LAST (Family) NAME: ______________________________________

FIRST (Given) NAME: _______________________________________

STUDENT NUMBER: ____

UNIVERSITY OF TORONTO
Faculty of Arts & Science

DECEMBER 2022 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

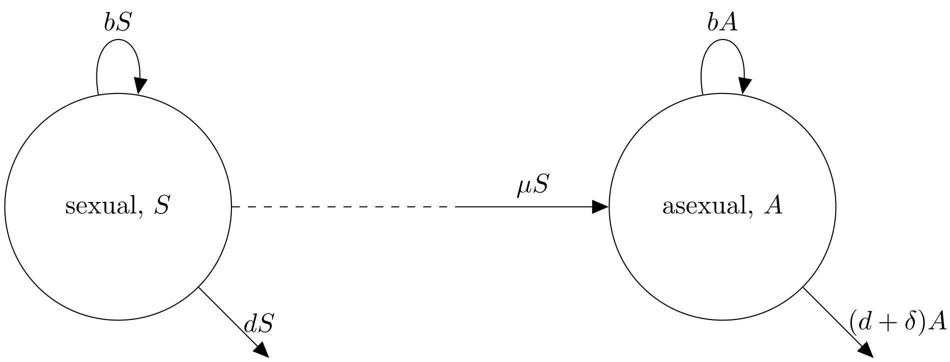
Exam Format and Grading Scheme:

3 questions, worth 40%, 40%, and 20%, respectively.

Students must hand in all examination materials at the end

Question 1 (40%) Roughly 99.9% of eukaryote species reproduce sexually at least some of the time. Why this is remains a bit of a conundrum (Otto 2009). Here we examine a model of one hypothesis.

Let the number of sexual species be S and the number of asexual species be A. Let sexual species go extinct at rate d and asexual species go extinct at an elevated rate $d + \delta$. Assume both types of species speciate at rate b. Let sexual species produce asexual species at rate μ (and assume that this does not affect the number of sexual species). A flow diagram for this model is drawn below.



(a) (8%) Write down the differential equations for the change in S and A over time.

> **Solution**
>
> We add the arrows coming in and subtract the (solid) arrows going out of each node, giving
> $$\frac{\mathrm{d}S}{\mathrm{d}t} = bS - dS$$
> $$\frac{\mathrm{d}A}{\mathrm{d}t} = bA - (d + \delta)A + \mu S$$

(b) (4%) We can write this system of equations in matrix form, $\frac{\mathrm{d}\vec{x}}{\mathrm{d}t} = \mathbf{M}\vec{x}$, with $\vec{x} = \begin{pmatrix} S \\ A \end{pmatrix}$. Write out the matrix $\mathbf{M}$.

> **Solution**
>
> $$\mathbf{M} = \begin{pmatrix} b - d & 0 \\ \mu & b - d - \delta \end{pmatrix}$$

(c) (8%) Calculate the eigenvalues of $\mathbf{M}$.

Solution

Because this is a lower triangular matrix the eigenvalues are just the diagonal el'ements, $\lambda_1 = b - d$ and $\lambda_2 = b - d - \delta$.

(d) (4%) Given that all parameters are positive, what is the leading eigenvalue?

Solution

If $\delta > 0$ then $b - d > b - d - \delta$, so $\lambda_1 = b - d$ is the leading eigenvalue.

(e) (8%) Calculate the right eigenvector associated with the leading eigenvalue.

Solution

The right eigenvector, $\vec{u}_1 = \begin{pmatrix} u_1 \\ u_2 \end{pmatrix}$, associated with eigenvalue λ_1 solves

$$\mathbf{M}\vec{u}_1 = \lambda_1 \vec{u}_1$$

Writing this out as a system of equations

$$\begin{aligned} (b-d)u_1 &= (b-d)u_1 \\ \mu u_1 + (b-d-\delta)u_2 &= (b-d)u_2 \end{aligned}$$

The first equation doesn't tell us anything. The second equation can be rearranged

$$\begin{aligned} \mu u_1 + (b-d-\delta)u_2 &= (b-d)u_2 \\ \mu u_1 &= (b-d)u_2 - (b-d-\delta)u_2 \\ \mu u_1 &= \delta u_2 \\ \frac{\mu}{\delta}u_1 &= u_2 \end{aligned}$$

We are free to choose one element and pick $u_1 = 1$. Then $u_2 = \mu/\delta$. The right eigenvector is then

$$\vec{u}_1 = \begin{pmatrix} 1 \\ \frac{\mu}{\delta} \end{pmatrix}$$

'

(f) (4%) Show that the fraction of species expected to be sexual in the long-term under this model is $\frac{\delta}{\delta+\mu}$.

Solution

The right eigenvalue associated with the leading eigenvalue gives the relative abundances of the variables in the long term. To convert these relative abundances into fractions we need them to sum to one, which we can do by dividing both elements by their sum,

$1 + \mu/\delta = (\delta + \mu)/\delta$. This gives

$$\vec{u}_1 = \begin{pmatrix} \frac{\delta}{\delta+\mu} \\ \frac{\mu}{\delta+\mu} \end{pmatrix}$$

so that the fraction of sexual species in the long term is $\frac{\delta}{\delta+\mu}$.

(g) (4%) Given the fraction of sexual species is p, what value of δ is needed under this model? Assuming we estimated $\mu = 0.001$ per million years, by how much does the extinction rate of asexual species need to be elevated above that of sexual species to account for the fact that 99.9% of species are sexual?

Solution

We want to set the long-term frequency $\frac{\delta}{\delta+\mu}$ equal to p and solve for δ

$$\begin{aligned} p &= \frac{\delta}{\delta + \mu} \\ p(\delta + \mu) &= \delta \\ \mu p &= \delta(1 - p) \\ \frac{\mu p}{1 - p} &= \delta \end{aligned}$$

And if we take $\mu = 0.001$ and $p = 0.999$ we get $\delta = 0.999 \approx 1$. I.e., the extinction rate of asexuals needs to be elevated by roughly 1 per million years.

Question 2 (40%) In lecture we focused on species interactions with only two species, e.g., competition and predation. These models have been extended to consider more complex communities and ecosystems.

Consider a simple ecosystem composed of a resource, a plant species, and a herbivore (Grover & Holt 1998). Let the density of resources be R, the density of plants be P, and the density of herbivores be H. Assume that resources continually arrive from elsewhere at rate DS. Let plants uptake reources at rate uPR and die at rate $(D+e)P$, where eP is recycled back into resources but DP is lost from the system. Let herbivores consume plants at rate vPH and die at rate $(D+d)H$, where only dH is recycled. The differential equations describing this system are

$$\begin{aligned}\frac{\mathrm{d}R}{\mathrm{d}t} &= DS - uPR + eP + dH \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= uPR - (D+e)P - vPH \\ \frac{\mathrm{d}H}{\mathrm{d}t} &= vPH - (D+d)H\end{aligned}$$

Assume all parameters are positive.

(a) (12%) Solve for the two equilibria of this model.

> **Solution**
>
> One of the easiest place to start is with the differential equation for H, since we can immediately see that $\frac{\mathrm{d}H}{\mathrm{d}t} = 0$ implies either that $H = 0$ or, after factoring out H, that $P = (D+d)/v$.
>
> Let's first look at the case where $H = 0$. Setting the differential equation for P equal to zero and plugging in $H = 0$ implies that $P = 0$ or, after factoring out P, that $R = (D+e)/u$.
>
> Now note that if both $H = 0$ and $P = 0$ then $\frac{\mathrm{d}R}{\mathrm{d}t}$ cannot be zero, which means that there is no equilibrium with both $H = 0$ and $P = 0$.
>
> If $H = 0$ and $R = (D+e)/u$ then the resource equation tells us
>
> $$\begin{aligned}0 &= DS - uPR + eP + dH \\ 0 &= DS - P(D+e) + eP \\ 0 &= DS - DP \\ P &= S\end{aligned}$$
>
> Thus one equilibrium is $\hat{R} = (D+e)/u$, $\hat{P} = S$, and $\hat{H} = 0$.
>
> Now let's consider the case where the herbivore equation tells us that $P = (D+d)/v$.

Setting the plant equation to zero and factoring out P, we know

$$\begin{aligned}0 &= uPR - (D+e)P - vPH \\ 0 &= uR - (D+e) - vH \\ H &= uR/v - (D+e)/v\end{aligned}$$

Now plugging this and $P = (D+d)/v$ into the resource equation and setting to zero we get

$$\begin{aligned}0 &= DS - uPR + eP + dH \\ 0 &= DS - uR(D+d)/v + e(D+d)/v + d(uR/v - (D+e)/v) \\ R(u(D+d)/v - du/v) &= DS + e(D+d)/v - d(D+e)/v \\ R(uD/v) &= DS + eD/v - dD/v \\ Ru &= Sv + e - d \\ R &= (Sv + e - d)/u\end{aligned}$$

Finally, we plug this into $H = uR/v - (D+e)/v$ to complete the second equilibrium: $\hat{R} = D(Sv + e - d)/u$, $\hat{P} = (D+d)/v$, and $\hat{H} = (Sv - d - D)/v$.

(b) (8%) Calculate the Jacobian for this system.

Solution

The Jacobian is

$$\begin{aligned}J &= \begin{pmatrix} \frac{\mathrm{d}}{\mathrm{d}R}\frac{\mathrm{d}R}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}P}\frac{\mathrm{d}R}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}H}\frac{\mathrm{d}R}{\mathrm{d}t} \\ \frac{\mathrm{d}}{\mathrm{d}R}\frac{\mathrm{d}P}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}P}\frac{\mathrm{d}P}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}H}\frac{\mathrm{d}P}{\mathrm{d}t} \\ \frac{\mathrm{d}}{\mathrm{d}R}\frac{\mathrm{d}H}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}P}\frac{\mathrm{d}H}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}H}\frac{\mathrm{d}H}{\mathrm{d}t} \end{pmatrix} \\ &= \begin{pmatrix} -uP & -uR + e & d \\ uP & uR - (D+e) - vH & -vP \\ 0 & vH & vP - (D+d) \end{pmatrix}\end{aligned}$$

(c) (4%) Show that the Jacobian evaluated at the herbivore-less equilibrium ($\hat{R} = (D+e)/u$, $\hat{P} = S$, and $\hat{H} = 0$) is

$$\mathbf{J}_0 = \begin{pmatrix} -uS & -D & d \\ uS & 0 & -vS \\ 0 & 0 & vS - (D+d) \end{pmatrix}$$

Solution

Plugging $R = \hat{R} = (D+e)/u$, $P = \hat{P} = S$, and $H = \hat{H} = 0$ in to the Jacobian above gives

$$\mathbf{J}_0 = \begin{pmatrix} -uS & -D & d \\ uS & 0 & -vS \\ 0 & 0 & vS-(D+d) \end{pmatrix}$$

(d) (8%) This matrix, $\mathbf{J}_0$, is block triangular with matrices $\mathbf{A} = \begin{pmatrix} -uS & -D \\ uS & 0 \end{pmatrix}$ and $\mathbf{B} = \begin{pmatrix} vS-(D+d) \end{pmatrix}$ along the diagonal. The eigenvalues of $\mathbf{J}_0$ are therefore the eigenvalues of these two matrices, $\mathbf{A}$ and $\mathbf{B}$. It turns out that $\mathbf{A}$ determines stability in the complete absence of the herbivore. Use the Routh-Hurwitz stability conditions for a 2x2 matrix (positive determinant and negative trace) to show that this herbivore-less equilibrium is always stable in the absence of the herbivore.

Solution

To use the Routh-Hurwitz conditions we need to calculate the determinant and trace, which are

$$\text{Det}(\mathbf{A}) = (-uS)(0) - (-D)(uS) = DuS$$

and

$$\text{Tr}(\mathbf{A}) = -uS + 0 = -uS$$

Given that all parameters are positive we then know that the Routh-Hurwitz stability conditions, $\text{Det}(\mathbf{A}) > 0$ and $\text{Tr}(\mathbf{A}) < 0$, are always satisfied.

(e) (4%) The remaining eigenvalue is $vS-(D+d)$, which determines the stability of the herbivore-less equilibrium when a few herbivores are introduced. What conditions on the parameters are required for instability of the herbivore-less equilibrium, i.e., for the herbivore to invade?

Solution

In continuous-time models instability requires the eigenvalues to be positive, so here we need $vS-(D+d)$ or $vS > D+d$ for the herbivore to invade. (Note that this is the same as the condition for biological vailidity of the herbivore equilibrium density, $\hat{H} > 0$.)

(f) (4%) It is perhaps surprising that the equilibrium density of the resource, $\hat{R}$, declines with the death rate of the herbivore, d, at the equilibrium with the herbivore present ($\hat{R} = D(Sv + e - d)/u$, $\hat{P} = (D+d)/v$, and $\hat{H} = (Sv-d-D)/v$), despite the fact that this death represents an inflow of resources via nutrient recycling. Explain in words why this makes sense biologically.

Solution

The density of resource declines with the death rate of the herbivore because a larger death rate means less herbivore, which in turn means more plants, which in turn means more resources. This is called a trophic cascade.

Question 3 (20%) In lecture we added stochasticity to the discrete-time exponential growth model, $n_{t+1} = Rn_t$, by assuming that the reproductive factor of each individual, R_i, was an independent Poisson random variable with mean λ, $R_i \sim \text{Poi}(\lambda)$. This is called demographic stochasticity since it results from randomness inherent in demography (birth and death). Given the current number of individuals, n_t, this model gives $\mathbb{E}(n_{t+1}) = \text{Var}(n_{t+1}) = \lambda n_t$.

Another source of stochasticity comes from the environment – environmental stochasticity. We can model this by assuming that in good time steps every individual has reproductive factor R_g while in bad time steps every individual has reproductive factor R_b, and assuming that the probability that a time step is a good time step, $R = R_g$, is p.

(a) (4%) Calculate the expected number of individuals in the next time step, $\mathbb{E}(n_{t+1})$, given n_t in the current time step under this model of environmental stochasticity.

Solution

$$\begin{aligned}
\mathbb{E}(n_{t+1}) &= \mathbb{E}(Rn_t) \\
&= \mathbb{E}(R)n_t \\
&= (\Pr(R = R_g)R_g + \Pr(R = R_b)R_b)n_t \\
&= (pR_g + (1-p)R_b)n_t
\end{aligned}$$

(b) (8%) Calculate the variance in the number of individuals in the next time step, $\text{Var}(n_{t+1})$, given n_t in the current time step under this model of environmental stochasticity.

Solution

We first calculate

$$\begin{aligned}
\mathbb{E}(n_{t+1}^2) &= \mathbb{E}((Rn_t)^2) \\
&= \mathbb{E}(R^2)n_t^2 \\
&= (\Pr(R = R_g)R_g^2 + \Pr(R = R_b)R_b^2)n_t^2 \\
&= (pR_g^2 + (1-p)R_b^2)n_t^2
\end{aligned}$$

and use this and the expectation calculated above to give

$$\begin{aligned}
\text{Var}(n_{t+1}) &= \mathbb{E}(n_{t+1}^2) - \mathbb{E}(n_{t+1})^2 \\
&= (pR_g^2 + (1-p)R_b^2)n_t^2 - (pR_g + (1-p)R_b)^2 n_t^2 \\
&= (pR_g^2 + (1-p)R_b^2)n_t^2 - (p^2R_g^2 + 2p(1-p)R_gR_b + (1-p)^2R_b^2)n_t^2 \\
&= (p(1-p)R_g^2 + p(1-p)R_b^2 - 2p(1-p)R_gR_b)n_t^2 \\
&= p(1-p)(R_g^2 + R_b^2 - 2R_gR_b)n_t^2 \\
&= p(1-p)(R_g - R_b)n_t^2
\end{aligned}$$

(c) (4%) Explain in words why this model of environmental stochasticity can produce more variance in the number of individuals in the next time step, as compared to our model of demographic stochasticity, even when it produces the same expected number of individuals in the next time step.

Solution

The key here is that under demographic stochasticity the reproductive factor of each individual is independent of all others. Under environmental stochasticity every individual has the same reproductive factor. Holding the expected reproductive factor constant, environmental stochasticity can therefore produce "boom" and "bust" time steps, leading to higher variance.

(d) (4%) To get a better sense of this model we run the following code in Python.

```
import numpy as np
import matplotlib.pyplot as plt

def enviro_stoch(Rg,Rb,p,n0,tmax=100):
    n = n0
    t = 0
    ns = []
    while t < tmax:
        ns.append(n)
        X = np.random.binomial(1,p) #1 with probability p, else 0
        if X == 1:
            R = Rg
        else:
            R = Rb
        n = R*n
        t = t+1
    return ns

fig, ax = plt.subplots()

for i in range(10):
    ns = enviro_stoch(Rg=1.2,Rb=0.9,p=0.5,n0=10)
    ax.plot(ns)

plt.show()
```

What is it that we have plotted?

Solution

We have plotted 10 replicates of the environmental stochasticity simulation (number of individuals over time) with the same parameters.