Dispersal Evolution in *Tribolium* Metapopulations; a Game Theory Approach

Authors: Kody Angell, Elijah Morales, and Bakari Wiltshire
Mentors: Jordy Rodriguez Rincon, Lucero Rodriguez Rodriguez, and John D. Nagy

July 19, 2024

Table of Contents

Dispersal

Definition

"...any movement of individuals or propagules that has potential consequences for gene flow across space"[Ronce, 2007].

Table: The costs & benefits of dispersal as described by Dieckmann et al. [1999]

Costs	Benefits
Inability to mate	Avoids inbreeding
Increases predation and parasites	Avoids intraspecific competition
Could settle in an unsuitable habitat	Avoids interspecific competition
Uses metabolic energy	Increases resource diversity

Takeaway

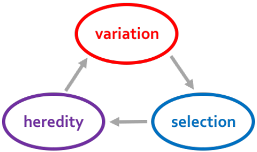
Evolutionary favored dispersal rate maximizes payoff (benefits − costs).

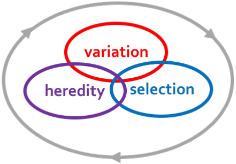
Basic Evolutionary Theory

Why is Natural Selection Important?

Natural selection is required for evolutionary payoff

Necessary and sufficient conditions for evolution by natural selection



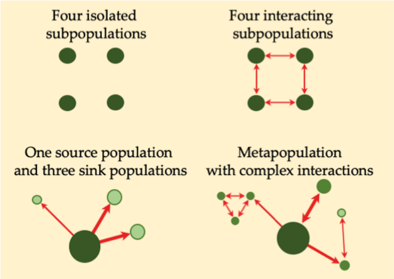


Source: [Darwin, 1859, Lewontin, 1970]

Overarching Research Goal

Metapopulation Definition

A metapopulation consists of many subpopulations connected by dispersal [Levins, 1969, 1970].



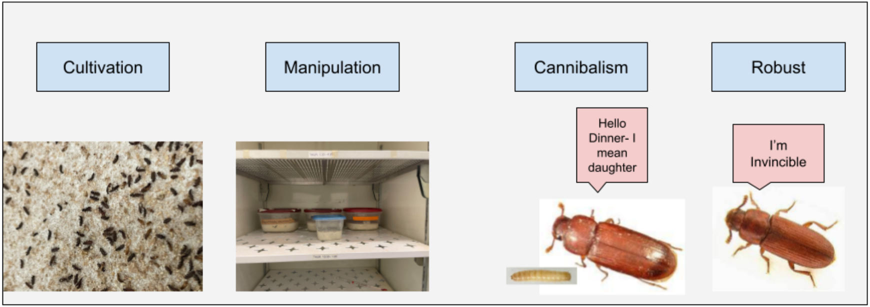
Research Question

How does natural selection determine dispersal rate in metapopulations?

Study Species

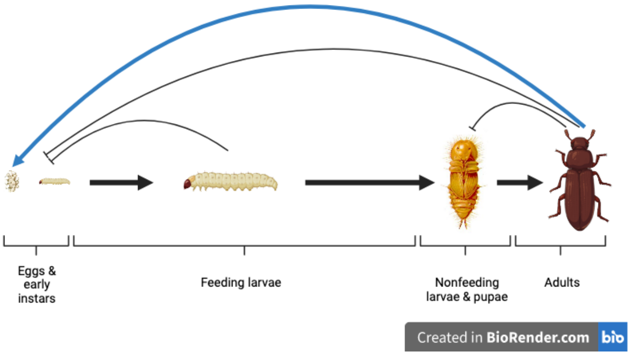
The flour beetle, a Tenebrionid beetle in the genus *Tribolium*, has features that make them a useful research organism.

Why Did We Choose *Tribolium?*



Tribolium Beetle Life History

- *Tribolium* beetle matures in 4 weeks [Park, 1934]
- Average life span is 1 year [Park, 1934]
- Can live up to 3 years [Park, 1934]



Tribolium Dispersal Evolves

Key Findings from Research

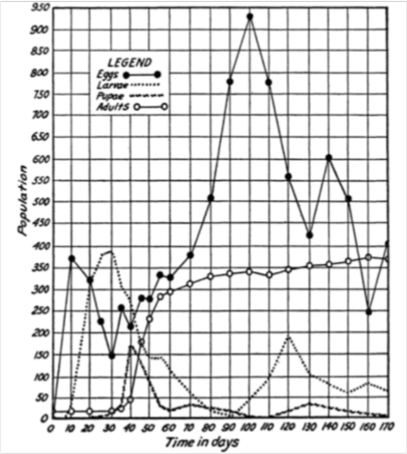
Ogden (1970a, 1970b)

- Dispersal rates in *Tribolium* can evolve due to natural selection acting on genetic variations in dispersal-related traits.
- Dispersal rates are affected by population density, food availability, and natal environment.

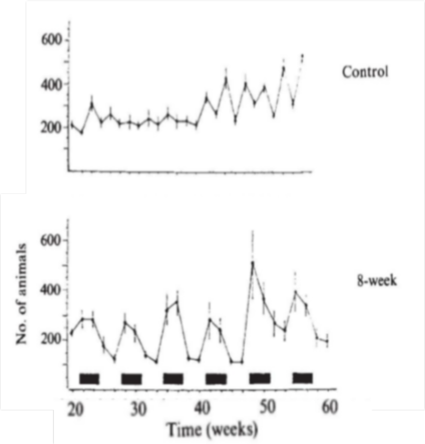
Pointer et al. (2023)

- Dispersal in *Tribolium* is oligogenic, meaning it is controlled by a few genes.
- Heritable traits linked to dispersal can evolve, providing a genetic basis for changes in dispersal behavior over generations.

Previous Studies on *Tribolium* Dynamics



Park [1934]



Jilson and Constantino [1980]

Current Studies on *Tribolium* Dynamics

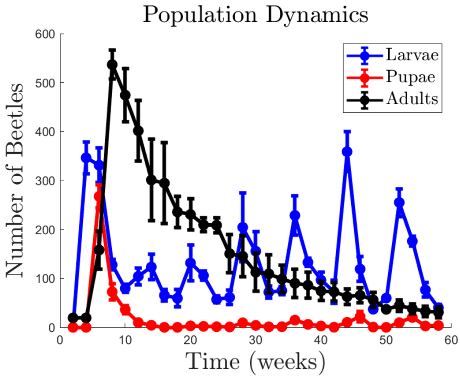
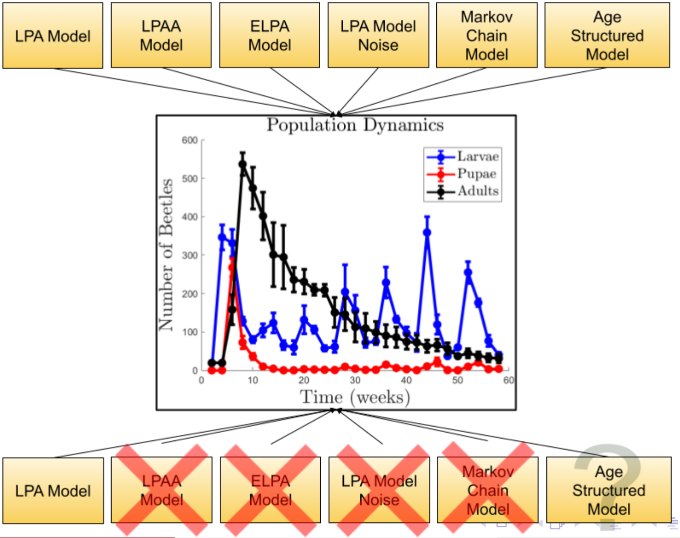


Figure: Our full data set of *Tribolium* population dynamics. Adults appear to dampen the oscillations of larvae

Next Step

We need to evaluate models that can reflect this data.

Goal: Find Model That Reflects Our Data



Mathematical Modeling - LPA Model

Variables

L_n = Number of feeding larvae at time step n
P_n = Number of non-feeding larvae, pupae and callow adults at time step n
A_n = Number of mature adults at time step n

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

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

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

Parameter	Definition
μ_a	The natural mortality proportion of adults
μ_l	The natural mortality proportion of larvae
b	The average larval recruitment, without cannibalism
c_{ea}	The cannibalism rate of eggs being eaten by adults
c_{el}	The cannibalism rate of eggs being eaten by larvae
c_{pa}	The cannibalism rate of pupae being eaten by adults

LPA Data Visualization

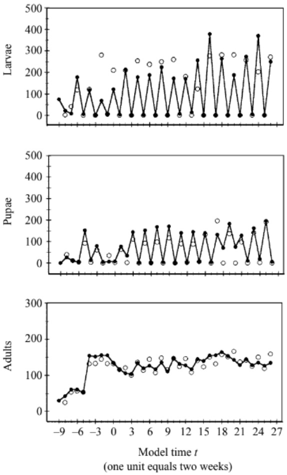


Figure: Costantino et al. [1998]'s display of LPA Model fitted with population dynamics from their lab

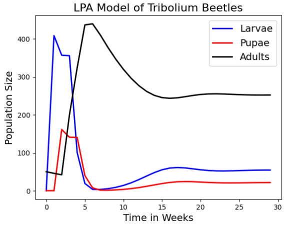


Figure: Brozak et al. [2024] best fit of training data

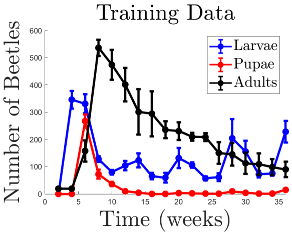


Figure: Brozak et al. [2024] best fit of training data

General Dynamics of the LPA Model

Theorem: Linear Stability for Discrete-Time Maps [Hale et al., 2012]

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 $|f'(x^*)| < 1$;
- **Unstable** if $|f'(x^*)| > 1$.

Jacobian of LPA at beetle-free equilibrium $(0, 0, 0)$:

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

Eigenvalues of discrete-time map

- If modulus of dominant eigenvalue is $> 1 \Rightarrow$ unstable system
- If modulus of dominant eigenvalue is $< 1 \Rightarrow$ stable system

Determining Conditions for Persistence

Getting around this problem

Use the concept of epidemiology with R_0 to determine how a disease spreads in a population. Here, $R_0 =$ The amount of adults *one* adult can produce.

Find R_0 by calculating the following cases.

1) The expected lifespan of an adult in a time unit
2) Number of eggs an adult will have per time unit
3) Proportion of eggs that attain adulthood

$$R_0 = P\{C|A,B\} \cdot E\left[B|L_a\right] \cdot E\left[L_a\right]$$

Determining Conditions for Persistence

$E\left[A\right]$:

The differential equation for the adult population is given by:

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

Solving this ODE:

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

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

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

Determining Conditions for Persistence

$E\left[B|A\right] \cdot E\left[A\right]$:
Given that an adult produces b viable eggs per time unit, the total number of eggs and adult will produce over its expected lifespan is:

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

$P\{C|A, B\}$: Since we are concerned with the stability of the beetle-free equilibrium where cannibalism is vanishingly rare $(0, 0, 0)$, the only mortality from larvae to adult is μ_l.

$$\implies P\{C|A, B\} = (1 - \mu_l)$$

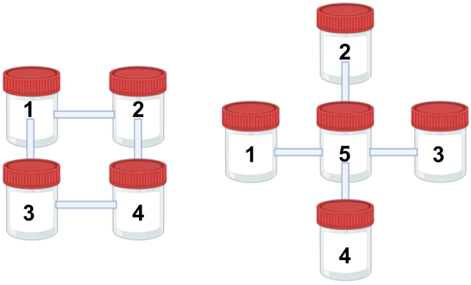
Determining Conditions for Persistence

The basic reproduction number R_0 for 1-patch is the product of the total number of eggs laid by an adult and the probability of an egg surviving to become an adult:

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

- $R_0 > 1 \implies$ the population will grow
- $R_0 < 1 \implies$ the population will go extinct

Application to Artificial Metapopulations



4-patch artificial metapopulation

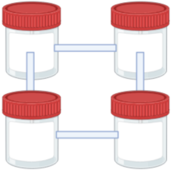
5-patch artificial metapopulation

LPA 4-Patch Metapopulation Model

4-Patch Model

$$L_{n+1,i} = be^{-c_{ea}A_{n,i} - c_{el}L_{n,i}} A_{n,i}$$
$$P_{n+1,i} = (1-\mu_l)L_{n,i}$$
$$A_{n+1,i} = P_{n,i} \underbrace{e^{-c_{pa}A_{n,i}}}_{\text{Cannibalism}} + \underbrace{(1-\mu_a)}_{\text{Survival}} \underbrace{(1-\gamma)}_{\text{Philopatric}} A_{n,i} + \underbrace{\gamma(1-\mu_a)(1-\epsilon)\left(A_{n,j} + A_{n,k}\right)}_{\text{Migration}}$$

i = current patch, j, k = adjacent patches, γ = dispersal rate, ϵ = cost of dispersal



LPA 5-Patch Metapopulation Model

5-Patch Model

Patches 1-4

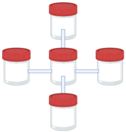
$$\begin{pmatrix} L_{n+1,i} \\ P_{n+1,i} \\ A_{n+1,i} \end{pmatrix} = \begin{pmatrix} 0 & 0 & be^{-c_{ea}A_{n,i}-c_{el}L_{n,i}} \\ 1-\mu_l & 0 & 0 \\ 0 & e^{-c_{pa}A_{n,i}} & (1-\mu_a)(1-\gamma)+\gamma(1-\mu_a)(1-\epsilon)A_{n,5} \end{pmatrix} \begin{pmatrix} L_{n,i} \\ P_{n,i} \\ A_{n,i} \end{pmatrix}$$

Adult Class in Patch 5

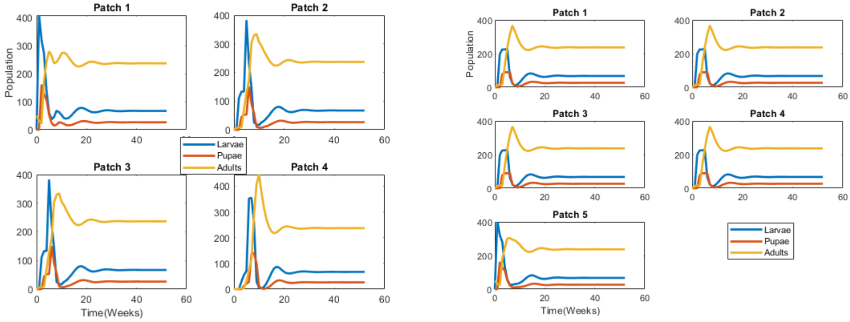
$$A_{n+1,5} = P_n \underbrace{e^{-c_{pa}A_{n,5}}}_{\text{Cannibalism}} + \underbrace{(1-\mu_a)}_{\text{Survival}} \underbrace{(1-\gamma)}_{\text{Philopatric}} + \underbrace{\gamma(1-\mu_a)(1-\epsilon)\sum_{j=1}^{4} A_{n,j}}_{\text{Migration from 4-patches}}$$

i = Current Patch

j, k = Adjacent Patches



Solution to the Metapopulation Models



R_0 for LPA Metapopulation Models

Using the same methods for viability conditions with the LPA, we utilized our version of R_0
Viability condition for the population

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

Resident Beetle vs Mutant Beetle

Resident Beetle

- Beetle type that begins a population
- Is the only beetle type in a population until it reaches equilibrium
- All resident beetles have the same dispersal rate

Mutant Beetle

- Beetle type that gets added to a population
- Has a different dispersal rate from the resident
- Each type of mutant is distinguished by their dispersal rate, otherwise are the same

Fitnesses in a 4-patch metapopulation

How We Got the Fitness Calculation

Average length of life of a beetle with the total number of eggs laid in the lifetime, the beetle must survive cannibalism as well as survive natural mortality.

Fitness of Residents:

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

Fitness of Mutants:

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

$E[A]$ = Average number of adults in the long run
$E[L]$ = Average number of larvae in the long run

ESS Equilibrium for Homogeneous Metapopulation

Invasion Exponent

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

It represents the long term growth rate of mutants in a population of residents. Technically is a Lyapunov exponent Metz et al. [1992]

- $\lambda > 0 \Rightarrow$ Mutant grows faster than resident, it can invade.
- $\lambda < 0 \Rightarrow$ Mutant population will decay, it can't invade.

ESS/Nash Equilibrium for Homogeneous Metapopulation

Relative Fitness in 4-patch:

$$\ln\left(\frac{F_m}{F_r}\right) = \ln\left(\frac{\mu_a + \gamma_r \epsilon}{\mu_a + \gamma_m \epsilon}\right).$$

Invasion Criterion:

$$\lambda > 0 \implies \ln\left(\frac{\mu_a + \gamma_r \epsilon}{\mu_a + \gamma_m \epsilon}\right) > 0 \quad \text{for mutant to invade}$$
$$\implies \gamma_r > \gamma_m$$

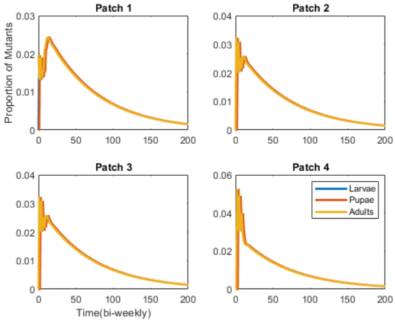
Key Result

Therefore, the ESS/Nash equilibrium is zero dispersal. Intuitively, there is no benefit to disperse because patches are identical.You only occur the cost.

Resident Vs Mutants (4-Patch)

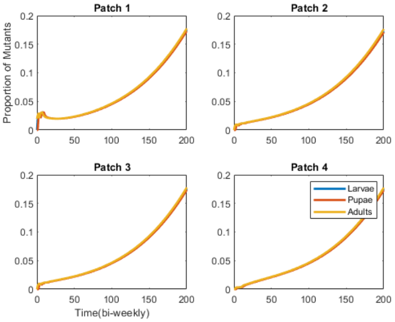
$\gamma_m > \gamma_r$

Mutant beetles disperse more



$\gamma_m < \gamma_r$

Resident beetles disperse more



Previous Literature

Previous literature by Metz et al., 1992, Hanski and Gilpin, 1991 proves that a homogenous metapopulation will not favor dispersal, and the ESS will always be zero.

Calculating Fitness in a 5-Patch Metapopulation

Can a 5-patch system generate the required heterogeneity?

Focusing on 5-patch

The process is similar for the 5-patch, with some adjustments for the different configuration

Fitness of Inner Patch for Class-α Beetle

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

Fitness of Outer Patches for Class-α Beetle

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

$\alpha \in \{r, m\}$

ESS/Nash Equilibrium for Homogeneous Metapopulation

Average Fitness of Class-α Beetles:

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

Calculating the relative fitness ends in the same result as the 4-patch model:

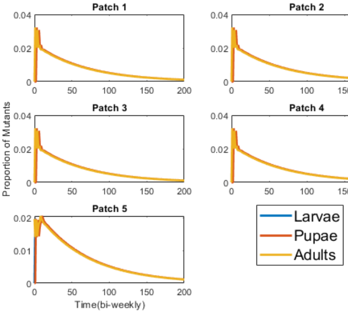
$$\underbrace{\gamma_r}_{\text{Resident Dispersal Rate}} > \underbrace{\gamma_m}_{\text{Mutant Dispersal Rate}}$$

This suggests that the 5-patch metapopulation does not create enough heterogeneity to influence dispersal.

Numerical Solution to a 5-Patch Metapopulation

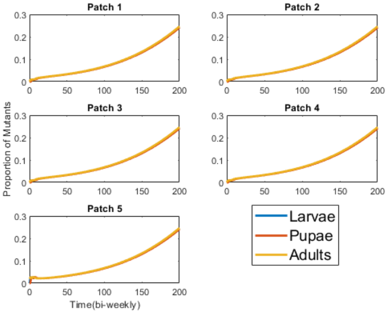
$\gamma_m > \gamma_r$

Mutant beetles disperse more



$\gamma_m < \gamma_r$

Resident beetles disperse more



The Next Step

- The 5-patch configuration on its own is not enough to generate heterogeneity.
- Extinction is a phenomena which occurs in nature.
- Local extinction is a primary reason for dispersal [Dieckmann et al., 1999]

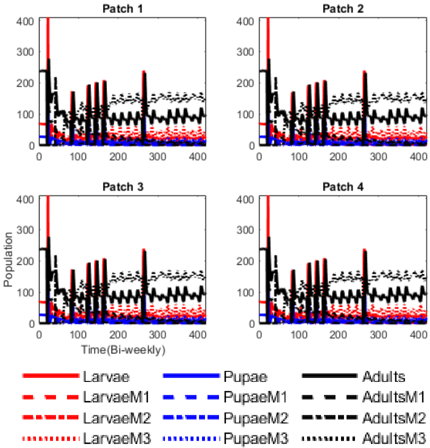
Next Question

Will emulating extinction in different patches generate enough heterogeneity for dispersal to evolve?

Computational Experiment

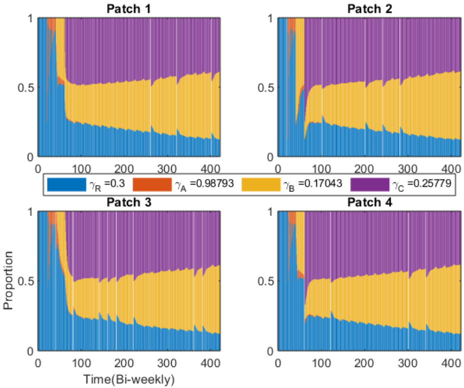
- Simulations started at the equilibrium points by running the LPA w/ cost model.
  Larvae- 67 Pupae- 26 Adults- 236
- After 20 time-steps, a patch will be selected at random to empty the patch, imitating extinction.
- The *Bakari* variable. The amount of mutant beetles added after 20 time-steps. Initially set to 0.01 beetles (cannot be applied to the patch chosen for extinction).
- Graphs are visualized as the total population individually using **line** graphs, and the proportion of each class (resident, mutant #1, mutant #2, and mutant #3) to the population using **bar** and **patch** graphs.

Random Extinction- Line Graph (4-patch)



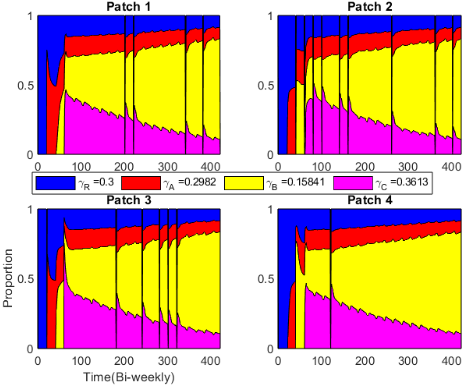
Simulation of dispersal evolution in a 4-patch metapopulation. The third mutant (dashed line) with γ 0.0684 takes over the population as well as the resident with 0.3 (solid line). Mutant #1: $\gamma = 0.7684$ Mutant #2: $\gamma = 0.5333$

Random Extinction- Bar Graph (4-patch)



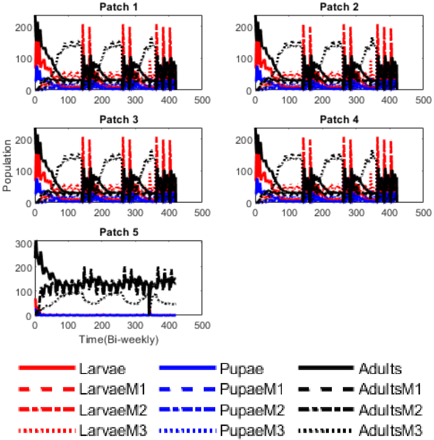
Predicted dispersal proportion during a 4-patch metapopulation simulation using a bar graph. Each white line showcases random extinction happening in random patches at each time step. The bar graph shows the proportion of shared space in each patch. The *Bakari* variable was raised to 1000 beetles.

Random Extinction- Patch Graph (4-patch)



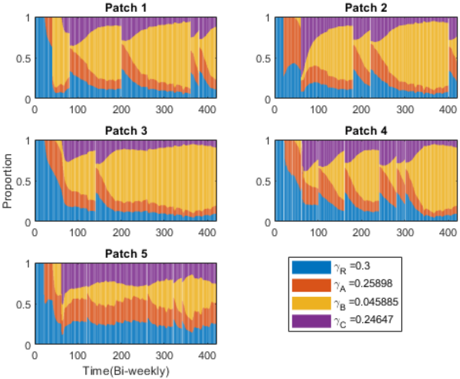
Simulation of the proportion of dispersal evolution in a 4-patch metapopulation using a patch graph. Each black line demonstrates a random extinction that occurs randomly in a patch at every time step. The patch graph shows how the different γ values determine the rate at which the classes take up the space. The *Bakari* variable was raised to 1000 beetles.

Random Extinction- Line Graph (5-patch)



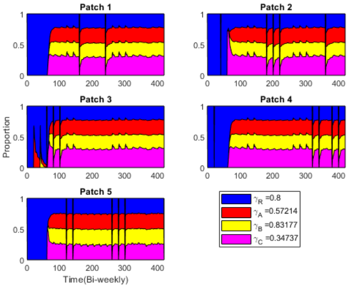
Simulation of dispersal evolution in a 5-patch metapopulation. The dispersal rates of the mutants were higher than the resident, causing them to eventually go extinct. The *Bakari* variable is set to 0.01 beetles. Mutant #1: $\gamma = 0.4155$ Mutant #2: $\gamma = 0.7543$ Mutant #3: $\gamma = 0.6933$

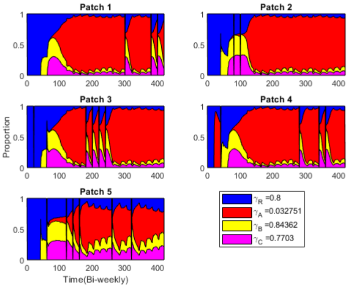
Random Extinction- Bar Graph (5-patch)



Predicted dispersal proportion during a 5-patch metapopulation simulation using a bar graph. The bar graph shows the proportion of shared space in each patch. The *Bakari* variable was raised to 1000 beetles.

Random Extinction- Patch Graph (5-patch)





Two simulations of the proportion of dispersal evolution in a 5-patch metapopulation using patch graphs. The graphs show how the different γ values determine the rate at which the classes take up the space. The *Bakari* variable was raised to 1000.

Specific Fitness of a Given Beetle in a Given Patch

Given:

1) Current position
2) Population configuration at time-step t

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

$$\frac{b(1-\mu_l)[(1-\gamma_\alpha)A + \frac{1}{2}\gamma_\alpha B + \frac{1}{2}\gamma_\alpha C]}{\mu_a + \gamma_\alpha \epsilon}$$

where,

- $A =$ some thing that represents the proportion that survived cannibalism in the current patch i
- $B =$ some thing that represents the proportion that survived cannibalism in the adjacent patch j
- $C =$ some thing that represents the proportion that survived cannibalism in the adjacent patch k

Specific Fitness of a Given Beetle of a Given Patch

Given:

1) Current position
2) Population configuration at time-step t

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

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

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

$$\frac{b(1-\mu_l)[(1-\gamma_\alpha)R+\gamma_\alpha E_5]}{\mu_a+\gamma_\alpha\epsilon}$$

where,

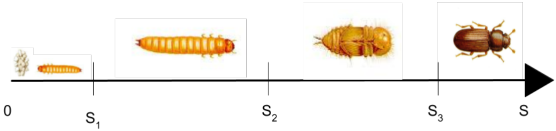
- $R =$ some thing that represents the proportion that survived cannibalism in the current patch i
- $E_k =$ something that represents the proportion that survived cannibalism in the surrounding patch(es) k of i in ascending order

Future Direction

We hope to create a better model that fits the population dynamics of *Tribolium*

Age-Structured Model

This model aims 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.



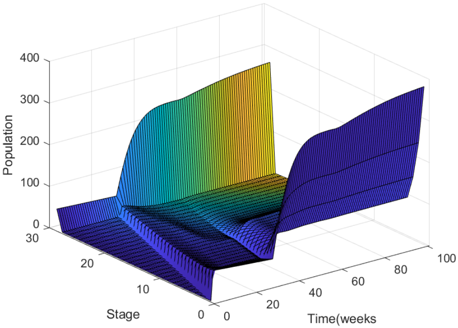
Age Structured Model

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

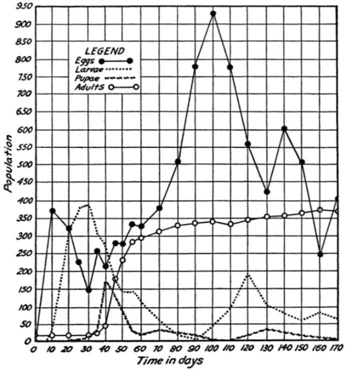
with

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

Age-Structured Model 3D Solution



3D visualization of age structured model



Park, 1934

Age-Structured Model 2D Solution

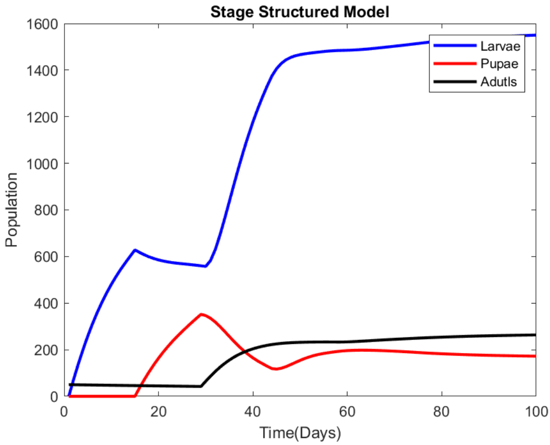
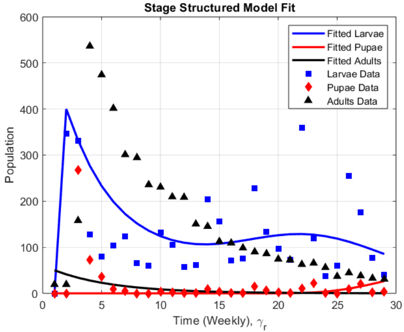


Figure: 2 Dimensional Stage Structure Model

Integrated separate sections of the age-structured model to make a two dimensional version of our age-structured model

Data Fitting Age-Structured Model



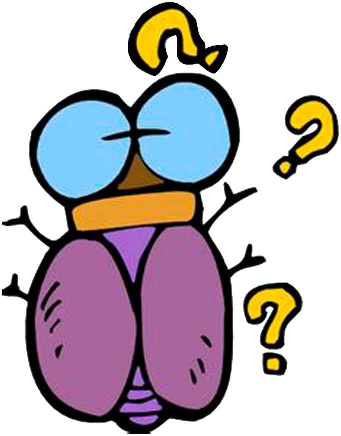
Fit Parameter	Description	Best Fit Values
c_{ea}	Cannibalism rate of eggs by adults	0.16142
c_{el}	Cannibalism rate of eggs by larvae	2.3609×10^{-14}
c_{pa}	Cannibalism rate of pupae by adults	1.5954
b	Birth rate of new eggs	11
μ_l	Natural death rate of feeding larvae	2.2682×10^{-8}
μ_a	Natural death rate of adults	0.23235

Conclusions

Major Findings

- If all patches are identical, then evolution will not evolve in these metapopulations
- It has been suggested that random extinctions can generate sufficient temporal and spatial heterogeneity in other models, but it is not clearly evident in our simulations

Questions?



D. Bonte, H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C. Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. Costs of dispersal. *Biological Reviews*, 87(2):290–312, 2012.

S. Brozak, S. Peralta, T. Phan, J. D. Nagy, and Y. Kuang. Dynamics of an (lpaa) model for *Tribolium* growth: Insights into population chaos. *SIAP - In Review*, 2024.

R. Costantino, J. Cushing, B. Dennis, R. A. Desharnais, and S. M. Henson. Resonant population cycles in temporally fluctuating habitats. *Bulletin of Mathematical Biology*, 60:247–273, 1998.

R. F. Costantino, R. A. Desharnais, J. M. Cushing, and B. Dennis. Chaotic dynamics in an insect population. *Science*, 275(5298):389–391, 1997.

C. Darwin. *On the Origin of Species by Means of Natural Selection*. Murray, 1859.

B. Dennis, R. A. Desharnais, J. Cushing, and R. Costantino. Nonlinear demographic dynamics: Mathematical models, statistical methods, and biological experiments. *Ecological Monographs*, 65(3):261–282, 1995.

U. Dieckmann, B. O'Hara, and W. Weisser. The evolutionary ecology of dispersal. *Trends in Ecology & Evolution*, 14(3):88–90, 1999.

J. Hale, H. Buttanri, and H. Kocak. *Dynamics and Bifurcations*. Texts in Applied Mathematics. Springer New York, 2012. ISBN 9781461244264. URL `https://books.google.com/books?id=xWLdBwAAQBAJ`.

I. Hanski and M. Gilpin. Metapopulation dynamics: Brief history and conceptual domain. *Biological journal of the Linnean Society*, 42(1-2): 3–16, 1991.

D. Jillson and R. Costantino. Growth, distribution, and competition of *Tribolium* castaneum and *Tribolium* brevicornis in fine-grained habitats. *The American Naturalist*, 116(2):206–219, 1980.

R. Levins. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control1. *Bulletin of the Entomological Society of America*, 15(3):237–240, 09 1969.

R. Levins. Extinction. *Lectures on Mathmatics in the Life Sciences*, 2: 77–197, 1970.

R. C. Lewontin. The units of selection. *Annual Review of Ecology and Systematics*, 1:1–18, 1970. ISSN 00664162.

J. A. Metz, R. M. Nisbet, and S. A. Geritz. How should we define 'fitness' for general ecological scenarios? *Trends in ecology & evolution*, 7(6): 198–202, 1992.

J. C. Ogden. Aspects of dispersal in *Tribolium* flour beetles. *Physiological Zoology*, 43(2):124–131, 1970.

T. Park. Observations on the general biology of the flour beetle, *Tribolium* confusum. *The Quarterly Review of Biology*, 9(1):36–54, 1934.

T. Park and M. B. Frank. The fecundity and development of the flour beetles, *Tribolium* confusum and *Tribolium* castaneum, at three constant temperatures. *Ecology*, 29(3):368–374, 1948.

M. D. Pointer, M. J. Gage, and L. G. Spurgin. Tribolium beetles as a model system in evolution and ecology. *Heredity*, 126(6):869–883, 2021.

M. D. Pointer, L. G. Spurgin, M. J. Gage, M. McMullan, and D. S. Richardson. Genetic architecture of dispersal behaviour in the post-harvest pest and model organism *Tribolium* castaneum. *Heredity*, 131(4):253–262, 2023.

O. Ronce. How does it feel to be like a rolling stone? ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.*, 38(1):231–253, 2007.

J. Starrfelt and H. Kokko. *The theory of dispersal under multiple influences*, pages 19–28. 09 2012. ISBN 9780199608898.