Basics of mathematical modelling - Autumn 2020

Project:

3-species model

Group: UEFK01

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Abstract

Stability and resilience are two decisive factors of an ecosystem's biomass and diversity, even its existence. Stability of an ecosystem is the consistency of the species' population living in it, whereas resilience refers to the adaptability of that ecosystem to new factors. These two characteristics are maintained by the interactions among species in that ecosystem; one species regulates others' populations based on their interaction; it might be predator-prey, competitors, or symbiosis, resulting in an equilibrium of that ecosystem. The ecosystem is stable if it is at equilibrium, or in a stable harmonic cycle with a steady frequency and density amplitude. Introducing new factors, such as human activities or foreign species, can significantly impact on an ecosystem's stability, and might even surpass the resilience of that ecosystem.

To understand the stability, resilience, and stable solutions of an ecosystem, several mathematical models for ecosystems have been studied, such as the Lotka-Volterra model of predator-prey and the Yodzis-Innes model, which takes the species biomass into account. In this project, we aim to exploit the Yodzis-Innes model of 3-species ecosystems with different parameter sets. Based on equilibrium points obtained from this model, we examine possible stable solutions of the ecosystems: an equilibrium point, a stable periodic orbit, and a chaotic solution.

Contents

List of Used Symbols

R, C, P	the population density of prey, consumer and predator, respectively
$\frac{dR}{dt}, \frac{dC}{dt}, \frac{dP}{dt}$	the population's grow rates of prey, consumer and predator, respectively
R_0, C_0	the half saturation density of the consumer and predator
mSMR	mass-specific standard metabolic rate
x_i	the mSMR of species *i*
y_i	the ingestion rate per unit metabolic rate of species *i*
m_i	the body mass of species *i*
a_{Ti}	allometric coefficient for metabolic rate regard the metabolic type of species *i*
EDT	Endotherm
VET	Vertebrate ectotherm
iVET	Invertebrate ectotherm

Introduction

Natural ecosystems consist of a large number of species interacting with each other. Through these interactions, the population dynamics of each species are affected. There are three main types of interaction: trophic (predator-prey), competition, and symbiosis [1]. Studying and modeling these interactions is important for example to understand and predict the underlying processes of environmental conservation, eco-evolutionary processes and to determine the harvest, hunting, and fishing limits [2, 3]. In this project, we are focusing on the stability and resilience of an ecosystem with predator-prey interaction.

The simplest model of predator-prey interaction is a two-species model. Its most common model was studied by Lotka and Volterra [4, 5, 6] in the early twentieth century. They assumed, that the response of the populations would be proportional to the product of their biomass densities, so that [7]:

$$\begin{cases} \dfrac{dR}{dt} = \alpha R - \beta RP \; (1) \\ \dfrac{dP}{dt} = \delta RP - \gamma P \; (2) \end{cases},$$

where R and P are the numbers of prey and predator respectively, dR/dt and dP/dt are their population's growth rates. Parameter α and γ are the rates of change in the absence of the other species and parameters β and δ describe the rate of change due to interaction between species. The first term of Equation (1) assumes the prey reproduces exponentially with the time constant α^{-1}. The term $-\beta RP$ represents the rate of predation upon the prey and is proportional to the rate that prey and predator meet (*RP*), which decreases the prey's growth rate. This "meeting rate" acts opposite in Equation (2), where it represents the consumption of the prey; therefore, it increases the growth rate of the predator population. The last term of the second equation represents the exponential decay rate of the predator population with the time constant of γ^{-1}.

Nevertheless, the Lotka-Volterra model makes some unrealistic assumptions. The prey population will grow exponentially even when the predator is not present, the predator will die out in the absence of the prey and predators can consume infinite quantities of the prey and consumption does not saturate at high prey densities. Yodzis and Innes (1992) responded to these unrealistic assumptions with a model with allometric relationships to relate production, metabolic, and maximum consumption rates to the species' body masses and their metabolic categories. [8, 9]

Stability and resilience are two utmost important characteristics of a natural ecosystem. While ecological stability refers to the consistency of population density of species living in an ecosystem, resilience is the ecosystem's capability to return to its stability after a perturbation either by the environment or foreign species. Holling (1973) described the effect of equilibrium points of an ecosystem consisting of two species, X and Y (Fig. 1**Error! Reference source not found.**), where their population densities are damped after a period of time. The phase plane (the left plane of Fig. 1) shows the relative trajectory of two population densities having the spiral form and directed toward the center node (a sink), resulting in a stable equilibrium point of the ecosystem. Moreover, more equilibrium points with various types can exist in one ecosystem; Fig. 2 shows six common types of equilibrium points, and the combination of these points altogether affects the trajectory of X's and Y's population density. These equilibrium points can be are considered as the simplest possible invariant set of population densities, where the population densities of species remain constant over the time, and can be estimated using mathematical models, such as Lotka – Volterra model or Yodzis – Innes model. [10]

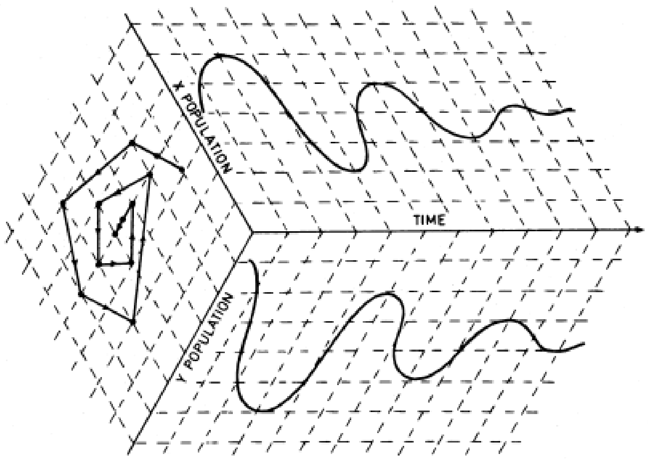

Fig. 1: Population density of two species X and Y over time are both damped and conversed to a constant value of density. The left plane shows their spiral trajectory directing toward a stable sink. (Figure from Holling 1973) [10]

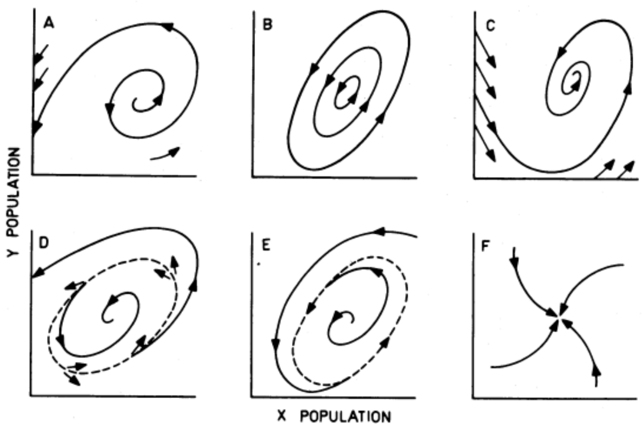

Fig. 2: Six common types of equilibrium points. (a) unstable equilibrium, (b) neutrally stable cycles, (c) stable equilibrium, (d) domain of attraction, (e) stable limit cycle, (f) stable node. (Figure from Holling 1973) [10].

By the effects of equilibrium points, there exists different types of stable solutions for an ecosystem. An equilibrium point is already a stable solution for an ecosystem, however, the resilience of the ecosystem at that equilibrium point might be very low to a small shifting in population densities. Then a periodic solution and a chaotic solution can become the alternative solutions of that ecosystem's stability, in which equilibrium points can still affect the population density by 'pushing' it away or 'pulling' it toward themselves. A stable periodic solution is where the population densities of each species oscillate with a specific frequency and amplitude. Even when a periodic solution can not be achieved, the ecosystem can converse to a chaotic solution, where the densities fluctuate due to the effect of 'strange attractor' in random-alike fashion.

The task of this project is to study 3-species Yodzis-Innes models with different parameter sets. We mainly aim to investigate the behavior of population densities near equilibrium points and to obtain three possible solutions to these models: equilibrium points, periodic solutions, and a strange attractor.

Method

The Yodzis-Innes model

$$\begin{cases} \dfrac{dR}{dt} = R(1-R) - x_c y_c \dfrac{CR}{R+R_0} \ (3) \\ \dfrac{dC}{dt} = x_c C\left(-1 + y_c \dfrac{R}{R+R_0}\right) - x_p y_p \dfrac{PC}{C+C_0} \ (4) \\ \dfrac{dP}{dt} = x_p P\left(-1 + y_P \dfrac{C}{C+C_0}\right) \ (5) \end{cases}$$

denoting:

- R, C, and P the population density of prey, consumer, and predator, respectively

$$\Omega = \{(R, C, P) \in \mathbb{R}^3 | R \geq 0;\ C \ \geq \ 0;\ P \ \geq \ 0\}$$

- dR/dt, dC/dt, and dP/dt their population's growth rates
- R_0 and C_0 the half saturation density of the consumer and predator
- x_i the mass-specific standard metabolic rate (mSMR) of species i; x_i scales allometrically with individual body size.
- y_i the ingestion rate per unit metabolic rate of species i; y_i is constrained by the metabolic type of the animals (endotherm (EDT), vertebrate ectotherm (VET), or invertebrate ectotherm (iVET)). The reference value of y_i is within the interval of $(1, y_{imax})$, where $y_{imax} = (1.6, 3.9, 19.4)$ for EDT, VET, and iVET, respectively.

Furthermore, the ratio of the predator's to prey's body mass, $m_p/m_c = (a_{TP}/a_{TC})^4 (x_C/x_P)^4$, can be used to estimate x_i. The allometric coefficient of metabolic rate appropriate to the metabolic type of species i, a_{Ti}, is (2.3, 0.5) for vertebrae and invertebrate, respectively.

Equilibrium points

Equilibrium points define a state of the system where it remained unchanged over time. When the start point is exactly at one of the equilibrium points, the density values stay constants despite the time t. Nevertheless, if the start point is closed by any of the equilibrium points, the solution might differ: The density can reach a periodic solution after a period of time, or converge to an stable equilibrium point (a sink).

To obtain the value of equilibrium points, we solve three derivatives of density equal to zeros. However, it is not feasible to obtain the equilibrium points' stability of a nonlinear system as this model; hence, it requires the linearization of the system at the equilibrium points.

Let $x' = f(x)$ (E) be a nonlinear system. Its linearization at the equilibrium point p can be denoted by a linear system whose solution is known, $z' = \ df_p z$ (L), where df_p is the differentiate of f at p. (E) and (L) are topologically equivalent if df doesn't contain imaginary eigenvalue. To achieve this condition at the equilibrium point p, p should be a hyperbolic equilibrium point, i.e. df_p doesn't contain imaginary eigenvalue $\mathfrak{I}\lambda_j = 0\ \forall j$.

The classification of equilibrium points in three-dimensional space was defined according to [11] and listed in Table 1. Because this is in three-dimension, an equilibrium point can be a combination of any type of two-dimensional equilibrium points.

Table 1: Classification of equilibrium points

Type	Condition
Non-hypobolic	$\exists j: \Re\lambda_j = 0$
Asymptotically stable (stable node)	$\begin{cases}\mathfrak{I}\lambda_j = 0\ \forall j \\ \Re\lambda_j < 0\ \forall j\end{cases}$
Unstable node	$\begin{cases}\mathfrak{I}\lambda_j = 0\ \forall j \\ \Re\lambda_j > 0\ \forall j\end{cases}$
Saddle (unstable)	$\begin{cases}\mathfrak{I}\lambda_j = 0\ \ \forall j \\ \exists j,k,j \neq k: \lambda_j\lambda_k < 0\end{cases}$
Stable focus	$\begin{cases}\exists j: \mathfrak{I}\lambda_j = 0 \\ \Re\lambda_j < 0\ \forall j\end{cases}$
Unstable focus	$\begin{cases}\exists j: \mathfrak{I}\lambda_j = 0\ , \\ \Re\lambda_j > 0\ \forall j\end{cases}$
Saddle focus (unstable)	$\begin{cases}\exists j: \mathfrak{I}\lambda_j = 0 \\ \exists j,k: \Re\lambda_j \times \Re\lambda_k < 0\end{cases}$

Since the densities are non-negative, we only focus on the positive equilibrium points.

Stable periodic orbit

Stable periodic orbit is the 'converged 'state of the Yodzis-Innes model, where none of the equilibrium points are stable. This state can be achieved after a period of time, depending on the distance of the starting point with the equilibrium, the further it is, the faster the convergence rate. Furthermore, the orbit shape is controlled by the equilibrium points: stable equilibrium points tends to pull the shape toward it, while unstable points push the orbit away. Even though the equilibrium points with a negative value are unrealistic, they can still affect the orbit shape. The convergence rate of the trajectory is affected by some parameters, which are R_0, C_0, and x_p

Strange attractor

Strange attractor can be another solution to the Yodzis-Innes model, where the solution is not periodic but the densities are able to reach a suitable value.

Solving steps

- Calculate the value of equilibrium points by setting all the derivatives equals to zeros
- Calculate the linearization of the system using the Jacobian matrix
- Define the types of each equilibrium point and its sign
- Plot the phase portrait to observe the system at and near-equilibrium points
- Choose random starting points and calculate their density trajectory over time
- Choose a starting point at each equilibrium point and calculate their density trajectory over time
- Choose a starting point near each equilibrium point and calculate their density trajectory over time

These steps were implemented using Matlab 2019b. The coding was attached along with this report.

Models

Plant – Crayfish – Catfish

In this example, we choose the consumer C crayfish, the predator P black bullhead (a type of catfish). The resource R can be any species that crayfish feeds on, but we assume it eats only plants so that the metabolic rate is constant.

- Crayfish is an iVET animal, which weighs ~20 g, and has an mSMR of 0.4-0.8 μmol O_2 g^{-1} h^{-1} [12]. Assuming its mSMR is 0.6 and it ingests 20 g of plant per day; hence, its ingestion rate per metabolic unit is ~1.5. Therefore, $x_c = 0.6, y_c = 1.5$.
- An adult black bullhead is a VET, which weighs ~5 kg, and has an mSMR of ~0.01 μmol O_2 g^{-1} h^{-1}. Broodfish can feed on 1-5% of their weight per day. However, their prey in our model is a crayfish, whose shell weighs the most, we assume the catfish needs to consume more, about 5% of their body weight. Hence, we choose $x_p = 0.01, y_p = 0.05/0.01 = 5$.

Let us choose the half-maximum densities, R_0 and C_0, which are 0.2 and 0.5, respectively. Consequently, the parameter set for this model is:

$$S_1 = \{R_0, C_0, x_c, y_c, x_p, y_p\} = \{0.2, 0.5, 0.6, 1.5, 0.0,1, 5\}$$

Six equilibrium points were obtained from this system (Table 2). Two of them were unrealistic as they contained negative densities. One equilibrium point had all densities positive, however, it was not asymptotically stable.

Fig. 3 (left) depicts the phase portrait of this system, and the effect of the equilibrium points on the relative trajectory of R, C, and P with a random starting point. These equilibrium points tend to “pull” and “push” the trajectory, forming a stable periodic orbit of the trajectory. Fig. 3 (right) depicts the densities plot over time, representing the stable periodic solution of the system. The trajectory eventually becomes stable after 400 days; the densities are all periodic with the frequency of 0.163 cycle/day. This means it takes about 6 days for the trajectory to complete one orbit.

Trajectories also change differently if it starts at an equilibrium points. If it starts at saddles and saddle focuses, the densities tend to remain constant over time. From non-hypobolic and other equilibrium points, the trajectory will converge to the periodic orbit with a specified frequency after a period of time, forming a stable periodic orbit. Furthermore, trajectories that start near equilibrium points will also follow the stable periodic orbit. Trajectories starting exactly at (upper left subfigure) and near (lower left subfigure) a saddle, a saddle focus and a non-hypobolic equilibrium point are shown in Fig. 4, Fig. 5 and Fig. 6 respectively. The periodic solution was shown on the right subfigures accordingly.

Since there exists a periodic solution for this system, we didn't obtain any strange attractor, even though it showed a strange orbit near the non-hypobolic equilibrium point as in Fig. 4.

Table 2: Equilibrium points of S1

Equilibrium points (R, C, P)	$(R, C, P) > 0$	Type	Biological condition
$(0 \quad 0 \quad 0)$	0	Saddle	No animal
$(1.0000 \quad 0 \quad 0)$	0	Saddle	Only resource
$(0.4000 \quad 0.4000 \quad 0)$	0	Non-hypobolic	No predator
$(0.8975 \quad 0.1250 \quad 0.3400)$	1	Saddle Focus	Stable
$(0 \quad 0.1250 \quad -1.5000)$	0	Saddle	Unrealistic
$(-0.0975 \quad 0.1250 \quad -3.6400)$	0	Saddle	Unrealistic

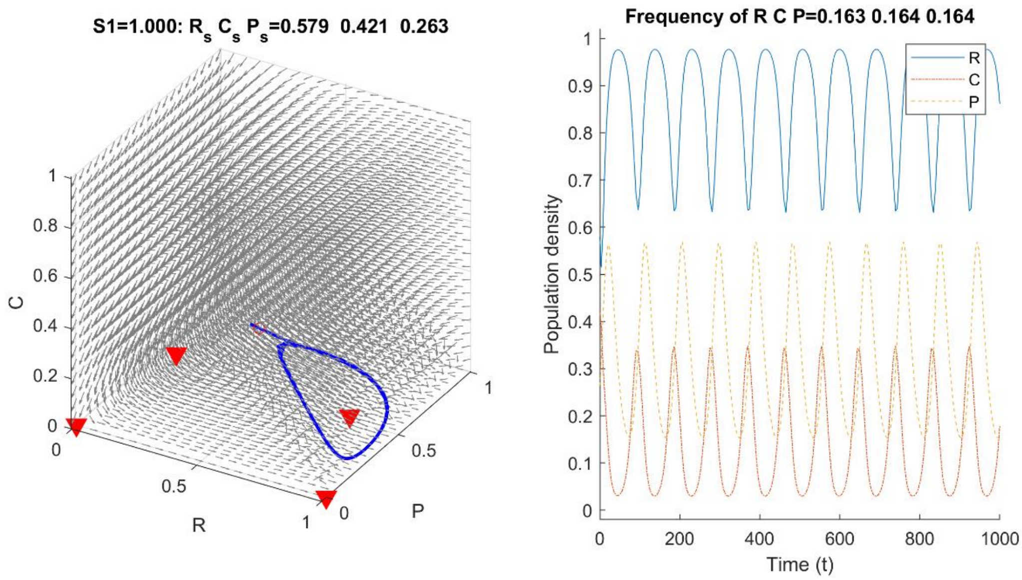

Fig. 3: Phase portrait (left), the relative trajectory of densities of a periodic solution of S1 (right)

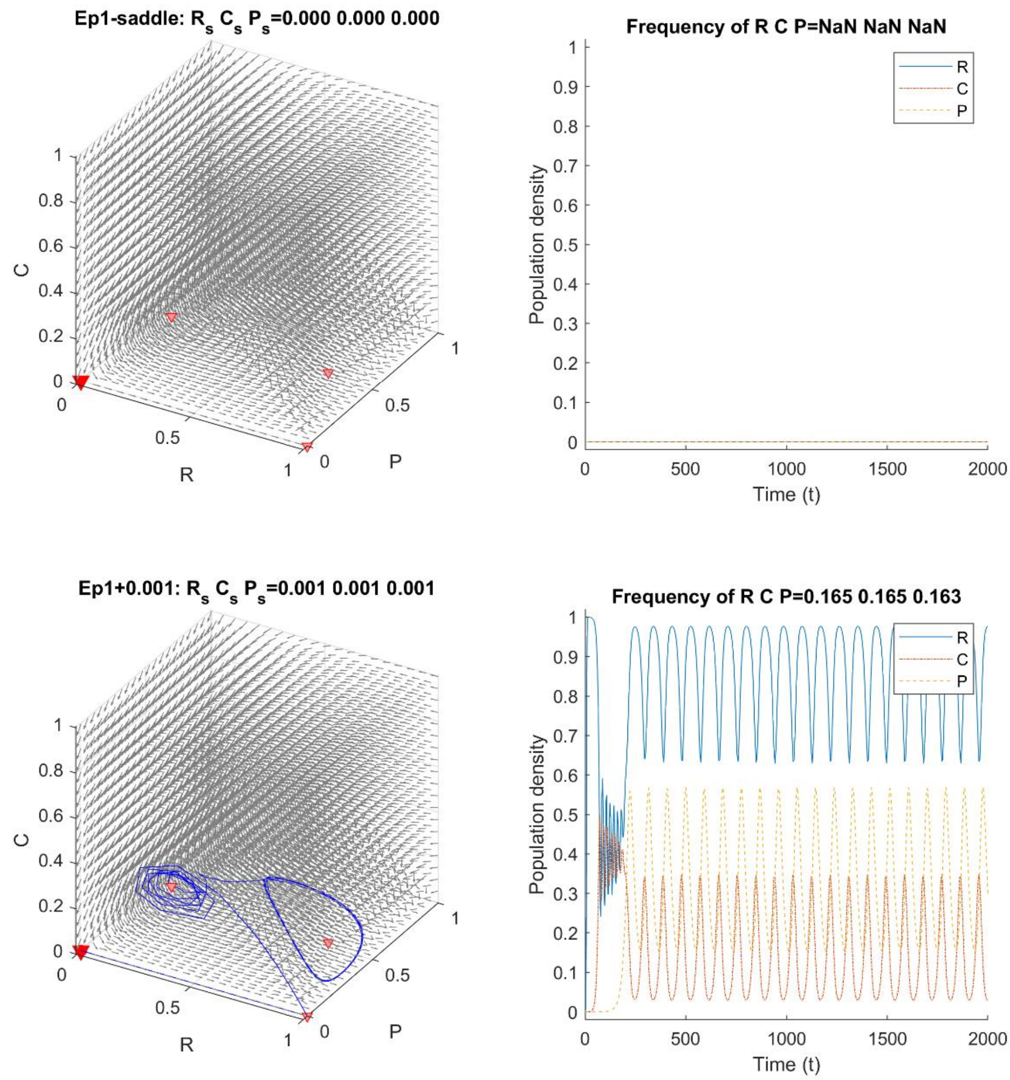

Fig. 4: Phase portrait (left column), the relative trajectory of densities of S1 (right column) starting at (upper row) and near a saddle (lower row).

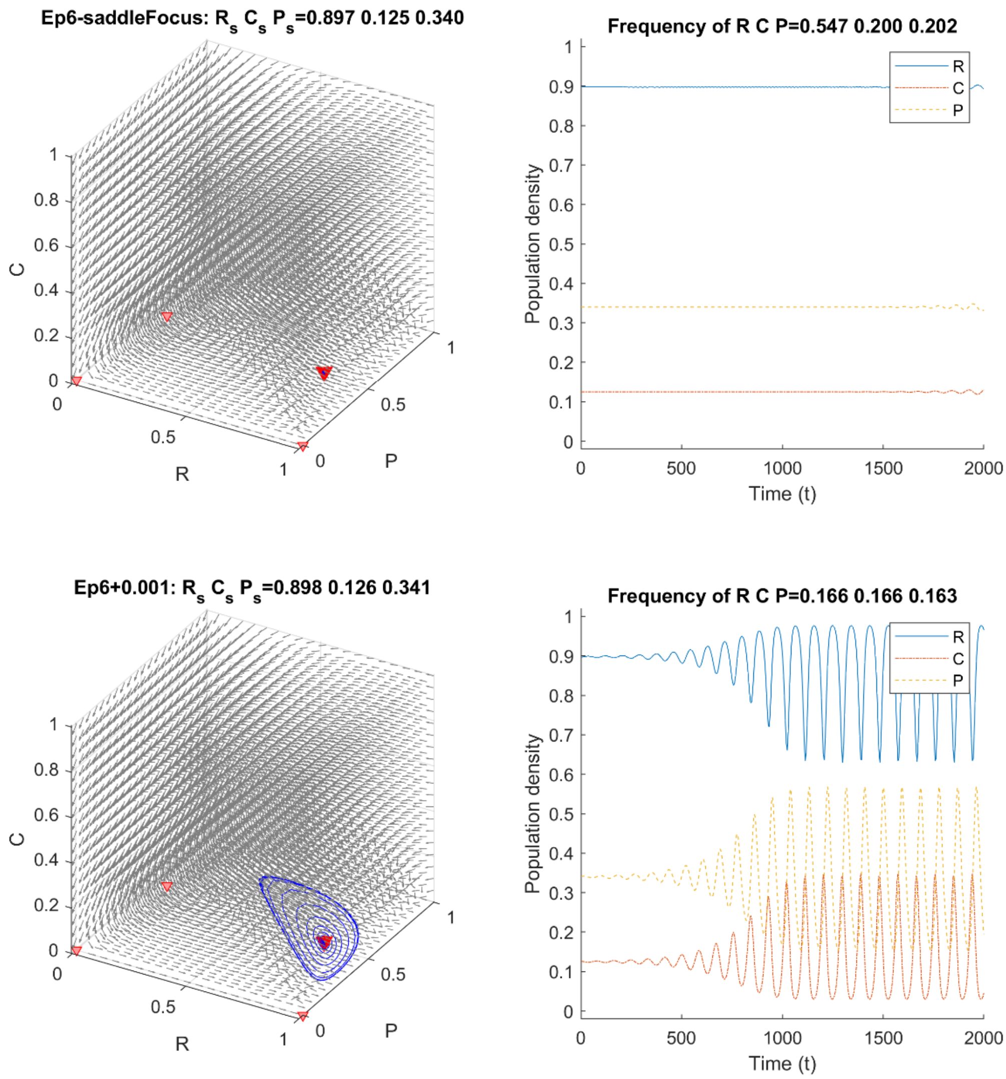

Fig. 5: Phase portrait (left column), the relative trajectory of densities of S1 (right column) starting at (upper row) and near a saddle focus(lower row).

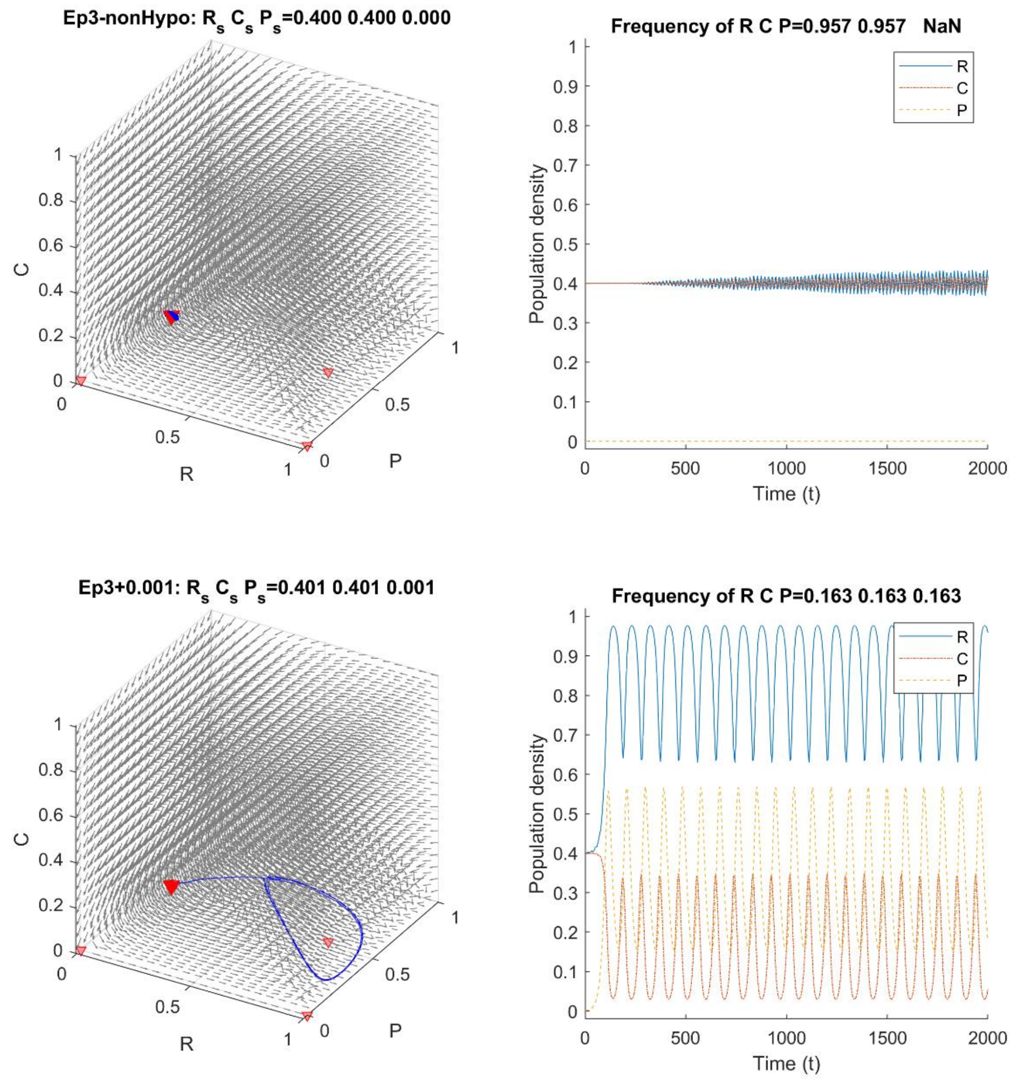

Fig. 6: Phase portrait (left column), the relative trajectory of densities of S1 (right column) starting at (upper row) and near a non-hypo equilibrium point (lower row).

Chaotic solution - Strange attractor

Here we represent the model with the parameter set provided in Task 3.

$$R_0 = 0.161 \qquad\qquad C_0 = 0.5$$

$$x_c = 0.4 \qquad\qquad y_c = 2.01$$

$$0.071 < x_p < 0.225 \qquad\qquad y_p = 5.0$$

We examined the model with five values of x_p: $x_p = (0.071, 0.110, 0.148, 0.187, 0.225)$, and observed that with all these values, the system converged to a semi-periodic solution. The relative trajectory of densities followed a special orbit after a period of time. This is a strange attractor, a chaotic solution of the system, as described in Task 3. Fig. 7 shows the variation of equilibrium points, the chaotic solution's mean frequency, and the density when $t \to \infty$. The upper subfigure represents the equilibrium points tend to have smaller values as x_p increases. On the lower-left subfigure, it shows the solution has the highest mean frequency when x_p is in the range of 0.148-0.187, and lowest when x_p=0.071. The lower-right subfigure depicts the population density at different values, the most affected density is of the predator (P), which become smaller as x_p increases, while R and C remain constant. We also observed that with the values in the middle range $(0.110, 0.148, 0.187)$, the trajectory converges to this solution faster than the system with x_p=0.071 or 0.225.

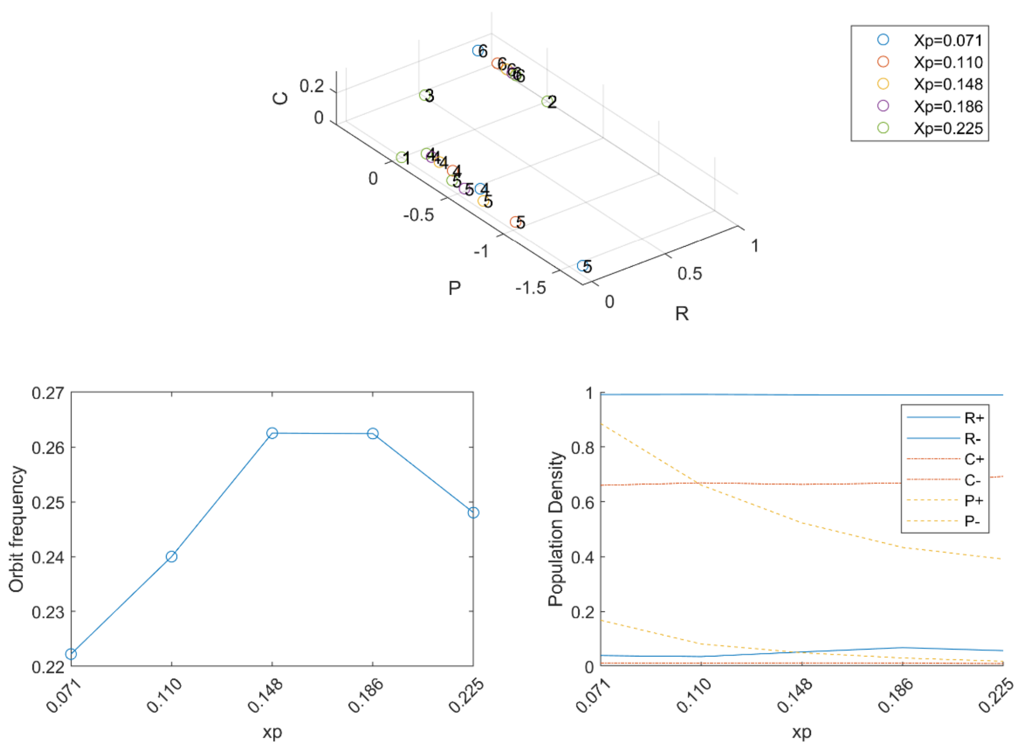

Fig. 7: The variation of equilibrium points (top), the dependence of chaotic solution's orbit frequency (bottom left) and population densities on the value of x_p (bottom right).

Below is an example of the system with x_p = 0.148: $S_{xp=0.148} = \{R_0, C_0, x_c, y_c, x_p, y_p\} = \{0.161, 0.5, 0.4, 2.01, 0.148, 5.0\}$. A list of equilibrium points was shown in Table 3. The phase portrait, equilibrium points and a random-starting trajectory were plotted in Fig. 8, left figure. The periodic solution was plotted on the right side of Fig. 8. The behavior of the trajectories at and near-equilibrium points are the same as in S1 (Blackworm- Crayfish - Catfish). We obtained one more type of equilibrium points in this system: unstable focus, and plotted it in Fig. 9. This unstable focus remains for all five values of x_p.

Table 3: Equilibrium point of S2 x_p = 0.148

Equilibrium points (R, C, P)	$(R, C, P) > 0$	Type	Biological condition
$(0 \quad 0 \quad 0)$	0	Saddle	No animal
$(1.0000 \quad 0 \quad 0)$	0	Saddle	Only resource
$(0.1594 \quad 0.3350 \quad 0)$	0	Unstable focus	No predator
$(0.9058 \quad 0.1250 \quad 0.1767)$	1	Saddle Focus	Stable
$(0 \quad 0.1250 \quad -0.2500)$	0	Saddle	Unrealistic
$(-0.0668 \quad 0.1250 \quad -0.8193)$	0	Saddle	Unrealistic

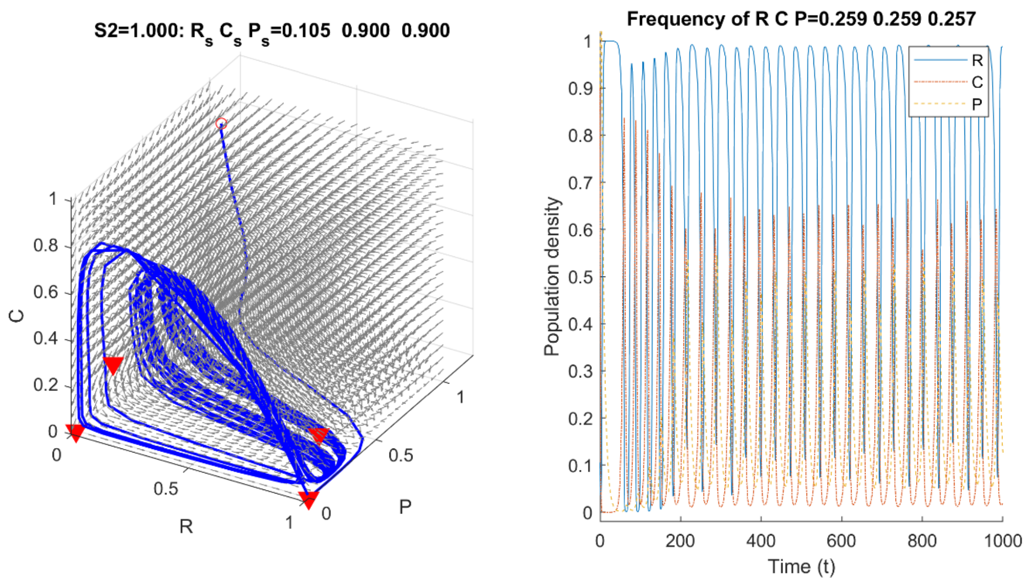

Fig. 8: Phase portrait (left), relative trajectory of densities (right) of a periodic solution of S2 for x_p=0.148

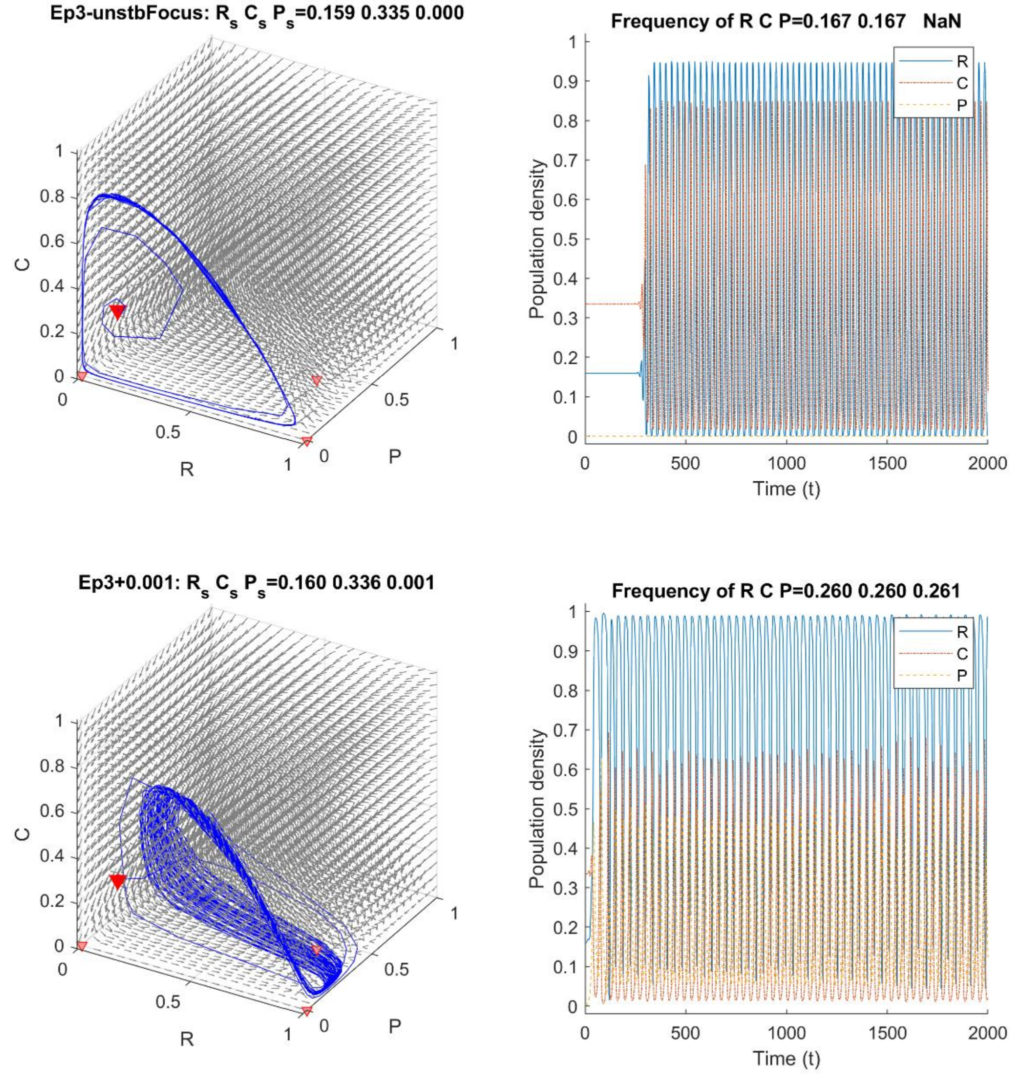

Fig. 9: Phase portrait (left column), the relative trajectory of densities of S2 for x_P=0.148 (right column) starting at (upper row) and near unstable-focus equilibrium point (lower row).

Discussion

In this project, the goal was to investigate a 3-species Yodzis-Innes model and the behavior of population densities near equilibrium points and to obtain three possible solutions to these models: equilibrium points, periodic solutions, and a strange attractor.

The solutions of two systems were presented in this study: Plant – Crayfish – Catfish (S_1) and provided systems in Task 3 (S_2). Both systems had six equilibrium points; two of these are (0, 0, 0) (no species) and (1, 0, 0) (only resources) as saddle-type equilibrium points. Biologically, these two points seem to be the solutions when the predator and consumers died out, there exists only resources (R = 1) or none of the three species exists. Besides these, both systems have two unrealistic equilibrium points and one all-positive saddle-focus node.

However, the orbits of these two systems are different. S_1 has a flat periodic orbit with a frequency of 0.165 cycle/day, while the second system has a chaotic solution. On the other hand, S_2 has a larger and curved orbit yet with a higher frequency (0.270 cycle/day). This difference is caused by two different equilibrium points: S_1 has the non-hypobolic equilibrium point (0.4, 0.4, 0) (Fig. 6) whereas S_2 has an unstable focus node (0.1594, 0.3350, 0) (Fig. 9).

The Yodzis-Innes model provides a biologically meaningful perspective to observe and predict the variation of the population density. It is flexible, as we can easily include more species in the model. The solution of the model is also easily implemented in computational software such as Matlab for a fast and accurate solution. However, this model has some drawbacks. First of all, this system is a self-contained system and the parameters are set constant, yet in reality, all of the parameters vary according to the surrounding environment. For example, the metabolic rate can be influenced by temperature, age, and food availability. Secondly, it could become mathematically cumbersome when used for more species and more complex networks. Thirdly, it requires the parameter to be carefully chosen, otherwise, the system can be biologically extreme. One of the extremes is when the population of prey is reduced to extremely low numbers and still recovers. In a real-life situation, the prey and consequently the predator would most likely go extinct. This issue is called and 'atto-fox problem'[1] [13].

To overcome some of these inaccuracies of the model a different type of models such as the individual-based model [14] or stochastic model [15] can be used. However, depending on the intended use and when keeping the drawbacks into consideration, we believe that the Yodzis-Innes model provides a reliable and fast model of a three-species ecosystem and insight into its dynamics, resilience, and stability.

[1] This term comes from a model, where population of foxes per squared kilometer decreases to 10^{-18} (prefix atto) before it recovers.

References

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Attachment

Attached with this report is the Matlab coding, UEFK01_3-species_model.zip. After extracting this file:

- Read readme.txt
- Run main.m
- The results are saved in Figures folder, according to the parameters $\{R_0, C_0, x_c, y_c, x_p, y_p\}$ and the two studied systems $\{S_1, S_2\}$
    - Run run_param.m: examine the changing of parameters affecting on the solution of the system
    - Run run_studied_system.m: produce the results of two studied systems.
- Details of how to use this program were described in each file.