University of Studies of Padua

Department of mathematics "Tullio Levi-Civita"

Bachelor degree in mathematics

A voter-like model for species coexistence in complex ecosystems

Supervisor:
Prof. Marco Formentin

Graduating student:
Giorgio Ferrero

Serial number: 1236232

Academic year 2021/2022
23rd september 2022

Introduction

Real world ecosystems support a striking amount of species, entwined to one another by a complex web of ecological interactions.
We would expect the presence of a large amount of species to destabilize the system (as seen in Robert May's work), but in real ecosystems we observe the opposite: more complex ecosystems tend to be more stable.
Explaining how this behavior emerges is an open problem in theoretical ecology.
In this thesis, we model an ecosystem as a voter-like model that emphasizes mutualistic interactions, which have historically been given less attention than competitive interactions (such as predation). We then find that cooperative interactions promote stability even as the number of species grows, showing a possible solution to the long standing paradox of species coexistence.
In chapter 1 we introduce the necessary notions: first we briefly describe continuous time Markov chains and how they can be constructed with Poisson point processes, then introduce the mean field limit, an important tool in the analysis of complex systems.
In chapter 2 we introduce our model and study its stability around its equilibrium, finding that in the case of mutualistic interactions and under loose assumptions about the network of interactions, complexity (both in the number of species and in the density of their interactions) encourages stability.

Contents

Chapter 1

Basics of Markov Chains and the Mean Field Limit

In this chapter we introduce the necessary notions for the analysis of the model: continuous time Markov chains, their representation through Poisson point processes, and the mean field limit.

1.1 Continuous time Markov Chains

Definition 1.1.1. Given a probability space $(\Omega, \mathcal{F}, \mathbb{P})$, where Ω is a sample space, $\mathcal{F}$ is a σ- algebra, and $\mathbb{P}$ is a probability measure, a stochastic process is a collection of random variables $\{X(t) : t \in T\}$, $X(t) : \Omega \to S$, where S is the state space of the process.

In our case $X(t)$ is the state of the system at time t. In particular, our model is a markovian and homogeneous process, meaning:

Definition 1.1.2 (Markov Process)**.** $(X(t))_{t\in\mathbb{R}^+}$ with values in S is a Markov process if $\forall\ i, j, i_1, ..., i_k \in E$, $\forall t, s > 0$, and $\forall\ 0 \leq s_1, ..., s_k \leq s$,

$$\mathbb{P}(X_{t+s} = j | X_s = i, X_{s_1} = i_1, ..., X_{s_k} = i_k) = \mathbb{P}(X_{t+s} = j | X_s = i)$$

Definition 1.1.3 (Homogeneous Markov Process)**.** A Markov process $(X_t)_{t\geq 0}$ is homogeneous if the transition probabilities between states at times s and

$t + s$ depend only on t, that is to say:

$$\mathbb{P}(X_{t+s} = j | X_s = i) = \mathbb{P}(X_t = j | X_0 = i)$$

In the case of a homogeneous markov chain, we can study it through its transition semigroup:

Definition 1.1.4. Given $(X_t)_{t \geq 0}$ homogeneous markov process, its transition semigroup is the matrix semigroup $P(t) = (p_{ij}(t))_{i,j \in E}$, where

$$p_{ij}(t) = \mathbb{P}(X_{t+s} = j | X_s = i)$$

Because we assumed the chain to be homogeneous, the transition semigroup is well defined.

We can easily prove that it has a semigroup structure:

$$p_{ij}(t+s) = \sum_{k \in E} p_{ik}(t) \cdot p_{kj}(s) \implies P(t+s) = P(t) \cdot P(s)$$

The best way to describe the chain is its infinitesimal generator:

Definition 1.1.5 (Infinitesimal Generator)**.** The infinitesimal generator of a homogeneous continuous time markov chain with transition semigroup $(P(t))_{t \geq 0}$ is

$$Q = \lim_{h \to 0^+} \frac{P(h) - \mathbb{I}}{h}$$

From the definition the following properties immediately follow:

- $\mathbb{P}(X_{t+h} = j | X_t = i) = p_{ij}(h) = h \cdot q_{ij} + o(h)$
- $\mathbb{P}(X_{t+h} = i | X_t = i) = p_{ii}(h) = 1 - h \cdot q_{ii} + o(h)$

In our particular case of a chain with a finite state space ($|E| < +\infty$), the following properties are true:

- $\inf_i q_{ii} > -\infty$
- $\sum_j q_{ij} = 0$

The infinitesimal generator perfectly describes the chain: this is expressed by the **Kolmogorov equations**:

Theorem 1.1.1 (Kolmogorov Equations). *Let* $(P(t))_{t\in\mathbb{R}^+}$ *be a transition semigroup on* E*, where* $|E| < +\infty$*, and let* Q *be the infinitesimal generator. Then the following equations hold:*

$$\frac{d}{dt}P(t) = P(t) \cdot Q \qquad \text{(Forward Equation)}$$

$$\frac{d}{dt}P(t) = Q \cdot P(t) \qquad \text{(Backward Equation)}$$

Therefore, given the obvious initial constraint $P(0) = \mathbb{I}$*, the transition semigroup can be expressed as*

$$P(t) = e^{Qt}$$

What's more, let $\mu(t) = (\mu_1(t), ..., \mu_{|E|}(t))$ *be the distribution of the chain at time* t*. Then we also have that*

$$\frac{d}{dt}\mu(t) = \mu(t) \cdot Q \qquad \text{(Global Equation)}$$

Therefore we have that the infinitesimal generator Q *determines the transition semigroup* $(P(t))_{t\in\mathbb{R}^+}$ *and thus, the entire chain.*

Now we want to find a clear way to represent a Markov chain with generator Q: to do so, we introduce homogeneous Poisson processes and the Competition Theorem:

1.1.1 Homogeneous Poisson Processes and the Competition Theorem

To define homogeneous poisson processes (from now forward, HPPs), we must first introduce the more general notion of Random Point Process (or RPP):

Definition 1.1.6 (Random Point Process). A Random Point Process is a sequence $(T_i)_{i\in N}$ of non-negative random values such that

- $T_0 = 0$
- $i > j \implies T_i > T_j$
- $\lim_{i\to+\infty} T_i = +\infty$

Given a random point process, we define:

- Its **sequence of interevents** $(S_i)_{i\geq 1}$, where $S_i = T_i - t_{i-1}$
- Its **counting process** $N(a, b] = |T \cap (a, b]|$. The nondecreasing stochastic process $(N(t))_{t\in\mathbb{R}^+}$, $N(t) = N(0, t]$ perfectly describes $(T_i)_{i\in N}$ and will be used as a substitute

As we've said before, we're interested in homogeneous poisson processes:

Definition 1.1.7 (Homogeneous Poisson Process)**.** The point process $(N(t))_{t\in\mathbb{R}^+}$ is a homogeneous poisson process with intensity $\lambda > 0$ if:

- For any sequence of times $0 \leq t_1 \leq ... \leq t_k$, $N(t_i, t_{i+1})$ are independent
- For any interval $(a, b] \subset \mathbb{R}^+$, $N(a, b] \sim Poi(\lambda(b - a))$

There is an equivalent, infinitesimal characterization of HPPs:

The point process $(N(t))_{t\in\mathbb{R}^+}$ is a homogeneous poisson process with intensity $\lambda > 0$ if:

- For any sequence of times $0 \leq t_1 \leq ... \leq t_k$, $N(t_i, t_{i+1})$ are independent
- $\mathbb{P}(N(t, t + dt] = 1) = \lambda \cdot dt + o(dt)$
- $\mathbb{P}(N(t, t + dt] > 1) = o(dt)$

A particularly important property of HPPs is the Competition Theorem:

Theorem 1.1.2 (Competition Theorem)**.** *Let $\hat{N} = (N_i)_{i\geq 1}$ be a family of indipendent HPPs with intensities $(\lambda_i)_{i\geq 1}$. Then:*

- *Two distinct HPPs in $\hat{N}$ have no points in common*

- *if* $\lambda = \sum_{i\geq 1} \lambda_i < +\infty$*,* $N(t) = \sum_{i\geq 1} N_i(t)$ *is a HPP with intensity* λ

This tells us that the superposition of a countable amount of HPPs, under certain conditions, is still an HPP.

We also have that, defining Z *as the first point of* N *and* J *as the index of the HPP that contains* Z*,*

- $\mathbb{P}(J = i, Z \geq a) = \mathbb{P}(J = i) \cdot \mathbb{P}(Z \geq a)$
- $\mathbb{P}(J = i) = \frac{\lambda_i}{\lambda}$
- $\mathbb{P}(Z \geq a) = e^{-\lambda a}$

Homogeneous Poisson Processes give us two ways to represent Markov chains:

1.1.2 Representations of Markov Chains

Assume that we have $\hat{Q} = (\hat{q}_{ij})_{ij\in E}$ matrix, with $|E| < +\infty$ and $0 < \hat{q}_i j < +\infty$, $i, j \in E$. We want to build a markov process with generator $\hat{Q}$.

We do it as follows: let $q^* \geq \sup_i \hat{q}_i = \sup_i \sum_{j\neq i} \hat{q}_{ij}$ and define the matrix $M = (m_{ij})_{i,j\in E}$ as follows:

- $m_{ii} = 1 + \frac{\hat{q}_{ii}}{q^*}$
- $m_{ij} = \frac{\hat{q}_{ij}}{q^*}$ for $i \neq j$

Then we have that M is a stochastic matrix, which means we can define $(\hat{X}_i)_{i\geq 1}$ as the Markov process with transition matrix M. Now let $\lambda = q^*$ and $N(t)$ be a homogeneous Poisson process of parameter λ. We define a homogeneous Markov process $(X_t)_{t\geq 0}$ as

$$X(t) = \hat{X}_{N(t)}$$

Let Q be this process's infinitesimal generator. We now prove that $Q = \hat{Q}$. Let P be the transition semigroup: then, from the last section's computations, we have, for $h << 1$,

$$\begin{aligned} p_{ij}(h) &= \mathbb{P}(N(h) = 1) \cdot \mathbb{P}(\text{The chain moves from i to j}) \\ &= q^* \cdot h \cdot m_{ij} + o(h) \\ &= \hat{q}_{ij} \cdot h + o(h) \end{aligned}$$

Which implies that $\lim_{h \to 0} p_{ij} = \hat{q}_{ij}$.

Another way to construct homogeneous Markov chains is by using the competition theorem: let Q be the generator, and assume that at time 0, the chain is at state I. Then for each state $j \neq I$, we define a Homogeneous poisson process $(N_t^j)_{t \geq 0}$ with rate q_{Ij}, and we put them in competition with each other. As in the competition theorem, let Z be the first point in the superposition, and J the index responsibile for it. Then, at time Z, we move the chain's state to J. By iterating this process, we can easily simulate homogeneous Markov Chains.
In the next section, we will show some examples of a particular type of homogeneous Markov process: interacting particle systems.

1.2 Interacting Particle Systems and examples

Interacting particle systems, intuitively, are homogeneous markov processes that describe how the state of the points of a lattice evolve over time. The points are linked by a graph, and the state of each point is influenced by the states of its neighbous. In our model, points will represent individuals in an ecosystem, and their states will represent their species.

Formally, interacting particle systems are homogeneous markov processes with state spaces of the form S^{Λ}, where S is called the **local state space** and Λ is called the **lattice**.

1.2.1 The Voter Model

The voter model is often used to model the evolution of populations. In its standard form, called the linear voter model, we have $S = \{0, 1, ..., k\}$, $\Lambda = \mathbb{Z}^d$ with a grid-like graph structure, and each site updates its state with rate 1, choosing state σ with probability proportional to the number of its neighbous with state σ.
Formally, we define $N_{x,i}(\sigma)$, where x is the system's state, i is a site, and $\sigma \in S$, as the number of neighbours of i with local state σ. Then we have that site i flips to value σ with rate $r_i^\sigma(x) = \frac{N_{x,i}(\sigma)}{\sum_{\tau \in S} N_{x,i}(\tau)}$.
Our model in Chapter 2 is a modified version of the linear voter model.

1.2.2 Ising-Potts Model

In Ising-Potts models, the sites of the lattice $\mathbb{Z}^d$ represent atoms in a crystal, with local state space $\{-1, 1\}$, which usually represents the direction of the atom's magnetic field. The local state is called the site's spin. Sites like or dislike having the same spin as their neighbours, depending on a parameter β, with each site updating its spin at rate 1.
Defining $N_{x,i}(\sigma)$ as in the voter model, we have that site i flips to value σ with rate $r_i^\sigma(x) = \frac{e^{\beta N_{x,i}(\sigma)}}{\sum_{\tau \in S} e^{\beta N_{x,i}(\tau)}}$.
As we can see, if $\beta > 0$, atoms tend to have the same spin as their neighbours, meaning that the model is ferromagnetic. If $\beta < 0$, the model is antiferromagnetic.
From these simple examples we can already see that in general we cannot solve interacting particle systems analytically , so we are interested in having ways to turn a complex model into a simpler one, while conserving some of the original model's properties. One of these methods is the **mean field limit**, which we will now discuss.

1.3 The Mean Field Limit

Taking the mean field limit of an interacting particle system means replacing Λ with the complete graph with N nodes, and then taking the limit $N \to \infty$.

In this section we'll find conditions under which, if $f(X(t))$ is a real function of interacting particle system X, under the mean field limit $f(t)$ evolves following a differential equation and is therefore deterministic.

We'll then show the mean field limit of the linear voter model and Ising model, and how their limiting differential equations behave.

1.3.1 Limiting differential equation

First we must give conditions under which a function of a Markov process is still a Markov process:

Let $X = (X_t)_{t\geq 0}$ be a Markov process with finite state space S, generator G, semigroup $(P_t)_{t\geq 0}$. Let T be another finite set, and $f : S \to T$ be a function. $\forall x \in S$, $y' \in T | f(x) \neq y'$, define

$$\mathcal{H}(x, y') = \sum_{x' \in S : f(x') = y'} G(x, x')$$

The total rate at which $f(X_t)$ jumps to y', when $X_t = x$.

Then we have that, if $\mathcal{H}(x, y') = H(f(x), y')$ (that is to say, the rate at which $f(X_t)$ jumps to y' depends only on $f(x)$), then $Y_t = f(X_t)$ is a Markov process with generator H.

Now, for each $N \geq 1$,let $X^N = (X_t^N)_{t\geq 0}$ be an interacting particle system with state space S_N, generator G_N and transition semigroup $(P_t^N)_{t\geq 0}$, and let $f_N : S_N \to \mathbb{R}$ be functions (when no confusion arises, we drop the N in the notation. We define the **quadratic variation** and **drift** of the process $f(X_t)$ as, respectively:

$$\alpha_N(x) = \alpha(x) = \sum_{x' \in S} G(x, x')(f(x') - f(x))^2$$

$$\beta_N(x) = \beta(x) = \sum_{x' \in S} G(x, x')(f(x') - f(x))$$

We make the following assumptions:

- That the functions f_N all take values in a closed interval $I \subset \mathbb{R}$, with left and right boundaries $I_- = infI$ and $I_+ = supI$, not necessarily finite;
- That there exists a globally Lipshitz function $b : I \in \mathbb{R}$ such that

$$\lim_{N \to \infty} \sup_{x \in S_N} |\beta_N(x) - b(f_N(x))| = 0$$

- That

$$b(I_-) \geq 0 \text{ if } I_- > -\infty \text{ and } b(I_+) \leq 0 \text{ if } I_+ < +\infty$$

Under these assumptions, the differential equation $\frac{d}{dt} y_t = b(y_t)$ has a single I-valued solution $(y_t)_{t \geq 0}$ for each initial state $y_0 \in I$. Then we haave the following theorem:

Theorem 1.3.1 (Limiting differential equation)**.** *Under the above conditions, with the following additional assumptions:*

1. *That $f_N(X_0)$ converges in probability to y_0;*
2. *That*

$$\lim_{N \to \infty} sup_{x \in S_N} \alpha_N(x) = 0$$

We have that, for each $T < \infty$ and $\epsilon > 0$,

$$\lim_{N \to \infty} \mathbb{P}(|f_N(X_t^N) - y_t)| \leq \epsilon \; \forall t \in [0, T]) = 1$$

Proof: Fix $T < +\infty$, $\epsilon > 0$, $y_0 \in I$. Let L be the Lipschitz constant of b, and set $\delta = \frac{1}{3} \epsilon e^{-LT}$.

Define the following events:

- $\Omega_0 = \{|f(X_0) - y_0| \leq \delta\}$
- $\Omega_1 = \{\int_0^T |\beta(X_t) - b(f(X_t))| dt \leq \delta\}$

- For $K > 0$, $\Omega_{K,2} = \{\int_0^T \alpha(X_t)dt \leq KT\}$

Thm 4.1 from [1] tells us that

$$\mathbb{P}\left(\sup_{t\in[0,T]} |f(X_t) - y_t| > \epsilon\right) \leq KT\delta^{-2} + \mathbb{P}(\Omega_0^c \cup \Omega_1^c \cup \Omega_2^c)$$

From assumption 1, we immediately have that $\lim_{N\to\infty} \mathbb{P}(\Omega_0^c) = 0$.
Let $A_N = \sup_{x\in S_N} \alpha_N(x)$, $B_N = \sup_{x\in S_N} |\beta_N(x) - b(f_N(x))|$. Then by hypothesis we have $A_N \to 0$, $B_N \to 0$ for $N \to \infty$. This implies that, for N sufficiently large,

$$\int_0^T |\beta(X_t) - b(f(X_t))|dt \leq B_N T \leq \delta \implies \mathbb{P}(\Omega_1^c) = 0$$

We also have that, $\forall N$,

$$\int_0^T \alpha(X_t)dt \leq A_N T \implies \mathbb{P}(\Omega_{A_N,2}^c) = 0$$

Thus by setting $K = A_N$, we have

$$KT\delta^{-2} + \mathbb{P}(\Omega_0^c \cup \Omega_1^c \cup \Omega_2^c) \leq \frac{4A_N T}{\delta^2} = 36 A_N \frac{Te^{2LT}}{\epsilon^2}$$

Which goes to 0 as $N \to \infty$ ■
For us, X_t^N will be the interacting particle system with lattice the complete graph with N vertices, and f_N will (usually) be the fraction of vertices with a certain local state.
It is important to note that the theorem is only valid for **fixed time intervals** $[0, T]$. It does not tell us how the mean field limit behaves at infinity. This is due to the fact that 'at infinity' the behaviour isn't deterministic, and the mean field limit can jump between solutions of $\frac{d}{dt}y_t = b(y_t)$.
We now show the mean field limits for the two models introduced in the last section.

1.3.2 Mean Field Limit of the linear voter model

We consider a linear voter model with state space $S = \{0, 1\}$.
Let $(X_t^N)_{t\geq 0}$ be the model with lattice Λ_N the complete graph with N ver-

tices, let G_N be its generator, S_N its state space, and let

$$\hat{X}_t^N = \frac{1}{N} \sum_{i \in \Lambda_N} X_t^N(i)$$

be the fraction of vertices with local state 1. Because of what was said on functions of Markov processes, we know that $\hat{X}_t$ is a Markov process. We want to study its behavior for $N \to \infty$.

We take f_N to be the identity function $\forall N \in \mathbb{N}$. We need the generator of $\hat{X}_t^N$:

$\hat{X}_t^N$ has state space $\hat{S}_N = \{0, 1/N, 2/N, ..., 1\}$, and can only jump from x to $x + 1/N$ or $x - 1/N$.

Let $r_+(x)$ be the rate at which it jumps from x to $x + 1/N$, and $r_-(x)$ the rate from x to $x - 1/N$. Then we have

$$r_+(x) = \sum_{x' \in S_N : \hat{X}^N = x + 1/N} G_N(x, x')$$

There are $N \cdot (1 - x)$ such states (1 for each possible vertex with local state 0), and each one of those vertices flips with rate x, which means that we have

$$r_+(x) = Nx(1 - x)$$

And with a similar reasoning we have

$$r_-(x) = Nx(1 - x)$$

We can now compute the drift and quadratic variation of $\hat{X}_t^N$:

$$\begin{aligned} \alpha_N(x) &= \sum_{x' \in \hat{S}_N} H(x, x')(x' - x)^2 \\ &= r_+(x)\frac{1}{N^2} + r_-(x)\frac{1}{N^2} \\ &= \frac{x(1 - x)}{2N} \\ \beta_N(x) &= \sum_{x' \in \hat{S}_N} H(x, x')(x' - x) \\ &= r_+(x)\frac{1}{N} - r_-(x)\frac{1}{N} \\ &= 0 \end{aligned}$$

All the conditions of the theorem are satisfied:

- The drift is uniformly approximated by $b = 0$
- The differential equation $\frac{d}{dt}y_t = 0$ admits a unique solution for all y_0
- $\lim_{N\to\infty} \sup_{x\in\hat{S}_N} \alpha_N(x) = 0$

So we have that the limit of $\hat{X}_t^N$ for $N \to \infty$ is a constant function, meaning that, in the mean field limit of the linear voter model, the fractions of sites with local states 1 or 0 remain constant.

1.3.3 Mean Field limit of the Ising Model

We consider an Ising model with local state space $S = \{-1, 1\}$. We substitute the lattice with the complete graph Λ_N, and define

$$N_{x,i}(\sigma) = \frac{1}{|\mathcal{N}_i|} \sum_{j\in\mathcal{N}_i} 1_{x(j)=\sigma}$$

The fraction of neighbours of i with local state σ, and fix the rate at which i flips to σ as

$$\frac{e^{\beta N_{x,i}(\sigma)}}{\sum_{\tau\in S} e^{\beta N_{x,i}(\tau)}}$$

We call X_t^N the markov process with these characteristics, with state space S_N, generator G_N, lattice Λ_N. For simplicity's sake, we count each node among its neighbours. By doing so, we have that $N_{x,i}(\sigma)$ does not depend on i and is the fraction of vertices with local state σ. We denote it with $N_x(\sigma)$. We now proceed in a similar way to the voter model: we have that the **average magnetization**

$$\hat{X}_t^N = \frac{1}{N} \sum_{i\in\Lambda_N} X_t^N(i)$$

Is a Markov process, with state space $\hat{S}_N = \{-1, -1 + 2/N, ..., 1 - 2/N, 1\}$. Let $r_+(x)$ be the rate at which it jumps from x to $x + 2/N$, and $r_-(x)$ the rate from x to $x - 2/N$. With the same reasoning we followed for the voter model, there are $NN_x(-1)$ sites that can flip to 1, and each one does so with rate $\frac{e^{\beta N_x(1)}}{e^{\beta N_x(-1)}+e^{\beta N_x(1)}}$. So we have

$$r_+(x) = N \cdot N_x(-1)\frac{e^{\beta N_x(+1)}}{e^{\beta N_x(-1)} + e^{\beta N_x(1)}}$$

And

$$r_-(x) = N \cdot N_x(+1)\frac{e^{\beta N_x(-1)}}{e^{\beta N_x(-1)} + e^{\beta N_x(1)}}$$

Obviously $x = N_x(+1) - N_x(-1)$ and $1 = N_x(+1) + N_x(-1)$, which gives us $N_x(+1) = (1+x)/2$ and $N_x(-1) = (1-x)/2$. We can then rewrite the rates as

$$\begin{aligned} r_+(x) &= N\frac{1-x}{2}\frac{e^{\beta\frac{x+1}{2}}}{e^{\beta\frac{x+1}{2}} + e^{\beta\frac{1-x}{2}}} \\ &= N\frac{1-x}{2}\frac{e^{\beta x/2}}{e^{\beta x/2} + e^{-\beta x/2}} \end{aligned}$$

And

$$r_-(x) = N\frac{1+x}{2}\frac{e^{-\beta x/2}}{e^{\beta x/2} + e^{-\beta x/2}}$$

Taking f_N the identity function again, we calculate the drift and quadratic variation of $\hat{X}_t^N$:

$$\begin{aligned} \alpha_N(x) &= (r_+(x) + r_-(x))\left(\frac{2}{N}\right)^2 \\ &= \frac{4}{N}\left(\frac{1-x}{2}\frac{e^{\beta x/2}}{e^{\beta x/2} + e^{-\beta x/2}} + \frac{1+x}{2}\frac{e^{-\beta x/2}}{e^{\beta x/2} + e^{-\beta x/2}}\right) \end{aligned}$$

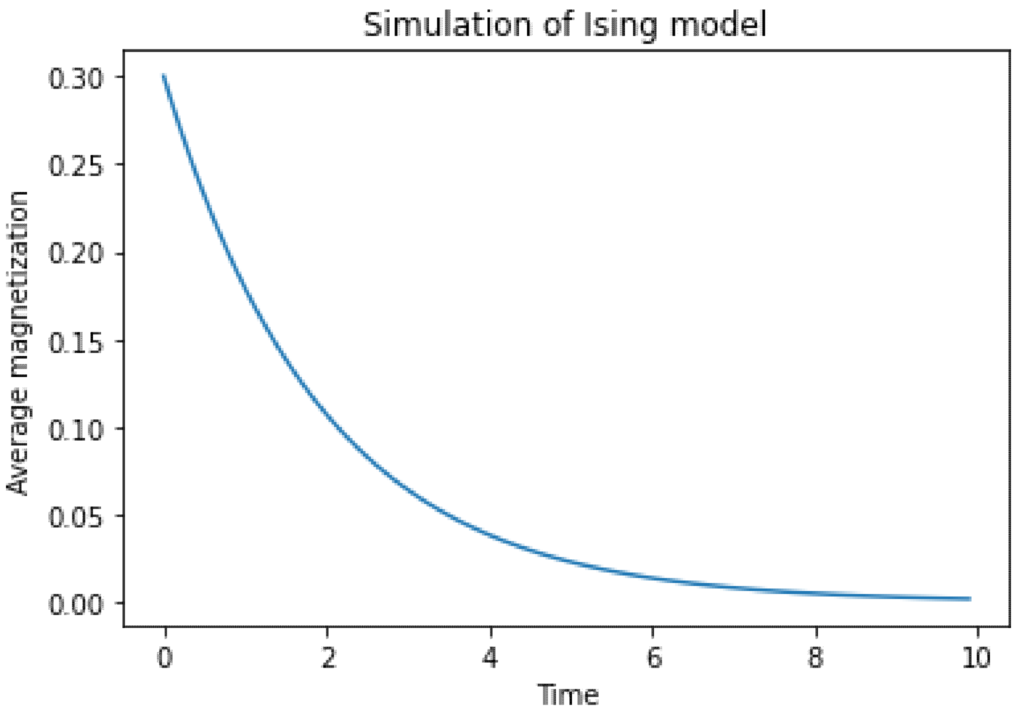
$$\begin{aligned} \beta_N(x) &= \frac{2}{N}\left(r_+(x) - r_-(x)\right) \\ &= (1-x)\frac{e^{\beta x/2}}{e^{\beta x/2} + e^{-\beta x/2}} + (1+x)\frac{e^{-\beta x/2}}{e^{\beta x/2} + e^{-\beta x/2}} \\ &= \frac{e^{\beta x/2} + e^{-\beta x/2}}{e^{\beta x/2} + e^{-\beta x/2}} - x \\ &= \tanh\left(\frac{1}{2}\beta x\right) - x \end{aligned}$$

The theorem's hypothesis are again all verified. We then have that, under the mean field limit, for any fixed time interval $[0, T]$, the average magnetization of the Ising model evolves following the differential equation

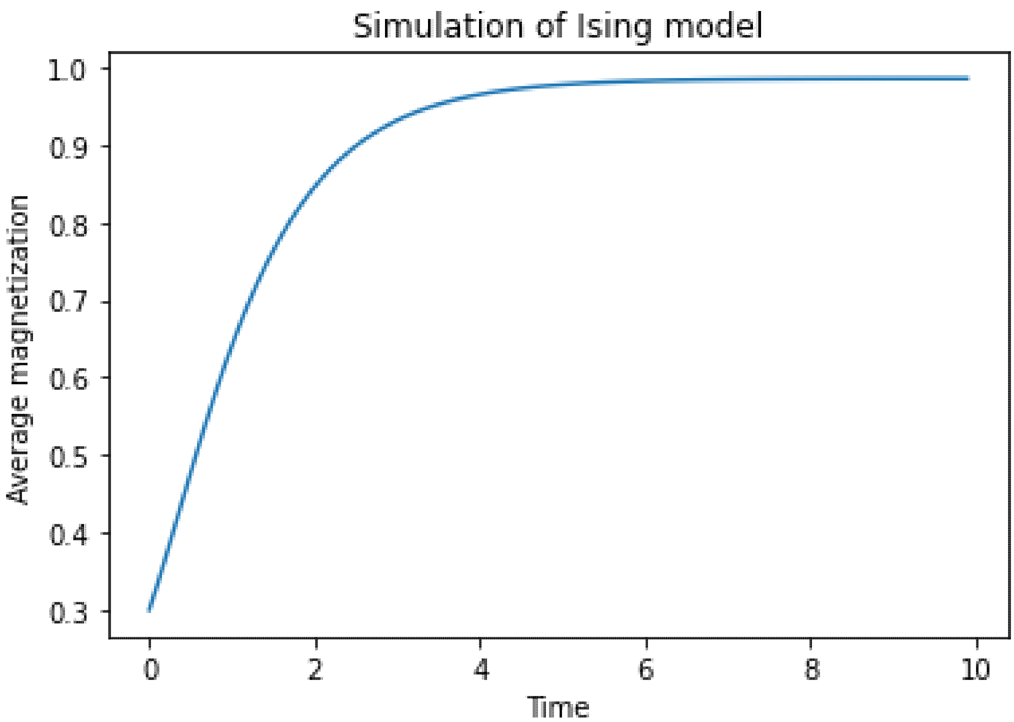
$$\frac{d}{dt}y_t = \tanh\left(\frac{1}{2}\beta y_t\right) - y_t$$

.

We study this equation's behavior: consider the function $f(x) = tanh(\frac{1}{2}\beta x) - x$, with domain $[-1, 1]$. We have $f(-1) > 0$, $f(1) < 0$, which implies that the function has at least one zero in its domain.
We have $f'(x) = \frac{1}{2}\beta(1 - tanh^2(\frac{1}{2}\beta x)) - 1 < \frac{1}{2}\beta - 1$. For $\beta < 2$, the function is strictly decreasing and has one and only zero in 0, which implies that the differential equation $\frac{d}{dt}y_t = tanh(\frac{1}{2}\beta y_t) - y_t$ has a single, stable, equilibrium point in 0, to which all solutions of the equation with $-1 \leq y_0 \leq 1$ converge.
For $\beta > 2$, the function has 3 zeros, $\{0, b, -b\}$ with $b > 0$ (the function is odd), with 0 being unstable and the other 2 stable.This means that the differential equation has 3 equilibria, 0 which is unstable, b to which all solutions with $y_0 > 0$ converge and $-b$ to which all solutions with $y_0 < 0$ converge.



(a) $\beta = 1$



(b) $\beta = 5$

Figure 1.1: Simulations of the behavior of the mean field limit of the Ising model, using the explicit Euler method, with $y_0 = 0.3$, $dt = 0.1$

Chapter 2

A voter-like model for species coexistence

2.1 Our approach to the problem

The first to analyze ecosystem stability from a theoretical standpoint was Robert May, who modeled ecosystems as a system of nonlinear differential equations, oscillating around an equilibrium point. May then modeled the matrix A that describes the system's dynamic around its equilibrium as a random matrix, and found that in the large S limit, stability becomes less and less likely as S increases. This theoretical result, that clashes with empirical observation, is known as May's paradox.
We now introduce a voter-like model, through which we intend to prove the importance of mutualistic interactions in ecosystems' stability, and highlight a possible path to reconciling biodiversity and stability.
Our approach differs from May's in that we first model the ecosystem's dynamic for each of its individuals as a stochastic process. We then take the mean field limit and find a deterministic model described by a series of differential equations, and study its stability around its equilibrium points. In this way A is determined by the ecosystem's dynamic, instead of being directly modeled as a random matrix.

2.2 Description of the model

We model an ecosystem as an interacting particle system, with lattice $\Lambda = \{1, ..., N\}$ the complete graph with N vertices, and local state space $\{1, ..., S\}$. Points of the graph represent individuals, and the local state represents that individual's species. We call η_z the species label at site z, with the system's state being given by $\eta(t) = (\eta_1(t), ..., \eta_N(t))$.
We model species interaction by introducing a directed graph on $\{1, ..., S\}$, where directed links represent ecological interactions.
The strength of these interactions is modeled by two matrices M and L, which describe cooperative and exploitative interactions respectively.
We require that M and L satisfy the following conditions:

- $\forall i, j = 1, ..., S$, $M_{ij} \geq 0$ (M models mutualistic interactions)
- $\forall i, j = 1, ..., S$, $L_{ij}L_{ji} < 0$ or $L_{ij} = L_{ji} = 0$ (L models competitive interactions)
- $\forall i, j = 1, ..., S$ $L_{ij}M_{ij} = 0$ (two species can interact either competitively or cooperatively, but not both)

$M_{ij} > 0$ means that the j-th species benefits from the presence of the i-th species, while $L_{kl} > 0 (< 0)$ and $L_{lk} < 0 (> 0)$ means that the l-th species exploits (is exploited by) the k-th species.
We ignore spacial effects for simplicity, as denoted by choosing the complete graph as lattice.
We describe the system's dynamics as a voter-like model, in which, for each site i, the individual is removed and replaced with one of species j at rate

$$\omega(j, \eta, M, L) = \hat{\eta}_j + \epsilon_1 \sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_j) + \epsilon_2 \sum_{k=1}^{S} \hat{\eta}_k L_{kj} \hat{\eta}_j \tag{2.1}$$

where θ is the Heaviside step function and $\hat{\eta}_j = \frac{\eta_j}{N}$.
For $\epsilon_1 = \epsilon_2 = 0$ we have the standard linear voter model, which we have already analyzed.

We fix the total number of individuals to account for the ecosystem's carrying capacity: a new individual comes into the ecosystem always at the expense of another (our model has no empty sites, and sites do not empty, only change labels).
Mutualistic and competitive interactions are modeled differently:

- Competitive interactions are **quadratic**, as they are modeled under the classic law of mass-action in chemical reactions, where the probability of interactions occurring is proportional to the number of individuals of both the involved species;

- Cooperative interactions are **linear**, as we make the assumption that they are mediated by some resource, which one species produces and the other benefits from.

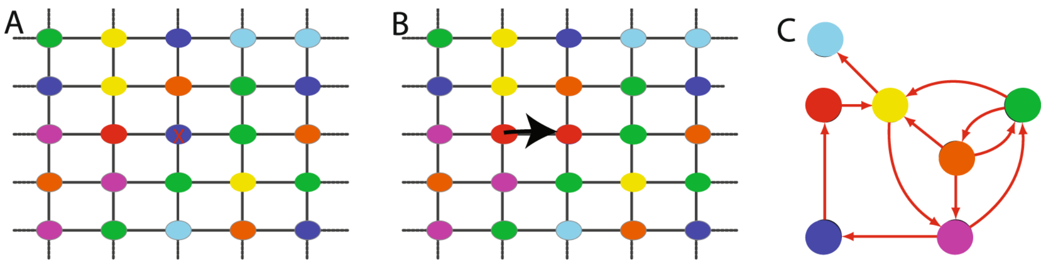


Figure 2.1: Visualization of the model's dynamic:
In figure A we see the lattice, with linked nodes representing neighbors;
in figure B we see how the system evolves: each node can flip its neighbors' states to its own with the rates described above;
in figure C we see a representation of the network of interactions between species: in the case of mutualistic interactions, a direct link between i and j means that the species j is aided by the presence of species i .
Image taken from [5]

We are unable to describe the behavior of the model as it is: to simplify it, we take the mean field limit, by sending $N \to \infty$, and study the behavior of the resulting deterministic model:

For each $\hat{\eta}_j$ we have $\hat{S} = \{1/N, 2/N, ..., N\}$.
$\hat{\eta}_j$ increases at rate $N \cdot \omega(j, \eta, M, L)$ (the total rate at which individuals flip to species j) and decreases at rate $N(\hat{\eta}_j) \sum_{k=1}^{S} \omega(k, \eta, M, L)$ (total rate at which individuals of species j flip to another species). We compute the drift and quadratic variation:

$$
\begin{aligned}
\beta_N(\hat{\eta}_j) &= \frac{1}{N} N \cdot \left(\omega(j, \eta, M, L) - \hat{\eta}_j \sum_{k=1}^{S} \omega(k, \eta, M, L) \right) \\
&= \hat{\eta}_j + \epsilon_1 \sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_j) + \epsilon_2 \sum_{k=1}^{S} \hat{\eta}_k L_{kj} \hat{\eta}_j \\
&- \hat{\eta}_j \left(\sum_{i=1}^{S} (\hat{\eta}_i + \epsilon_1 \sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_i) + \epsilon_2 \sum_{k=1}^{S} \hat{\eta}_k L_{kj} \hat{\eta}_i \right) \\
&= \epsilon_1 \sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_j) + \epsilon_2 \sum_{k=1}^{S} \hat{\eta}_k L_{kj} \hat{\eta}_j \\
&- \hat{\eta}_j \sum_{i,k=1}^{S} (\epsilon_1 \ \hat{\eta}_k M_{kj} \theta(\hat{\eta}_i) + \epsilon_2 \hat{\eta}_k L_{kj} \hat{\eta}_i)
\end{aligned}
$$

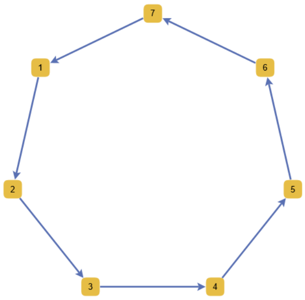
$$
\begin{aligned}
\alpha_N(\hat{\eta}_j) &= \frac{1}{N^2} N \left(\omega(j, \eta, M, L) + \hat{\eta}_j \sum_{k=1}^{S} \omega(k, \eta, M, L) \right) \\
&\to 0 \text{ as } N \to \infty
\end{aligned}
$$

We can then write the limiting differential equation:

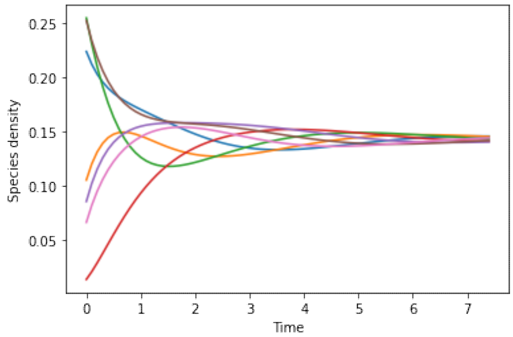
$$
\frac{d}{dt} \hat{\eta}_j = \epsilon_1 \sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_j) + \epsilon_2 \sum_{k=1}^{S} \hat{\eta}_k L_{kj} \hat{\eta}_j - \hat{\eta}_j \sum_{i,k=1}^{S} (\epsilon_1 \ \hat{\eta}_k M_{kj} \theta(\hat{\eta}_i) + \epsilon_2 \hat{\eta}_k L_{kj} \hat{\eta}_i) \tag{2.2}
$$

From now on, we assume the only interactions between species are mutualistic:$\epsilon_2 = 0$. This gives us

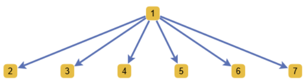
$$
\frac{d}{dt} \hat{\eta}_j = \epsilon_1 \left(\sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_j) - \hat{\eta}_j \sum_{i,k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_i) \right) \tag{2.3}
$$



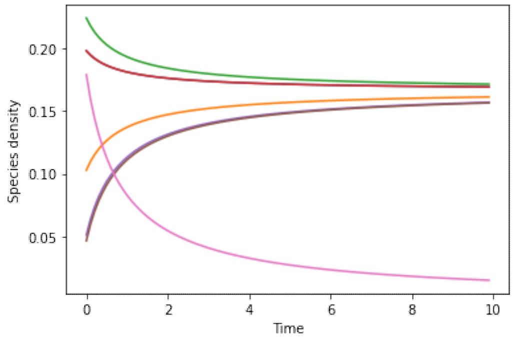
(a) Cyclic network



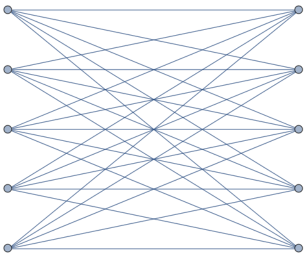
(b) System evolution for cyclic network



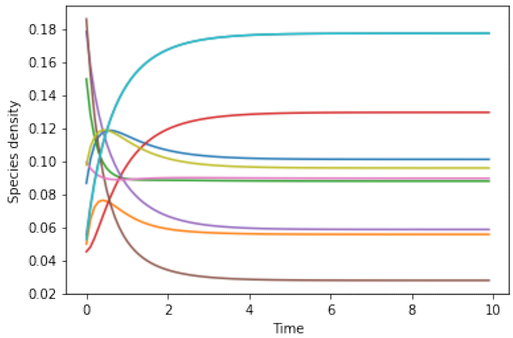
(c) Supporting species



(d) System evolution with supporting species



(e) $K_{5,5}$



(f) System evolution for bipartite graph

Figure 2.2: Figures(a) and (b): interaction network and system evolution for a cyclic network

Figures(c) and (d): a single species supports all others. Observe how the supporting species goes extinct for $t \to \infty$

Figures (e) and (f): dynamic of a random bipartite graph, obtained from $K_{5,5}$ by keeping each directed link with probability $1/2$

2.3 Unsupported species and equilibrium points

As shown in Figure 2.2b, unsupported species (that is to say, species that have an indegree of 0 in the interaction network) are extinct at equilibrium: we can easily prove this by looking at equation (2.3): by setting $\frac{d}{dt}\hat{\eta}_j = 0\ \forall j$, we get

$$\hat{\eta}_j = \frac{\sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_j)}{\sum_{i,k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_i)} \tag{2.4}$$

Let $m = (m_i)$ be an equilibrium point: if species j is unsupported, we have $M_{ij} = 0\ \forall i$, which implies $\sum_{k=1}^{S} \hat{\eta}_k M_{kj} \theta(\hat{\eta}_j) = 0$, therefore $m_j = 0$, meaning that species j is extinct at all equilibrium points of the system.
The presence of unsupported species can cause a chain of extinctions: the extinction of an unsupported species may cause other species to become unsupported, and then extinct. To solve this issue, we **prune** the network of interactions $\hat{S}$:

1. If there are any nodes in $\hat{S}$ with an indegree of 0, we remove those nodes and any links from and to those nodes (in matrix terms, if node k has an indegree of 0, we remove the $k-th$ row and column of M)

2. We repeat step 1, until all nodes have an indegree of at least 1. The resulting network is called a **pruned** network

From now on,we assume that any network we analyze is pruned.
In a pruned network, at equilibrium, $\hat{\eta}_j \neq 0\ \forall j$. We observe that such equilibrium points are the positive left eigenvectors of M such that the sum of their components is 1: from equation (2.4), let m be the equilibrium point, and assume $m_i > 0\ \forall i$: then we have

$$m_i = \frac{(m^T M)_i}{\sum_{k=1}^{S} (m^T M)_k} \tag{2.5}$$

Which is exactly what we wanted to prove.

An important category of pruned networks are **strongly connected** networks, which we know to be equivalent to asking that M is irreducible. In this case, we can apply the Perron-Frobenius theorem, which tells us that:

- The spectral radius r of M is an eigenvalue, and the only positive one;
- M has only two eigenvectors with positive entries:the right and left r-eigenvectors.

Because of what said above, this implies that we have a single (feasible) equilibrium point, in which all entries are positive.
When we will choose how to model the matrix M, we will do so in a way such that $M_{ij} > 0 \implies M_{ji} > 0$, which lets us separate the network into strongly connected clusters, which can be studied separately.

2.4 Linearization and Stability

We want to study the system's stability: this means studying its behavior around its equilibrium points, which is determined by the sign of $Re(z)$, for z eigenvalue of the matrix that describes the behavior of the system around its equilibrium.
In particular, for the system to be stable, we want $Re(z) < 0\ \forall z$ eigenvalue. Let $m = (m_i)$ be an equilibrium point, that we assume to have all positive entries. Let $A = (A_{ij})$ be the linearized matrix: then we have

$$A_{ij} = \frac{d}{d\hat{\eta}_j} \frac{d}{dt} \hat{\eta}_i \bigg|_{\hat{\eta}=m}$$

Substituting equation (2.3), we get

$$\begin{aligned}
A_{ij} &= \frac{d}{d\hat{\eta}_j}\epsilon_1\left(\sum_{k=1}^{S}\hat{\eta}_k M_{ki}\theta(\hat{\eta}_i) - \hat{\eta}_i\sum_{l,k=1}^{S}\hat{\eta}_k M_{kl}\theta(\hat{\eta}_l)\right)\Bigg|_{\hat{\eta}=m} \\
&= \epsilon_1\left(M_{ij}^T - \delta_{ij}\sum_{l,k=1}^{S}\hat{\eta}_k M_{kl}\theta(\hat{\eta}_l) - \hat{\eta}_i\sum_{k=1}^{S}M_{jk}\right)\Bigg|_{\hat{\eta}=m} \qquad (2.6)\\
&= \epsilon_1\left(M_{ij}^T - \delta_{ij}\sum_{l,k=1}^{S}m_k M_{kl} - m_i\sum_{k=1}^{S}M_{jk}\right)
\end{aligned}$$

To study A's eigenvalues, we first have to choose how to model the matrix M as a random matrix:

- We set the diagonal to 0: $M_{ii} = 0\ \forall i \in \{1, ..., S\}$
- Each off-diagonal pair (M_{ij}, M_{ji}) is set to (0,0) with probability $1 - C$ and is drawn from a bivariate Gaussian distribution of means (μ, μ) with $\mu > 0$ and covariance matrix $(\sigma^2, \rho\sigma^2, \rho\sigma^2, \sigma^2)$ with probability C. C represents the probability that two species interact and is called **connectance**.

By modeling M this way, we've chosen to loosen our hypothesis on the sign of m_{ij}: instead of assuming $m_{ij} > 0\ \forall i, j$, we model m_{ij} as a random variable with **mean** $\mu > 0$.

As we've said before, we have $M_{ij} > 0 \implies M_{ji} > 0$, which means that the interaction graph $\hat{S}$ can be divided into strongly connected components, where each component can be considered a distinct ecosystem, independent from the others.

We define:

- The mean of M's off-diagonal elements $\mu_M = C\mu$
- The variance $\sigma_M^2 = \mathbb{E}[(m_{ij} - \mu_M)^2] = C(1 - C)\mu^2 + C\sigma^2$
- The correlation $\rho_M = cov(m_{ij}, mji)/\sigma_M^2 = \frac{\rho\sigma^2 + (1-C)\mu^2}{\sigma^2 + (1-C)\mu^2}$

We study the system's behavior in the large S limit: we assume that the interaction network is strongly connected, which implies
$\sum_{i=1}^{S} M_{ij} \sim (S-1)\mu_M \; \forall j \in \{1, ..., S\}$ (by the law of large numbers), which means M has leading eigenvalue $\lambda_M = (S-1)\mu_M$, with left eigenvector $m = (m_i)_{1\leq i\leq S}$, with $m_i \sim 1/S$. We then have

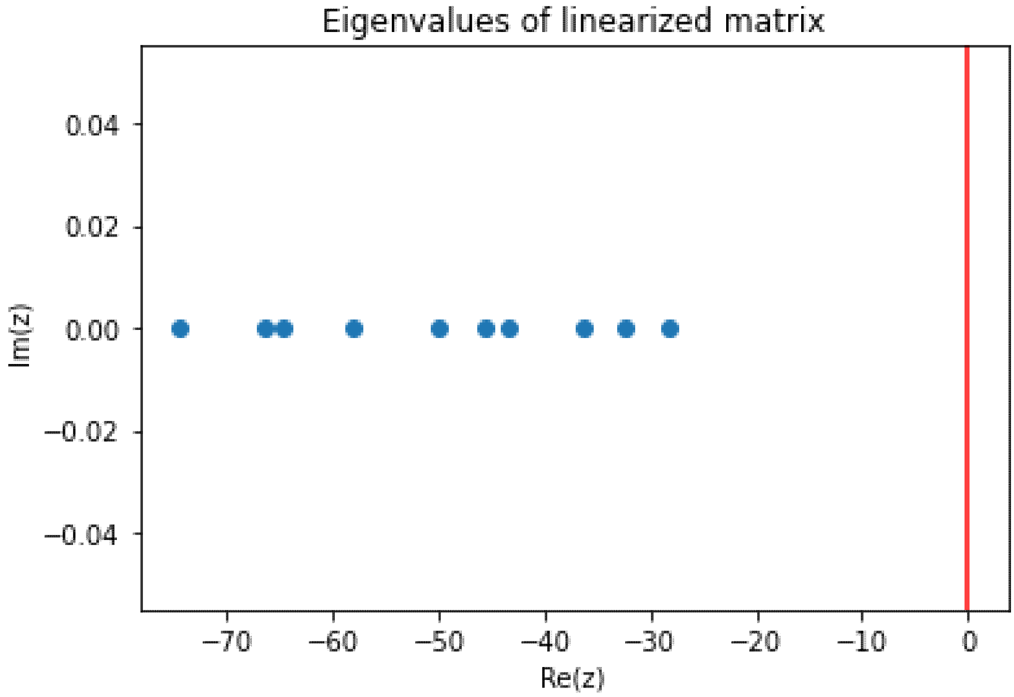
$$\begin{aligned} A'_{ij} = \frac{A_{ij}}{\epsilon_1} &= M^T_{ij} - \delta_{ij} \sum_{l,k=1}^{S} m_k M_{kl} - m_i \sum_{k=1}^{S} M_{jk} \\ &\sim M^T_{ij} - \delta_{ij}(S-1)\mu_M - \mu_M \\ &= (M^T_{ij} - \mu_M) - \delta_{ij}(S-1)\mu_M \end{aligned}$$

Let $M' = (m'_{ij})_{1\leq i,j\leq S}$, with $m'_{ij} = M^T_{ij} - \mu_M + \delta_{ij}\mu_M$. We have $A' = M' - S\mu_M \mathbb{I}$, which implies that A''s eigenvalues are M''s eigenvalues, shifted by $-S\mu_M$.
M' is a random matrix, with diagonal elements set to 0 and off-diagonal pairs set to $(-\mu_M, -\mu_M)$ with probability $(1-C)$ and drawn from a bivariate Gaussian distribution of mean $((1-C)\mu, (1-C)\mu)$ and covariance matrix $(\sigma^2 . \rho\sigma^2, \rho\sigma^2, \sigma^2)$ with probability C. M' has mean 0, variance σ_M^2 and covariance ρ_M (variance and convariance are invariants by translation).
This implies that M''s eigenvalues in the large S limit are uniformly distributed on an ellipse with center in 0 and semi-axis $\sqrt{S}\sigma_M(1+\rho_M)$ (real) and $\sqrt{S}\sigma_M(1-\rho_M)$ (imaginary) [2]. We then have, for each eigenvalue z of A',

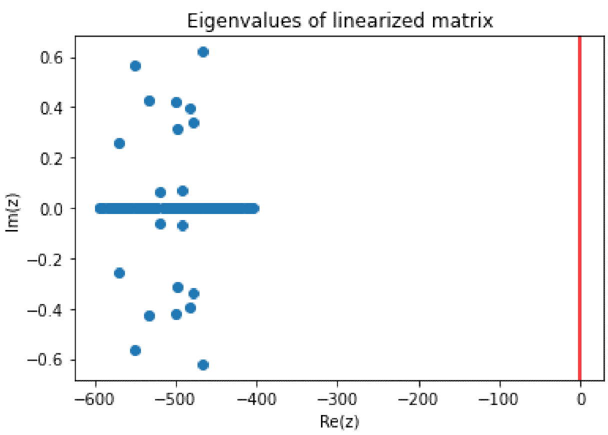
$$Re(z) \leq \sqrt{S}\sigma_M(1+\rho_M) - S\mu_M$$

Which implies that if $\mu_M \geq \sigma_M(1+\rho_M)/\sqrt{S}$, the equilibrium is stable with probability 1 (A has the same eigenvalues as A', multiplied by ϵ_1: it's equivalent to analyze A' or A for stability).
The condition also tells us that:

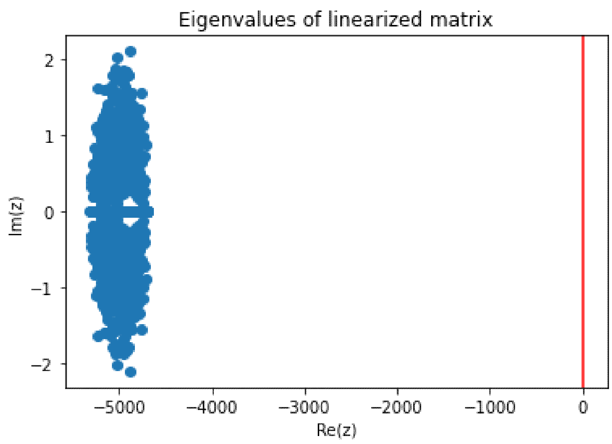
- As S increases, so does the system's stability: more complex ecosystems are more stable in this model;
- The stability also increases with μ_M: the system grows more stable as the strength of its interactions increases.



(a) S=10



(b) S=100



(c) S=1000

Figure 2.3: Eigenvalues of A, with μ=10,σ=1,ρ=0.5,C=0.5. Observe how the ellix shape becomes more and more visible as S increases

Conclusions

Ecosystems are inherently complex, as they are composed of large amounts of individuals, interacting with one another via a dense network of interactions.

Due to this, they display emergent non trivial behavior, such as the apparent link between complexity and stability.

Our goal was to show the importance of mutualistic interactions and the impact that the topology of the interaction network has on the system's behavior.

By modeling ecosystems as interacting particle systems driven by a voter-like dynamic, we have analyzed the negative impact that unsupported species have on biodiversity at equilibrium and found a sufficient condition for all species to coexist. We then studied its stability, finding a positive link between it and complexity, showing that mutualistic interactions are an important piece of the puzzle of ecosystem stability.

In this thesis we have focused on showing the link between cooperative interactions and stability: further analysis of the model could focus on its behavior when competitive interactions are also accounted for, and how the system oscillates around its equilibrium points.

Appendix A

Python Codes

A.1 Ising simulation

```
def Ising_simulation(y0,step,iter,beta):
  y=[]
  t=[step*i for i in range(iter)]
  drift=numpy.tanh(0.5*beta*y0)-y0
  y.append(y0)
  for i in range(iter-1):     #Simulation with explicit Euler method
    y0=y0+drift*step
    y.append(y0)
    drift=numpy.tanh(0.5*beta*y0)-y0
  plt.plot(t,y)
  plt.ylabel('Average magnetization')
  plt.xlabel('Time')
  plt.title('Simulation of Ising model')
```

A.2 Simulation of voter-like model

```
def simulate(M,dt,iter,nu,S):
  A=[[] for i in range(S)]   #Stores hystory of simulation
  M.transpose()
  for i in range(S):
    A[i].append(nu[i])
  for i in range(iter-1):   #Iteration with explicit Euler
    for j in range(S):
      nu[j]=max(nu[j],0)
    v=np.matmul(M,nu)
    v.transpose()
    v1=sum(v)
    nu_delta=v-v1*nu    #Drift of the system
    nu=nu+dt*nu_delta
    for j in range(S):
      A[j].append(nu[j])

  times=[i*dt for i in range(iter)]   #Create plot
  for i in range(S):
    plt.plot(times,A[i])
  plt.xlabel('Time')
  plt.ylabel('Species density')
```

A.3 Eigenvalues of A

```
def generate_matrix(S,mu,sigma,rho,C):
  M=np.zeros((S,S))            #Build matrix M
  for i in range(1,S):
    for j in range(i):
      if random.random()< C:
        [M[i][j],M[j][i]]=np.random.multivariate_normal([mu,mu],
        [[sigma**2,rho*(sigma**2)],[rho*(sigma**2),sigma**2]])
  A=np.zeros((S,S))   #Build linearized matrix A
  for i in range(0,S):
    for j in range(0,S):
      A[i][j]=M[j][i]-C*mu
      if i==j:
        A[i][j]=A[i][j]-(S-1)*C*mu
  return A

def plot_eigenvalues(A):      #Plot eigenvalues of matrix A
  eigenvalues=np.linalg.eig(A)[0]
  Re=[z.real for z in eigenvalues]
  Im=[z.imag for z in eigenvalues]
  plt.scatter(Re,Im)
  plt.axvline(x=0,color='r',label='Stability Barrier')
  plt.title('Eigenvalues of linearized matrix')
  plt.xlabel('Re(z)')
  plt.ylabel('Im(z)')
  plt.show()
```

Bibliography

[1] R.W.R. Darling and J.R. Norris. Differential equation approximations for Markov chains.*Probab. Surveys 5* (2008), 37-79.

[2] Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* 483, 205 (2012).

[3] Garlaschi Stefano, Statistical Physics approach to ecological and biological topics. Ph.D in Physics thesis. Universitá degli studi di Padova, 2021

[4] Swart, Jan M. A course in interacting particle systems. *arXiv preprint* arXiv:1703.10007 (2017).

[5] Tu, C. & Suweis, S. & Grilli, J. *et al.* Reconciling cooperation, biodiversity and stability in complex ecological communities. *Sci Rep* 9, 5580 (2019). https://doi.org/10.1038/s41598-019-41614-2

[6] Brémaud Pierre, Markov Chains, Gibbs Fields, Monte Carlo Simulation and Queues. Springer Charm, 1999