

LAST (Family) NAME: _____

FIRST (Given) NAME: _____

STUDENT NUMBER: _____

**UNIVERSITY OF TORONTO
Faculty of Arts & Science**

DECEMBER 2021 EXAMINATIONS

**EEB430H1 & EEB1430H1 (all sections)
Mathematical modeling in ecology and evolution**

**Duration: 3 hours
Aids Allowed: None**

Exam Reminders:

- Fill out your name and student number on the top of this page.
- If a scantron and/or exam booklets are required: Ensure you fill in your name and student number on the scantron and/or exam booklet(s)
- Do not begin writing the actual exam until the announcements have ended and the Exam Facilitator has started the exam.
- As a student, you help create a fair and inclusive writing environment. If you possess an unauthorized aid during an exam, you may be charged with an academic offence.
- Turn off and place all cell phones, smart watches, electronic devices, and unauthorized study materials in your bag under your desk. If it is left in your pocket, it may be an academic offence.
- When you are done your exam, raise your hand for someone to come and collect your exam. Do not collect your bag and jacket before your exam is handed in.
- If you are feeling ill and unable to finish your exam, please bring it to the attention of an Exam Facilitator so it can be recorded before leaving the exam hall.
- In the event of a fire alarm, do not check your cell phone when escorted outside.

Special Instructions:

Answer in the exam booklets

Exam Format and Grading Scheme:

4 questions, worth 20%, 30%, 40%, and 10%, respectively.

Students must hand in all examination materials at the end

Question 1 (20%) Here we investigate the demography of a mustard plant, *Boechera stricta*, following Cotto *et al.* (2019).

B. stricta has two key stages: immature (non-reproductive) and mature (reproductive). A fraction s_I of immature individuals survive each year, of which a proportion m mature. Each mature individual produces f seeds that survive to become immature individuals in the following year, and a proportion s_M of mature individuals survive and remain mature.

- (a) (4%) Write down recursion equations for the number of immature, I , and mature, M , individuals. Write out the corresponding transition matrix, \mathbf{M} .
- (b) (4%) Write down the characteristic polynomial for \mathbf{M} .

Cotto *et al.* (2019) used published data to estimate parameter values for *B. stricta* and found that the two eigenvalues are approximately $\lambda = 3$ and $\lambda = 1/2$. With their estimated parameter values the right eigenvector associated with $\lambda = 3$ is approximately $\begin{pmatrix} 1/10 \\ 9/10 \end{pmatrix}$ and the right eigenvector associated with $\lambda = 1/2$ is approximately $\begin{pmatrix} 11/10 \\ -1/10 \end{pmatrix}$. The left eigenvector associated with $\lambda = 3$ is approximately $(1 \quad 15)$ and the left eigenvector associated with $\lambda = 1/2$ is approximately $(1 \quad -1/10)$. Use these estimates in your answers below.

- (c) (4%) What is the leading eigenvalue? Is the population expected to grow or decline?
- (d) (2%) What fraction of the population do we expect to be reproductively mature in the long-run?
- (e) (2%) What is the reproductive value of a mature individual relative to an immature individual?
- (f) (4%) The general solution for this system can be written $\vec{n}(t) = \mathbf{A}\mathbf{D}^t\mathbf{A}^{-1}\vec{n}(0)$. Write out the entries of \mathbf{D} and \mathbf{A} .

Question 2 (30%) Here we analyze a model to understand how species compete for essential nutrients (e.g., plants need certain inorganic nutrients to grow). Our approach follows Loreau (2011).

Let R represent the available stock of an essential nutrient, which flows into the system at rate I and is lost from the system at rate qR . Let N_1 be the biomass of a plant species that requires this nutrient. We assume the plants uptake the nutrient at a rate of a_1RN_1 , of which e_1 is converted into new plant biomass. Plant biomass is lost at a rate of m_1N_1 . The rate of change in the nutrient stock and plant biomass is then

$$\begin{aligned}\frac{dR}{dt} &= I - qR - a_1RN_1 \\ \frac{dN_1}{dt} &= e_1a_1RN_1 - m_1N_1.\end{aligned}$$

- (a) (10%) Find all equilibria of this model.
- (b) (10%) Use the Jacobian to determine when the equilibrium with the plant present, $\hat{N}_1 > 0$, is stable (assuming all parameters are positive). [Hint: look at the sign of the trace and determinant.] We'll call the value of R at this equilibrium the "R star" of species 1, R_1^* .
- (c) (2%) Now consider a second plant species whose dynamics follow

$$\frac{dN_2}{dt} = e_2a_2RN_2 - m_2N_2.$$

If it were the only plant species present, with $N_2 > 0$, use this equation to get the equilibrium value of the resource. We call this the "R star" of the second species, R_2^* .

- (d) (4%) Now to understand how competition for essential nutrients works, replace R with R_1^* in the equation for $\frac{dN_2}{dt}$. Dividing by N_2 gives the growth rate of species 2 when it attempts to establish in a habitat where only species 1 was present beforehand. Show that species 2 can only establish when $R_2^* < R_1^*$.
- (e) (4%) What does it mean, biologically, that a species can only replace another when it has a lower R^* ?

Question 3 (40%) Here we analyze a “Levene-type” model to understand how environmental heterogeneity can produce genetic polymorphism. This treatment follows Doebeli (2011).

Imagine a species occupying two environments, which we’ll call patch 1 and patch 2. Each generation, an individual with trait value x survives to reproductive age with probability $w_1(x) = e^{-(x+d)^2/(2\sigma^2)}$ if it is in patch 1 or with probability $w_2(x) = e^{-(x-d)^2/(2\sigma^2)}$ if it is in patch 2. That is, trait value $x = -d$ maximizes survival in patch 1 and trait value $x = d$ maximizes survival in patch 2. The parameter d determines how different the two patches are while σ (assumed to be positive) describes how quickly survival drops off as trait values deviate from those maximizing survival (larger σ cause slower drop offs). Survivors produce offspring, asexually, of which cN from patch 1 and $(1-c)N$ from patch 2 are chosen to start the next generation (e.g., c , which is between 0 and 1, could be the quality of patch 1 relative to patch 2). We assume the total population size across the two patches, N , is constant. The offspring then randomly disperse into the two habitat patches to start the next generation.

Now imagine a population where individuals have either trait x or trait y . The frequency of y in the next generation is then determined by the sum of the classic haploid selection recursion in each patch, weighted by the contribution of each patch to the next generation,

$$q(t+1) = c \frac{q(t)w_1(y)}{(1-q(t))w_1(x) + q(t)w_1(y)} + (1-c) \frac{q(t)w_2(y)}{(1-q(t))w_2(x) + q(t)w_2(y)}.$$

Here we’ll do an evolutionary invasion analysis, assuming x is the resident trait value and y is the trait value of a rare mutant. To find the invasion fitness of a rare mutant we take the derivative of $q(t+1)$ with respect to $q(t)$ and evaluate at $q(t) = 0$, giving

$$\lambda(y, x) = c \frac{w_1(y)}{w_1(x)} + (1-c) \frac{w_2(y)}{w_2(x)}.$$

- (a) (10%) Calculate the selection gradient, $D(x) = \left. \frac{\partial \lambda(y, x)}{\partial y} \right|_{y=x}$, which describes the direction of evolution from x . [Hint: using the chain rule, the derivative of $f(x) = e^{-(x-a)^2/(2\sigma^2)}$ is $-(x-a)/\sigma^2 f(x)$.]
- (b) (4%) At a singular strategy, \hat{x} , there is no directional selection. Show that $\hat{x} = d(2c-1)$ is a singular strategy.
- (c) (4%) Calculate $\left. \frac{dD(x)}{dx} \right|_{x=\hat{x}}$, describing how the selection gradient changes with the resident strategy near the singular point.
- (d) (2%) When is \hat{x} convergence stable? (Hint: use your answer in (c).)
- (e) (10%) Calculate $\left. \frac{\partial^2 \lambda(y, x)}{\partial y^2} \right|_{y=\hat{x}, x=\hat{x}}$, describing the curvature of the fitness function when the resident trait value is at the singular strategy.
- (f) (4%) Assuming the two patches contribute equally, $c = 0.5$, show that \hat{x} is evolutionarily *unstable* when $\sigma < d$. (Hint: use your answer in (e).)
- (g) (4%) Give a biological interpretation for why we see evolutionary instability at \hat{x} when d is large relative to σ (assuming $c = 0.5$). Note that $\hat{x} = d(2c-1)$ represents a strategy that is a compromise between the two patches.
- (h) (2%) Given the parameter values are such that \hat{x} is convergent stable but not evolutionarily stable, how does environmental heterogeneity affect genetic polymorphism?

Question 4 (10%) Here we use probability theory to derive a classic result in the coalescent model, a model which describes how alleles sampled from present-day individuals have lineages that “coalesce” into common ancestors as we look into the past.

- (a) (2.5%) In a diploid population of constant size N , the probability the lineages of two sampled alleles coalesce in the previous generation is the probability they have the same parent allele. When we choose parent alleles at random this is $1/(2N)$. If the two sample lineages do not coalesce in that generation the probability of them coalescing in the generation before that is again $1/(2N)$, and so on. What is the name (or equation) of the probability distribution that most accurately describes the number of generations until the two lineages coalesce, $\Pr(T = t)$?
- (b) (2.5%) Given it takes $T = t$ generations until the two lineages coalesce, there will be a branch of length t leading from each sampled allele to their most recent common ancestor. That means the two sampled alleles are separated by $2t$ generations. Given mutations – all of which are unique – occur *continuously* at a rate of μ per generation, what is the name (or equation) of the probability distribution that most accurately describes the number of mutations that occur in $2t$ generations, $P(M = m|2t)$?
- (c) (2.5%) Use the law of total expectation to write the expected number of mutations, $\mathbb{E}(M)$, as a sum of conditional expectations, where the conditioning is the time until coalescence, $\mathbb{E}(M|T = t)$.
- (d) (2.5%) We find that the answer to (c) can be written $\mathbb{E}(M) = 2\mu\mathbb{E}(T)$. Based on your answer in (a), what is $\mathbb{E}(T)$? You now have the expected number of mutational differences between two randomly sampled alleles!