Università degli studi di Padova

Physical Models of Living Systems

Master Degree in Physics of Data, 2022-2023

Nicola Zomer

December 18, 2022

Contents

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:

$$\frac{dR}{dt} = \mu(R) - cRN \tag{1}$$
$$\frac{dN}{dt} = (\gamma cR - d)N \tag{2}$$

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

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

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.

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

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

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

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

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

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

$$\frac{dN}{dt} = \tilde{a} - \tilde{b}N \tag{7}$$

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:

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

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

$$C = N_0 - \frac{\tilde{a}}{\tilde{b}} \tag{9}$$

1.1.1 Numerical comparison

Let's consider the following set of parameters:

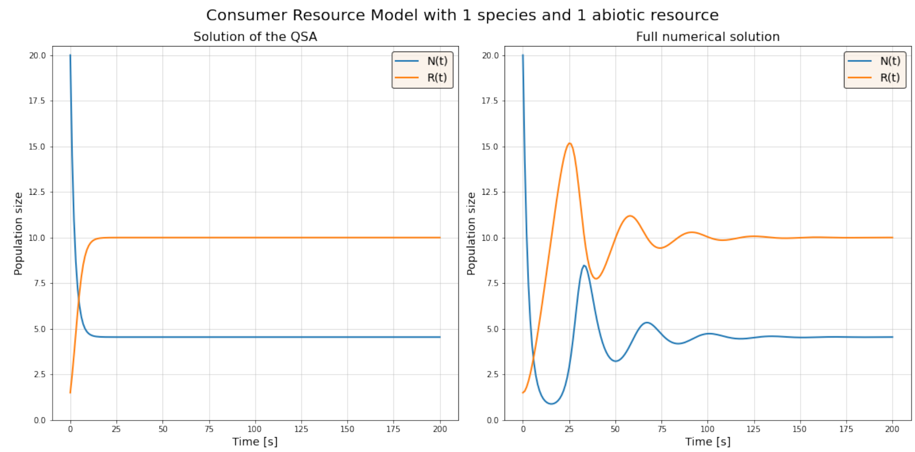
$$k_s = 1, \quad c = 0.02, \quad d = 0.4, \quad \gamma = 2 \tag{10}$$

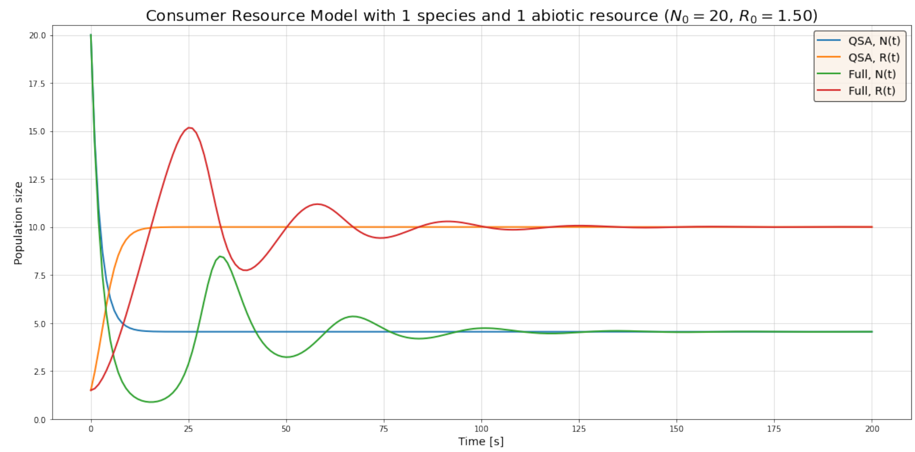
and the initial condition:

$$N(t = 0) = N_0 = 20 \tag{11}$$

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

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:

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

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:

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

In this case, we have that:

$$A(x) = \frac{x}{\tau}\left(1 - \frac{x}{K}\right) \tag{15}$$
$$B(x) = \frac{\sigma}{\tau}x^2 \tag{16}$$

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

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

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

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

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.

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

Integrating on both sides we obtain:

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

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

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

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

$$\int P^*(x)dx = 1 \tag{21}$$

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

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

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[1]. 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:

$$\frac{dx}{dt} = ax - pxy \tag{23}$$
$$\frac{dy}{dt} = -cy + pxy \tag{24}$$

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:

$$\begin{cases} \frac{dx}{dt} \overset{!}{=} 0 \\ \frac{dy}{dt} \overset{!}{=} 0 \end{cases} \implies \begin{cases} 0 = ax - pxy \\ 0 = -cy + pxy \end{cases} \tag{25}$$

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:

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

We obtain:

$$J_0 = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix} \qquad J_1 = \begin{pmatrix} 0 & -c \\ a & 0 \end{pmatrix} \tag{27}$$

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:

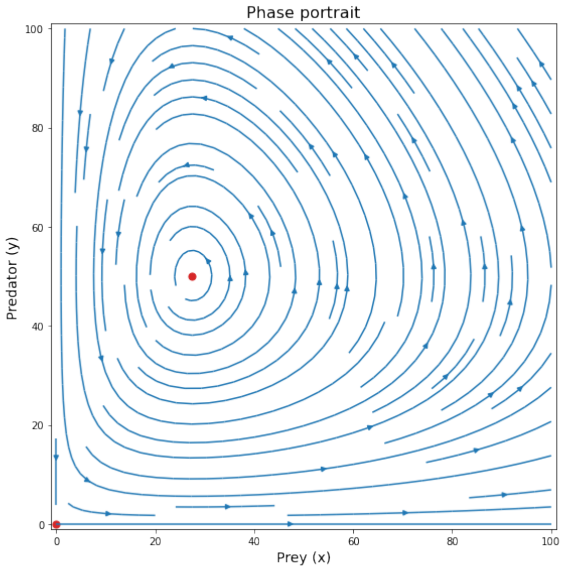
$$\lambda_1^0 = a \qquad \lambda_2^0 = -c \tag{28}$$
$$\lambda_1^1 = -i\sqrt{ac} \qquad \lambda_2^1 = i\sqrt{ac} \tag{29}$$

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.

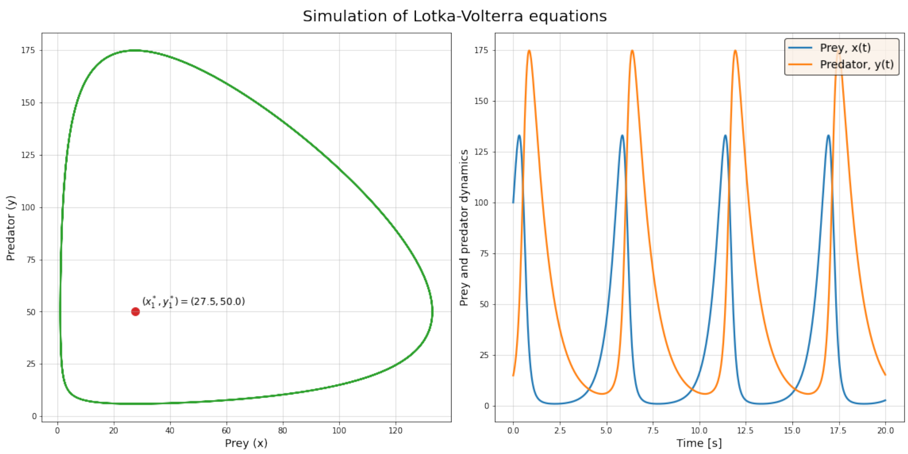
This results can be understood also by looking at the phase portrait corresponding to the Lotka-Volterra equations we are studying:



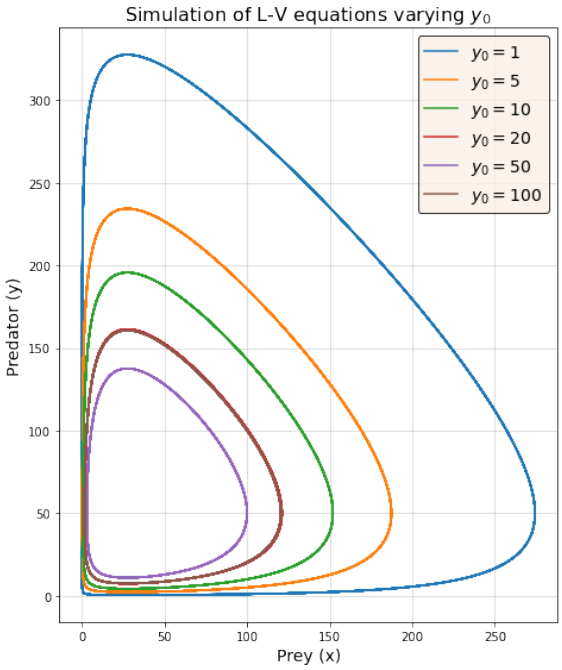
3.3 Simulation results

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:

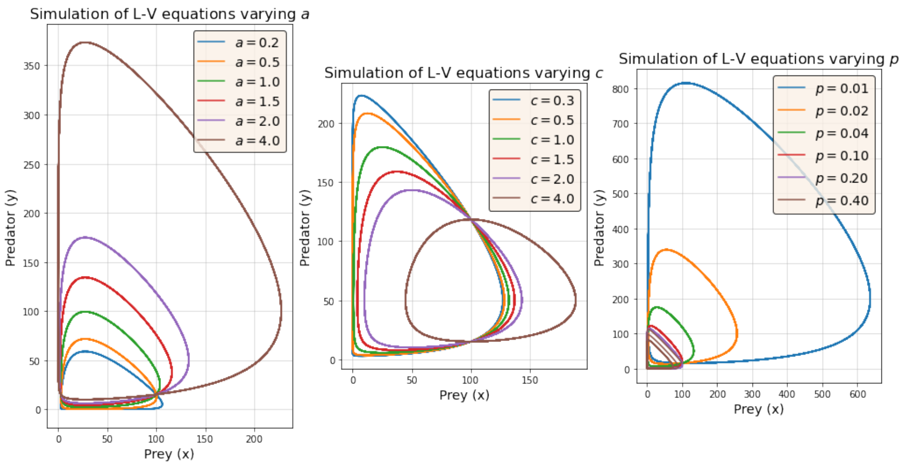
- $a = 2$
- $c = 1.1$
- $p = 0.04$



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 a SxS 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,..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[1]: 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:

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

which can be solved through the saddle point approximation.

Optional. Create a time series $\lambda(t)$, with $t = 1, 2, ..., T$ where at each time t, the value of λ 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

Introduction

A neuronal avalanche is a cascade of synchronized activity in a neuronal network. In practice, it can be defined as a sequence of time bins characterized by the spiking of at least one neuron in each bin. We define the size and the duration of the avalanche as, respectively, the number of neurons firing simultaneously and the time between the first and the last neural activity. Experimentally, both size and duration distributions are approximated by a power law.

We denote with $P_>(t|\lambda_1, \lambda_2, ..., \lambda_n)$ the probability of having an avalanche of duration longer than $t = n \cdot dt$, given the sequence of firing rates λ_i. In this case, we are considering correlated and time-independent firing rates, such that $\lambda_i = \lambda$ for all t and for all neurons.

Moreover, we consider a population of N neurons and we define $dt \equiv \delta/N$, such that in the continuum limit $N \to \infty$ and $dt \to 0$, while δ is fixed. Notice that this implies that the number of time intervals $n \equiv t/dt$ can be written as $n = Nt/\delta$.

The avalanche duration probability

We saw in class that the probability that at least one neuron spikes in $[t_i, t_i + dt]$ is given by:

$$1 - (1 - \lambda_i dt)^N \tag{31}$$

Then, $P_>$ can be computed recursively, assuming as boundary condition $P_>(0|\vec{\lambda}) = 1$:

$$P_>(t|\vec{\lambda}) = \prod_{i=1}^{n} \left[1 - (1 - \lambda_i dt)^N\right] \tag{32}$$

Given the assumption that all $\lambda_i = \lambda$ are the same, we can rewrite this as:

$$P_>(t|\vec{\lambda}) = P_>(t|\lambda) = \left[1 - (1 - \lambda dt)^N\right]^n \tag{33}$$

The value of λ is sampled from a generic distribution $\lambda \sim Q(\lambda)$. Then, we can marginalize over it to obtain the avalanche duration probability $P_>(t)$:

$$\begin{aligned} P_>(t) &= \int_0^\infty d\lambda P(\lambda) P_>(t|\lambda) = \\ &= \int_0^\infty d\lambda Q(\lambda) \left[1 - (1 - \lambda dt)^N\right]^n \end{aligned}$$

In the continuum limit we have that:

$$\lim_{\substack{N\to\infty \\ dt\to 0 \\ \delta \text{ const}}} (1 - \lambda_i dt)^N = \lim_{\substack{N\to\infty \\ dt\to 0 \\ \delta \text{ const}}} \left(1 - \lambda_i \frac{\delta}{N}\right)^N = e^{-\delta\lambda} \tag{34}$$

Finally, putting all together and imposing that the firing rates are exponentially distributed $Q(\lambda) = \gamma e^{-\gamma\lambda}$ we get the integral presented in equation (30), to be solved using the Saddle Point approximation:

$$P_>(t) = \gamma \int_0^\infty d\lambda \cdot \exp(-\gamma\lambda) \cdot [1 - \exp(-\delta\lambda)]^n \tag{35}$$

The Saddle Point approximation

In a general setting, the Saddle Point approximation is a method that can be used to approximate a function near a particular critical point, i.e. a saddle point. A saddle point is characterized by the fact that the derivatives in orthogonal directions are all zero (indeed it is a critical point), but it is not a local extrema of the function.

The idea behind the Saddle Point approximation is that, near a saddle point, a function can be approximated by a quadratic function. This can be used for approximating an integral, as we will do here.

Theorem 6.1 (***Saddle Point approximation***)

Let $f(\mathbf{x})$ be a function with a single minimum at $\mathbf{x_0}$ and such that:

$$I_f = \int_D e^{-Nf(\mathbf{x})}\, \mathrm{d}^d\mathbf{x} \qquad D \subset \mathbb{R}^d \tag{36}$$

Suppose that $\mathbf{x_0}$ is not on the boundary of D, meaning that there exists some $r > 0$ so that the sphere centred on $\mathbf{x_0}$ of radius r is entirely inside D:

$$\exists r > 0 \text{ s.t. } \{\mathbf{x} \in \mathbb{R}^d \colon |\mathbf{x} - \mathbf{x_0}| < r\} \subset D$$

Then, it is possible to prove that:

$$I_f \equiv \int_D e^{-Nf(\mathbf{x})}\, \mathrm{d}^d\mathbf{x} = e^{-Nf(\mathbf{x_0})} \left(\frac{2\pi}{N}\right)^{d/2} [\det(\partial_\alpha \partial_\beta f(\mathbf{x_0}))]^{-1/2} \cdot \left[1 + O\left(\frac{1}{N}\right)\right] \qquad N \gg 1 \tag{37}$$

where $\partial_\alpha \partial_\beta f(\mathbf{x_0})$ is the Hessian of $f(\mathbf{x})$ evaluated at $\mathbf{x} = \mathbf{x_0}$.

In the 1-dimensional case, equation (37) becomes:

$$I_f \equiv \int_{D \subset \mathbb{R}} e^{-Nf(x)} \mathrm{d}x = e^{-Nf(x_0)} \sqrt{\frac{2\pi}{N|f''(x_0)|}} \cdot \left[1 + O\left(\frac{1}{N}\right)\right] \qquad N \gg 1 \tag{38}$$

Essentially, the Saddle Point approximation states that an integral of the form presented in (36) can be approximated, provided that N is large, with the value of the integrand calculated at its maximum (up to a multiplicative Gaussian factor).

Solution of the integral

At this point, we can apply this approximation to solve the integral (30). We define:

$$I_n \equiv \frac{1}{\gamma} P_>(t) = \int_0^\infty d\lambda \cdot \exp(-\gamma\lambda) \cdot (1 - \exp(-\delta\lambda))^n = \int_0^\infty e^{-nf(\lambda)} \tag{39}$$

where

$$f(\lambda) \equiv \frac{\gamma\lambda}{n} - \log[1 - \exp(-\delta\lambda)] \tag{40}$$

In order to use the Saddle Point approximation, first we have to find the critical point of $f(\lambda)$ by setting its first derivative to zero.

$$f'(\lambda) = \frac{\gamma}{n} - \frac{\delta}{e^{\delta\lambda} - 1} \stackrel{!}{=} 0 \quad \Rightarrow \quad \lambda_0 = \frac{1}{\delta} \log\left(1 + \frac{\delta n}{\gamma}\right) \tag{41}$$

Then, we need to evaluate $f''(\lambda)$ in λ_0 to find the curvature of f at the critical point:

$$f''(\lambda) = \frac{\delta^2 e^{\delta\lambda}}{(e^{\delta\lambda}-1)^2} \quad \Rightarrow \quad f''(\lambda_0) = \left(\frac{\gamma}{n}\right)^2 \left(1+\frac{\delta n}{\gamma}\right) > 0 \tag{42}$$

Notice that $f(\lambda)$ has a single minimum at λ_0 and λ_0 is not on the boundary of $D = [0, \infty)$. Indeed, $\delta, n, \gamma > 0$ so also $\lambda_0 > 0$. The conditions of the theorem (6.1) are therefore satisfied.

Next, using the Saddle Point approximation, for large n, we have that:

$$I_n = e^{-nf(\lambda_0)} \sqrt{\frac{2\pi}{n|f''(\lambda_0)|}} = \frac{1}{\gamma}(1+\theta)^{-\frac{n}{\theta}} \left[\frac{\theta}{1+\theta}\right]^n \sqrt{\frac{2\pi n}{1+\theta}} \quad , \quad \theta \equiv \frac{\delta n}{\gamma} \tag{43}$$

Where we used the fact that at the critical point the value of f is:

$$\begin{aligned} f(\lambda_0) &= \left\{\frac{\gamma\lambda}{n} - \log[1-\exp(-\delta\lambda)]\right\}\Bigg|_{\lambda=\lambda_0} = \\ &= \log\left[1+\frac{\delta n}{\gamma}\right]^{\frac{\gamma}{\delta n}} - \log\left[\frac{\frac{\gamma}{\delta n}}{1+\frac{\gamma}{\delta n}}\right] \end{aligned}$$

The avalanche duration probability is simply obtained by multiplying I_n by γ. Finally, we can rewrite $P_>(t)$ in terms of t using the definition θ and the relation between (δ, n, N, t):

$$\left.\begin{aligned} n &= \tfrac{Nt}{\delta} \\ \theta &= \tfrac{\delta n}{\gamma} \end{aligned}\right\} \quad \Rightarrow \quad \theta = \frac{Nt}{\gamma} \tag{44}$$

Notice also that $n/\theta = \gamma/\delta$. We obtain:

$$\boxed{P_>(t) = \sqrt{\frac{2\pi\gamma}{\delta}} \left(1+\frac{Nt}{\gamma}\right)^{-\frac{\gamma}{\delta}} \left[\frac{Nt}{Nt+\gamma}\right]^{\frac{Nt}{\delta}+\frac{1}{2}}} \tag{45}$$

In the limit $t \to \infty \iff n \to \infty$ we have that $\left[\frac{Nt}{Nt+\gamma}\right]^{\frac{Nt}{\delta}+\frac{1}{2}} \to e^{-\frac{\gamma}{\delta}}$ which is constant, so the behaviour of avalanche duration probability $P_>(t)$ is a power law with exponent $-\frac{\gamma}{\delta}$.

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:

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

as a function of the free parameter τ_I. Simulate a trajectory in the stable regime and one in the limit cycle regime (different τ_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.