Two-prey-one-predator system: coexistence of sheep, *guanaco*, and puma in the Patagonia region

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The modeling of ecological systems, like two or more competing species with or without considering the environment, can help understand the necessary conditions for sustainable coexistence of them. One example of practical interest is in the northern Patagonia of Argentina[1,2]. The *puma* (cougar) and *guanaco* are native species of that region that have coexisted for thousand of years in a predator-prey relation before the introduction of sheep in the XIX century. That changed the Patagonia steppes equilibrium, with the puma shifting to predate preferentially the sheep, while the *guanaco* had to compete with the sheep for grass.

We propose the following set of equations to model a system of three species, being two preys in a hierarchical competition and one predator:

$$\begin{aligned}\dot{x} &= c_x x - \mu_x xz - \frac{x^2}{k_x} - \mu_{xy} xy \\ \dot{y} &= c_y y - \mu_y yz - \frac{y^2}{k_y} \\ \dot{z} &= c_z z\,(x+y) - e_z z\end{aligned} \tag{1}$$

We have x as the inferior competitor (sheep), y as superior (*guanaco*), and z as the predator (puma). About the constants, c_j controls the population increase of the species j, μ_j tells us about predation of prey j, μ_{xy} is about competition between the preys. k_j is the carrier capacity of the species j, and finally, e_z is the predator extinction rate.

Unlike the *guanaco*, which evolved along with its predator, the sheep is less adapted to flee from the puma, so it is an easier prey. The sheep and *guanaco* also share an almost identical diet, out of 80 plant species, they share 76, which puts the species in direct competition for forage and water. Under natural conditions, the *guanaco* is the superior competitor, better adapted to the local ecosystem; a herd of *guanacos* has the ability to displace a flock of sheep.

The system of differential equations has nine parameters. However, we can take advantage of the fact that dependent variables have no specific meaning. These equations model the changes in the population of each species, but we do not have an exact interpretation of what $x = 1$ means, for example. It can be 1 animal, 1 herd, or up to 1 kg of biomass. So we can do some manipulations to get the following reduced system:

$$\begin{aligned}\dot{x} &= c_x x - \mu_{xy} xy - \mu_x xz - \frac{x^2}{k_x} \\ \dot{y} &= y - yz - \frac{y^2}{k_y} \\ \dot{z} &= z\,(x+y) - e_z z\end{aligned} \tag{2}$$

The parameters in the equations 2 are not the same as in the equations 1, they are the results of basic operations between the previous variables. We chose to use the same parameters name for notation ease. While there is no absolute meaning for the x, y, z quantities, if any of them is zero, it means that the corresponding species is extinct. Therefore, the most interesting result that the model can show is which species is alive when the system reaches equilibrium, so we will focus on them. A good start is to understand how each variable affects the survival of each species. To investigate it we can use artificial neural networks. The *perceptron* is a basic model of neurons for linear binary classification with supervised learning. The neuron works by assigning a weight to each input, this weight is a measure of the importance of the input to the desired output[3]. We build a simple model where the inputs of each neuron are the 6 independent variables of the system, and the output is the situation of one of the species in the equilibrium state of the system.

After performing a training scheme with 1250 inputs produced via a numerical solution of the system of equations, we performed a validation with 5000 inputs produced in the same way. Each neuron was responsible for predicting whether one species was alive or not in the steady state, they correctly predicted more than 90% of all situations. The weight of each neuron is illustrated in figure 1.

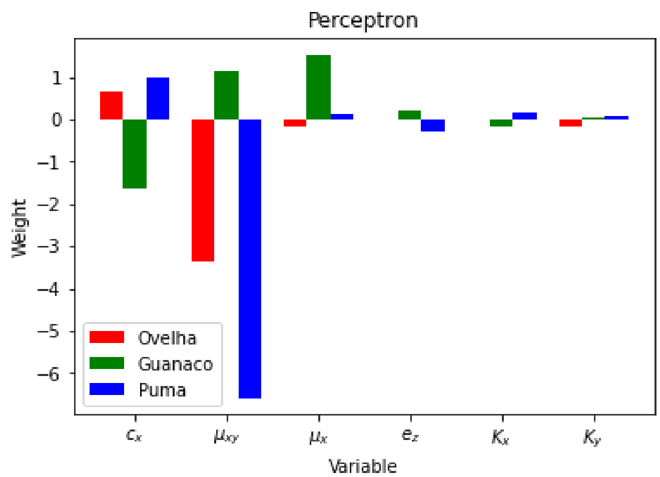

Figure 1. Neuron weights.

Each neuron also has its own variable called bias. Bias tells us the resistance against its activation, and more important than the absolute values of the weights of each input is its ratio against bias. Then, we changed the magnitude of each weight vector to share the same bias for a better comparison.

These results show us that for the range of values we chose to create the dataset, the system is more sensitive to some variables than others, we can also see how each variable affects each species. This helps to get an idea of how we can get from one specific state to another.

A ternary is a graph that allows us to visualize how the system changes according to three variables. If we have 5 variables, we can build 10 different subsets made with 3 different variables each. We can build a graph with 10 ternary graphs arranged in a circle. It will not show us how the system changes according to 5 variables at the same time, but it is difficult to even for us to understand, but it helps us to see how the system changes according to 5 variables in different ways by looking at each ternary graph. We still have one more variable in our system, we can animate the graph using the time to see how the system changes for the last variable.

Returning to the perceptron weights, we can see that if we start from the coexistence of three species, we can reach any other state keeping k_x constant. So we chose to leave k_x to change over time. In figure 2 we can see how the variables are organized in the graph and the final state of the system for different ranges of values.

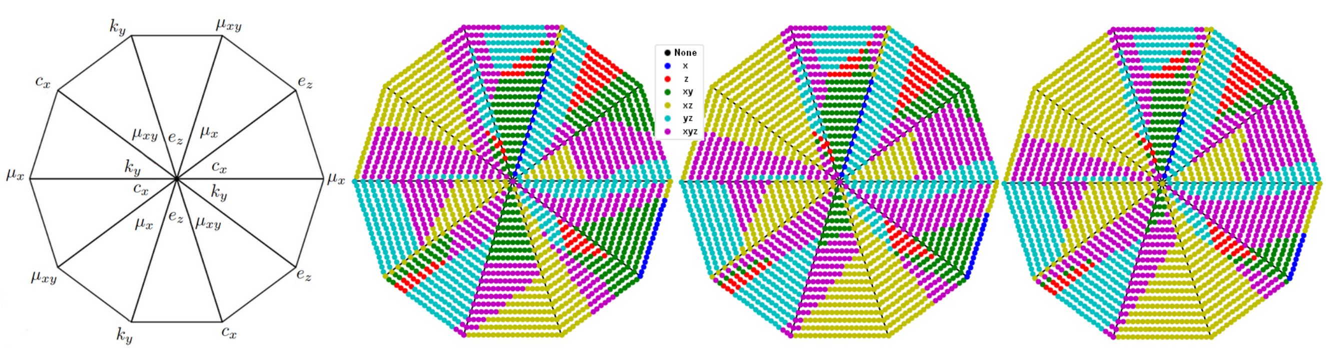

Figure 2. k_x increases from left to right.

We can see that we can reach almost every state by changing μ_{xy}, e_z, and k_y. The only state that is not represented in the graphs is when all are extinct, to reach this result we need to choose a lower value for e_z. This is a counter-intuitive special situation when the predator grows so large that it drives the prey to extinction and then collapses the entire ecosystem. We can see that these 3 variables change the system in different ways. And it is not just about magnitudes, but also, and mainly, whether they contribute to each species' survival or extinction. As a counter-example, we can see that c_x and μ_{xy} affect sheep and puma in the same way and *guanaco* in the opposite situation, they only have differences in the signal, beyond the magnitudes. Similar situations are for e_z and k_x, μ_x and k_y.

Now we can have a broad understanding of how the system responds to each variable and which path we can choose to take the system from one initial state to another. This is interesting to use as a resource for decision-making.

But if the person behind the decision does not have a certain mathematical background, he can limit himself to the proposed model. Making changes to the equation-based model, solving, and interpreting may require some specific mathematical knowledge.

Agent-based modeling is a different type of modeling where we leverage coding and computing tools. The main idea is that the phenomenon can be modeled using just agents and then writing some simple rules for the interaction between these agents[4]. In this way, we do not model the phenomenon we want to observe directly, it is achieved as an emergent phenomenon of the whole system. And if we want to make some changes to the model, we can do it in an easy way by changing the rules of interactions between agents.

Therefore, we tried to reproduce the results achieved by the system of equations using agent-based modeling. We can define some variables, specifically $k_x = 0.5/c_x$ and $k_y = 0.5$, so we have a probabilistic interpretation of our set of equations that can help us build our agent-based model. The comparison for a specific set of parameters can be seen in figure 3.

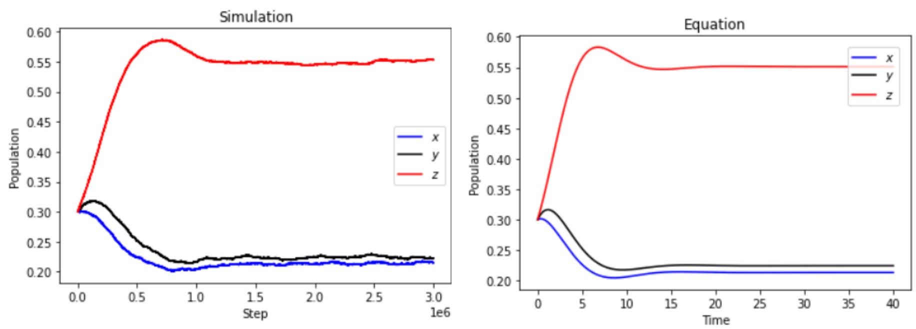

Figure 3. On the left, the simulation of the model, and on the right, the numerical solution of the set of equations.

The similarity is remarkable. In this simple model, each population is represented by an agent with the main attribute we can interpret as the percentage of some total area covered by the animal, and methods are related to reproduction, predation, natural death, and competition. All methods have a one-to-one relationship with the terms of our set of equations. It is easy to think of many ways to improve this model, but this simplicity and strong relationship to the set of equations make it an interesting toy model to explore and a good starting point.

We believe that the agent-based model, with the equation-based model and the tools, exposed earlier to understand and explore the system form an interesting framework to be a “something to think about it”, that different researchers can take advantage of and use it as a laboratory to explore some assumptions and ideas in a quantitative way. We hope to contribute to the development of the field and can help in the decision-making process on the management of ecosystems in a sustainable way.

Keywords: mathematical ecology, agent-based model, two-prey-one-predator system, machine learning.

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