

Università degli studi di Padova

# Physical Models of Living Systems

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# 1 Homework Week 01

Tasks:

1. Solve the Quasi Stationary Approximation of the Consumer Resource Model with 1 species and 1 abiotic resource and compare it numerically with the full solution. Optional: find a regime of parameters where the QSA is good. Remember to check that parameters you choose and initial condition for  $R$  and  $N$  should be so that  $R^*$  in the QSA is not negative.
2. Write the Fokker Plank Equation associated to the stochastic logistic equation with environmental noise and solve for the stationary solution  $P^*$ . Optional: compare analytical and numerical simulation of the SDE.

## 1.1 Exercise 1

Let  $N(t)$  be the size of the population and  $R(t)$  the amount of resources available. The Consumer Resource Model with 1 species and 1 abiotic resource is described by the following system of differential equations:

$$\frac{dR}{dt} = \mu(R) - cRN \quad (1)$$

$$\frac{dN}{dt} = (\gamma cR - d)N \quad (2)$$

For abiotic resources,  $\mu(R)$  is given by the Monod function:

$$\mu(R) = \frac{R}{k_s + R} \quad (3)$$

In order to solve the system using the QSA, first we need to find the stationary solution of equation (1), which corresponds to assuming  $R$  is fixed at equilibrium.

$$0 \stackrel{!}{=} \frac{dR}{dt} = \frac{R}{k_s + R} - cRN \Big|_{R=R^*} \quad (4)$$

Using the fact that  $R^* = \text{const} \neq 0$  we can solve it for  $R^*$ :

$$(1 - cNk_s)R - cNR^2|_{R=R^*} = 0 \implies R^* = \frac{1 - cNk_s}{cN} \quad (5)$$

This solution can be substituted in equation (2), leading to a linear ordinary differential equation for the population  $N(t)$ :

$$\frac{dN}{dt} = \left[ \frac{\gamma(1 - cNk_s)}{N} - d \right] N \quad (6)$$

If we define  $\tilde{a} = \gamma$  and  $\tilde{b} = \gamma ck_s + d$  we can rewrite the equation as:

$$\frac{dN}{dt} = \tilde{a} - \tilde{b}N \quad (7)$$

The general solution can be found solving the corresponding homogeneous equation and adding a particular solution, which can be found for example by looking at the stationary state.

$$\text{Homogeneous: } \dot{N} = -\tilde{b}N \Rightarrow N(t) = Ce^{-\tilde{b}t}$$

$$\text{Stationary state: } 0 \stackrel{!}{=} \dot{N} = \tilde{a} - \tilde{b}N \Rightarrow N(t) = \frac{\tilde{a}}{\tilde{b}}$$

So the full solution of the QSA of the Consumer Resource Model with 1 species and 1 abiotic resource is given by:

$$N(t) = Ce^{-\tilde{b}t} + \frac{\tilde{a}}{\tilde{b}} \quad (8)$$

and the multiplicative constant  $C$  can be determined imposing the initial condition  $N(t=0) = N_0$ , which leads to:

$$C = N_0 - \frac{\tilde{a}}{\tilde{b}} \quad (9)$$

### 1.1.1 Numerical comparison

Let's consider the following set of parameters:

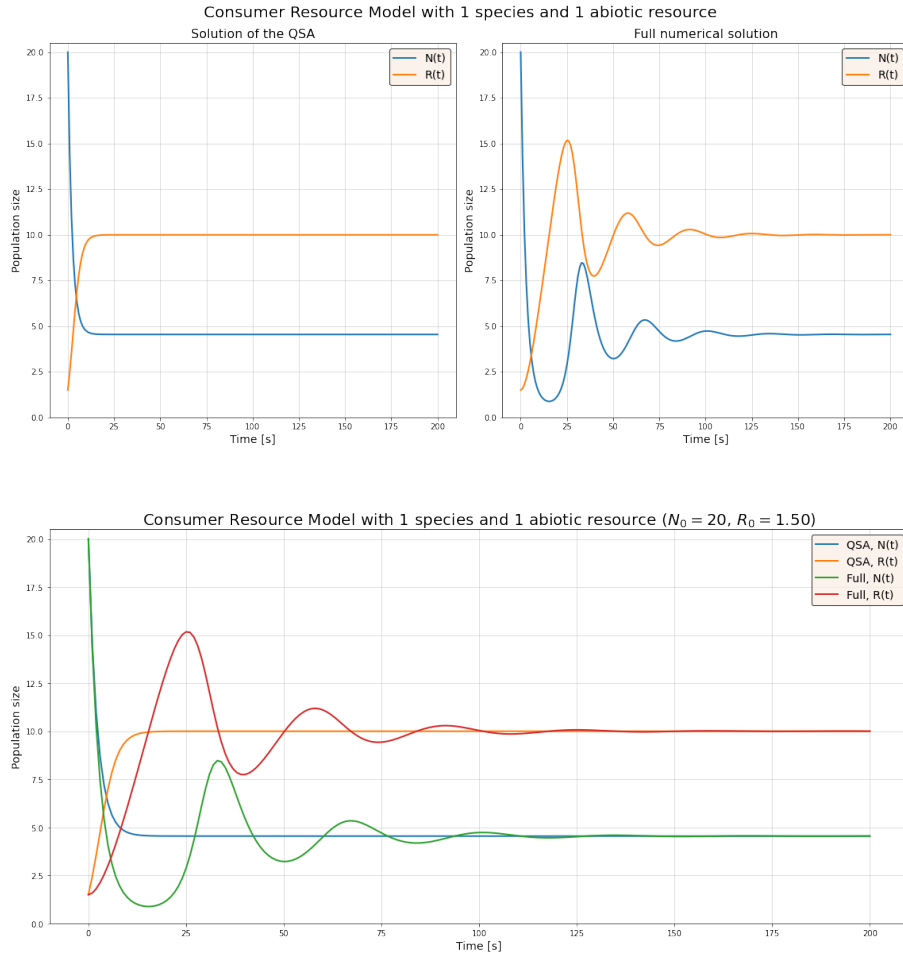
$$k_s = 1, \quad c = 0.02, \quad d = 0.4, \quad \gamma = 2 \quad (10)$$

and the initial condition:

$$N(t = 0) = N_0 = 20 \quad (11)$$

$$R(t = 0) = \frac{1 - cN_0k_s}{cN_0} = 1.5 \quad (12)$$

The following plots are obtained by simulating the evolution of  $N(t)$  and  $R(t)$  for  $t \in [0, 200]$  with the above set of parameters and initial condition. Through them it is possible to compare numerically the QSA solution with the full one.



For more details, see the corresponding notebook: [hw01\\_Dynamics\\_of\\_Single\\_Species.ipynb](#).

## 1.2 Exercise 2

Given the stochastic logistic equation with environmental noise:

$$\frac{dx}{dt} = \frac{x}{\tau} \left( 1 - \frac{x}{K} \right) + \sqrt{\frac{\sigma}{\tau}} x \xi(t) \quad (13)$$

where  $\xi(t)$  is Gaussian white noise, it is possible to identify  $A(x)$  and  $B(x)$  such that the previous equation can be reformulated as:

$$\frac{dx}{dt} = A(x) + \sqrt{B(x)} \xi(t) \quad (14)$$

In this case, we have that:

$$A(x) = \frac{x}{\tau} \left(1 - \frac{x}{K}\right) \quad (15)$$

$$B(x) = \frac{\sigma}{\tau} x^2 \quad (16)$$

At this point it is possible to write the associated Fokker Plank equation:

$$\begin{aligned} \frac{\partial P}{\partial t} &= -\frac{\partial}{\partial x} [A(x)P(x)] + \frac{1}{2} \frac{\partial^2}{\partial^2 x} [B(x)P(x)] = \\ &= -\frac{\partial}{\partial x} \left[ \frac{x}{\tau} \left(1 - \frac{x}{K}\right) P(x) \right] + \frac{1}{2} \frac{\partial^2}{\partial^2 x} \left[ \frac{\sigma}{\tau} x^2 P(x) \right] \end{aligned} \quad (17)$$

To find the stationary solution  $P^*$  we have to impose that  $\frac{\partial P}{\partial t} \stackrel{!}{=} 0$ . Defining the flux:

$$J(x) = -\frac{x}{\tau} \left(1 - \frac{x}{K}\right) P(x) + \frac{1}{2} \frac{\partial}{\partial x} \left[ \frac{\sigma}{\tau} x^2 P(x) \right] \quad (18)$$

we have that  $\frac{\partial P}{\partial t} = 0 \iff \frac{\partial J(x)}{\partial x} = 0 \iff J(x) = \text{const.} = 0$ , where the last equal is achieved by imposing the boundary condition  $J(0) = 0$ . We are left with a first order differential equation,  $J(x)|_{P(x)=P^*} = 0$ , which can be solved by separation of variables.

$$\begin{aligned} J(x) &= 0 \\ \Rightarrow -\frac{x}{\tau} \left(1 - \frac{x}{K}\right) P(x) + \frac{\sigma}{\tau} x P(x) + \frac{1}{2} \frac{\sigma}{\tau} x^2 \frac{dP(x)}{dx} &= 0 \\ \Rightarrow \frac{1}{P(x)} \frac{dP(x)}{dx} &= \frac{2}{x} \left(\frac{1}{\sigma} - 1\right) - \frac{2}{\sigma K} \end{aligned}$$

Integrating on both sides we obtain:

$$\ln P(x) = 2 \left(\frac{1}{\sigma} - 1\right) \ln x - \frac{2}{\sigma K} x + C \quad (19)$$

and, finally, taking the exponential and redefining the constant  $C$  we have the stationary solution:

$$P^*(x) = C \exp \left\{ 2 \left(\frac{1}{\sigma} - 1\right) \ln x - \frac{2}{\sigma K} x \right\} \quad (20)$$

To find  $C$  we have to impose the normalization condition on  $P^*(x)$  and solve the corresponding equation:

$$\int P^*(x) dx = 1 \quad (21)$$

The integral can be solved using the Gamma function and the final expression of the stationary distribution is:

$$P^*(x) = \frac{1}{\Gamma\left(\frac{2}{\sigma}\right)} \exp \left\{ 2 \left(\frac{1}{\sigma} - 1\right) \ln x - \frac{2}{\sigma K} x \right\} \quad (22)$$

## 2 Homework Week 02

Infer the number of species from data of a forest sampled in 1% of the total area. Each row of the file represent a different species, and the number indicates the species abundance (i.e., the number of individuals). Perform the analysis to infer the number of species at the whole scale ( $p=1$ ). You can work in small group of 2/3 people.

### 2.1 Solution

The solution can be found in the repository of the course<sup>[1]</sup>. The notebook is developed together with Tommaso Amico and Andrea Lazzari, and it can be accessed via the following link: [hw02\\_Spatial\\_Scaling\\_RSA.ipynb](#).

### 3 Homework Week 03

Consider the Lotka-Volterra equations:

$$\frac{dx}{dt} = ax - pxy \quad (23)$$

$$\frac{dy}{dt} = -cy + pxy \quad (24)$$

Tasks:

1. Find the stationary solutions.
2. Do the stability analysis of the stationary solutions. Is there any stable solution?
3. (optional) Simulate Eqs.(23)-(24) with different parameters. Is there a range of parameters where do you observe sustained oscillations?

#### 3.1 Stationary solutions

Stationary solutions are characterized by:

$$\begin{cases} \frac{dx}{dt} \stackrel{!}{=} 0 \\ \frac{dy}{dt} \stackrel{!}{=} 0 \end{cases} \implies \begin{cases} 0 = ax - pxy \\ 0 = -cy + pxy \end{cases} \quad (25)$$

The solutions of this system are:

- $x_0^* = y_0^* = 0$
- $x_1^* = \frac{c}{p}, y_1^* = \frac{a}{p}$

so we found 2 stationary points,  $(x_0^*, y_0^*) = (0, 0)$  and  $(x_1^*, y_1^*) = (\frac{c}{p}, \frac{a}{p})$ . Notice that the first solution corresponds to the extinction of both species.

#### 3.2 Stability analysis

For each stationary point, we have to compute the Jacobian of the system in it:

$$J_i = \begin{pmatrix} \partial_x f_1 & \partial_y f_1 \\ \partial_x f_2 & \partial_y f_2 \end{pmatrix} \bigg|_{x_i^*} = \begin{pmatrix} a - py & -px \\ py & px - c \end{pmatrix} \bigg|_{x_i^*} \quad (26)$$

We obtain:

$$J_0 = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix} \quad J_1 = \begin{pmatrix} 0 & -c \\ a & 0 \end{pmatrix} \quad (27)$$

Writing the linearized equations around the stationary point, we know that stability is determined by the largest real part of the Jacobian's eigenvalues. The eigenvalues corresponding to  $J_0$  and  $J_1$  are, respectively:

$$\lambda_1^0 = a \quad \lambda_2^0 = -c \quad (28)$$

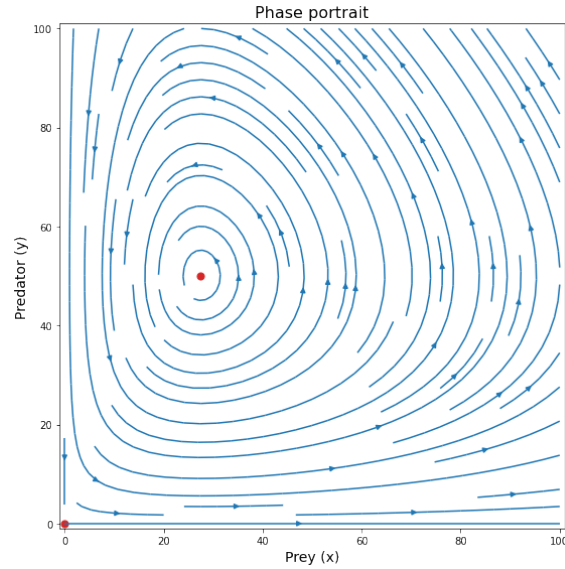
$$\lambda_1^1 = -i\sqrt{ac} \quad \lambda_2^1 = i\sqrt{ac} \quad (29)$$

where we used the fact that  $a, c > 0$ .

As  $\lambda_1^0 = a > 0$ , the first stationary point  $x_0^*$  is unstable. Moreover, since the eigenvalues are one positive and one negative, the stationary point in  $(0, 0)$  is a saddle point. This is a very important result. Indeed, if it were stable, both species populations could be attracted to it. This would result in an extinction process for different non-zero initial condition. However, this does not happen because this fixed point is unstable, which means that according to the model it is difficult for the extinction of both species to occur.

On the other side, in the second stationary point we have that  $Re(\lambda_1^1) = Re(\lambda_2^1) = 0$ , which corresponds to a neutral or critical situation. In general, all typical behaviours are possible in this case (unstable focus, stable focus, saddle point, etc.), together with another one, namely a centre, which is a closed orbit that is neutrally stable. Since the imaginary part of  $x_1^*$  is nonzero, or in other words  $x_1^*$  is complex, and the system is conservative, there exist closed orbits about the fixed point, and we expect an oscillatory, periodic behaviour around the it.

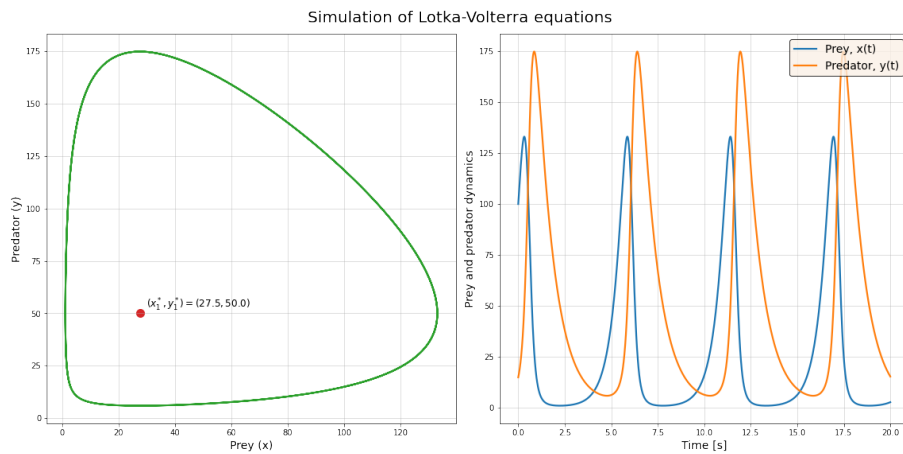
This results can be understood also by looking at the phase portrait corresponding to the Lotka-Volterra equations we are studying:



### 3.3 Simulation results

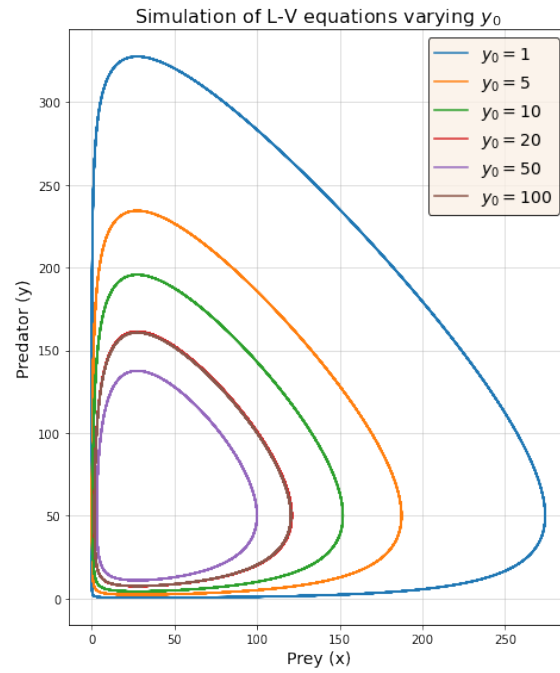
This section shows some simulation results. The corresponding notebook is available at the following link: [hw03\\_Lotka\\_Volterra.ipynb](#). First, a simulation is performed setting  $x(0) = 100$ ,  $y(0) = 15$  as initial conditions and using the following set of parameters:

- $a = 2$
- $c = 1.1$
- $p = 0.04$

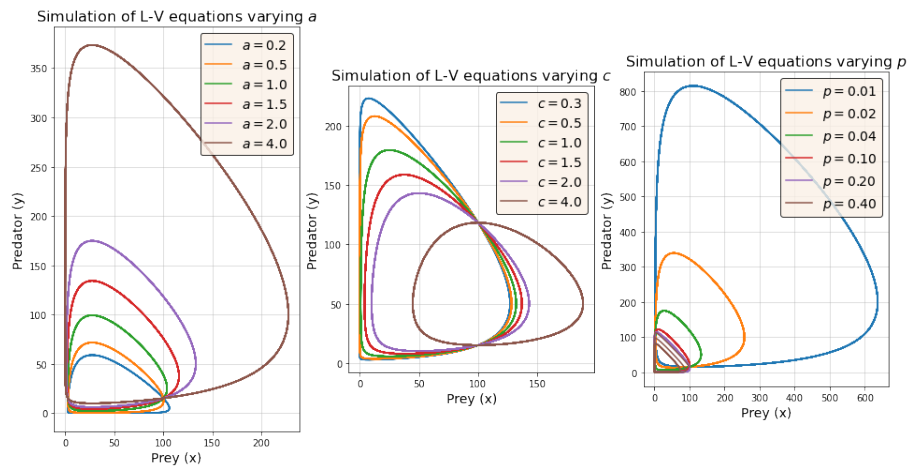


Then, to better visualize the oscillatory and periodic behaviour we simulate the dynamics with the same set of parameters, varying the initial size of the predator's population.





Finally, the same plot is obtained by varying  $a$ ,  $c$  or  $p$ , respectively. In all cases reported the graphs show the presence of sustained oscillations. The resulting plots are shown here:



## 4 Homework Week 04

Assignment:

1. Generate a random  $S \times S$  matrix with  $C$  non zero entries and  $1-C$  zeros ( $C$  is between zero and one). Set the diagonal to  $-d$ . The non-zero elements are drawn from a given distributions. Calculate the eigenvalues. Repeat different realizations and plot all the eigenvalues in the complex plane [Real part (x-axis) and imaginary part (y-axis)]. Compare this result with the expectations from the circular law.
2. Generate the same as above but for mutualistic structure and find how the maximum real eigenvalues scales with  $S$  (use  $S=20,30,40,\dots,100$ ) and compares your numerical finding with the analytical expectations (we did not explicitly have calculated this in class).
3. Analyse the food web using the metrics we have seen in class. The file represent the weighted adjacency matrix of the food web. For the analysis you can binarize (zero and one) the matrix. You find the file in the google drive.
4. (optional) Calculate the same as 1) but with for the cascade model or for the nested mutualistic network.

### 4.1 Solution

The solution is fully developed in a Jupyter Notebook: [hw04\\_Ecological\\_Interactions.ipynb](#) [1].

## 5 Homework Week 05, 06

Consider a consumer resource model where the supply rate is  $s(c) = \omega c(1 - c/K)$  and the resource concentration  $r(c) = c$  is linear, for  $S = 5$  species and  $R = 5$  resources. Assign the metabolic strategies at random from a Uniform Distribution between  $[0, 0.2]$ , while set all other parameters to 1 and choose the death rate small enough as you prefer.

1. Perform the simulations of the full CRM model and compare the stationary solution you find numerically with those obtained analytically.
2. Set  $w = 10$  and do the simulation of the quasi stationary approximation (finding first  $c^*$  and then simulating  $n(t, c^*)$ ) and compare it with the simulations of the full CRM (keeping fix the metabolic strategies in the two cases for a given realization). Do several (e.g.  $>20$ ) realizations of the dynamics to obtain a statistics of the species population stationary states in the two cases, represent each population through a Box-Whisker Plot both for the full CRM and the GLV and compare the two.
3. Does the quasi-stationary approximation works if  $w = 0.1$ ? Why?

### 5.1 Solution

The solution is carried out in the following Jupyter Notebook, which is publicly accessible from the course repository<sup>[1]</sup>: [hw05\\_Generalized\\_Consumer\\_Resource\\_Model.ipynb](#).

## 6 Homework Week 07

Calculate the avalanche duration probability  $P_{>}(t)$  if  $\lambda_i = \lambda$  for all  $t$  and all neurons. This leads, as only sketched in class, to the following integral:

$$\gamma \int_0^\infty d\lambda \cdot \exp(-\gamma\lambda) \cdot (1 - \exp(-\delta\lambda))^n \quad (30)$$

which can be solved through the saddle point approximation.

**Optional.** Create a time series  $\lambda(t)$ , with  $t = 1, 2, \dots, T$  where at each time  $t$ , the value of  $\lambda$  is extracted from an exponential distribution. Then simulate  $N = 100$  independent heterogeneous Poisson processes, where each one describes the spikes events of a single neuron, but all have the same time dependent rate parameter  $\lambda(t)$ .

### 6.1 Calculation of the avalanche duration probability

### 6.2 Simulation of independent heterogeneous Poisson processes

## 7 Homework Week 08

Study the stability of the excitatory-inhibitory two neurons system (Eq. 7.5 in the notes) for the parameters:

- $M_{EE} = 1.25$ ,  $M_{IE} = 1$ ,  $M_{EI} = -1$ ,  $M_{II} = 0$ ;
- $h_E = 10\text{ Hz}$ ,  $h_I = -h_E$ ;
- $\tau_E = 10\text{ ms}$

as a function of the free parameter  $\tau_I$ . Simulate a trajectory in the stable regime and one in the limit cycle regime (different  $\tau_I$ ).

### 7.1 Stability study

### 7.2 Simulation in the stable regime

### 7.3 Simulation in the limit cycle regime

## References

- [1] Nicola Zomer. *Github Repository of Physical Models of Living Systems*. Nov. 2, 2022. URL: [https://github.com/NicolaZomer/Physical\\_Models\\_of\\_Living\\_Systems](https://github.com/NicolaZomer/Physical_Models_of_Living_Systems).