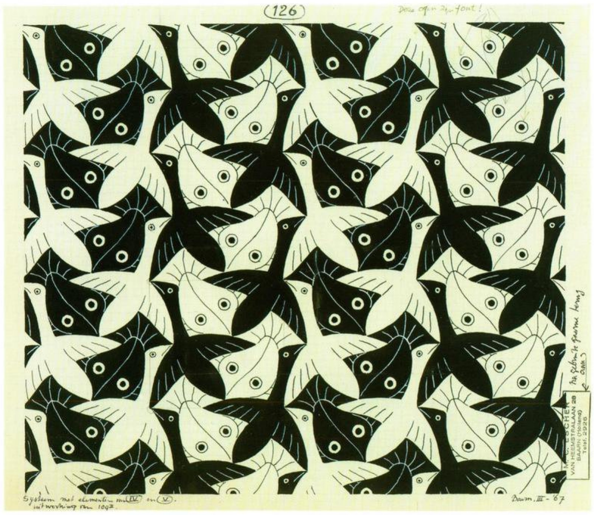
UNIVERSITY OF TORONTO

Faculty of Arts and Science
Ecology and Evolutionary Biology



Mathematical modeling in ecology and evolution

(EEB430/1430)

Midterm Exam – October 19, 2022

Available Time: Two hours

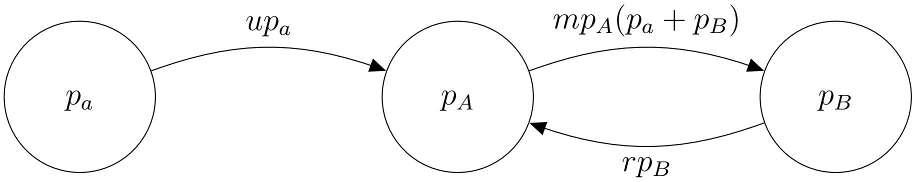
Permitted Materials: Pen/pencil

Guidelines:

1. The front page lists the materials you can use during this exam. Any other materials are not allowed. This includes mobile devices.
2. Write your name and student number on the booklet provided, answer the questions in the booklet, and hand the booklet in at the end of the exam.
3. Show/explain how you arrive at your answers.
4. Please write clearly.

NB. This is an individual exam. Good luck!

Question 1 [10/20 points] Puneeth Deraje is studying a phenomenon called "paramutation", where a "paramutable" allele (A) can be converted to another allele (B) when it pairs with a "paramutator" allele (a or B) in a heterozygote. This conversion is, however, unstable, causing the B allele to reset to the A allele over time. Puneeth also considers mutation from the a allele to the A allele. Below is a flow diagram for a continuous-time version of this model, tracking the frequencies of each allele in the absence of selection.



a. [1 points] Write down the differential equations corresponding to this flow diagram.

Answer

Add the flows coming in and subtract the flows going out

$$\frac{\mathrm{d}p_a}{\mathrm{d}t} = -up_a$$
$$\frac{\mathrm{d}p_A}{\mathrm{d}t} = up_a - mp_A(p_a + p_B) + rp_B$$
$$\frac{\mathrm{d}p_B}{\mathrm{d}t} = mp_A(p_a + p_B) - rp_B$$

b. [3 points] At equilibrium $p_a = 0$. Since the frequencies sum to 1 we can write $p_B = 1 - p_A$ and reduce the above to a single differential equation in terms of p_A

$$\frac{\mathrm{d}p_A}{\mathrm{d}t} = -mp_A(1 - p_A) + r(1 - p_A)$$

Solve for the equilibrium frequencies of the A allele.

Answer

Set the differential equation equal to zero and solve for $\hat{p}_A$

$$0 = -m\hat{p}_A(1 - \hat{p}_A) + r(1 - \hat{p}_A)$$
$$0 = (-m\hat{p}_A + r)(1 - \hat{p}_A)$$

which implies $\hat{p}_A = 1$ or $\hat{p}_A = r/m$.

c. [1 points] Determine when the equilibrium $\hat{p}_A = r/m$ is biologically valid.

Answer

Since p_A is a frequency it must be within 0 and 1, inclusive. That requires r and m to have the same sign (they are both rates, and so both are positive), $m \neq 0$, and $r \leq m$.

d. [3 points] Determine when the equilibrium $\hat{p}_A = r/m$ is locally stable.

Answer

Since p_A is a frequency it must be within 0 and 1, inclusive. That requires r and m to have the same sign (they are both rates, and so both are positive), $m \neq 0$, and $r \leq m$. We first take the derivative of the differential equation with respect to p_A

$$\frac{\mathrm{d}}{\mathrm{d}p_A}\frac{\mathrm{d}p_A}{\mathrm{d}t} = -m(1+2\hat{p}_A) - r$$

and then evaluate at $p_A = \hat{p}_A = r/m$

$$\begin{aligned}\left.\frac{\mathrm{d}}{\mathrm{d}p_A}\frac{\mathrm{d}p_A}{\mathrm{d}t}\right|_{p_A=\hat{p}_A=t/m} &= -m(1+2r/m) - r \\ &= -m + r\end{aligned}$$

For stability in continuous time we need this derivative to be less than zero. Here that means we need $r < m$.

e. [1 points] Explain what $r < m$ means biologically.

Answer

Based on the description of the system and the flow diagram, r is the reset rate and m is the rate at which A paramutates in heterozygotes. The inequality $r < m$ therefore means that the rate of reset is less than the paramutation rate. This is why we need this to be true for the B allele to exist in the long term; from the point of view of a rare B allele ($p_A \approx 1$), it's "birth rate" is m and its "death rate" is r, and so it will only persist if $r < m$.

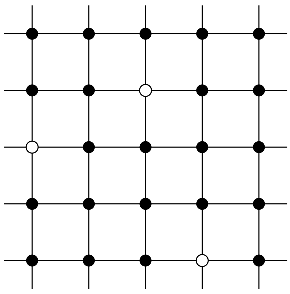
f. [1 points] We could solve the differential equation for p_A using seperation of variables and partial fractions, but instead we decide to just use Python. Briefly describe what each line below does.

```
from sympy import *
var('m,r,t')
p = Function('p')(t)
de = Eq(diff(p,t), (-m*p+r)*(1-p))
dsolve(de)
```

Answer

1. import the symbolic Python library
2. define the parameters and variables we will use
3. define the function we wish to solve for
4. define the differential equation we wish to solve
5. solve the differential equation

Question 2 [10/20 points] Sydney Ackermann is studying population dynamics on a lattice, where individuals disperse and compete for vertices (intersections of lines in the diagram below, where filled dots represent occupied vertices and empty dots represent vacant vertices).



Here we'll consider an approximation of a simplified version of her discrete-time model, where, in each time step, 1) a fraction d of individuals die, 2) each survivor gives birth to b offspring, and 3) each offspring disperses to a randomly chosen vertex on a $k \times k$ lattice (creating k^2 vertices). She only allows one individual to exist at each vertex, and so when an offspring lands on an occupied vertex it either dies or displaces the resident. Taking a small enough time step, the expected population size in the next time step is

$$n_{t+1} = n_t \left(1 + b\left(1 - \frac{n_t}{k^2}\right) - d\right)$$

where $1 - n_t/k^2$ is the fraction of vertices that are currently empty.

a. [3 points] Find the equilibria of this model.

Answer

We set $n_{t+1} = n_t = \hat{n}$ and solve for $\hat{n}$

$$\hat{n} = \hat{n}\left(1 + b\left(1 - \frac{\hat{n}}{k^2}\right) - d\right)$$

which means that $\hat{n} = 0$ is one equilibrium and dividing by $\hat{n}$

$$
\begin{aligned}
1 &= \left(b\left(1 - \frac{\hat{n}}{k^2}\right) - d\right) \\
1 &= 1 + b\left(1 - \frac{\hat{n}}{k^2}\right) - d \\
0 &= b\left(1 - \frac{\hat{n}}{k^2}\right) - d \\
d/b &= 1 - \frac{\hat{n}}{k^2} \\
1 - d/b &= \frac{\hat{n}}{k^2} \\
k^2(1 - d/b) &= \hat{n}
\end{aligned}
$$

b. [1 points] Determine when the equilibrium $\hat{n} = k^2(1 - d/b)$ is biologically valid.

Answer

We assume $d \geq 0$ and $b \geq 0$ since they are rates, which guarantees that $\hat{n} \leq k^2$, which is the maximum number of individuals that can fit on the lattice. Since the number of individuals must be non-negative we need $d \leq b$.

c. [3 points] Determine when the equilibrium $\hat{n} = k^2(1 - d/b)$ is locally stable.

Answer

We first take the derivative of the recursion with respect to n_t. Using the product rule we have

$$
\frac{\mathrm{d}n_{t+1}}{\mathrm{d}n_t} = \left(1 + b\left(1 - \frac{n_t}{k^2}\right) - d\right) - n_t b/k^2
$$

Now we evaluate at $n_t = \hat{n} = k^2(1 - d/b)$

$$
\begin{aligned}
\left.\frac{\mathrm{d}n_{t+1}}{\mathrm{d}n_t}\right|_{n_t=\hat{n}=k^2(1-d/b)} &= \left(1 + b\left(1 - \frac{k^2(1 - d/b)}{k^2}\right) - d\right) - k^2(1 - d/b)b/k^2 \\
&= 1 - (1 - d/b)b \\
&= 1 - (b - d)
\end{aligned}
$$

And in discrete time we need this derivative to be between -1 and 1 for stability, meaning that we need

$$\begin{aligned} -1 &< 1-(b-d) \\ -2 &< -(b-d) \\ 2 &> b-d \end{aligned}$$

and

$$\begin{aligned} 1-(b-d) &< 1 \\ -(b-d) &< 0 \\ b-d &> 0 \end{aligned}$$

d. [1 points] Explain why the population does not occupy all the vertices at equilibrium when $d > 0$ even when the birth rate is higher than the death rate, $b > d$.

Answer

In this model some individuals die every time step, which creates empty vertices, and while enough offspring may be produced to fill those empty spots, there are always some empty spots that don't get landed on.

e. [1 points] We decide to simulate this recursion in Python. We start by defining a function to create a generator

```
def n(t0, n0, b, d, k, max=500):
    '''generator for lattice model'''
    t = t0
    nt = n0
    while t < max:
        yield nt
        t = t + 1
        nt = nt*(1 + b*(1-nt/k**2) - d)
```

and then supply parameter values of interest to make the generator

```
ns = n(0,1,0.1,0.05)
```

at which point we get an error: `n() missing 1 required positional argument: 'k'`. How do we fix this error?

Answer

The function `n` requires us to provide 5 parameter values but we have only given 4, so we need to provide 1 more, eg, `ns = n(0,1,0.1,0.05,10)`.

f. [1 points] Now imagine that a fraction p of offspring disperse off the lattice, and die. Write down the recursion equation for this extended model.

Answer

We multiply the fraction of offspring landing on an empty vertex $(1 - n_t/k^2)$ by the fraction that don't disperse off, $(1 - p)$, giving

$$n_{t+1} = n_t \left(1 + b\left(1 - \frac{n_t}{k^2}\right)(1 - p) - d\right)$$

——— *End of Exam* ———