Dispersal evolution in *Tribolium* metapopulations; a game theory approach[★]

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Abstract

Dispersal is a critical ecological process that influences population dynamics, gene flow, and species distribution across landscapes. Factors that affect dispersal rate include environmental variability, habitat fragmentation, density-dependent interactions, and interspecific interactions. In metapopulations, dispersal connects multiple subpopulations. Which reduces risk of local extinctions and increases metapopulation persistence. Proximate causes of dispersal include genetics and environmental connectivity. However, the mechanisms by which natural selection influences dispersal rates under varying environmental conditions remain unclear. Here we show that the evolution of dispersal rates can be predicted under various environmental conditions. By expanding the famous LPA model of *Tribolium* population dynamics to a metapopulation context, we confirmed that environmental homogeneity leads to the evolution of a zero dispersal rate. Using evolutionary game theory, we predict ESS dispersal rates in *Tribolium* beetles in both 4-patch and 5-patch metapopulations when catastrophic extinctions occur on individual patches. These results will be tested using data from experiments in our lab. However, our models can be

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applied to more general population configurations and sources of environmental stochasticity. These findings can be applied to broader ecological and evolutionary studies, offering insights into the mechanisms that govern species survival and adaptation in fragmented landscapes. Our methods offer a powerful tool for researchers aiming to predict organismal dispersal patterns using existing data. This approach can enhance conservation strategies, habitat management, and ecological forecasting by offering precise predictions of dispersal behavior and its impact on population stability.

Contents

1. Introduction

Dispersal is defined as “any movement of individuals or propagules that has potential consequences for gene flow across space” (Ronce, 2007). This evolutionary trait affects fitness within a population and can influence population dynamics. Dispersal can be beneficial, yet also risky. Dispersal can increase genetic variation by limiting inbreeding, allow individuals to avoid competition and/or fill empty habitats. However, dispersal expends metabolic energy, exposes organisms to increased predation and other deadly threats both during immigration and in the new habitat. It can also force organisms into less suitable habitats. The combination of costs and benefits determine how natural selection operates on dispersal rate. For understanding the rate of dispersal, Lewontin (1970) lists three necessary and sufficient conditions for evolution by natural selection. First, there must be variation in dispersal probability among individuals in a population. Second, this variation must be at least partially heritable. Lastly, the trait must correlate with reproductive success. There are other factors which operate to determine dispersal rate. One of these reasons is local extinctions within a population. Dispersal can be influenced by kin competition, successional dynamics, habitat turnover rates, and spatial structure of a landscape (Dieckmann et al., 1999).

Dispersal is especially important within metapopulations as they are vital for understanding species persistence and spatial population dynamics . A metapopulation is comprised of many subpopulations connected by dispersal (Levins, 1969, 1970). If each of the subpopulations consist of equal environmental conditions, then there will be no need for an individual to disperse (Hanski and Gilpin, 1991) . If each subpopulation has different environmental conditions where dispersal may increase fitness, then individuals are more likely to disperse. For a species long-term existence, dispersal and colonization are needed processes as they enable populations to recover from local extinctions and maintain genetic diversity across landscapes (Wang and Altermatt, 2019).

Dispersal can be density-independent or density-dependent though it is very rare to naturally see density-independent dispersal in an ecological setting. In homogeneous metapopulations, density-independent dispersal has no effect on the metapopulation stability. However, if the metapopulation is heterogeneous, then density-independent dispersal may stabilize the metapopulations. With density-dependence, a positive dispersal may destabilize homogeneous metapopulations. Whereas a negative density-dependent dispersal will stabilize the homogeneous metapopulations. This indicates that dispersal is too costly to increase the fitness of dispersing organisms (Tromeur et al., 2016). It is worth noting that within homogeneous populations there can be evolutionary dynamics as because space itself can count as an evolutionary parameter (Ochocki and Miller, 2017).

Evolution based dispersal strategy doesn’t always maximize population size or minimize the probability of extinction, so metapopulations might not always be beneficially impacted (Parvinen et al., 2012). Furthermore, emigration within density-dependant dispersal might have different density thresholds (Parvinen et al., 2012). Overall, it is important to determine dispersal cost and how a species fitness might change with their dispersal rate. This is especially important as dispersal within metapopulations may have extremely varying results for the dispersing individuals. We wish to specifically study how natural selection determines dispersal rate in metapopulations

In order to effectively study evolutionary based dispersal within metapopulations, we chose to look at *Tribolium* beetles. The flour beetle, a Tenebrionid beetle in the genus *Tribolium*, have features that make them an important research organism. First, they have adapted to live in flour or other household mediums as well as rotten logs, and natural locations (Park, 1934).

Their ease of manipulation in laboratory settings and robustness make them ideal for experiments that bridge mathematical predictions with empirical data. Additionally, Tribolium beetles exhibit unique behaviors, such as cannibalism, which have been extensively documented and provide valuable insights into population dynamics and dispersal tendencies. The cannibalism of *Tribolium* also creates a non-linear feedback system (**?**). An additional feature that makes *Tribolium* a viable study species is how easy they are to manipulate in a lab, this allows us to compare our mathematical predictions to real life data. Furthermore, These creatures are incredibly robust, so they are hard to kill. *Tribolium* also contains the unique evolutionary trait of cannibalism. Though these creatures often eat younger members of the species, they never eat themselves into extinction (Park and Frank, 1948). Due to their unique characteristics, *Tribolium* have been studied for nearly 100 years. Their characteristics, population dynamics, and dispersal likelihood have been meticulously investigated.

Tribolium beetles dispersal is largely oligogenic (Pointer et al., 2023), but can also be influenced by different biological traits. These traits include number of mating's by males, duration of mating by males, total reproductive fitness, timing of reproductive fitness, development time, and longevity (Pointer et al., 2024). *Tribolium* beetles are more likely to disperse when in ideal humidity and temperature conditions. They also tend to disperse when faced with a dense population . Dispersal rates in *Tribolium* can evolve due to natural selection acting on genetic variations in dispersal-related traits. Dispersal rates are also affected by population density, food availability, and natal environment (Ogden, 1970).

All organisms face a cost with dispersal, and *Tribolium* are no exception. A high tendency for dispersal is notably linked to reduced mating effort, diminished early reproductive investment, slower development of offspring laid later, and extended lifespan in female *Tribolium* beetles (Pointer et al., 2024). We are interested to see how dispersal evolves within metapopulations by using *Tribolium*

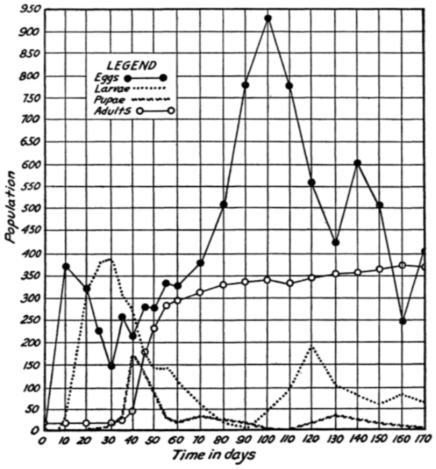

Figure 1: Park, 1934 population dynamics of *Tribolium* separated into eggs, larvae, pupae, and adults. This is with 25g of medium which was changed every two weeks.

This paper will provide deeper insights into the evolutionary dynamics of dispersal and its implications for population stability and species survival. In order to study the evolution of dispersal, we first need an accurate model of population dynamics for *Tribolium* beetles within a metapopulation.

1.1. Population Dynamics Data Set

In our search for an accurate model, we first need a data set. We looked at two different data sets created by previous researchers. Park (1934) and Jillson and Costantino (1980) both collected data sets of the population dynamics of *Tribolium* which are displayed below.

Figure (2) displays the population dynamics of *Tribolium* as a single population dynamics. This figure indicates that the overall population dynamics of *Tribolium* exhibit oscillatory behavior. Meanwhile, Figure (1) separates the population into eggs, larvae, pupae, and adults and shows how these oscillations primarily occur in larvae and pupae.

In terms of current research with *Tribolium* population dynamics, we utilized a comprehensive data set generated by our lab. This data set includes population dynamics from four distinct populations of *Tribolium* beetles, each cultivated under controlled conditions.

The experimental setup involved four separate containers, each with 50 grams of medium composed of 5% yeast and 95% white flour. Each container was initially stocked with 20 mature *Tribolium* adults. Following standard *Tribolium* husbandry practices, the medium was completely replaced every two weeks. During each medium change, larvae, pupae, adults, and eggs were extracted and transferred to fresh medium. The number of

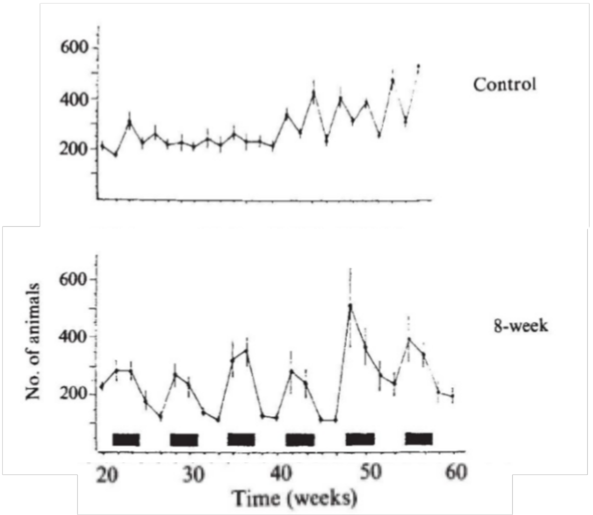

Figure 2: Jillson and Costantino, 1980 total population dynamics of *Tribolium*, The entire population of beetles were counted at each time step. The control group is with no media change occurring, while the 8 week group is part of a study conducted. The black blocks represent the *Tribolium* living in 32g of medium, while no block indicates the *Tribolium* living in 8g of medium.

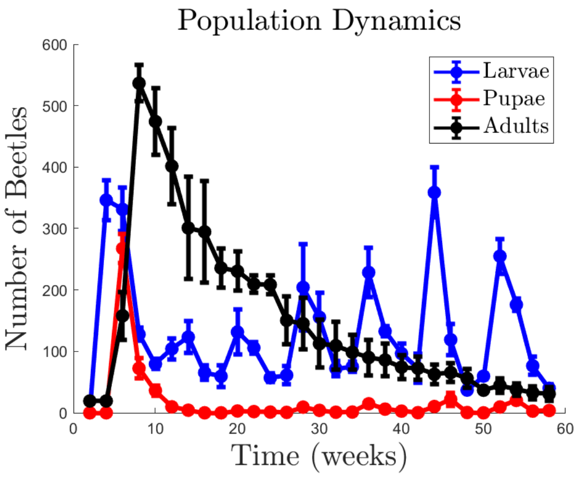

Figure 3: Our full data set of *Tribolium* population dynamics. Adults appear to dampen the oscillations of larvae

larvae, pupae, and adults in a population were counted and recorded. The mean population size for all four containers, along with the standard error of the mean (SEM) bars, was plotted against time.

We compared our population dynamics to both Park, 1934 and Jillson and Costantino, 1980's population dynamics. In order to compare our population dynamics with the dynamics from Jillson and Costantino, 1980; Park, 1934 we plotted both the larvae, pupae, and adults individually, as well as plotted the total population sum.

We compared our total population data as seen in Figure (4) to (Jillson and Costantino, 1980)'s data as portrayed in Figure (2). Both of these populations show oscillations. However, a key difference is Figure (4) has a downward trend of the entire population where Figure (2) has the adult population increasing within the control group.
We further compared our population dynamic data in Figure (3) to data in (Park, 1934) (Figure (1)). While (Park, 1934)'s data does have larval oscillations, ours are more frequent. Furthermore, our adults have a downward trend whereas (Park, 1934)'s have adults appear to reach a steady state.

For the purpose of this paper, we plan on using the *Tribolium* dynamics from our specific lab. Therefore, our goal is to find a model that matches our specific population dynamics of *Tribolium*. In order to do so we subsequently divided our data into two categories: training data and predictive data. The training data covers the first 36 weeks of the population's life cycle, while the predictive data extends from week 36 to 58. We will compare a variety of potentially viable models with this data.

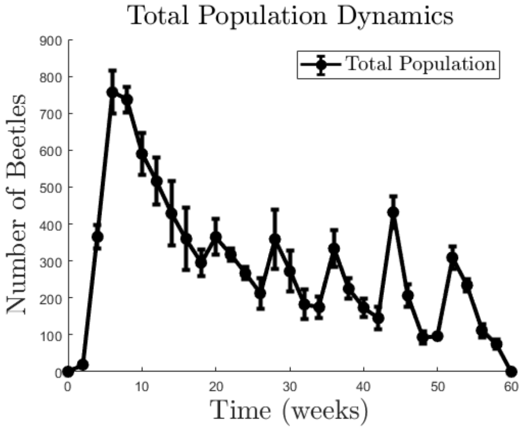

Figure 4: Our population dynamics of the sum of adult, pupae, and larvae. This is the average of four different populations with SEM bars plotted.

2. Model Review

2.1. LPA Model

In our search for viable models that exhibit the population dynamics of *Tribolium* we first resorted back to previous research. There is a variety of research both biological and mathematical on *Tribolium* as*Tribolium* beetle's population dynamics has been a long-standing subject of interest, especially due to their non-linear chaotic behavior. In 1995, Dennis et al. (1995) created the original population dynamic model of *Tribolium* beetles. This model, known as the LPA model, focuses on the life stages of Larvae (L), Pupae (P), and Adults (A) of Tribolium beetles,described by the following equations

$$\begin{aligned} L_{n+1} &= bA_n e^{-c_{ea}A_n - c_{el}L_n}, \\ P_{n+1} &= L_n(1-\mu_l), \\ A_{n+1} &= P_n e^{-c_{pa}A_n} + A_n(1-\mu_a). \end{aligned} \tag{1}$$

We do a detailed mathematical derivation of Dennis et al.'s (1995) model expressed in the system above. Let L_n represent the number of feeding larvae, P_n denotes the number of non-feeding larvae, pupae, and callow adults, and A_n represent the number of mature adults at time step n. The model assumes all stages will move to the next stage every time-step, except for adults, the amount of eggs the adults lay is constant, and oviposition

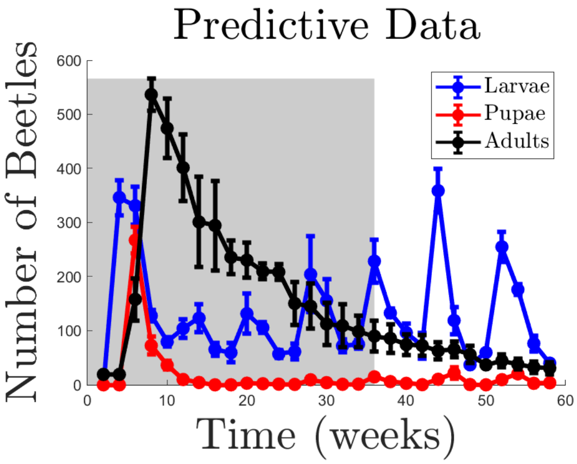

Figure 5: The population dynamics of *Tribolium* separated into training and predictive data. The gray shaded area represents the training data whilst the non-shaded region is the predictive data

and cannibalism occur simultaneously at each unit time step. To derive the Larvae compartment of the model, we assume adults eat eggs at rate c_{ea} while larvae eat eggs at rate c_{el}. Additionally, there is no competition for eggs between individuals given that there is a high proportion of eggs compared to the number of adults and larvae at all times. These assumptions mean the cannibalism of adults and larvae on eggs is independent. Lastly, births occur at the beginning of the time step while deaths occur at the end.

Larvae Compartment: To analyze the number of larvae in any given next-generation, we first examine the rate at which the egg population increases, considering the rate at which adults and larvae cannibalize eggs before they become larvae. Let $E(t)$ be the number of eggs at time t:

$$\frac{dE}{dt} = (-c_{ea}A_n - c_{el}L_n)E$$

To analyze the number of larvae in any given next-generation, we must first analyze the rate at which the egg population is increasing. This can be done by observing the rate at which adults and larvae cannibalize eggs before they become larvae. Considering adult and larvae cannibalism, let $E(t)$ be number of eggs at time t:

$$\frac{dE}{dt} = (-c_{ea}A_n - c_{el}L_n)E$$

$$\frac{dE}{dt} = (-c_{ea}A_n - c_{el}L_n)E$$

Solving this by separation of variables:

$$\int \frac{1}{E} dE = \int (-c_{ea}A_n - c_{el}L_n) dt$$

Integrating both sides:

$$\ln E \Big|_{E(n)}^{E(n+1)} = (-c_{ea}A_n - c_{el}L_n)\Big|_{n}^{n+1}$$

$$\ln \frac{E(n+1)}{E(n)} = -c_{ea}A_n - c_{el}L_n$$

$$\frac{E(n+1)}{E(n)} = e^{-c_{ea}A_n - c_{el}L_n}$$

Let $E(n) = bA_n$, then:

$$E(n+1) = bA_n e^{-c_{ea}A_n - c_{el}L_n}$$

Therefore, the number of larvae in the next generation is:

$$L_{n+1} = \underbrace{bA_n}_{\text{Recruitment}} \underbrace{e^{-c_{ea}A_n - c_{el}L_n}}_{\text{Cannibalism}}$$

Pupae Compartment: The number of pupae in the next generation is the number of larvae that survive the previous time-step:

$$P_{n+1} = \underbrace{(1-\mu_l)}_{\text{Survival}} L_n$$

Adult Compartment: The number of adults in the next time step considers both pupae becoming adults and the survival of current adults. The number of pupae that survive cannibalism and emerge as adults is $P_n e^{-c_{pa}A_n}$. The proportion of adults that survive is $(1-\mu_a)$:

Table 1: The parameters, definition, and values of the LPA model with Dennis et al. 1995.

Parameter	Definition	Value
b	Number of viable eggs per adult	11.68
μ_a	Natural death rate of adults	0.6
μ_l	Natural death rate of larvae	0.5129
c_{ea}	Cannibalism of adults on eggs	0.0110
c_{el}	Cannibalism of larvae on eggs	0.0110
c_{pa}	Cannibalism of adults on pupae	0.0178

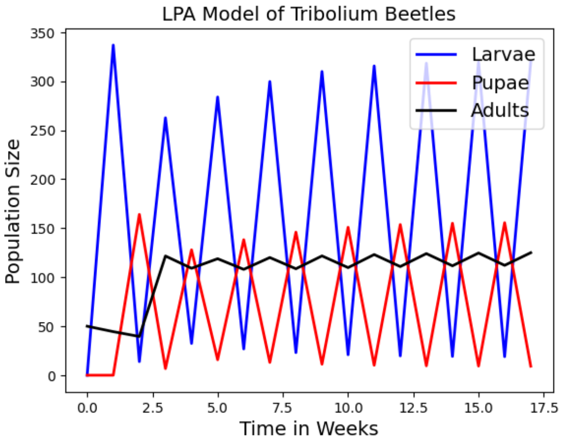

Figure 6: Solution to the LPA model with parameter values from (Dennis et al., 1995, see Table 1).

$$A_{n+1} = P_n \underbrace{e^{-c_{pa}A_n}}_{\text{Cannibalism}} + A_n \underbrace{(1-\mu_a)}_{\text{Survival}}$$

Thus, Dennis et al.'s Dennis et al. (1995) LPA model is summarized as follows:

$$\begin{pmatrix} L_{n+1} \\ P_{n+1} \\ A_{n+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & be^{-c_{ea}A_n - c_{el}L_n} \\ 1-\mu_l & 0 & 0 \\ 0 & e^{-c_{pa}A_n} & 1-\mu_a \end{pmatrix} \begin{pmatrix} L_n \\ P_n \\ A_n \end{pmatrix} \tag{2}$$

The parameters are shown in Table 1.

Dennis et al. (1995) used the parameter values shown in Table 1. It is worth noting that though these parameters are biologically reasonable for *Tribolium* beetles, these values were specifically used due to the oscillations they cause the model to portray. Thus, their

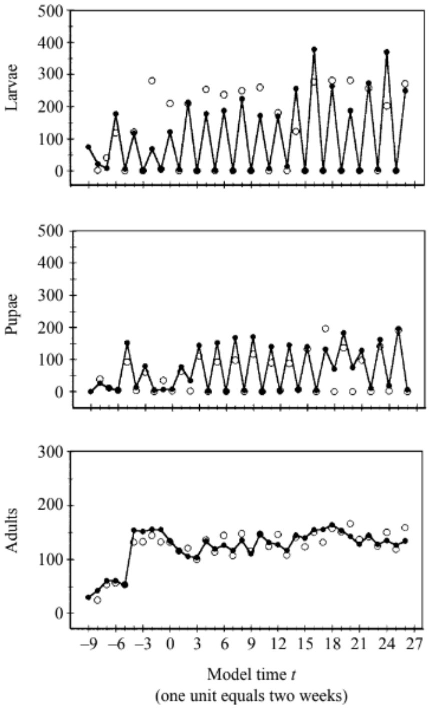

Figure 7: Costantino et al., 1998 population dynamics of *Tribolium*. Their population dynamics contained high oscillations within the pupae and larvae from their data collection.

model causes nonlinear chaotic dynamics and oscillations within each group. This can be observed with the projected oscillations. However, (Costantino et al., 1998) did end up with *Tribolium* beetles to have large oscillations in their population data. Their LPA model is reflected of the oscillations they saw in their populations. However, they did also specifically manipulate different things to get these effects.

Additional modeling such as bifurcation diagrams have been reflected with the LPA model. Figure 8 shows the bifurcation diagram of model (1) and represents the sum of larvae, pupae, and adults with the Liapunav exponent. Cannibalism of pupae by adults is used as the bifurcating parameter. Each arrow indicates different asymptotic dynamical regions where the experimental treatments are placed. Their primary result is that even in these chaotic dynamics, extinction is exceedingly rare.

Brozak Brozak et al. (2024) expanded the study of the original LPA model to best match our training data showcasing the population dynamics of *Tribolium* beetles. The LPA equations remained consistent, however each specific variable was optimized to fit the data.

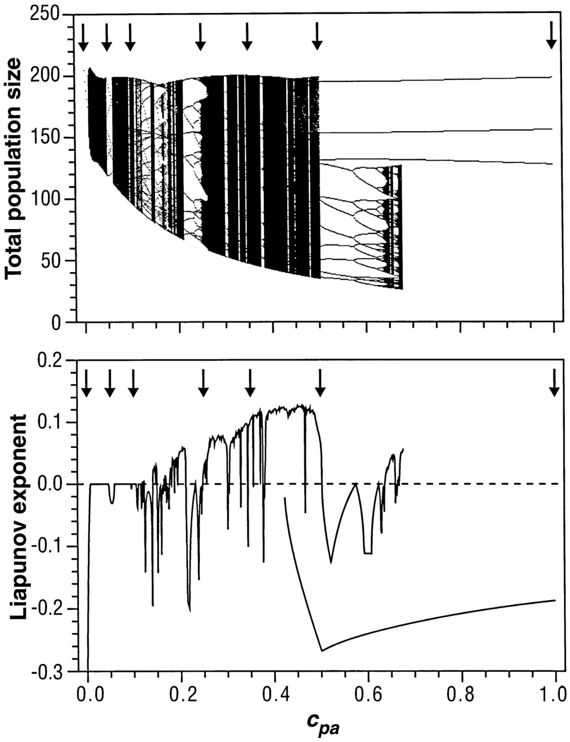

Figure 8: Bifurcation diagram directly from the Costantino et al. (1997) paper.

Table 2: Parameters, Definition, and Values of the LPA Model with Brozak et al. Data

Parameter	Definition	Brozak
b	Number of viable eggs per adult	20
μ_a	Natural death rate of adults	0.0842
μ_l	Natural death rate of larvae	0.6053
c_{ea}	Cannibalism of adults on eggs	0.0179
c_{el}	Cannibalism of larvae on eggs	0.0003
c_{pa}	Cannibalism of adults on pupae	1.0760×10^{-13} height

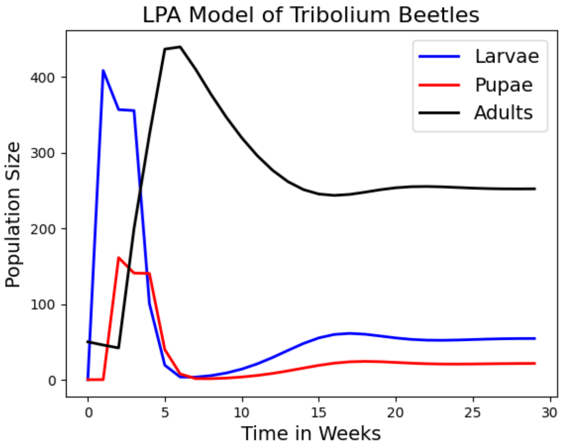

Figure 9: LPA model with Brozak et al. parameters

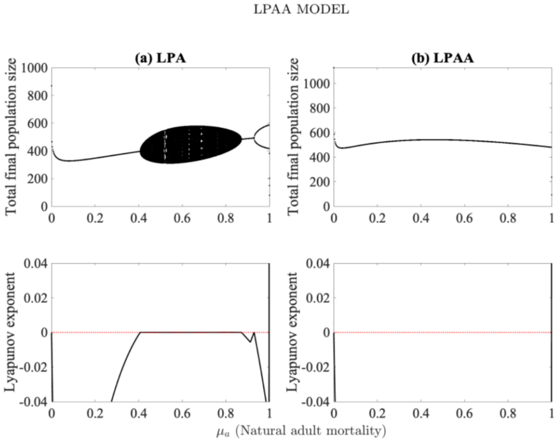

Figure 10: Brozak et al. Bifurcation with μ_a

Brozak compared her LPA model in a bifurcation diagram focusing on μ_a which is the natural adult mortality. The stability results for extinction and positive steady states matched the original LPA model. However, with Brozak's LPA model with μ_a as the bifurcation parameter, no chaotic dynamics occurred.

2.2. *Cushing et al. LPA with Noise Model (1998)*

The original LPA model does not consider for demographic or environmental stochasticity; therefore, Cushing et al. (1998) added noise to the system to study its effect. Specifically, they introduce a random vector, $\begin{pmatrix} E_1 & E_2 & E_3 \end{pmatrix}$, which has has a multivariate normal distribution with a mean of zero. The equation is expressed below.

$$\begin{aligned} L_{n+1} &= bA_n e^{-c_{el}L_n - c_{ea}A_n + E_1} \\ P_{n+1} &= L_n(1-\mu_l)e^{E_2} \\ A_{n+1} &= P_n^{-c_{pa}A_n} + A_n(1-\mu_a)e^{E_3} \end{aligned} \tag{3}$$

The larvae term is dependent on how many eggs are laid by adults coupled with how many of those eggs survive cannibalism by larvae and pupae. The noise causes subtle variations in the formula to account for any environmental shifts or factors. The pupae is simply the amount of larvae which survive past the larval stage, once again with random noise added. The adult term is depended on current adults surviving as well as the new pupae becoming adults.

The most concerning factor of the LPA model with noise is that it does not adhere to the necessary requirements of the conservation equation. It allows for adult beetles to enter the population without being born or immigrating. This was a concern with the model, in addition the added environmental stochasticity does not better fit the model to the training data.

2.3. Discrete-Time Markov Chain

We used the birth and death process to model dynamics for larvae, pupae, and adults. This is for representing the average probability of each stage moving to the next stage, independent of previous stages. We built the model with stochastic considerations in order to compare it with the classical discrete time LPA model. We assume that the number of eggs follow a Poisson distribution with the mean 2λ. The total number of offspring in a single time step born to the population is λA_n. We define the natural mortality has probability of dying which will be different for each class. Between n and $n+1$ all number of individuals are binomially distributed with means $\mu_l L_n$, $\mu_p P_n$, $\mu_a A_n$. This is for larvae, pupae, and adults respectively. We assume the probability that the eggs survive hatching is $e^{-c_{ea}A_n}$. The number of eggs and larvae that survive cannibalism will be binomially distributed with the probability across λA_n trails. Therefore, the number of eggs/larvae which survive cannibalism from large larvae is binomially distributed with the probability of $e^{-c_{el}L_n}$. Similarly, the number of pupae that survive cannibalism by adults is defined as e^{-cpaA_n}.

We further assume that after each time step, adults lay eggs. After the eggs are laid, then cannibalism of both larvae and pupae will occur. Then, natural mortality will occur. After that, all survivors will advance 1 age class except adults who will remain as so until they die.

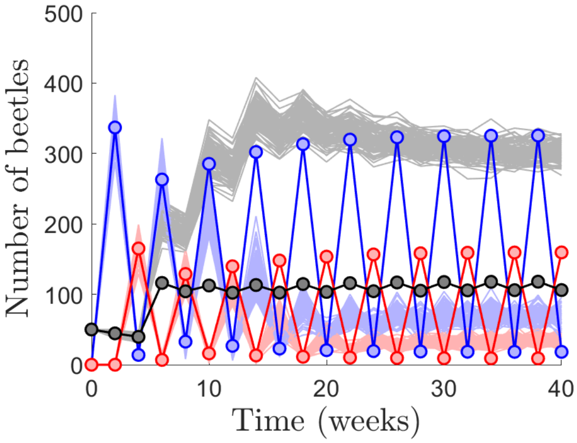

Figure 11: Mean value of 100 runs of discrete time Markov chain compared to original LPA model. The Markov chain is faded whilst the original LPA model are the solid lines.

Parameters from the original LPA model (Dennis et al., 1995) was used in this discrete-time Markov chain.

One of the major issues with the Markov model is that it implies beetles can stay in each life stage for weeks, which is simply not biologically accurate. This specific Markov chain we utilize uses a smaller time step which does not align with our work.

2.4. *ELPA Model*

We decided to recast the LPA Model in continuous time instead of discrete. In order to do so, we are holding a variety of assumptions and parameters for the continuous time model. Our first assumption is that adults lay eggs at a constant rate of λ. Second, $\mu_{ij}J$ is the per capita rate at which i are being eaten by j. Furthermore, every stage has a natural death rate but eggs and pupae death rates are so small, they're negligible. Lastly, any stage that cannibalizes increases their fitness and lifespan by decreasing their death rate.

We also carry the additional assumptions regarding the timeline of lifestages for *Tribolium*. The average time to get from an egg to larvae is 3 days, the average time to get from larvae to pupae is 11 days, and the average time to get from pupae to adult is 14 days

Our variables for the continuous time model are E, L, P and A where E equals the total number of eggs, L equals the total number of larvae, P equals the total number of pupae, and A equals the total number of adults. The continuous time model is expressed below

Table 3: The ELPA Model parameters, definitions and values with D as number of days.

Parameter	**Definition**	**Units**	**Value**
λ	Oviposition rate of viable eggs	$\frac{1}{D \cdot adult}$	13
μ_{ea}	Cannibalism rate of an Egg eaten by an Adult	$\frac{1}{D \cdot adult}$	–
μ_{el}	Cannibalism rate of an Egg eaten by a Larvae	$\frac{1}{D \cdot adult}$	–
μ_{la}	Cannibalism rate of a Larvae eaten by an Adult	$\frac{1}{D \cdot adult}$	–
μ_{pa}	Cannibalism rate of a Pupae eaten by an Adult	$\frac{1}{D \cdot adult}$	–
α_e	Average time of eggs to hatch	$\frac{1}{D}$	$\frac{1}{3}$
α_l	Average transformation time from Larvae to Pupae	$\frac{1}{D}$	$\frac{1}{11}$
α_p	Average transformation time from pupae to adult	$\frac{1}{D}$	$\frac{1}{14}$
δ_{max}	Maximum death rate for Adults	$\frac{1}{D}$	$\frac{\ln 2}{14}$
δ_{min}	Minimum death rate for Adults	$\frac{1}{D}$	$\frac{\ln 2}{364}$
γ_{max}	Maximum death rate for Larvae	$\frac{1}{D}$	$4 \ln 2$
γ_{min}	Minimum death rate for Larvae	$\frac{1}{D}$	$\frac{\ln 2}{14}$

with the following parameters.

$$\begin{aligned}
\frac{dE}{dt} &= \lambda A - \mu_{ea} A E - \mu_{el} L E - \alpha_e E \\
\frac{dL}{dt} &= \alpha_e E + -\mu_{la} A L - \alpha_l L - \Gamma L \\
\frac{dP}{dt} &= \alpha_l L - \mu_{pa} A P - \alpha_p P \\
\frac{dA}{dt} &= \alpha_p P - \Delta A
\end{aligned} \tag{4}$$

where $\Gamma = \gamma_{max} \cdot e^{-\kappa_l \mu_{el} E} + \gamma_{min}$ and $\Delta = \delta_{max} \cdot e^{-\kappa_a(\mu_{ea} E + \mu_{la} L + \mu_{pa} P)} + \delta_{min}$.

Additionally, κ is our predation efficiency parameter and D is day.

The explanation of each term in the ELPA model is as follows:

$$\begin{aligned}
\frac{dE}{dt} &= \underbrace{\lambda A}_{\text{eggs laid}} \underbrace{-\mu_{ea}AE-\mu_{el}LE}_{\text{cannibalism}} - \underbrace{\alpha_e E}_{\text{Hatching}} \\
\frac{dL}{dt} &= \underbrace{\alpha_e E}_{\text{Eggs to Larvae}} + \underbrace{-\mu_{la}AL}_{\text{Cannibalism}} - \underbrace{\alpha_l L}_{\text{Larvae to Pupae}} - \underbrace{\Gamma L}_{\text{Natural Death}} \\
\frac{dP}{dt} &= \underbrace{\alpha_l L}_{\text{Larvae to Pupae}} - \underbrace{\mu_{pa}AP}_{\text{Cannibalism}} - \underbrace{\alpha_p P}_{\text{Pupae to Adult}} \\
\frac{dA}{dt} &= \underbrace{\alpha_p P}_{\text{Pupae to Adult}} - \underbrace{\Delta A}_{\text{Adult Death}}
\end{aligned}$$

Since this model is continuous, we define each stage with an ODE. The first stage is the rate of the growth of eggs. We define it as viable eggs being born per adult with the cannibalism of adults and larvae upon the eggs being accounted for. We also account for the average time necessary for each egg to hatch, or how long it will be in the egg stage.

The second stage is focusing on each individual as they are larvae. We start with the eggs that successfully moved out of the egg stage and into the larvae stage. We then account for adults cannibalizing on larvae and the time it takes for a larvae to become a pupae. Finally we account for natural death of the larvae with a decreasing death function.

The third stage demonstrates the pupae. We start with all of the larvae that become pupae before accounting for the cannibalism of adults on pupae. Additionally, we ensure that the average time of a pupae becoming an adult is added.

Finally the adult stage starts with pupae becoming adult. We then account for adults leaving the population due to natural death and cannibalism whilst also assuming that the cannibalism adults partake in increases their fitness.

We fit the ELPA data using Trust Region Reflective Algorithm. The scipy optimize tool corrfit in python is utilized to show correct data fitting.

The following parameters demonstrated the fitted values of the ELPA model.

All of these parameters are biologically reasonable. However, this model does not accurately model the training data.

2.5. Age-Structured Model

We created a model aimed to address the limitations of simpler models like the LPA model by capturing the continuous progression and interactions across various developmental stages, which are critical for understanding the population dynamics more precisely. This age-structured population model divides the beetle population into different

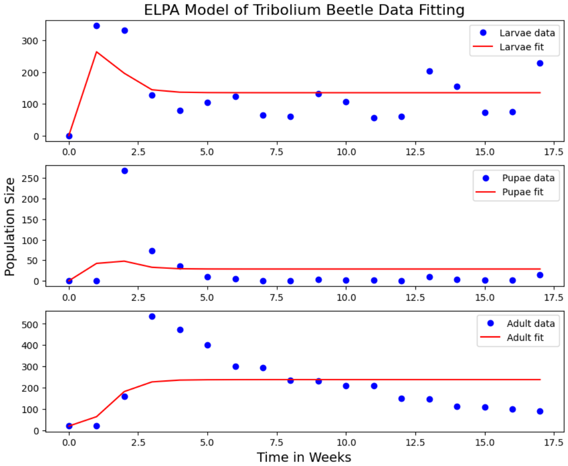

Figure 12: Data fitting for larvae, pupae, and adults with the ELPA model

Table 4: The best fit values for the ELPA model adjacent to the parameters and definitons.

Parameter	Definition	Fitted Values
c_{ea}	Cannibalism rate of an egg eaten by an adult	0.3327
c_{el}	Cannibalism rate of an egg eaten by a larvae	0.0009
c_{la}	Cannibalism rate of a larvae eaten by an adult	0.0161
c_{pa}	Cannibalism rate of a pupae eaten by an adult	1.7907×10^{-5}
α_e	Average time of eggs to hatch	1.7908
α_l	Average transformation time from larvae to pupae	0.7009
α_p	Average transformation time from pupae to adult	3.2945
λ	Oviposition rate of viable eggs	116.2452
δ_{max}	Maximum death rate for adults	6.9332
δ_{min}	Minimum death rate for adults	0.3977
γ_{max}	Maximum death rate for larvae	1.2670
γ_{min}	Minimum death rate for larvae	0.0042
κ	Time it takes to eat enough to decrease death rate by $\frac{1}{2}$	19.8272

stages: 0-s_1(eggs and early instar larvae), s_1-s_2(feeding larvae), s_2-s_3(non-feeding larvae, pupae, and callow adults), and s_3-∞(adults). The population density within each stage is governed by a partial differential equation (PDE), and the adult population is described by an ordinary differential equation (ODE). The transitions between stages are governed by boundary and continuity conditions. The objective of this model is to describe the dynamics of a beetle population as it transitions through various life stages. The model aims to capture the effects of growth, cannibalism, and natural death rates on the population density across different stages. By solving these equations, not only can we generalize it to analyze evolution of dispersal, but understand how the population evolves over time and identify key factors influencing population stability and growth. We define the population density $p(s,t)$ as different PDEs for different intervals of the stage variable s.

$$\frac{\partial p}{\partial t} = \begin{cases} -\underbrace{g(s)\frac{\partial p}{\partial s}}_{\text{Development}} \underbrace{-c_{ea}A(t) - c_{el}\int_{s_1}^{s_2} p(s,t)\,ds,}_{\text{Cannibalism}} & s \in (0, s_1), \\ -g(s)\frac{\partial p}{\partial s} - \underbrace{\mu_l p(s,t),}_{\text{Mortality}} & s \in [s_1, s_2), \\ -g(s)\frac{\partial p}{\partial s} - \underbrace{c_{pa}A(t)}_{\text{Cannibalism}}, & s \in [s_2, s_3), \end{cases} \tag{5}$$

with

$$\frac{\mathrm{d}A}{\mathrm{d}t} = \underbrace{g(s)p(s_3,t)}_{\text{Maturation}} - \underbrace{\mu_a A(t).}_{\text{Mortality}}$$

Since the age-structured model (5) is an accumulation of PDE's we need to ensure there are viable boundary conditions as well as continuity conditions. We define our boundary condition (B.C.) as

$$p(0,t) = bA(t) \quad \text{at } s = 0.$$

Furthermore, our continuity conditions are defined as

$$\frac{\partial p(s_1,t)}{\partial t} = g(s_1)p(s_1,t) \quad \text{at } s = s_1$$
$$\frac{\partial p(s_2,t)}{\partial t} = g(s_2)p(s_2,t) \quad \text{at } s = s_2$$

The parameters and variable for our age-structured model is described by the table below.

Table 5: The parameters and variables for the age-structured model.

Parameter/Variable	**Description**
$p(s,t)$	Population density at stage s and time t
$A(t)$	Adult population at time t
$g(s)$	Growth function
c_{ea}	Cannibalism rate of eggs by adults
c_{el}	Cannibalism rate of eggs by larvae
c_{pa}	Cannibalism rate of pupae by adults
b	Birth rate of new eggs
μ_l	Natural death rate of feeding larvae
μ_a	Natural death rate of adults
s_1, s_2, s_3	Stage boundaries

We then preform a discretization of our age-structured model. We define the eggs and early instar larvae which is ($s \in (0, s_1)$) as

$$p_i^{n+1} = p_i^n + \Delta t\left(g\frac{p_{i-1}^n - p_i^n}{\Delta s} - c_{ea}A^n - c_{el}\sum_{j=s_1/\Delta s}^{s_2/\Delta s} p_j^n \Delta s\right)$$

Our feeding larvae which is from ($s \in [s_1, s_2)$) is defined as:

$$p_i^{n+1} = p_i^n + \Delta t\left(g\frac{p_{i-1}^n - p_i^n}{\Delta s} - \mu_l p_i^n\right)$$

Furthermore, we define the non-feeding larvae, pupae, and callow adults as ($s \in [s_2, s_3)$)

$$p_i^{n+1} = p_i^n + \Delta t\left(g\frac{p_{i-1}^n - p_i^n}{\Delta s} - c_{pa}A^n\right)$$

Lastly, the adults ($s \in [s_3, \infty)$) are defined as:

$$A^{n+1} = A^n + \Delta t\left(g p_i^n - \mu_a A^n\right)$$

The boundary condition for this is:

$$p_0^{n+1} = bA^n \quad \text{at } s = 0,$$

with the Continuity Conditions (C.C.) being:

$$p_{s_1/\Delta s}^{n+1} = p_{s_1/\Delta s}^n + \Delta t \cdot g \cdot p_{s_1/\Delta s}^n \quad \text{at } s = s_1$$

Table 6: Model Parameters and Variables for Age Structured Model

Parameter/Variable	**Description**
$p(s,t)$	Population density at stage s and time t
$A(t)$	Adult population at time t
$g(s)$	Growth function
c_{ea}	Cannibalism rate of eggs by adults
c_{el}	Cannibalism rate of eggs by larvae
c_{pa}	Cannibalism rate of pupae by adults
b	Birth rate of new eggs
μ_e	Natural death rate of eggs and early instar larvae
μ_l	Natural death rate of feeding larvae
μ_p	Natural death rate of non-feeding larvae, pupae, and callow adults
μ_a	Natural death rate of adults
s_1, s_2, s_3	Stage boundaries

$$p^{n+1}_{s_2/\Delta s} = p^{n}_{s_2/\Delta s} + \Delta t \cdot g \cdot p^{n}_{s_2/\Delta s} \quad \text{at } s = s_2.$$

The parameter's and variables for our model is defined in the table below.

We then calculated the R_0 of our age structured model. There are 3 events which must happen for our R_0 value.The first is adults will survive long enough to grow from size s_3 to some $s \in [s_3, \infty)$. Second, adults will breed at the size s. Lastly, eggs will survive long enough to grow from size s_0 to s_3. Therefore, R_0 is all these probabilities multiplied which gives us the following equation: $P\{C|A,B\} \cdot P\{B|A\} \cdot P\{A\}$

For P{A}, A(t) is the number of adults in this cohort at time $t \geq t_0$ and can only leave by dying at rate μ_a.For an adult beetle, we start by solving the differential equation for its survival:

$$\Longrightarrow \frac{dA}{dt} = -\mu_a A(t), \quad \frac{ds}{dt} = g$$

Solving this ODE, we get:

$$A(t) = A_0 e^{-\mu_a t}$$

Additionally, the expected lifespan of an adult is given by the mean of the exponential distribution:

$$\frac{1}{\mu_a}$$

We then look at P$\{B|A\}$. The birth rate of new eggs per adult is given by b. Since an adult lives on average $\frac{1}{\mu_a}$ time units, the total number of eggs laid by an adult is:

$$\frac{b}{\mu_a}$$

Finally, we must calculate our P$\{C|A,B\}$ value. Since we are determining where the beetle-free equilibrium $(0,0,0)$ changes stability, then survival throughout the stages are unaffected by cannibalism. Similarly to the adults, all stages $s \in [0, s_3)$ only leave their cohort due to natural mortality.
Hence,

$s \in [0, s_1)$:

$$\frac{dE}{dt} = -\mu_e E$$

$$\vdots$$

$$\boxed{E(t) = E_0 e^{-\mu_e t}}$$

$s \in [s_1, s_2)$:

$$\frac{dL}{dt} = -\mu_l L$$

$$\vdots$$

$$\boxed{L(t) = L_0 e^{-\mu_l t}}$$

$s \in [s_2, s_3)$:

$$\frac{dP}{dt} = -\mu_p P$$

$$\vdots$$

$$\boxed{P(t) = P_0 e^{-\mu_p t}}$$

$$\implies \boxed{R_0 = \frac{b E_0 L_0 P_0 e^{-(\mu_e+\mu_l+\mu_p)t}}{\mu_a}}$$

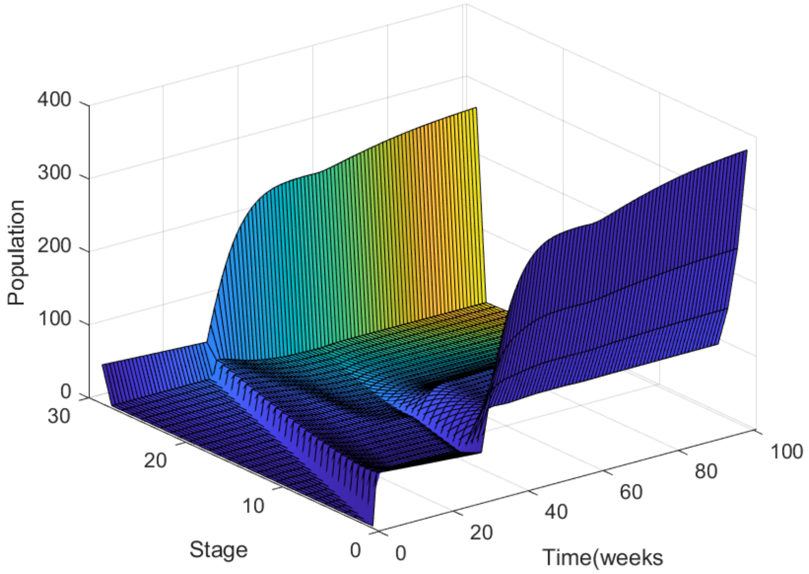

Figure 13: Age Structured Model 3D

■

After that, we created a 3D rendition of the Age Structured Model yields the following image.

By utilizing integration we formed the following 2D rendition of the Stage Structured Model.

We fit the age structured model to our training data utilizing least squares optimization.

The best fit values we received from our age- structured model are biologically accurate. However the b value is a bit low. We attempted to adjust our age-structured model by adding a natural juvenile mortality function. We define this function as

$$\mu_j(s) = \begin{cases} \mu_e, & \text{if } s \in [0, s_1) \\ \mu_l, & \text{if } s \in [s_1, s_2) \\ \mu_p, & \text{if } s \in [s_2, s_3) \end{cases}$$

The population density $p(s,t)$ for this reworked model is described by different PDEs for different intervals of the stage variable s:

$$\frac{\partial p}{\partial t} = \begin{cases} -g(s)\frac{\partial p}{\partial s} - c_{ea}A(t) - c_{el}\int_{s_1}^{s_2} p(s,t)\,ds - \mu_j(s)p(s,t), & \text{if } s \in (0, s_1) \\ -g(s)\frac{\partial p}{\partial s} - \mu_j(s)p(s,t), & \text{if } s \in [s_1, s_2) \\ -g(s)\frac{\partial p}{\partial s} - c_{pa}A(t) - \mu_j(s)p(s,t), & \text{if } s \in [s_2, s_3) \end{cases} \tag{6}$$

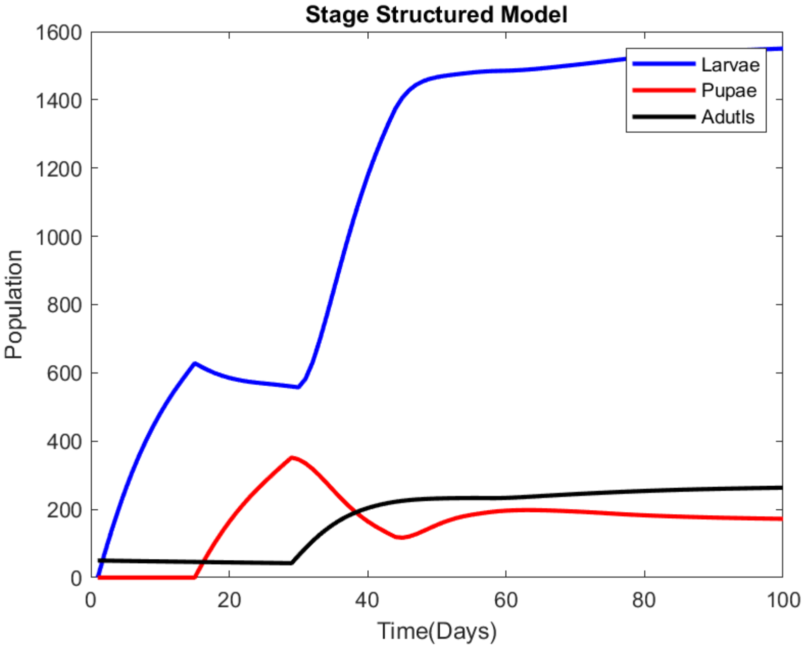

Figure 14: 2 Dimensional Stage Structure Model

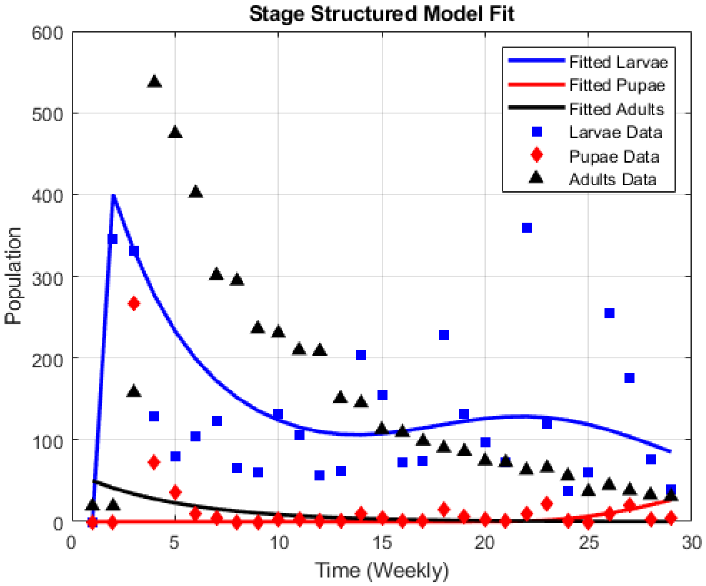

Figure 15: Best data fitting for the age structured model.

Table 7: Parameters and Best Fit Values of the Age Structured Model

Parameter/Variable	Description	Best Fit Values
$p(s,t)$	Population density at stage s and time t	N/A
$A(t)$	Adult population at time t	N/A
g	Growth rate	N/A
c_{ea}	Cannibalism rate of eggs by adults	0.16142
c_{el}	Cannibalism rate of eggs by larvae	2.3609×10^{-14}
c_{pa}	Cannibalism rate of pupae by adults	1.5954
b	Birth rate of new eggs	11
μ_l	Natural death rate of feeding larvae	2.2682×10^{-8}
μ_a	Natural death rate of adults	0.23235
s_1, s_2, s_3	Stage boundaries	N/A

We continue to govern the adult population $A(t)$ as an ODE which is defined below.

$$\frac{dA}{dt} = gp(s_3,t) - \mu_a A(t), \quad \text{if } s \in [s_3, \infty)$$

Our boundary conditions and continuity conditions remain the same as they were in our original age-structured model. We are still working on the optimization and data fitting of our new model.

2.6. Potential Fallacies

None of these models are able to accurately predict the larval oscillations we see within our data set. A leading hypothesis for the larval oscillations is that it is driven by adult cannibalism (Costantino et al., 1998; Jillson and Costantino, 1980). However, the data set tells another story. As adult population decrease, larval oscillations are appearing to increase which means that adult cannibalism is not responsible for the large oscillations. The models we reviewed did take adult cannibalism into account, but we believe there is a better reasoning for why these larval oscillations are occurring.

We hold two viable hypotheses for these larval oscillations. The first hypothesis has to do with intraspecific competition between larvae. Larger larvae cannibalize smaller larvae. This unique form of both competition and predation may produce the chaotic dynamics seen. The Rosenzweig-MacArthur Model could be a viable method for testing this

The second hypotheses is that the larval oscillations are driven by the medium change of *Tribolium* beetles. It is standard practice within researchers of *Tribolium* to change their medium every two weeks (Park, 1934; Jillson and Costantino, 1980; Park and Frank, 1948). While adults, pupae, larvae, and eggs are carefully extracted, it is near impossible

Table 8: LPA Forcing Function Best Fit Values

Parameters	**Definition**	**Value**
μ_a	The natural mortality proportion of adults	0.0842
μ_l	The natural mortality proportion of larvae	0.6053
μ_g	**The mortality due to medium change**	0.359
b	The average larval recruitment, without cannibalism	20
c_{ea}	The cannibalism rate of eggs being eaten by adults	0.0179
c_{el}	The cannibalism rate of eggs being eaten by larvae	0.0003
c_{pa}	The cannibalism rate of pupae being eaten by adults	0.0

to filter out the eggs within a flour environment. The eggs of these beetles will adapt to best match the environment of medium (Park, 1934). If all of the eggs aren't being filtered out during the medium change, then we might be adding an environmental forcing function, shifting the population dynamics.

A further experiment in our lab provides insight into this conundrum. Peralta's experiment consisted of studying *Tribolium* dynamics with different medium changes. put 40 adult beetles into cup A with 50g medium. Each time step she split the original cup evenly between two cups. She split the beetles evenly, as well as putting 25g of the old medium into each cup. Then, she added 25g of fresh medium into each cup. She only split each cup letter once. For example, after she split cup A at time step 1, she no longer touched cup A and didn't change the medium at all. She did the experiment with a two week and a four week time step.

2.7. LPA with Forcing Function

We hypothesized that the medium changes are an environmental factor which is causing these oscillations. It is vital to reiterate that this is firmly a hypothesis and has not been proven. In order to account for this hypothesis, we added a forcing function to the original LPA model (Dennis et al., 1995).

$$\begin{pmatrix} L_{n+1} \\ P_{n+1} \\ A_{n+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & (1-\mu_g)be^{-c_{ea}A_n - c_{el}L_n} \\ 1-\mu_l & 0 & 0 \\ 0 & e^{-c_{pa}A_n} & 1-\mu_a \end{pmatrix} \begin{pmatrix} L_n \\ P_n \\ A_n \end{pmatrix}$$

We decided to use parameters estimated by Brozak et al. (2024) to fit to our data. We then performed optimization analysis to find a best fit for μ_g. More specifically, we used the least-squares regression method to minimize the difference between our data set and the simulations done setting different values of μ_g. We set lower and upper bounds for μ_g

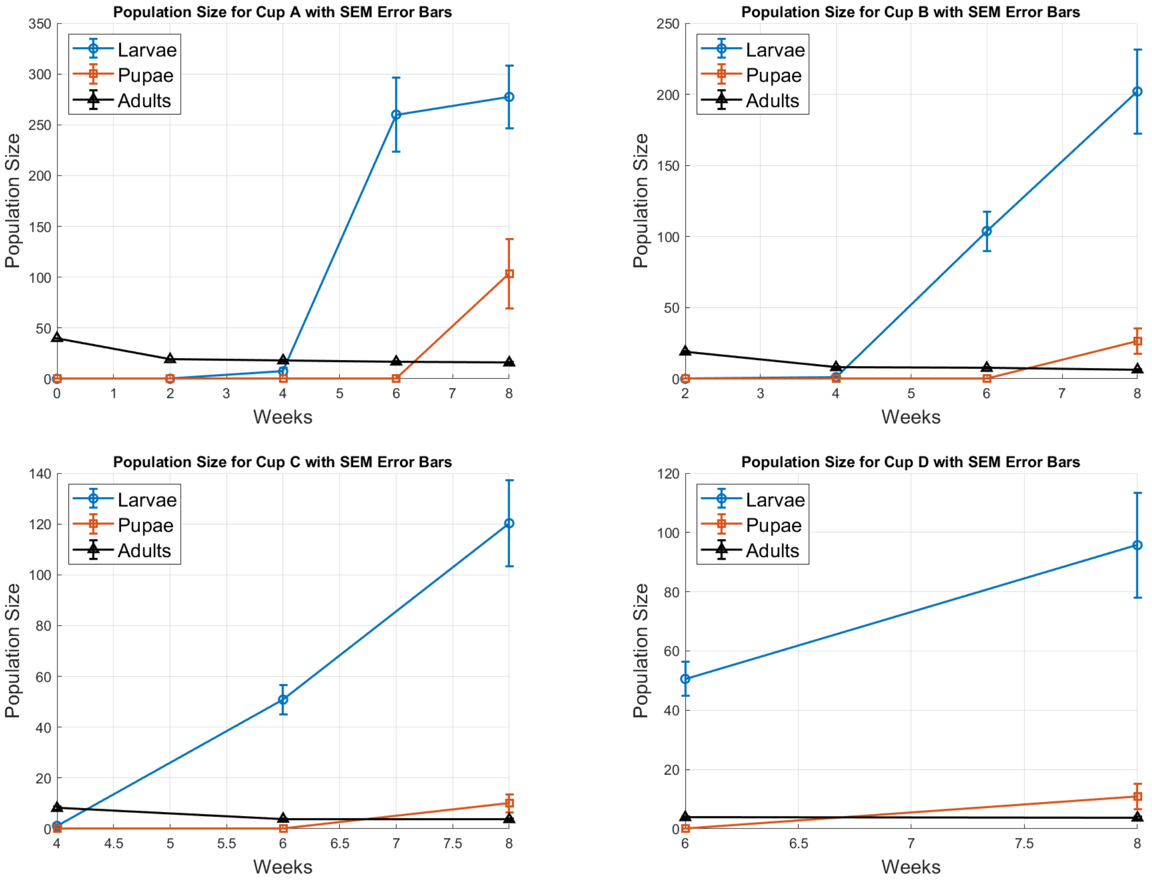

Figure 16: These are the results from Peralta's Experiment which was conducted over 8 weeks. Each time step is 2 weeks long. (a) demonstrates the medium being changed on week 2 when cup A was split into cups A and B. The medium was not changed for the rest of the experiment. (b) shows Cup B which is half of the original cup A. It was split at Time Step 2, and was then left unchanged for the rest of the experiment. (c) displays cup C which is half of the original cup B. It was split at Time Step 3, and was then left unchanged for the rest of the experiment. (d) Shows Cup D which is half of the original cup C. It was split at Time Step 4, and was then left unchanged for the rest of the experiment.]

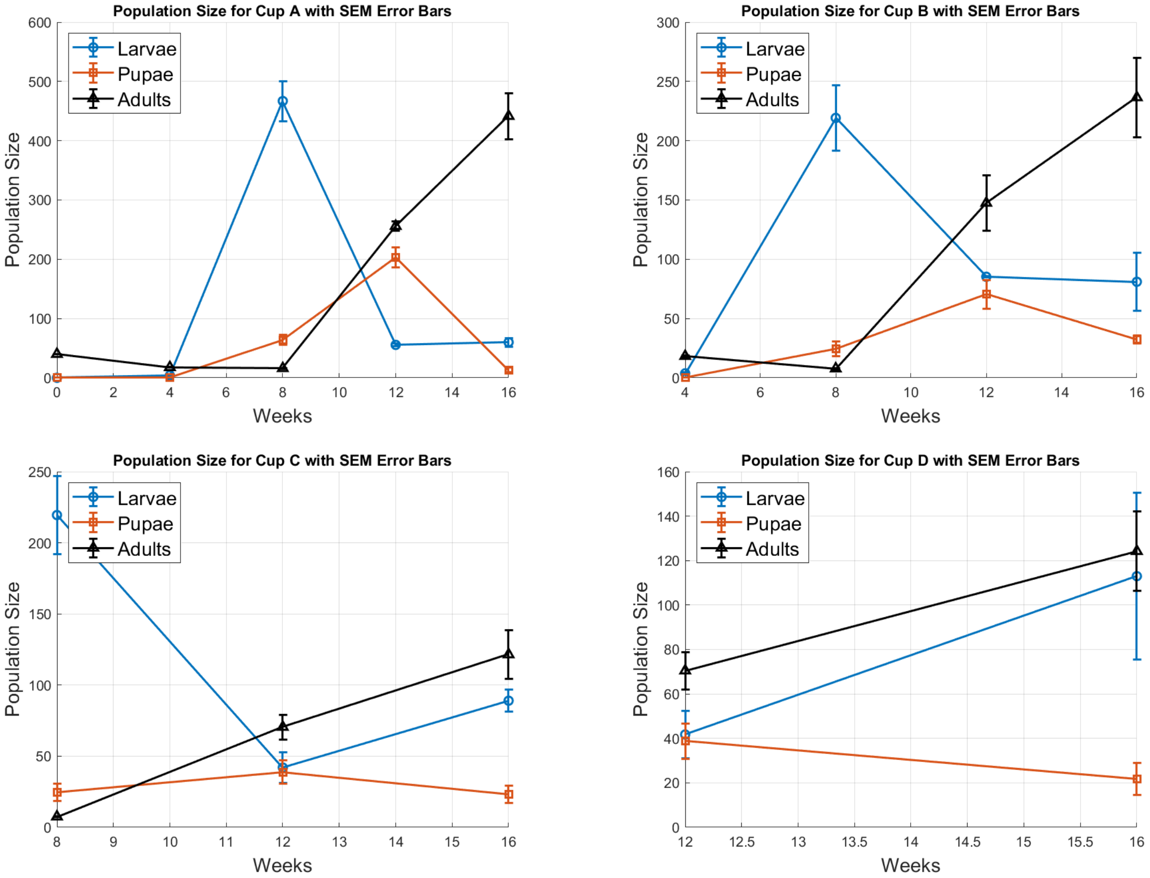

Figure 17: These are the results from Brozak et al., 2024 which was conducted over 16 weeks. Each time step is 4 weeks long.(a) begins the experiment where 40 adult beetles are placed. After 4 weeks, cup A was split into cups A and B. An equal number of beetles were placed into a and b, furthermore the 50g of old medium was split evenly between cup a and cup b. 25 of fresh medium was placed into cup a and cup b. demonstrates the medium being changed on week 4 when cup A was split into cups A and B. The medium was not changed for the rest of the experiment. (b) shows Cup B which is half of the original cup A. It was split at Time Step 2, and was then left unchanged for the rest of the experiment. (c) displays cup C which is half of the original cup B. It was split at Time Step 3, and was then left unchanged for the rest of the experiment. (d) is a visual representation of Cup D which is half of the original cup C. It was split at time step 4, and was then left unchanged for the rest of the experiment.]

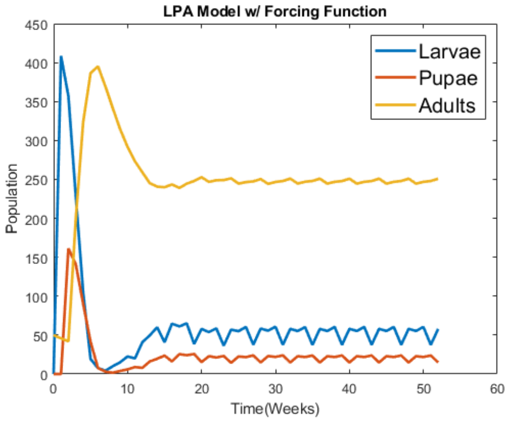

Figure 18: LPA model with forcing function implemented every 4 weeks

to be 0 and 1, respectively. The bounds were setting to represent the proportion of larvae dying due to the medium change. We performed the analysis using function built in the SciPy Python package Virtanen et al. (2020).

While this does not fit our data any better, it is still a potentially viable hypothesis where a biologically study should be conducted.

3. Materials and Methods

We reviewed a variety of models to accurately represent our data on the population dynamics of *Tribolium*. However, all models contained issues in best fitting our data. While we have valid hypothesis for why, we still wish to predict evolution of dispersal with one of the models demonstrated above. We wish to continue evolving our age structured model as we do believe it will eventually be an accurate representation of our data. However, we decided to continue our studies with dispersal utilizing the LPA model. The LPA model is an incredibly robust and well-studied model. There isn't another model that significantly fits our data better, and the LPA model is biologically accurate. We used this model to determine how natural selection determine the dispersal rate of *Tribolium* beetles under various environmental conditions. The first thing we need in order to accurately study the evolution of dispersal within *Tribolium* with the LPA is to determine the linear stability of the LPA model.

3.1. Calculating R_0 for LPA

In order to determine linear stability for the LPA model, we utilize (Hale et al., 2012) linear stability for discrete-time maps theorem, which is as follows:

Consider an equilibrium x^* of a discrete-time map of the form $x_{n+1} = f(x_n)$, where $f(x) \in C^1$ and $f'(x^*) \neq 0$. Then x^* is asymptotically stable if $|f'(x^*)| < 1$ and unstable if $|f'(x^*)| > 1$.

We found our Jacobin of our beetle free equilibrium $0,0,0$ to

$$\mathbf{J}_{(0,0,0)} = \begin{bmatrix} 0 & 0 & b \\ 1-\mu_l & 0 & 0 \\ 0 & 1 & 1-\mu_a \end{bmatrix}$$

If the modulus of dominant eigenvalue is > 1 then it is an unstable system. However, if the modulus of dominant eigenvalue is < 1 then it is a stable system. While there is a general solution to a cubic equation, we decided to utilize a concept from epidemiology R_0. The basic reproduction number R_0, in our context, is the expected number of adult beetles that a single adult beetle will produce over its lifetime. We are interested in the beetle-free equilibrium $(0,0,0)$, where the population is zero. This equilibrium is where we want to determine the threshold R_0 which tells us whether the population will grow or go extinct.

There are three causes we must consider, and calculate their probabilities to find R_0. We must consider the expected lifespan of an adult, the number of eggs an adult will lay in its lifetime, and the probability of eggs surviving long enough to grow into an adult.

The differential equation for the adult population is given by:

$$\frac{dA}{dt} = -\mu_a A$$

By separating variables, we solve this differential equation:

$$\frac{1}{A} dA = -\mu_a dt.$$

We then integrate both sides to get

$$\int \frac{1}{A} dA = -\mu_a \int dt$$
$$\ln|A| = -\mu_a t + C.$$

We then must solve for A where we get

$$A = C_1 e^{-\mu_a t}, \quad (C_1 > 0).$$

By then adding the initial condition $A(0) = A_0$

$$A(t) = A_0 e^{-\mu_a t}.$$

The expected lifespan $E[L_a]$ is given by the mean of the exponential distribution, which is:

$$E[L_a] = \frac{1}{\mu_a}.$$

We then must find the number of eggs laid by an adult. Given that an adult produces b viable eggs per time unit, the total number of eggs an adult will produce over its expected lifespan is:

$$b \cdot E[L_a] = \frac{b}{\mu_a}.$$

To find the probability that an egg survives and transitions through each stage to become an adult, we consider the survival probabilities at each stage.

The egg to larvae stage must survive cannibalism by adults and larvae which provides the following equation:

$$P\{A\} = e^{-(c_{ea} \int_0^t A(\tau) d\tau + c_{el} \int_0^t L(\tau) d\tau)}.$$

Next, we look at larvae becoming pupae where they must survive to become a pupae, we then get,

$$P\{B|A\} = 1 - \mu_l.$$

For the pupae to adult stage, a beetle must survive cannibalism by adults which provides this equation:

$$P\{C|A, B\} = e^{-c_{pa} \int_0^t A(\tau) d\tau}.$$

Therefore, the overall probability that an egg will survive through all stages to become an adult is:

$$P\{E \to A\} = P\{A\} \cdot P\{B|A\} \cdot P\{C|A, B\}.$$

When we substitute the probabilities we get:

$$P\{E \to A\} = e^{-(c_{ea} \int_0^t A(\tau)d\tau + c_{el} \int_0^t L(\tau)d\tau)} \cdot (1 - \mu_l) \cdot e^{-c_{pa} \int_0^t A(\tau)d\tau}.$$

At the beetle-free equilibrium $(0, 0, 0)$, there are no beetles present, hence any integral over the population densities $A(t)$, $L(t)$, etc., will be zero because the integrands are zero.

This implies that $P\{E \to A\} = (1 - \mu_l)$

The basic reproduction number, R_0, is the product of the total number of eggs laid by an adult and the probability of an egg surviving to become an adult:

$$R_0 = \frac{b(1 - \mu_l)}{\mu_a}$$

3.2. Metapopulation

We now wish to apply the previous LPA results to study dispersal. In order to accurately measure dispersal within *Tribolium*, we need to ensure the *Tribolium* have the ability to disperse. We created artificial metapopulations which allows us to study how the beetles move in a laboratory setting. Only the adult *Tribolium* beetles have the ability to move between metapopulations. The metapopulations used are either 4-patch or 5-patch metapopulations.

The 4-patch metapopulation as seen on the left hand side of Fig 7 demonstrates the four equal patches. Each cup is identical and has equal length tubing connecting the cups. The beetle is able to move freely between cups adjacent to their current residential patch. The 5-patch metapopulation is no longer identical. Only the middle cup contains connections to four different cups. A beetle must go through the middlemost cup to disperse to another cup.

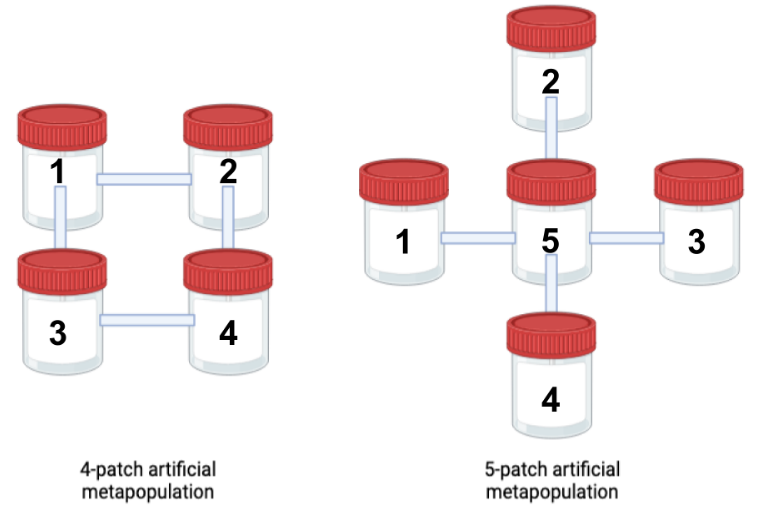

Figure 19: A visual representation of both a 4-patch and 5-patch metapopulation used to study dispersal

4. Results

We adjusted the original LPA model of Dennis et al. (1995) to account for dispersal within a 4-patch and 5-patch metapopulation environment. All original parameters and assumptions hold for this adjusted model. We have also added a few additional parameters. The additional parameters added were γ and ϵ. γ is necessary, as it accounts for the random chance that an adult will disperse. ϵ is necessary as dispersal will always have a cost associated with it. We don't need to add a parameter for the benefit of dispersal, as we will account for that within heterogeneous metapopulations. We represent the current patch a beetle is in as i, and the patches adjacent to that individual beetle as j and k.

4.1. LPA 4-Patch

With these parameters and assumption, we then adjusted the LPA model to account for dispersal in a 4-patch metapopulation and obtained the following equations. We hold the same assumptions as the original LPA model. Our additional assumptions is that beetles will only disperse into an adjacent patch. Furthermore, we assume that there is an equal change of beetles dispersing into the different adjacent patches.

Table 9: LPA with Dispersal Parameters

Parameter	Definition
b	Number of viable eggs per adult
μ_a	Natural death rate of adults
μ_l	Natural death rate of larvae
c_{ea}	Cannibalism of adults on eggs
c_{el}	Cannibalism of larvae on eggs
c_{pa}	Cannibalism of adults on pupae
γ	Chance of adult leaving any patch
ϵ	Chance of adult dying due to dispersal (cost)

$$\begin{pmatrix} L_{n+1,i} \\ P_{n+1,i} \\ A_{n+1,i} \end{pmatrix} = \begin{pmatrix} 0 & 0 & be^{-c_{ea}A_{n,i}-c_{el}L_{n,i}} \\ 1-\mu_l & 0 & 0 \\ 0 & e^{-c_{pa}A_{n,i}} & (1-\mu_a)(1-\gamma) \end{pmatrix} \begin{pmatrix} L_{n,i} \\ P_{n,i} \\ A_{n,i} \end{pmatrix} + \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2}\gamma(1-\mu_a)(1-\epsilon)(A_{n,j}+A_{n,k}) \end{pmatrix}$$

Since adults are the only ones who disperse, the larvae and pupae derivation is the same as before. The adult derivation is as follows:

$$A_{n+1,i} = P_n \underbrace{e^{-c_{pa}A_{n,i}}}_{\text{Cannibalism}} + \underbrace{(1-\mu_a)}_{\text{Survival}} \underbrace{(1-\gamma)}_{\text{Philopatric}} A_{n,i} + \underbrace{\frac{1}{2}\gamma(1-\mu_a)(1-\epsilon)(A_{n,j}+A_{n,k})}_{\text{Migration}}$$

We then crafted a numerical representation of these equations. As (Brozak et al., 2024) parameters best fit our population dynamics data, we used her best fit values for the visual representation as shown below.

Figure (20) represents how *Tribolium* will disperse within the 4-patch metapopulation. All of the beetles start in patch 1. At the next time step, patch 2 and patch 3 become filled with adults who begin reproducing. Patch 4 takes longer for a viable population to grow as beetles first must disperse to either patch 2 or patch 3 before dispersing into patch 4.

Additionally, using the same assumptions and parameters, we derived a formula for a 5-patch metapopulation.

4.2. LPA 5-Patch

Patches 1-4

$$\begin{pmatrix} L_{n+1,i} \\ P_{n+1,i} \\ A_{n+1,i} \end{pmatrix} = \begin{pmatrix} 0 & 0 & be^{-c_{ea}A_{n,i}-c_{el}L_{n,i}} \\ 1-\mu_l & 0 & 0 \\ 0 & e^{-c_{pa}A_{n,i}} & (1-\mu_a)(1-\gamma) \end{pmatrix} \begin{pmatrix} L_{n,i} \\ P_{n,i} \\ A_{n,i} \end{pmatrix} + \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \frac{1}{4}\gamma(1-\mu_a)(1-\epsilon)A_{n,5} \end{pmatrix}$$

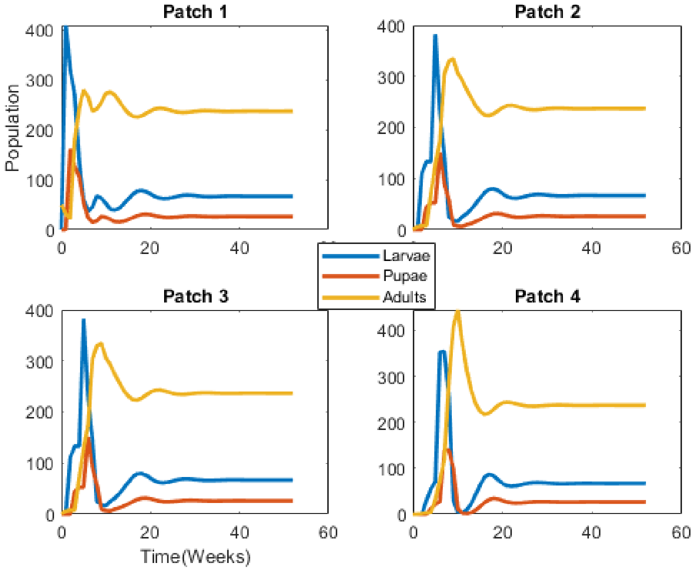

Figure 20: Predicted dispersal within a 4-patch metapopulation utilizing (Brozak et al., 2024) best fit parameters

Adult Class in Patch 5

$$\begin{pmatrix} L_{n+1,5} \\ P_{n+1,5} \\ A_{n+1,5} \end{pmatrix} = \begin{pmatrix} 0 & 0 & be^{-c_{ea}A_{n,5}-c_{el}L_{n,5}} \\ 1-\mu_l & 0 & 0 \\ 0 & e^{-c_{pa}A_{n,5}} & (1-\mu_a)(1-\gamma) \end{pmatrix} \begin{pmatrix} L_{n,5} \\ P_{n,5} \\ A_{n,5} \end{pmatrix} + \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \gamma(1-\mu_a)(1-\epsilon)\sum_{j=1}^{4} A_n, j \end{pmatrix}$$

The LPA 5-Patch model holds all of the same derivations as the 4-patch LPA model. We then introduced a different formula specifically for patch 5, as that patch is different from all of the other patches. All beetles start in this patch and all beetles must go through patch 5 to disperse to any other patch.

$$A_{n+1,5} = P_n \underbrace{e^{-c_{pa}A_{n,5}}}_{\text{Cannibalism}} + \underbrace{(1-\mu_a)}_{\text{Survival}} \underbrace{(1-\gamma)}_{\text{Sedentary}} A_{n,5} + \underbrace{\gamma(1-\mu_a)(1-\epsilon)\sum_{j=1}^{4} A_{n,j}}_{\text{Immigration from 4-patches}}$$

Figure (21) displays how dispersal happens within a 5-patch metapopulation. Beetles begin in patch five, which means a population establishes first in that patch. Afterwards, beetles have an equal chance of dispersing into patches 1-4 which means that the predicted dispersal is even throughout all of those patches. The population dynamics are the exact same in those 4 patches.

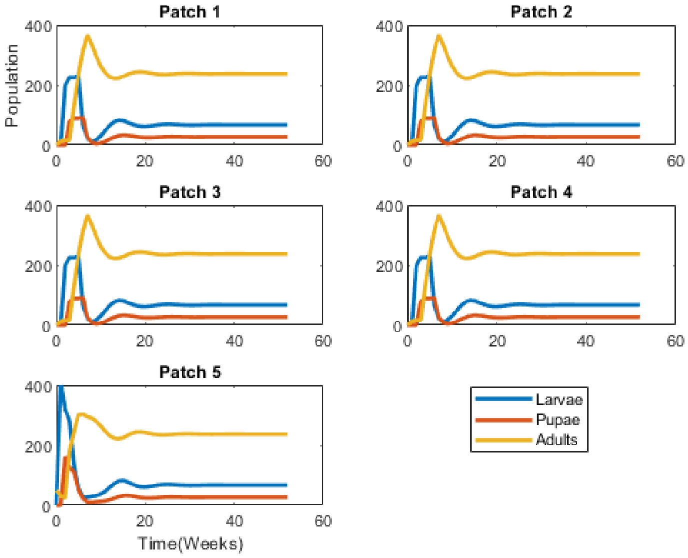

Figure 21: Predicted dispersal within a 5-patch metapopulation.

R_0 Metapopulation

Earlier, we derived the R_0 for the LPA model in a single population patch. Now, we wish to determine the R_0 for the artificial metapopulations. The R_0 holds true for both the 4-patch and 5-patch metapopulations. We used the exact same methods for viability conditions with the LPA. The only difference is we introduce γ as the dispersal rate and ϵ as the cost of dispersal . This is added to the mortality of adults, as now adults face death both by natural consequences and by dispersal. The full proof will be in the appedix.

R_0 for both 4 & 5 patch metapopulation models:

$$R_0 = \frac{b(1-\mu_l)}{\mu_a+\gamma\epsilon}$$

where γ is dispersal rate and ϵ is the cost of dispersal

The basic reproduction number R_0, in our context, is the expected number of adults that a single adult will produce over its lifetime. We are interested in the beetle-free equilibrium $(0,0,0)$, where the population is zero. This equilibrium is where we want to determine the threshold R_0 which tells us whether the population will grow or go extinct The R_0 is the same for both the 4-patch and 5-patch artificial metapopulation.

4.3. Applications to evolution

The construction of artificial metapopulations using the adjusted LPA models allows us to delve into the evolutionary dynamics of dispersal in a structured and controlled manner. By simulating the life cycle and dispersal behaviors of Tribolium beetles across multiple interconnected patches, we can investigate how dispersal strategies evolve in response to varying environmental pressures and habitat configurations.

The primary advantage of our artificial metapopulation models lies in their ability to capture the interplay between local population dynamics and dispersal. By incorporating realistic parameters such as cannibalism rates, natural death rates, and the costs associated with dispersal, these models provide a reliable framework for studying the adaptive significance of dispersal.

By adjusting parameters such as dispersal rate (γ) and dispersal cost (ϵ), we can simulate different evolutionary scenarios and observe how these factors influence the fitness of Tribolium beetles. For instance, we can explore how increased dispersal costs affect the propensity of beetles to move between patches and identify the conditions under which dispersal traits are favored by natural selection.

Using the models, we can introduce small mutations in dispersal traits and analyze their impact on population dynamics. By comparing the fitness of mutant and resident strategies, we can determine whether a particular dispersal rate is an Evolutionary Stable Strategy (ESS) – one that, if adopted by the population, cannot be invaded by any alternative strategy. This approach helps us understand the long-term evolutionary outcomes of dispersal behaviors.

Our models allow us to simulate metapopulations in heterogeneous environments, where patches differ in terms of resource availability, predation pressure, and other ecological factors. This heterogeneity can have significant implications for the evolution of dispersal, such as adaptive responses to environmental changes. By varying the conditions across patches, we can study how Tribolium beetles adjust their dispersal strategies to optimize their fitness. For example, in environments where some patches offer higher reproductive success or lower mortality risks, beetles may evolve higher dispersal rates to exploit these favorable conditions.

4.4. ESS 4-Patch

To determine fitness we have to analyze the persistent equilibrium. This now means that the process of maturing through the larval to adult stage will be affected by cannibalism and natural mortality.

Fitness of Residents:

$$F_r = \frac{be^{-c_{ea}E[A]-c_{el}E[L]-c_{pa}E[A]}(1-\mu_l)}{\mu_a+\gamma_r\epsilon} \tag{7a}$$

Fitness of Mutants:

$$F_m = \frac{be^{-c_{ea}E[A]-c_{el}E[L]-c_{pa}E[A]}(1-\mu_l)}{\mu_a+\gamma_m\epsilon} \tag{7b}$$

In order to calculate the relative fitness, we define our invasion exponent as the measuring the exponential rate of divergence or convergence of nearby trajectories in phase space. More formally, our invasion exponent is a dominant Lyapunov exponent. Since our world is variable and nonlinear, then our best measure of available fitness is based on dominant Lyapunov exponents When our invasion exponent is positive that indicates that small differences in fitness lead to exponential divergence, signifying strong selection pressure favoring the mutant. A negative Lyapunov exponent indicates convergence, meaning the mutant is less fit. Metz et al., 1992. We calculate our relative fitness as

$$\lambda = \ln\left(\frac{F_m}{F_r}\right)$$

We can then analyze our invasion exponent by

$$\begin{aligned}
\ln\left(\frac{F_m}{F_r}\right) &= \ln\left(\frac{\mu_a+\gamma_r\epsilon}{\mu_a+\gamma_m\epsilon}\right)\\
\implies \ln\left(\frac{\mu_a+\gamma_r\epsilon}{\mu_a+\gamma_m\epsilon}\right) &> 0 \quad \text{for mutant to invade}\\
\implies \frac{\mu_a+\gamma_r\epsilon}{\mu_a+\gamma_m\epsilon} &> 1\\
\implies \mu_a+\gamma_r\epsilon &> \mu_a+\gamma_m\epsilon\\
\implies \gamma_r &> \gamma_m.
\end{aligned}$$

This demonstrates that evolution will tend dispersal to 0. Which implies there is no benefit to disperse to identical patches. We demonstrate visually as well in which we create a visual representation of which beetle type survives when γ_m is greater than γ_r and when γ_m is less than γ_r.

Figure (22) represents that the beetles with the smaller dispersal rate will survive in a 4-patch population when compared to those with a higher dispersal rate. Our results are expected as in a homogenous metapopulation, there is not benefit to dispersal. The

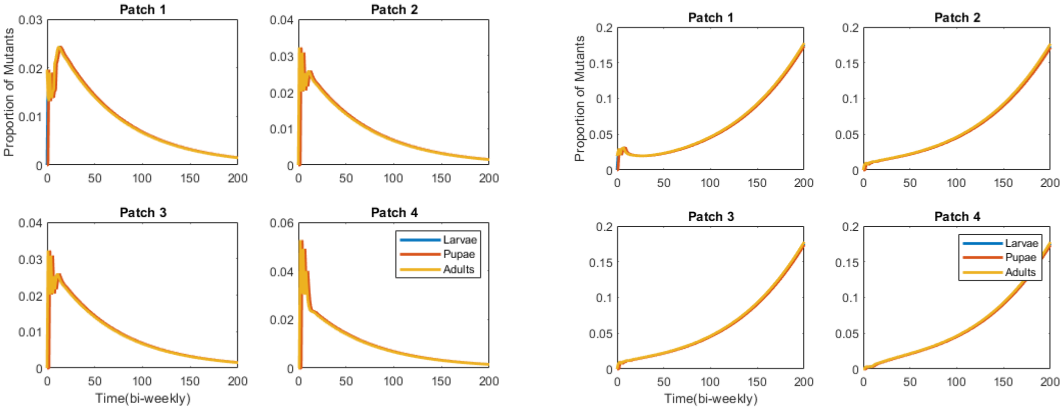

Figure 22: The figure to the left represents when $\gamma_m > \gamma_r$. Since the mutants have a higher dispersal rate than the residents, they will die out as evolution will tend dispersal to 0. The right figure demonstrates that one the dispersal rate of mutants is less than that have residents, $\gamma_m < \gamma_r$, then the mutants will invade as dispersal tends to zero.

only thing dispersal does is increase your chance of dying due to dispersal. We have seen this result in literature such as Hanski and Gilpin, 1991 which states a homogenous metapopulation will not favor dispersal, and the ESS will always be zero. However, we wish to discover if a 5-patch metapopulation can generate enough heterogeneity where the ESS might not be zero, and if dispersal could be favored.

4.5. ESS 5-Patch

To calculate the evolutionary stability strategy for a 5-patch metapopulation, the process is similar, with some adjustments for the different configuration of inner and outer patches. We introduce the idea of a class-α beetle where $\alpha \in r, s$

We define the fitness of a class-α beetle inside of the inner patch as

$$F_{\text{in},\alpha} = \frac{be^{-c_{ea}E[A_{\text{in}}]-c_{el}E[L_{\text{in}}]-c_{pa}E[A_{\text{in}}]}(1-\mu_l)}{\mu_a+\gamma_\alpha\epsilon}.$$

The fitness of outer patch class-α as beetle is defined as

$$F_{\text{out},\alpha} = \frac{be^{-c_{ea}E[A_{\text{out}}]-c_{el}E[L_{\text{out}}]-c_{pa}E[A_{\text{out}}]}(1-\mu_l)}{\mu_a+\gamma_\alpha\epsilon}.$$

We can then define our overall fitness of the class-α as

$$F_\alpha = E[A_{\text{in}}]F_{\text{in},\alpha}+4E[A_{\text{out}}]F_{\text{out},\alpha}.$$

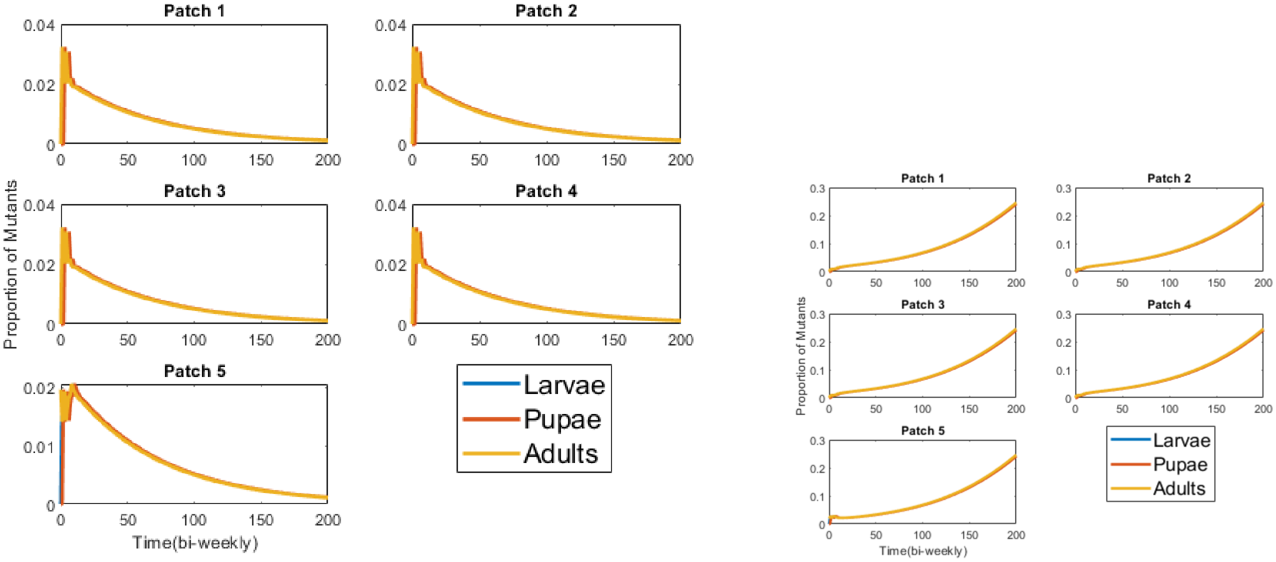

Figure 23: The figure to the left represents when $\gamma_m > \gamma_r$. Since the mutants have a higher dispersal rate than the residents, they will die out as evolution will tend dispersal to 0. The right figure demonstrates that one the dispersal rate of mutants is less than that have residents, $\gamma_m < \gamma_r$, then the mutants will invade as dispersal tends to zero.

However, when we evaluate the relative fitness, we get the same result as the 4-patch model

$$\gamma_r > \gamma_m.$$

This suggests that the 5-patch metapopulation does not create enough heterogeneity to influence dispersal. We can demonstrate this result visually as well.

The 5-patch metapopulation does not generate enough heterogeneity for dispersal to evolve past zero. The ESS still remains 0.

4.6. Random Extinctions

Since a 5-patch metapopulation does not generate enough heterogeneity, we looked at random events in nature that has the potential to generate a heterogeneous environment. We looked at local extinctions which is a common phenomena in nature. Furthermore, local extinctions is a primary reason for dispersal (Dieckmann et al., 1999). We wished to see if emulating extinction in different patches will generate enough heterogeneity for dispersal to evolve.

We created simulations in both 4-patch and 5-patch models where random extinction would occur. This computational experiment involved running the LPA model for a specified amount of time to obtain the equilibrium points. Using Table 21, the starting amount of larvae, pupae, and adults is 67, 26, and 236, respectively. After 20 time-steps, a patch will be selected at random to empty the patch, imitating extinction.

The γ values chosen for the mutants were randomly chosen each simulation between 0 and 1; the dispersal rate of a resident beetle is fixed to 0.3. We realized that is pretty low and the probability of the mutant γ's is higher than 0.3 is pretty high. So for the 5-patch models, the resident dispersal rate is set to 0.8. Next, a fraction of a mutant beetle will be added in a random patch, excluding the patch selected for extinction. If we introduced a mutant into a patch destined for extinction, we would be unable to see if the mutant had the ability to invade.

The differences in dispersal rate (γ) caused fluctuations in all patches, although they are all relatively similar with the stochastic factors. The graphs were also plotted using the proportion of each class (resident, mutant #1, mutant #2, and mutant #3) to the entire population, shown in Figure (36). It is important to note the bar graphs represent the proportion of space each class takes up. With this in mind, the patch graph expresses the proportion in a different way- showing the change proportion depending on the γ's. Although adding a fraction of a beetle truly shows the evolution of dispersal, no conclusions can be drawn from it as the changes are so slow, it is near invisible to the naked eye.

To fix this issue, we increased the amount of mutant beetles added every 20 time-steps to 1000. This does not affect whether they can take over or go extinct as dispersal rate is the only indicator of each beetles individual fitness. Each time a new mutant was added, a new color appeared in the graph. There are only 3 mutants, totaling up to 4 types of beetles in this experiment. Seeing as that random extinction occurs and wipes a singular patch population to zero, the proportion can be undefined. This is solved by setting it to zero causing dips and dark lines on the graphs. Representative graphs were chosen for this section. For the full list of graphs used for this project, see Appendix. In the 4-patch simulations, we see a monomorphic pattern where the beetle type with the lowest dispersal rate take over the rest. The 5-patch however, it is showing a pattern representing polymorphism.

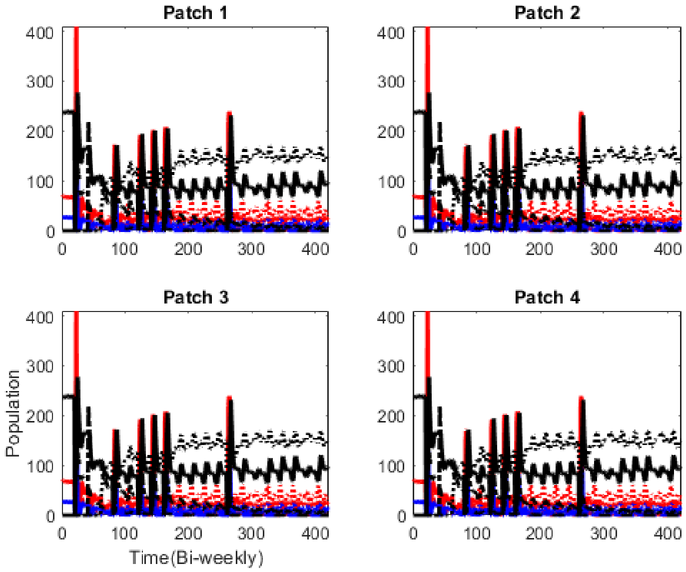

Figure 24: Simulation of dispersal evolution in a 4-patch metapopulation in a line graph. The third mutant (dashed line) with γ 0.0684 takes over the population along with the resident (solid line). The vertical lines represent the random extinction occurrences.
Resident: $\gamma = 0.3$ Mutant #1: $\gamma = 0.7684$ Mutant #2: $\gamma = 0.5333$ Mutant #3: $\gamma = 0.0684$

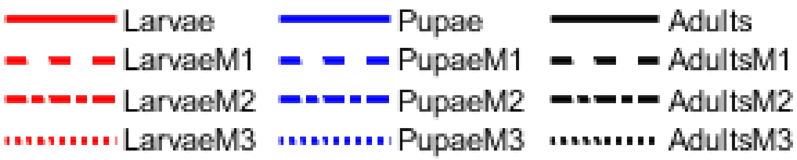

Figure 25: Legend

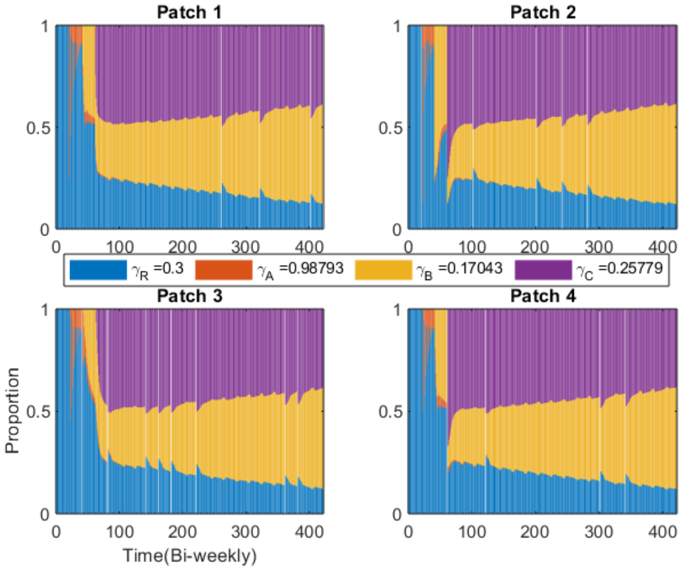

Figure 26: Simulation of dispersal proportion in a 4-patch metapopulation using a bar graph. This representation is the most interesting because it shows every scenario. The first mutation has a γ of .988, meaning they will disperse 98.8% of the time, forcing them into extinction in 2 years. Visually, the first mutant is barely seen. When the second mutation gets added with a dispersal rate of 0.17, they take over everything and will eventually be the only species to live on. When the third mutation gets added with a γ of 0.25, they fall into extinction at almost the same rate as the resident because of how close the γ's are.

4.6.1. Numerical solution of 4 and 5 patch dispersal

We now wish to mathematically prove our results. We do this by calculating the specific fitness of a given beetle in a given patch.

Suppose a 4-patch metapopulation where L_i, P_i, A_i determines the Larvae, Pupae and Adult population in patch $i \in \{1,2,3,4\}$ respectively.

Given the current position and population configuration at time-step t we can determine the specific fitness of a class-α beetle.

Let: $\Psi_1 = e^{-c_{ea}A_i - c_{el}L_i - c_{pa}A_i}$, $\Psi_2 = e^{-c_{ea}A_j - c_{el}L_j - c_{pa}A_j}$, and $\Psi_3 = e^{-c_{ea}A_k - c_{el}L_k - c_{pa}A_k}$

where $\Psi_{1,2,3}$ is the cannibalism force. i represents the patch of the beetle's current position, and j,k are the adjacent patches to i.

Specific Fitness of Class-α Beetle in 4-patch:

$$\frac{b(1-\mu_l)[(1-\gamma_\alpha)\Psi_1 + \frac{1}{2}\gamma_\alpha\Psi_2 + \frac{1}{2}\gamma_\alpha\Psi_3]}{\mu_a + \gamma_\alpha\epsilon}$$

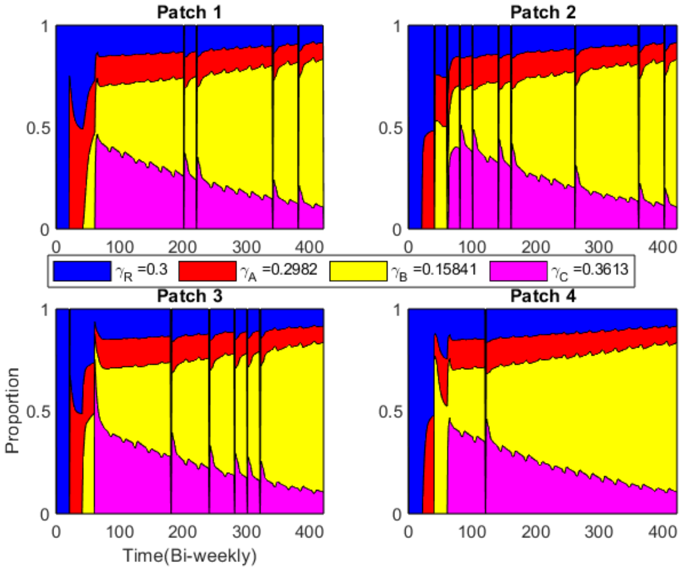

Figure 27: Simulation of the proportion of dispersal evolution in a 4-patch metapopulation using a patch graph. This is similar to Figure (26). The main difference is how the different classes (resident and mutants #1-3) are proportioned. Unlike the bar graphs where the classes are taking up space, the patch graph shows how the different γ values determine the rate at which the classes take up the space. The further away the γ value is from the resident (0.3), the longer it takes to take over or fall to extinction. The colors blue, red, yellow, and magenta represent the resident, mutant 1, 2, and 3, respectively. The breaks in the graph designate the proportion being undefined as random extinction occurs.

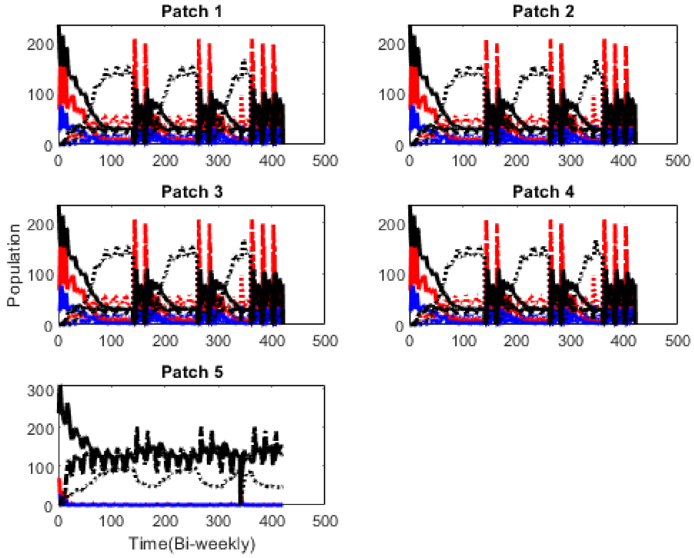

Figure 28: Simulation of dispersal evolution in a 5-patch metapopulation. The colors have the same representation as the previous 4-patch figure. The resident dispersal rate has been set to 0.3. Mutant #3 has the lowest dispersal rate, allowing it to grow over the rest of the population. Patch 5 always displays a different pattern because the odds of a beetle arriving is higher than the outer 4 patches because they have to go through it. The vertical lines represent the random extinction occurrences.
Resident: $\gamma = 0.3$ Mutant #1: $\gamma = 0.5316$ Mutant #2: $\gamma = 0.8732$ Mutant #3: $\gamma = 0.0545$

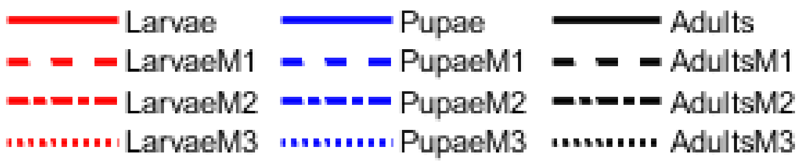

Figure 29: Legend

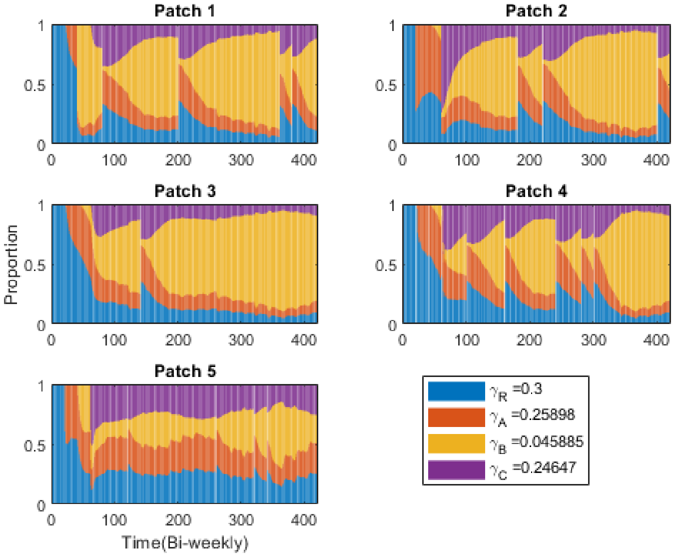

Figure 30: Simulation of dispersal evolution in a 5-patch metapopulation using a bar graph. The resident dispersal rate has been set to 0.3. The second mutation, with a of 0.045 grows into the proportion of the other beetles, but it is interesting to note of the proportion decrease at the very end.

Suppose a 5-patch metapopulation where L_i, P_i, A_i determines the population in patch $i \in \{1,2,3,4,5\}$.

Given the current position and population configuration at time-step t we can determine the specific fitness of a class-α beetle.

Let: $\Psi_i = e^{-c_{ea}A_i - c_{el}L_i - c_{pa}A_i}$ and $\Psi_k = e^{-c_{ea}A_k - c_{el}L_k - c_{pa}A_k}$

where $\Psi_{i,k}$ represents the cannibalism force. i represents the patch of the beetle's current position and k represents the surrounding patches of i. Note that $i,k \in \{1,2,3,4,5\}$ and $k \neq i$.

Specific Fitness of Class-α Beetle in 5-patch Outer Patches:

$$\frac{b(1-\mu_l)[(1-\gamma_\alpha)\Psi_i + \gamma_\alpha \Psi_5]}{\mu_a + \gamma_\alpha \epsilon}$$

Specific Fitness of Class-α Beetle in 5-patch Inner Patch:

$$\frac{b(1-\mu_l)[(1-\gamma_\alpha)\Psi_5 + \frac{1}{4}\gamma_\alpha \sum_{j=1}^{4} \Psi_j]}{\mu_a + \gamma_\alpha \epsilon}$$

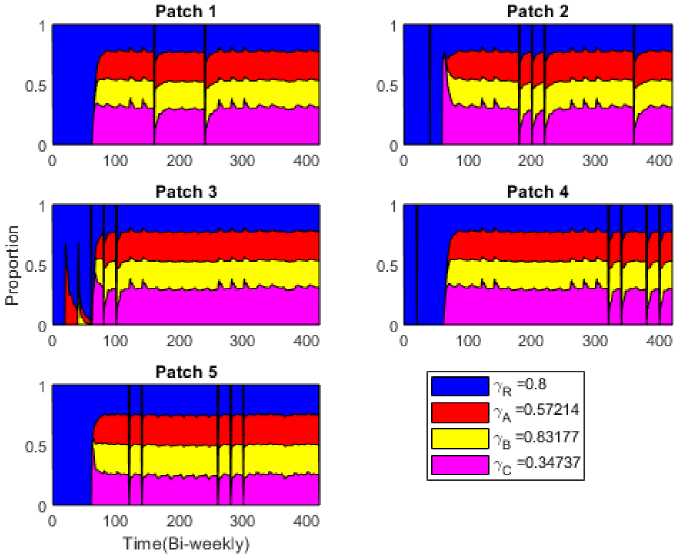

Figure 31: Simulation of predicted dispersal proportion in a 5-patch metapopulation using a patch graph. This graph shows that the 5-patch expresses a polymorphic pattern. The resident dispersal rate has been set to 0.8. In the beginning when we introduce the first and second mutant, they immediately die out. But it is when we add in the third mutation, we notice the mutants return and they all coexist. This is because the mutants never completely went extinct, but had a proportion of $3*10^{-7}$ so when the third mutation came in it changed the required dispersal rate so they can coexist.The breaks in the graph designate the proportion being undefined as random extinction occurs.

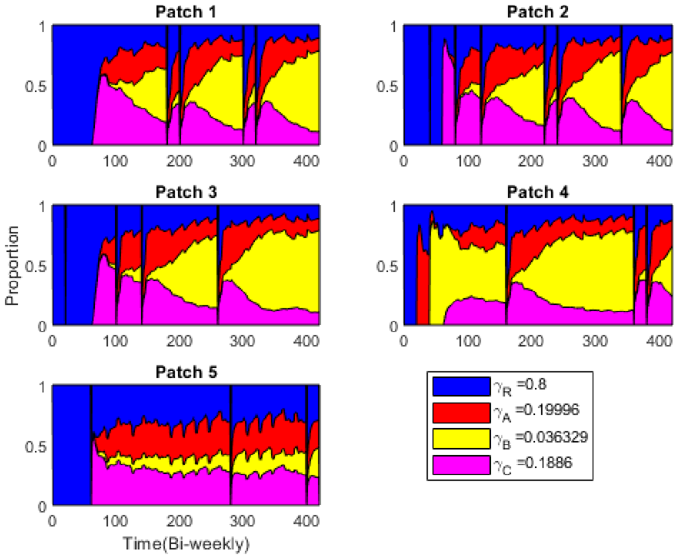

Figure 32: Simulation of predicted dispersal proportion in a 5-patch metapopulation using a patch graph. This figure shows how the 5-patch models can show a polymorphic pattern, but still runs the possibility of showing monomorphism as time progresses. The resident dispersal rate has been set to 0.8. The noticeable feature is that the γ value for the second mutant is so low that it still impacts the graphs in a big way, regardless of the random extinctions. The breaks in the graph designate the proportion being undefined as random extinction occurs.

5. Discussion

Our study provides the necessary and sufficient conditions to prove that homogeneous 4-path and 5-path metapopulations do not generate enough heterogeneity for dispersal to evolve. This finding aligns with established theories in metapopulation dynamics, particularly those proposed by Hanski and Gilpin, 1991, which suggest that in a homogeneous environment, dispersal tends to be minimized due to the lack of selective pressure favoring movement between identical patches. In such scenarios, a mutant beetle with a different dispersal rate will either outcompete the residents, driving them to extinction, or fail to establish, resulting in the mutant's extinction.

By introducting random extinctions within the 4-path metapopulation, we observed evidence suggesting that high mutant γ values introduced did not influence the population dynamics of the other patches, resulting in uniformity across the metapopulation. This outcome is consistent with the notion that local extinctions alone do not introduce sufficient heterogeneity to shift the evolutionary stable strategy (ESS) away from zero.

The 5-patch model, however, presented an interesting case of potential polymorphism, where mutants and residents could coexist. Yet, similar to the 4-patch model, it also exhibited patterns of monomorphism, where the ESS tends to the lowest dispersal. This duality suggests that while the 5-patch structure introduces some level of complexity, it may not be enough to sustain long-term polymorphism under the conditions tested. A plausible hypothesis for these results is that the simulations might not have run for a sufficient duration to capture the full evolutionary dynamics.

Doebeli and Ruxton provided a comprehensive overview of the evolution of dispersal within metapopulations, highlighting that the ecological dynamics are driven by both local dynamics and the dispersal rate of each patch. They argue that in metapopulations exhibiting non-equilibrium dynamics, the ESS can be nonzero. Our findings, which show no evolution of dispersal within randomly extinct patches, suggest that either the heterogeneity introduced by random extinctions is insufficient, or other factors are influencing the ESS towards zero.

Our model's assumption of non-biased dispersal may also contribute to these results. Ogden, 1970 demonstrated that *Tribolium* dispersal is often sex-biased and influenced by environmental conditions such as humidity or flour conditioning. Additionally, (Robertson and Cushing, 2011) found that adults tend to disperse away from juveniles, indicating that intra-specific interactions play a significant role in dispersal behavior. These factors are not accounted for in our model and could potentially affect the evolution of dispersal rates.

Future research should explore the conditions under which metapopulations might exhibit polymorphism or lead to a dominant beetle dispersal rate. Specifically, it would be valuable to extend the simulation's duration to capture long-term evolutionary trends and potential shifts in dispersal strategies. Incorporating sex-biased dispersal, environmental preferences, and interactions between life stages would reflect more realistic dispersal behavior. Additionally, considering the impact of temporally varying environments, where patches change in connectivity over time, could create dynamic selective pressures for dispersal.

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Appendix

Full calculation of R_0 for Metapopulations

There are four causes we must consider, and calculate their probabilities to find R_0. We must consider the expected lifespan of an adult, the cost an adult will face when they disperse, the number of eggs an adult will lay in its lifetime, and the probability of eggs surviving long enough to grow into an adult.

The differential equation for the adult population is given by:

$$\frac{dA}{dt} = -\mu_a A$$

By separating variables, we solve this differential equation:

$$\frac{1}{A} dA = -\mu_a dt.$$

We then integrate both sides to get

$$\int \frac{1}{A} dA = -\mu_a \int dt$$
$$\ln |A| = -\mu_a t + C.$$

We then must solve for A where we get

$$A = C_1 e^{-\mu_a t}, \quad (C_1 > 0).$$

By then adding the initial condition $A(0) = A_0$

$$A(t) = A_0 e^{-\mu_a t}.$$

The expected lifespan $E[L_a]$ is given by the mean of the exponential distribution, which is:

$$E[L_a] = \frac{1}{\mu_a}.$$

We then must have γ for dispersal rate and ϵ as the cost of dispersal. This will affect the expected lifespan $E[L_a]$.

$$E[L_a] = \frac{1}{\mu_a + \gamma\epsilon}.$$

We then must find the number of eggs laid by an adult. Given that an adult produces b viable eggs per time unit, the total number of eggs an adult will produce over its expected lifespan is:

$$b \cdot E[L_a] = \frac{b}{\mu_a + \gamma\epsilon}.$$

To find the probability that an egg survives and transitions through each stage to become an adult, we consider the survival probabilities at each stage.
The egg to larvae stage must survive cannibalism by adults and larvae which provides the following equation:

$$P\{A\} = e^{-(c_{ea}\int_0^t A(\tau)d\tau + c_{el}\int_0^t L(\tau)d\tau)}.$$

Next, we look at larvae becoming pupae where they must survive to become a pupae, we then get,

$$P\{B|A\} = 1 - \mu_l.$$

For the pupae to adult stage, a beetle must survive cannibalism by adults which provides this equation:

$$P\{C|A,B\} = e^{-c_{pa}\int_0^t A(\tau)d\tau}.$$

Therefore, the overall probability that an egg will survive through all stages to become an adult is:

$$P\{E \rightarrow A\} = P\{A\} \cdot P\{B|A\} \cdot P\{C|A,B\}.$$

When we substitute the probabilities we get:

$$P\{E \rightarrow A\} = e^{-(c_{ea}\int_0^t A(\tau)d\tau + c_{el}\int_0^t L(\tau)d\tau)} \cdot (1 - \mu_l) \cdot e^{-c_{pa}\int_0^t A(\tau)d\tau}.$$

At the beetle-free equilibrium $(0,0,0)$, there are no beetles present, hence any integral over the population densities $A(t)$, $L(t)$, etc., will be zero because the integrands are zero.

This implies that $P\{E \to A\} = (1-\mu_l)$

The basic reproduction number, R_0, is the product of the total number of eggs laid by an adult and the probability of an egg surviving to become an adult:

$$R_0 = \frac{b(1-\mu_l)}{\mu_a+\gamma\epsilon}$$

Additional Graphs of Dispersal Simulations

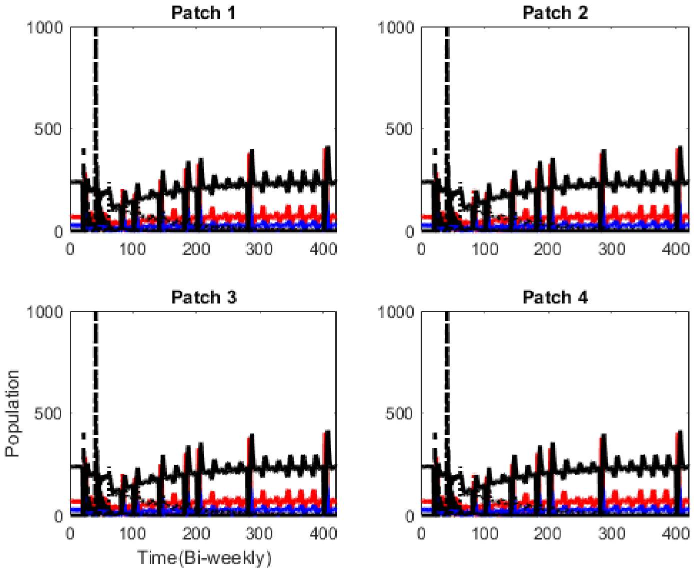

Figure 33: Simulation of dispersal evolution in a 4-patch metapopulation in a line graph. The vertical lines represent the random extinction occurrences. Shown in the figures, the difference in dispersal rates allow the mutant beetles to either take over the residents, or fall into extinction. The resident (solid line), having the smallest γ takes over the population. Other mutations (dashed lines) with γ's 0.98, 0.96, and 0.57 go extinct. Resident: $\gamma = 0.3$ Mutant #1: $\gamma = 0.9820$ Mutant #2: $\gamma = 0.9690$ Mutant #3: $\gamma = 0.5766$

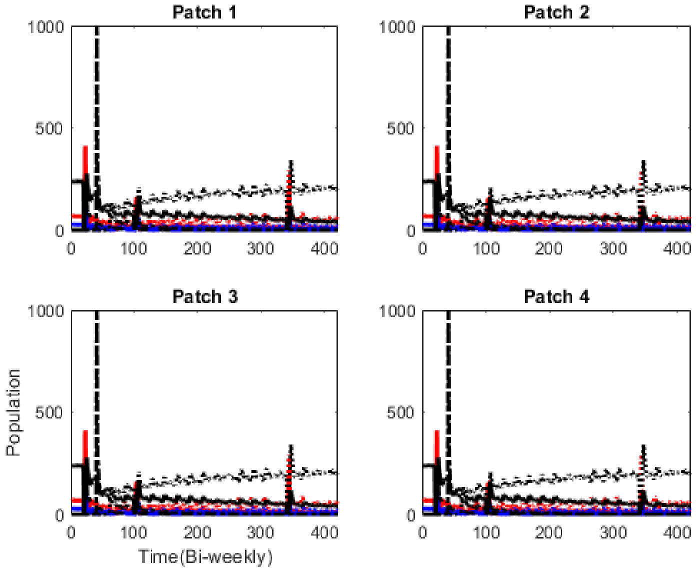

Figure 34: Simulation of dispersal evolution in a 4-patch metapopulation using a line graph. Although smaller than the last simulation, the third mutation that disperses at a rate of 0.1715 lives while the other strands go extinct because they have the smallest γ. The first mutation (long-dashed line) has a γ of 0.8665 and immediately falls to extinction. The vertical lines represent the random extinction occurrences.
Resident: $\gamma = 0.3$ Mutant #1: $\gamma = 0.8665$ Mutant #2: $\gamma = 0.6890$ Mutant #3: $\gamma = 0.1715$

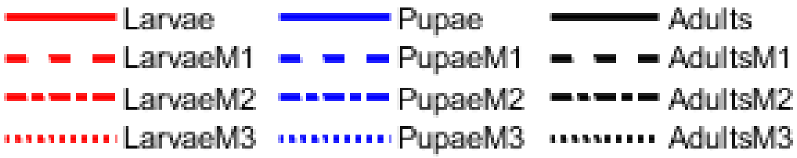

Figure 35: Legend

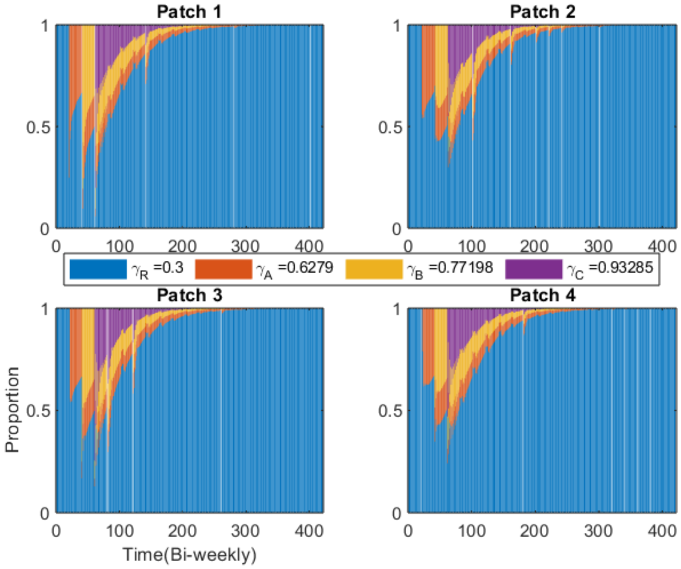

Figure 36: Simulation of dispersal evolution proportion in a 4-patch metapopulation using a bar graph. It is important to note that the proportion represented here is the amount of space each class takes up. The resident beetle (blue) has the lowest γ value, meaning it disperses the least. All mutants have a very high dispersal rate, killing them into extinction after just 7.5 years.

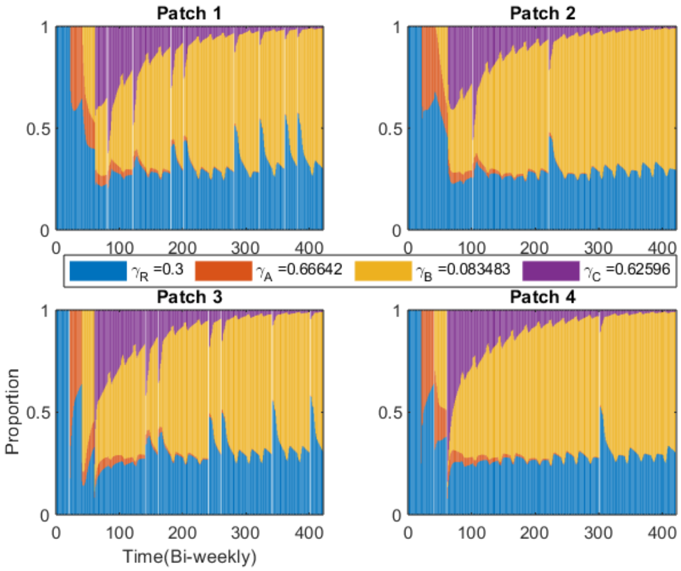

Figure 37: Simulation of dispersal evolution proportion in a 4-patch metapopulation using a bar graph. When the first mutant beetle gets added to the population with a dispersal rate of 0.6, they die out almost immediately. Visually, they get pushed down by the second mutation, which has a γ of 0.08 allowing them to take over the other mutants. Additionally, the dispersal rate of the third mutation is lower than the resident, killing them too.

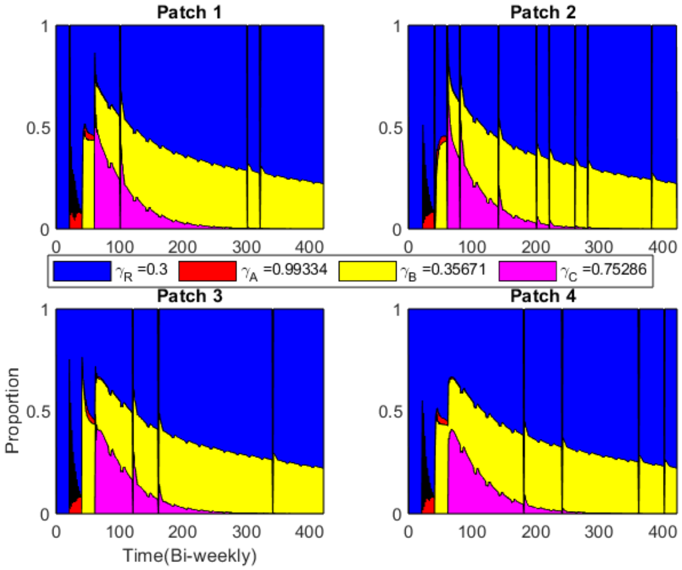

Figure 38: Simulation of dispersal proportion in a 4-patch metapopulation using a patch graph. The high γ values cause the beetles to go extinct. The breaks in the graph designate the proportion being undefined as random extinction occurs.

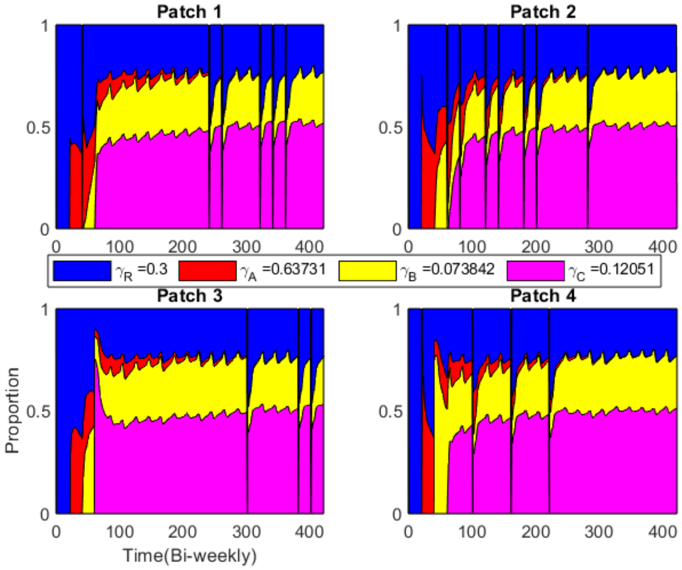

Figure 39: Predicted dispersal proportion during a 4-patch metapopulation simulation using a patch graph. The low γ values allow the mutant beetles to take over the population. The breaks in the graph designate the proportion being undefined as random extinction occurs.

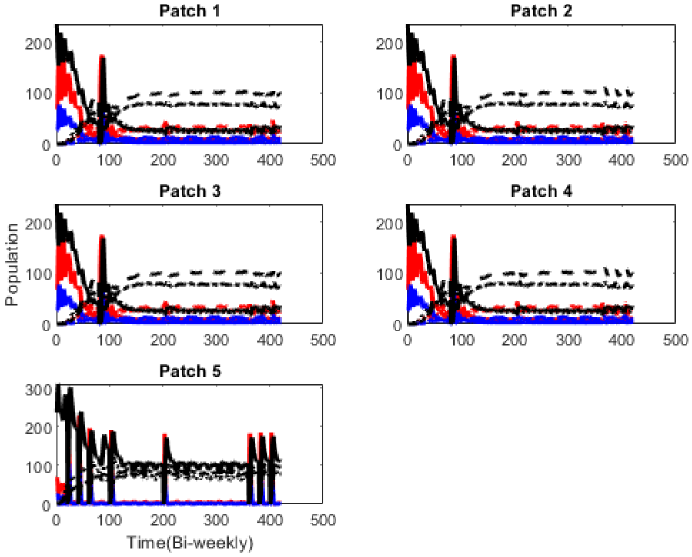

Figure 40: Simulation of dispersal evolution in a 5-patch metapopulation. The colors red, blue, and black represent the larvae, pupae, and adults, respectively. The resident dispersal rate has been set to 0.3. The vertical lines represent the random extinction occurrences. As represented, all mutants are smaller than the resident's dispersal rate (0.3), so they all take over the resident.
Resident: $\gamma = 0.3$ Mutant #1: $\gamma = 0.0675$ Mutant #2: $\gamma = 0.0690$ Mutant #3: $\gamma = 0.1668$

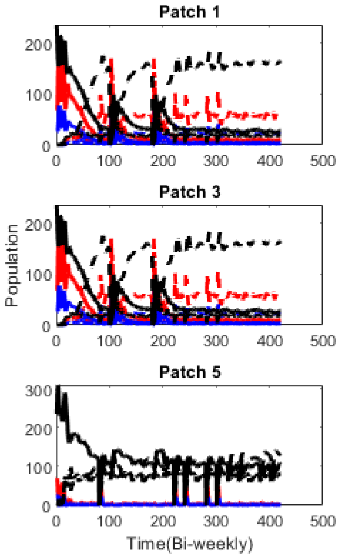

Figure 41: Simulation of dispersal evolution in a 5-patch metapopulation. The colors have the same representation as the previous figure. The resident dispersal rate has been set to 0.3. The vertical lines represent the random extinction occurrences. This graph is interesting because of the diversity of the γ values, they all coexist.

Resident: $\gamma = 0.3$ Mutant #1: $\gamma = 0.0787$ Mutant #2: $\gamma = 0.9331$ Mutant #3: $\gamma = 0.6029$

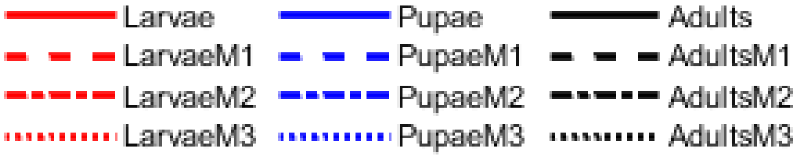

Figure 42: Legend

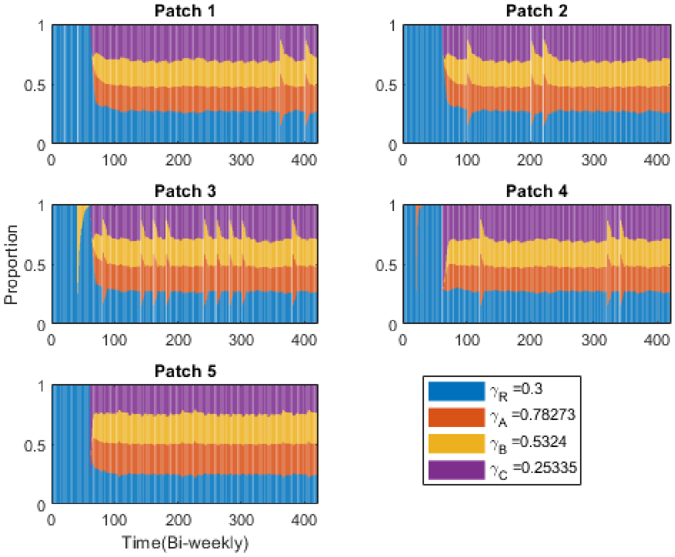

Figure 43: Simulation of dispersal proportion in a 5-patch metapopulation using a bar graph. The resident dispersal rate has been set to 0.3. In a similar case as the previous figure, all beetles coexist regardless of their γ values.

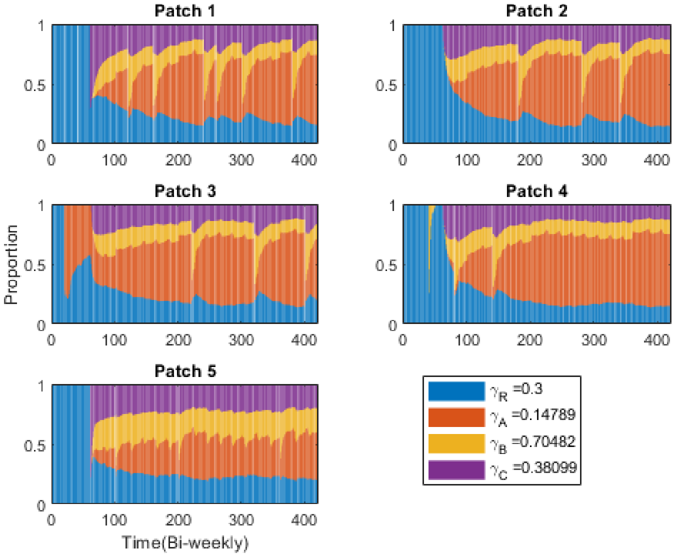

Figure 44: Simulation of dispersal proportion in a 5-patch metapopulation using a bar graph. The resident dispersal rate has been set to 0.3. The dispersal rate of the second mutant is too high, which lowers the fitness so the proportion is the lowest.

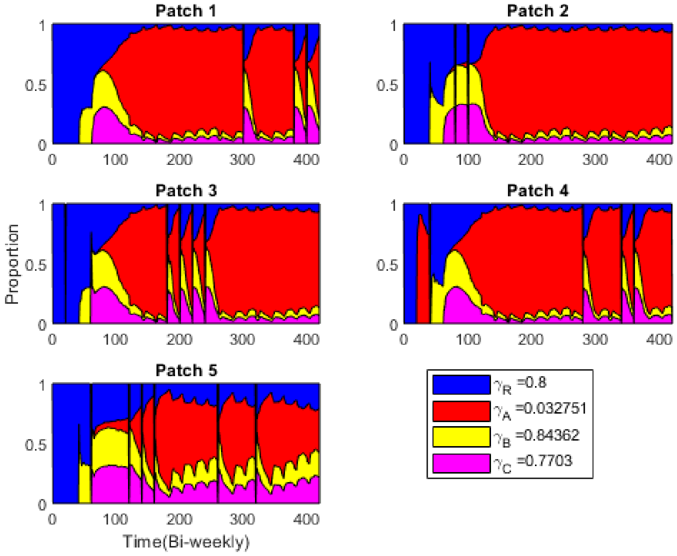

Figure 45: Simulation of dispersal proportion in a 5-patch metapopulation using a patch graph. The breaks in the graph designate the proportion being undefined as random extinction occurs. This allows the population to refresh and take longer to go extinct, take over, or coexist. The resident dispersal rate has been set to 0.8. The dispersal rate of the first mutant which is 0.03, allows it to take over the rest of the population.

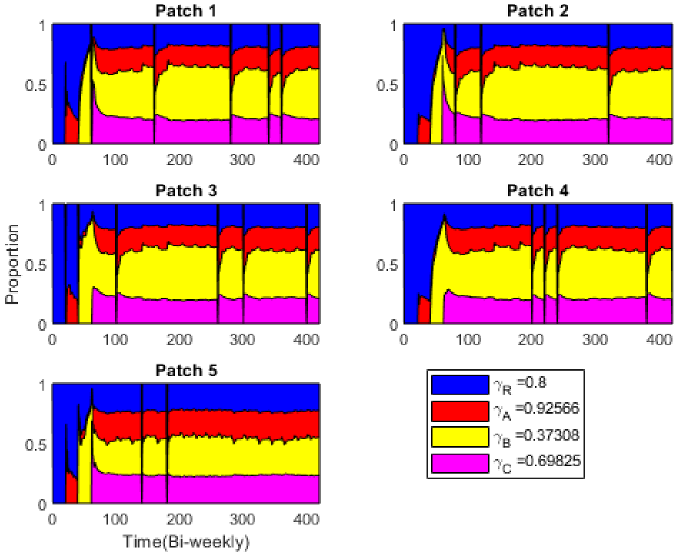

Figure 46: Simulation of predicted dispersal proportion in a 5-patch metapopulation using a patch graph. Follows the same extinction observation as the previous figure. The resident dispersal rate has been set to 0.8. The breaks in the graph designate the proportion being undefined as random extinction occurs. This graph is also interesting because a mutant is not taking over any of the other mutants or resident.