Exercise 3: Dynamics of interacting populations

Part 1: Mutualism in the two-species Lotka-Volterra model.

The two-species Lotka-Volterra model is defined by the equations

$$\dot{x} = f_x(x, y) = r_x x + c_x x^2 + c_{xy} x\, y\,, \tag{1a}$$
$$\dot{y} = f_y(x, y) = r_y y + c_y y^2 + c_{yx} y\, x\,. \tag{1b}$$

Consider (1) with mutualism ($c_{xy}, c_{yx} > 0$) and intraspecific competition ($c_x, c_y < 0$). One distinguishes two basic types of mutualism:

- With *obligate mutualism*, neither species can survive without the presence of the other species. We then have $r_x, r_y < 0$.
- With *facultative mutualism*, the other species is helpful, but not essential. This is characterized by $r_x, r_y > 0$.

1.1 First consider the case of obligate mutualism. Draw possible isocline configurations, add flow arrows, determine the equilbria and perform a stability analysis. You should find two qualitatively different parameter regimes. Can you exclude periodic orbits? What is the biological interpretation of the different regimes (examples)?

1.2 Do the same for the case of facultative mutualism. Discuss under what conditions this model might or might not make reasonable predictions. How could we make the model more realistic (by going beyond the Lotka-Volterra scheme)?

Part 2: SIR model with births, deaths, and vaccination.

Consider a population with equal per capita birth and death rates (given by μ), such that the total population size N remains constant. We model the spread of a disease assuming that newborns can be vaccinated, such that they acquire life-long immunity. We can then extend the basic SIR model to include an additional P compartment (of permanently immune individuals), such that $S + I + R + P = N$. Assume that a fraction σ of new-borns is vaccinated. Then the dynamics of the population is described by the following equations:

$$\dot{S} = \mu(1-\sigma)N - c\frac{I}{N}S - \mu S \tag{2a}$$

$$\dot{I} = c\frac{I}{N}S - rI - \mu I \tag{2b}$$

$$\dot{R} = rI - \mu R \tag{2c}$$

$$\dot{P} = \mu\sigma N - \mu P \tag{2d}$$

2.1 Find the equilibria of this system of equations and investigate their stability. What is the basic reproductive ratio R_0? Use this to derive the minimum vaccination fraction required to prevent outbreaks of the disease. What vaccination fraction do we need for $R_0 = 15$ (measles)? In this context, discuss the meaning of *herd immunity*.

2.2 Temporal immunity: Modify the above equations to describe a scenario in which immunity is not life-long, such that recovered individuals can become susceptible to re-infection with rate d. Analyse this model to determine how the vaccination threshold for herd immunity depends on d. Interpret your results.

2.3 Vaccinating adults: Assume that non-infected individuals can be vaccinated throughout their lifetime and that this occurs at a constant rate κ. We assume that immunity is life-long. Modify the above equations to include this scenario and again derive the new threshold for herd immunity.

Part 3: SEIR model

Some diseases such as COVID-19 are characterised by a latency period in which infected individuals are unlikely to transmit the infection to other susceptible individuals. Such individuals are referred to as 'exposed' individuals. This leads to the SEIR model, which is described by the following equations:

$$\dot{S} = \mu N - c\frac{I}{N}S - \mu S \tag{3a}$$

$$\dot{E} = c\frac{I}{N}S - \alpha E - \mu E \tag{3b}$$

$$\dot{I} = \alpha E - rI - \mu I \tag{3c}$$

$$\dot{R} = rI - \mu R \tag{3d}$$

3.1 Non-dimensionalise these equations to identify the smallest set of parameters that describe the dynamics. Interpret these new parameters in terms of the different time scales in the problem.

3.2 Investigate the stability of the disease-free equilibrium to determine the threshold reproductive ratio R_0 above which outbreaks occur.

3.3 Consider a scenario where R_0 is above the threshold required to prevent outbreaks. Derive an expression for the initial rate of spread of the disease starting from a very low number of infected individuals. How does the initial rate of spread depend on the latency period: derive limiting expressions when the latency period is much higher or much lower than other time scales. Based on your results, discuss a quantitative criterion for when it is important to account for exposed (but non-infectious) individuals in models of disease dynamics.
Hint: Assume that birth/death rates are much lower than other rates, and set these to zero (as a first approximation) in your expression for the initial rate of spread.

3.4 Bonus: Find estimates for the parameters of this model for the case of COVID-19 on the internet and discuss which parameters are known with higher or lower certainty.