UNIVERSITY OF TORONTO

Faculty of Arts and Science
Department of Ecology and Evolutionary Biology

Mathematical modeling in ecology and evolution

(EEB314/1430)

Test 1 – September 22, 2025

Available Time: 50m

Permitted Materials: Pen/pencil

Question 1 (13/13 points) Transposable elements are small segments of DNA that selfishly replicate themselves within a genome, often at a cost to the individual. They are found across the tree of life to a widely varying degree, e.g., they make up about 85% of the maize (corn) genome but only about 2% of the baker's yeast genome. To better understand the factors determining the number of transposable elements in a genome, Charlesworth and Charlesworth (1983) built a model. The model assumes that the transposable elements replicate at per capita rate u and are lost at per capita rate v, giving growth rate $\lambda = u - v$, which we will assume is positive. It also assumes there are T places in a genome where the transposable elements can exist and the fitness of an individual with n transposable elements in their genome is w_n. Finally, fitness is assumed to decline linearly with the number of transposable elements, $w_n = 1 - ns$, each reducing fitness by amount s. Putting this all together, they determined that the mean number of transposable elements per individual changed at rate

$$\frac{\mathrm{d}\bar{n}}{\mathrm{d}t} = \bar{n}\lambda - \bar{n}\left(1 - \frac{\bar{n}}{T}\right)\left(\frac{s}{1 - \bar{n}s}\right).$$

(a) (3 points) Show how to find the two equilibria of this model, $\hat{\bar{n}} = 0$ and

$$\hat{\bar{n}} = \frac{\lambda - s}{s(\lambda - 1/T)}.$$

We'll refer to these as the zero and nonzero equilibria, respectively.

Answer

Setting the rate of change to 0 and $\bar{n} = \hat{\bar{n}}$,

$$0 = \hat{\bar{n}}\lambda - \hat{\bar{n}}\left(1 - \frac{\hat{\bar{n}}}{T}\right)\left(\frac{s}{1 - \hat{\bar{n}}s}\right),$$

which gives $\hat{\bar{n}} = 0$. Otherwise we can divide by $\hat{\bar{n}}$ and rearrange,

$$\begin{aligned}
0 &= \lambda - \left(1 - \frac{\hat{\bar{n}}}{T}\right)\left(\frac{s}{1 - \hat{\bar{n}}s}\right) \\
\left(1 - \frac{\hat{\bar{n}}}{T}\right)\left(\frac{s}{1 - \hat{\bar{n}}s}\right) &= \lambda \\
\left(1 - \frac{\hat{\bar{n}}}{T}\right)s &= (1 - \hat{\bar{n}}s)\lambda \\
\hat{\bar{n}}s(\lambda - 1/T) &= \lambda - s \\
\hat{\bar{n}} &= \frac{\lambda - s}{s(\lambda - 1/T)}.
\end{aligned}$$

(b) (3 points) Show how to determine that the nonzero equilibrium is biologically valid when either

(a) $1/T \leq s \leq \lambda$ or

(b) $\lambda \leq s \leq 1/T$.

Answer

Here $\bar{n}$ is the mean number of transposable elements in a genome with T potential loci. That means the biologially valid range is $0 \leq \bar{n} \leq T$. The nonzero equilibrium is zero when $\lambda = s$ and is greater than zero when the numerator and denominator have the same sign. This requires either

(a) $s < \lambda$ and $1/T < \lambda$, or

(b) $\lambda < s$ and $\lambda < 1/T$.

In case a the equilibrium is less than or equal to T when

$$\begin{aligned}
\frac{\lambda - s}{s(\lambda - 1/T)} &\leq T \\
\lambda - s &\leq s(\lambda - 1/T)T \\
\lambda - s &\leq s\lambda T - s \\
\lambda &\leq s\lambda T \\
1 &\leq sT \\
1/T &\leq s.
\end{aligned}$$

In case b the sign flips,

$$\begin{aligned}
\frac{\lambda - s}{s(\lambda - 1/T)} &\leq T \\
\lambda - s &\geq s(\lambda - 1/T)T \\
\lambda - s &\geq s\lambda T - s \\
\lambda &\geq s\lambda T \\
1 &\geq sT \\
1/T &\geq s.
\end{aligned}$$

Putting all this together, the nonzero equilibrium is valid when either

(a) $1/T \leq s \leq \lambda$ or

(b) $\lambda \leq s \leq 1/T$.

(c) (4 points) Using the product and chain rules we have

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}\bar{n}}\left(\frac{\mathrm{d}\bar{n}}{\mathrm{d}t}\right) =& \lambda - \left(1 - \frac{\bar{n}}{T}\right)\left(\frac{s}{1 - \bar{n}s}\right) \\
& - \bar{n}\left(\frac{s}{1 - \bar{n}s}\right)\left(\left(1 - \frac{\bar{n}}{T}\right)\left(\frac{s}{1 - \bar{n}s}\right) - \frac{1}{T}\right).
\end{aligned}$$

Show how to determine that stability of the zero equilibrium requires $\lambda < s$ and stability of a valid nonzero equilibrium requires $1/T \leq s < \lambda$. (Hint: from part a you may have noticed that

$$\left(1-\frac{\bar{n}}{T}\right)\left(\frac{s}{1-\bar{n}s}\right)=\lambda$$

at the nonzero equilibrium.)

Answer

Evaluating the derivative at the zero equilibrium,

$$\frac{\mathrm{d}}{\mathrm{d}\bar{n}}\left(\frac{\mathrm{d}\bar{n}}{\mathrm{d}t}\right)_{\bar{n}=0} = \lambda - s.$$

Stability requires this to be negative, i.e., $\lambda < s$.

Evaluating the derivative at the nonzero equilibrium, using the hint,

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}\bar{n}}\left(\frac{\mathrm{d}\bar{n}}{\mathrm{d}t}\right)_{\bar{n}=\frac{\lambda-s}{s(\lambda-1/T)}} &= -\hat{n}\left(\frac{s}{1-\bar{n}s}\right)(\lambda-1/T)\Big|_{\bar{n}=\frac{\lambda-s}{s(\lambda-1/T)}} \\
&= -\frac{\lambda-s}{s(\lambda-1/T)}\left(\frac{s}{1-\frac{\lambda-s}{\lambda-1/T}}\right)(\lambda-1/T) \\
&= -(\lambda-s)\left(\frac{1}{1-\frac{\lambda-s}{\lambda-1/T}}\right) \\
&= -\frac{(\lambda-s)(\lambda-1/T)}{s-1/T}
\end{aligned}$$

This is negative in case a but not in case b.

(d) (2 points) Under this model, what needs to be true for an initially rare transposable element to be able to increase but not increase indefinitely?

Answer

To be able to increase when rare we need the zero equilibrium to be unstable, implying weak enough selection (cost), $s < \lambda$. We also need for there to be a valid and stable nonzero equilibrium, which implies case a, $1/T \leq s < \lambda$. The condition $1/T \leq s$ means that there are enough loci for the transposable element to occupy.

(e) (1 points) Assuming transposable elements are at the nonzero equilibrium, which of the following may explain the larger number of transposable elements in maize vs. baker's yeast?

(a) transposable elements have a smaller s in maize than yeast

(b) transposable elements have a larger T in maize than yeast

Answer

It is perhaps surprising that the equilibrium number of transposable elements declines with the number of locations for transposable elements in the genome, T, in this model. Therefore weaker selection against transposable elements, a smaller s, is the correct answer.

——— *End of Exam* ———