Problem Set: The Many Uses of Eigenvectors in Evolutionary Dynamics

Please show all work and represent your answers in simplest possible form.

Question #1 (50 points)

This question will be concerned with reactive strategies. Suppose that we have two reactive strategies, S_1 and S_2, playing a repeated prisoner's dilemma with payoff matrix $\begin{array}{ccc} & C & D \\ C & R & S \\ D & T & P \end{array}$. Let p_i be the probability that player S_i will cooperate after their oponent has cooperated in the previous round and let q_i be the probability that player S_i will cooperate after their oponent has defected in the previous round. In each round, the game is in one of the four states: CC (if both players cooperate in this round), CD (if the first player cooperates and the second defects), DC, and DD. We will denote these fours states as 1, 2, 3 and 4, respectively.

1a) (25 points)

(i) Write down the matrix $M = [m_{ij}]$, where m_{ij} is the probability that the game will be in state i after it was in state j in the previous round ($i, j \in \{1, 2, 3, 4\}$).

(ii) Assume that in the n-th round, the game is in state i with probability $x_i(n)$, for $i \in \{1, 2, 3, 4\}$. Write down the formulas for $x_i(n+1)$, the probability that the game is in state i in round $(n+1)$, in terms of $x_i(n)$ and m_{ij}, $i, j \in \{1, 2, 3, 4\}$. Rewrite your result as an equation that uses the terms $\vec{x}(n+1)$, $\vec{x}(n)$ and M ($\vec{x}(n)$ is the vector with entries $x_i(n)$).

(iii) The stationary distribution of this game is $\vec{x} = \lim_{n\to\infty} \vec{x}(n)$. What relation does $\vec{x}$ satisfy? Can you rephrase it in terms of eigenvectors and eigenvalues?

(iv) Using Mathematica, find the stationary distribution $\vec{x}$ in terms of q_i and $r_i = p_i - q_i$, $i = 1, 2$. If we let $s_1 = \frac{q_2 r_1 + q_1}{1 - r_1 r_2}$ and $s_2 = \frac{q_1 r_2 + q_2}{1 - r_1 r_2}$, can you rewrite $\vec{x}$ in terms of s_1 and s_2? (Hint: Check the help documentation on the "Eigensystem" command.)

(v) What is the expected payoff for strategy S_1 versus S_2 in one round of the game (after enough rounds)?

1b) (25 points)

(i) (7 points) Assume strategy S_1 is a TFT strategy with errors (say that it "accidentally defects" 1% of the time and forgives just 1% of the time). Calculate the expected payoff from 1a)(v) for this strategy playing against itself.

(ii) (7 points) Assume strategy S_2 is a GTFT strategy with errors (say that it "accidentally defects" 1% of the time and forgives 30% of the time). Calculate the expected payoff from 1a)(v) for this strategy playing against itself.

(iii) (8 points) Using the same strategies in (i-ii), compute the expected payoff of S_1 versus S_2, and of S_2 versus S_1.

(iii) (3 points) From the above, what statements can you make about invadability of S_1 by S_2 and vice-versa?

Question #2 (50 points)

Use the quasispecies equation. You may use Mathematica to compute any eigenvalues/eigenvectors of matrices.

Consider three strains: S1, S2, and S3, with fitnesses $f_1 = 1$, $f_2 = 1 - a$, $f_3 = 1 - 2a$, for $a \in (0, 0.5)$.

The rate of deleterious mutation is $u \in (0, 1)$. (Offspring of S1 mutate to S2 at rate u; offspring of S2 mutate to S3 at rate u.)

The rate of back-mutation is $v \in (0, 1)$. (Offspring of S2 mutate to S1 at rate v; offspring of S3 mutate to S2 at rate v.)

In all questions that ask about equilibrium, assume that all initial frequencies are positive. (There will always be a globally stable equilibrium to which all interior trajectories converge.)

2a) (10 points)

(i) (3 points) Write down the matrix $Q = [q_{ij}]$, where q_{ij} is mutation from type j to type i. (Note: This matrix is the *transpose* of the one described on p. 33 of the text.)

(ii) Write down the matrix $W = [w_{ij}] = [f_j q_{ij}]$ **(3 points)**. In words, briefly describe what the entry $w_{2,3}$ means and why its value is what it is **(4 points)**.

2b) (28 points)

Assume that there is no back-mutation ($v = 0$). Use the matrix W to answer the following:

(i) Prove: The equilibrium frequency of S3 is positive, for all possible parameter values.

(ii) What condition holds if and only if the equilibrium frequency of S1 is positive? (Hint: It is a very simple inequality using a and u.)

(iii) Prove: The equilibrium frequency of S1 is positive if and only if the equilibrium frequency of S2 is positive.

(iv) Use $a = 0.1$, $u = 0.03$. What are the equilibrium frequencies of the three strains?

2c) (12 points)

Now use the parameters $a = 0.01$, $u = 0.04$. Define $b = \frac{v}{u}$, the relative effectiveness of back-mutation.

Plot the equilibrium frequencies of the 3 strains on one graph, varying b between 0 and 1. Please submit the work/code that you used to produce the graph.

(If you can't figure out how to plot a continuous graph in Mathematica, you may output the frequencies for $b = 0$, 0.2, 0.4, 0.6, 0.8, 1 and create a graph from this data.)