Homework assignment

Please send your homeworks to jgrilli@ictp.it by **31/01/2022**. The subject of the email should read: *EcoEvo HA*

I. EXERCISES

You are *very* encouraged to discuss with others about the exercises. You can work on the exercises individually or as a group. There is no grade bonus or penalty in doing the exercise individually or with others. It is really just your choice. But if you do exercises with others, please do a joint submission.

A. More realistic model of fishery

Consider the equation

$$\frac{dn(t)}{dt} = rn(t)\left(1 - \frac{n(t)}{K}\right) - p(n(t)) \ , \tag{1}$$

which describes the population dynamics of some species of fish. The (analytic) function $p(n(t))$ is the rate of fishing as a function of the population abundance $n(t)$. Assume that

$$\lim_{n\to\infty} p(n) = p_\infty > 0 \ , \tag{2}$$

$$p(0) = 0 \ , \tag{3}$$

$$p'(0) = p_0 > 0 \ ., \tag{4}$$

and

$$p'(n) > 0 \ \forall n \geq 0 \tag{5}$$

1. Describe the ecological implications of these assumptions. Define $\phi(n) = p(n)/n$. What does $\phi(n)$ describes?
2. Assume that

$$p(n) = \frac{p_\infty p_0 n}{p_\infty + p_0 n} \ . \tag{6}$$

Describe the fixed points and the bifurcations in the system.
3. Try to generalize the previous result to a larger class of functions. What is the minimal set of conditions on $p(n)$ (or $\phi(n)$) you need to assume in order to obtain qualitatively the same phenomenology obtained in point 2?
4. Choose another function $p(n)$ which satisfies the assumptions that you find in point 3 and describe the fixed point and bifurcation in that system.

B. Large linear systems

Consider the linear system of equation

$$\frac{dx_i(t)}{dt} = \sum_{j=1}^{N} A_{ij} x_j \quad \text{for } i = 1, 2, \ldots, N \ , \tag{7}$$

where $A_{ii} = -1$ and the off-diagonal elements A_{ij} are independent random variables with mean 0 and variance σ^2/N, drawn from your favourite distribution (provided that it has finite moments). Describe the stability of the fixed point x^* at different values of σ. Use $N = 547$ and your favourite distribution.

C. More than two trophic levels

Consider the following 4 species:

- Species 1 grows logistically (in absence of other species) and is consumed by species 2 and 3.
- Species 2 and 3 go to extinction in absence of species 1.
- Species 4 consumes both species 2 and 3 and goes to extinction if species 2 and 3 are both absent.

1) Write a non-linear system of equations which describe the dynamics of those 4 interacting populations. You can make all the assumptions you want, as long as you clearly state the assumptions and simplifications you are making.
2) Use analytical and/or numerical methods to study the attractors of the equations you wrote. Describe the region of parameters where all the 4 species coexists (if such a region exists).
3) What did you learn from this model?

D. Density dependence

Consider the stochastic dicrete-time process defined by the following transition probabilities

$$M_{n\to n+1} = \frac{N-n}{N}\frac{n}{N}\left(1-q\frac{n}{N}\right) \tag{8}$$

and

$$M_{n\to n-1} = \frac{n}{N}\frac{N-n}{N}\left(1-q\frac{N-n}{N}\right) \ , \tag{9}$$

where $0 \leq q \leq 1$ and $M_{n\to n}$ is appropriately defined by the normalization condition. Study the fixation probability. You are free to use numerical simulations and/or analytic calculations, and encouraged to use both. What is the behavior in the limit $N \gg 1$? What is the interpretation of the parameter q?

E. Mutation asymmetry or selection?

Your friend knocks at your door asking for help. She is a yeast microbiologist working on experimental evolution. She ran an experiment on ethanol tolerance in *S. cervisiae*, where she measured (for many replicates) the relative frequency of ethanol tolerant individuals. The molecular mechanism of ethanol tolerance is still unknown and it is not clear if the mutation from ethanol tolerance to ethanol intolerance and the reverse mutation occur equally likely. In her experiment there is no ethanol, but the ethanol tolerant phenotype might be under selection pressure for other unknown reason. She is not sure of whether her data can be explained by an asymmetry in the mutation rates or by selection on one of the two phenotypes. Can you help your friend? If no, why? If yes, what should she measure to distinguish between the two alternative scenarios?

F. Fitness speed

Consider a population of size N. An invidiual belongs to a fitness class k with fitness $\exp(ks_0)$. When a mutation occurs (with probability U), the fitness class of the mutant is $k+l$ where l is an integer drawn from a distribution $g(l)$.

In this exercise you have to simulate the process with $g(l) = \delta_{l,-1}$ (see below on suggestions on what to simulate and how). Study the speed of adaptation, i.e. the large time behavior of the average fitness $\bar{f}(t) = \sum_k e^{ks_0} n_k(t)/N$, as a function of N (you are free to choose the values of s_0 and U, provided that $0 < s_0 \ll 1$ and $0 < U \ll 1$. Use this freedom well).

What do you expect in the limit $N \to \infty$? Describe what is happening in your simulations.

How to simulate the process. Let $n_k(t)$ be the number of individuals in class k at time t (tip: many classes are empty, do not use your computer memory to store thousands of zeros). Let's define $x_k(t) = e^{ks_0} n_k(t)/(N\bar{f}(t))$. Generate values $\tilde{n}_k(t+1)$ from a multinomial distribution with weights $x_k(t)$, i.e.

$$P(\{\tilde{n}.\}) = \frac{N!}{\prod_k \tilde{n}_k!} \prod_k (x_k(t))^{\tilde{n}_k} \ . \tag{10}$$

By definition $\sum_k \tilde{n}_k(t+1) = N$. Some of this individuals will mutate. The number of mutant m_k in class k will be binomially distributed

$$P(m_k) = \binom{\tilde{n}_k}{m_k} U^{m_k} (1-U)^{\tilde{n}_k - m_k} \ , \tag{11}$$

where U is the mutation probability. The mutated individuals will go to class $k-1$ (since $g(l) = \delta_{l,-1}$). The population at time $t+1$ will be therefore given by

$$n_k(t+1) = \tilde{n}_k(t+1) + m_{k+1} - m_k \ . \tag{12}$$