

Expanding Lotka-Volterra: Improving Predator-Prey Models and Exploring Models for Competition and Mutualism

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1 Abstract

Our project aims to explore various models of different types of interacting populations by analyzing their behavior, effectiveness, and accuracy. We will reference Lotka-Volterra, a simple but flawed model, as the introductory model to "jump off" to other kinds of models. We will explore models that build upon Lotka-Volterra to more accurately reflect how populations behave. We will also explore models that can model behaviors that Lotka-Volterra cannot as effectively. We will be using *Mathematical Biology: I. An Introduction* by J.D. Murray to find and examine different models of interacting populations. The aspect we are most interested in is exploring how the behaviors of a model can reflect the complex organic systems of the real world. It will be interesting to explore and understand the flaws of Lotka-Volterra and see how the tools we learn in class can be applied to construct more accurate models, as well as explore new types of interactions populations have and how we can model those behaviors as well. Our goal is to gain a wider and deeper understanding of how real world populations interact, as well as how the topics we learn in this class can be applied in the real world. We begin by introducing Lotka-Volterra, and present some of the different ways populations can interact beyond predator-prey: competition and mutualism.

2 Lotka-Volterra

Lotka-Volterra is a mathematical model that models the relationship between predators and their prey and how their populations change over time. $N(t)$ represents the prey population and $P(t)$ represents the predator population both at time t .

$$\frac{dN}{dt} = N(a - bP), \frac{dP}{dt} = P(cN - d)$$

With a , b , c and d being all positive constants. There are four assumptions of the Lotka-Volterra model:

- The prey population would infinitely increase without any predators.
- The job of the predator population is to limit the prey population to a stable ratio between predators and prey.
- The predator population would become extinct if there is no prey population.
- The prey population contributes to the growth of the predator population.

To analyze the model, the first thing to do is to nondimensionalize it, resulting in these equations:

$$\frac{du}{d\tau} = u(1 - v), \frac{dv}{d\tau} = \alpha v(u - 1)$$

Then linearizing it can determine the stability and singularity of the states:

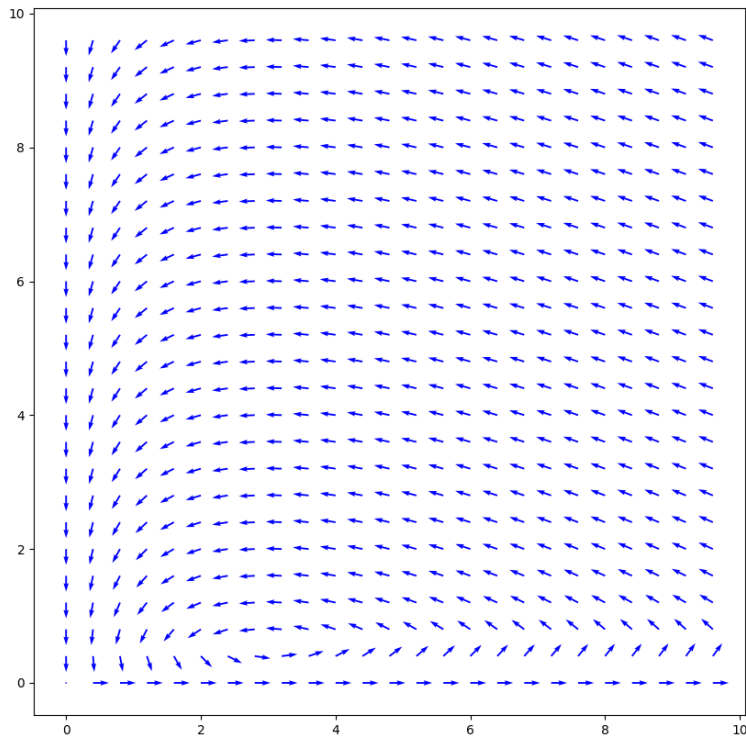


Figure 1: Vector field

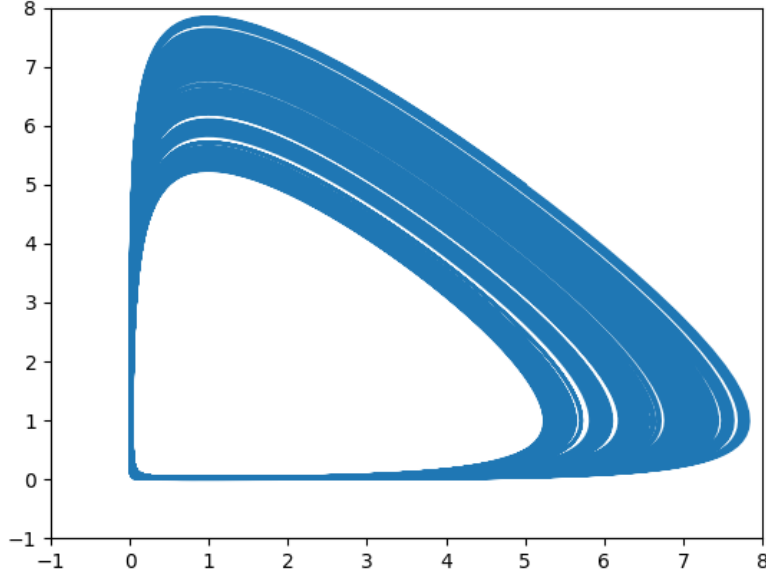


Figure 2: Phase plane trajectories

Lotka-Volterra can be thought of as our reference model since the four assumptions of the model have many flaws. It is also a rather simplistic, naive model; for instance, the model allows populations to become negative under certain conditions. It also cannot not readily model behaviors such as competition and mutualism. We thus start with a more realistic version of Lotka-Volterra, and move to explore new models that can simulate behaviors that Lotka-Volterra cannot.

3 Realistic Predator-Prey Models

This variation of the predator-prey system, described in section 3.3 of *Mathematical Biology*, makes adjustments to the original Lotka-Volterra model to more accurately reflect the real world. One such way it does this is by bounding the growth rates of the prey, as originally it is unbounded in the absence of predation. These rates are thus bounded based on the prey and predator densities:

$$\frac{dN}{dt} = NF(N, P), \frac{dP}{dt} = PG(N, P) \quad (1)$$

F and G depend on interaction, species, etc. We could say that prey satisfies a logistic growth in the absence of predators, so we could have:

$$F(N, P) = r \left(1 - \frac{N}{K} \right) - PR(N) \quad (2)$$

$R(N)$ is the predation term and K is the constant carrying capacity. To elaborate on the predation term, it is a response to the change in prey density. Saturation of large N reflects limited predator capability when prey is abundant. Lastly, we can adjust G in Lotka-Volterra to have a more sophisticated model:

$$G(N, P) = k \left(1 - \frac{hP}{N} \right), G(N, P) = -d + eR(N) \quad (3)$$

These models are all possible models that are more realistic than Lotka-Volterra, and there certainly exist more. The specific equation we choose to analyze is:

$$\frac{dN}{dt} = N \left[r \left(1 - \frac{N}{K} \right) - \frac{kP}{N + D} \right] \quad (4)$$

$$\frac{dP}{dt} = P \left[s \left(1 - \frac{hP}{N} \right) \right] \quad (5)$$

We can nondimensionalize this for easier analysis using the following variables:

$$u = \frac{N}{K}, v = \frac{hP}{K}, \tau = rt, a = \frac{k}{hr}, b = \frac{s}{r}, d = \frac{D}{K}$$

Which results in:

$$\frac{du}{d\tau} = u(1 - u) - \frac{auv}{u + d} \quad (6)$$

$$\frac{dv}{d\tau} = bv \left(1 - \frac{v}{u} \right) \quad (7)$$

3.1 Stability and Visualizations

The most notable difference with this model and Lotka-Volterra is how changing parameters, namely b , results in different behaviors. In other words, we can see that a uniform steady state solution can bifurcate to an oscillatory solution.

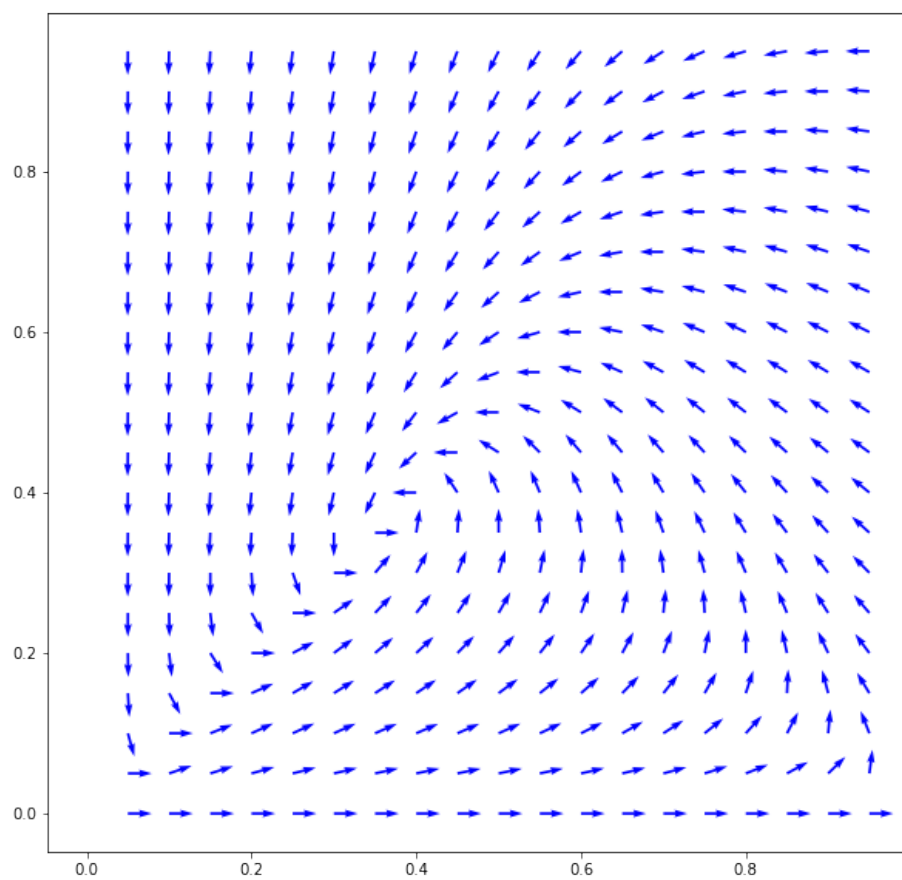


Figure 3: Uniform Steady State

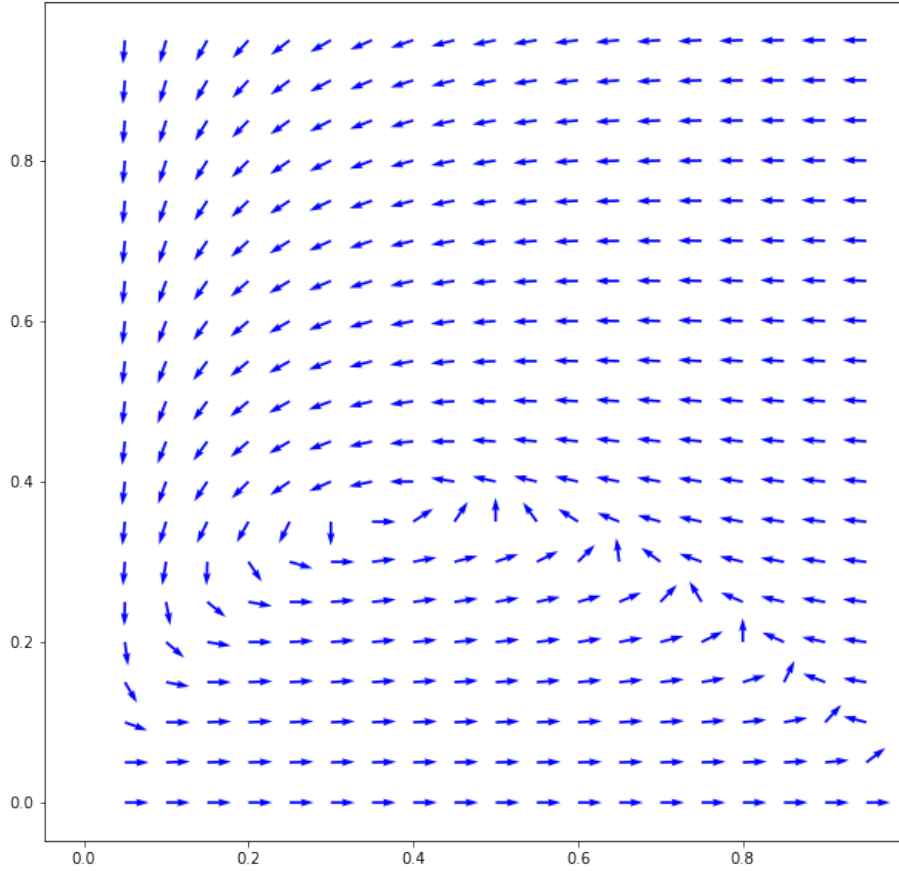


Figure 4: Oscillatory (Limit Cycle)

3.2 Findings

We can see an obvious difference between the realistic model and the original Lotka-Volterra model. When changing the parameters, we can observe completely distinct behaviors. The most important aspect is that with a slight perturbation from the limit cycle, the solution tends to zero. This is in stark contrast to Lotka-Volterra, which features closed cycles that would *not* see this behavior. This reflects a key behavior in a more realistic ecosystem: if a prey population increases, it encourages growth of the predator. With more predators, the prey decline, which causes the predators to decline. This allows prey to increase, and thus we see oscillation. However, these oscillations can grow and decay, which is what the realistic model depicts.

One difficulty I ran into was an error in the book. They have a subtraction instead of multiplication when nondimensionalizing their system, which causes the phase portraits to not look correct. The equations here are the right ones.

4 Competition Models

Competing populations compete for the same limited food source or in some other ways like territory to inhibit each other's growth. To model this behavior, we could base our model off of Lotka-Volterra with logistic growth of each species in absence of the other, but we present an alternative, simpler model (section 3.5, *Mathematical Biology*) that reflects the same properties of the more complicated model. Note that this model is not a conservative system, unlike Lotka-Volterra.

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right] \quad (8)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right] \quad (9)$$

the constants are defined as follows:

- $r_1, K_1, r_2, K_2, b_{12}, b_{21}$ are positive constants, where the r 's are the linear birth rates and K 's are carrying capacities.
- b_{12} represents competitive effect of N_2 on N_1 , and b_{21} represents competitive effect of N_1 on N_2 .

To make analysis easier, we also will nondimensionalize the model. We will use the following variables:

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12} \frac{K_2}{K_1}, \quad a_{21} = b_{21} \frac{K_1}{K_2}$$

This achieves the following equations which we will use in our analysis:

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) \quad (10)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1) \quad (11)$$

4.1 Stability and Visualizations

For this model, we have four cases, which depends on the constants, particularly a_{12} and a_{21} . Each case will have a phase portrait showing stability behavior, with nullclines as $1 - u_1 - a_{12}u_2 = 0$ and $1 - u_2 - a_{21}u_1 = 0$, represented in red. All cases also use $\rho = 1$, which represents a growth rate ratio of 1. This does not significant affect the behavior of the model, as it merely changes the steepness of certain arrows yet not affecting the overall behavior/trajectories. We find several critical points, which are derived in *Mathematical Biology I*, pg. 96. These critical points are $(0, 0)$, $(0, 1)$, $(1, 0)$, and a fourth positive stability point in certain cases. Note that $(0, 0)$ is always unstable.

4.1.1 Case 1

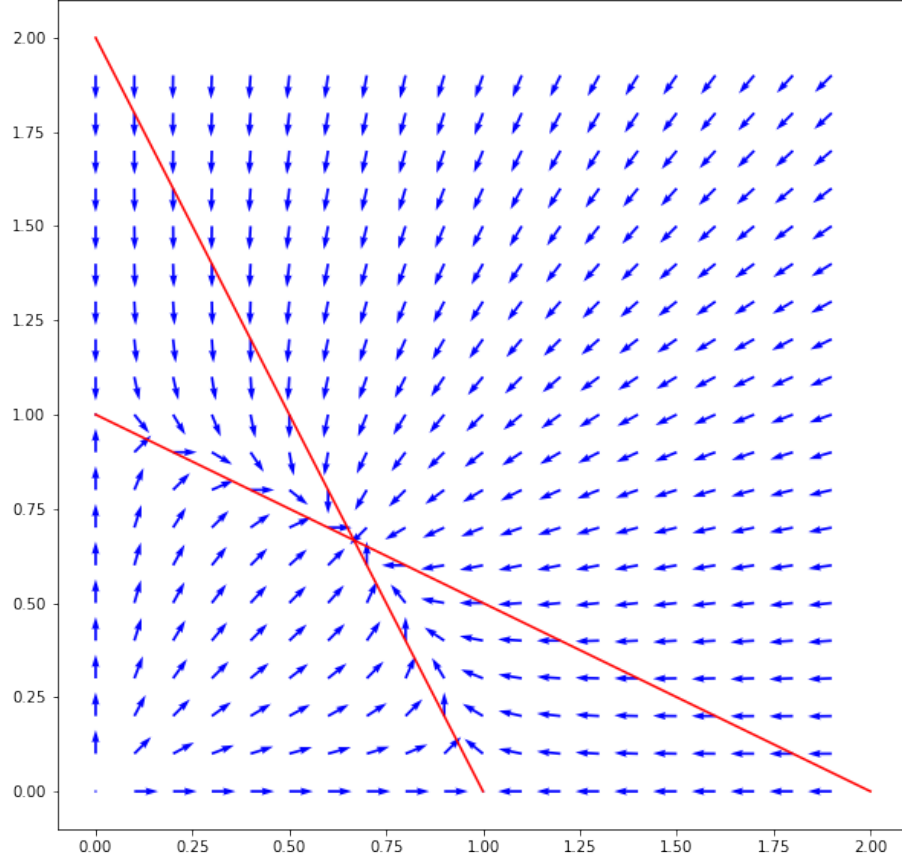


Figure 5: Case 1 with condition $a_{12} < 1, a_{21} < 1$. Here, $a_{12} = 0.5$ and $a_{21} = 0.5$

In this case we observe a very clear positive stability point, which serves as an attractor. While changing constants may change the location of this point, the stability point remains positive as the constants satisfy the conditions for this case. Though we already know $(0, 0)$ is unstable, we can see that $(0, 1)$ and $(1, 0)$ are also unstable. Thus we can assume that no matter the initial value of the populations, in this case the populations will reach a balanced equilibrium where both populations exist together, always competing. To elaborate, this behavior occurs since as the a constants are based off of the carrying capacities K_1, K_2 and the competition aggression b_{12}, b_{21} , the carrying capacities are approximately the same, and the aggression is weak enough that the species can coexist.

4.1.2 Case 2

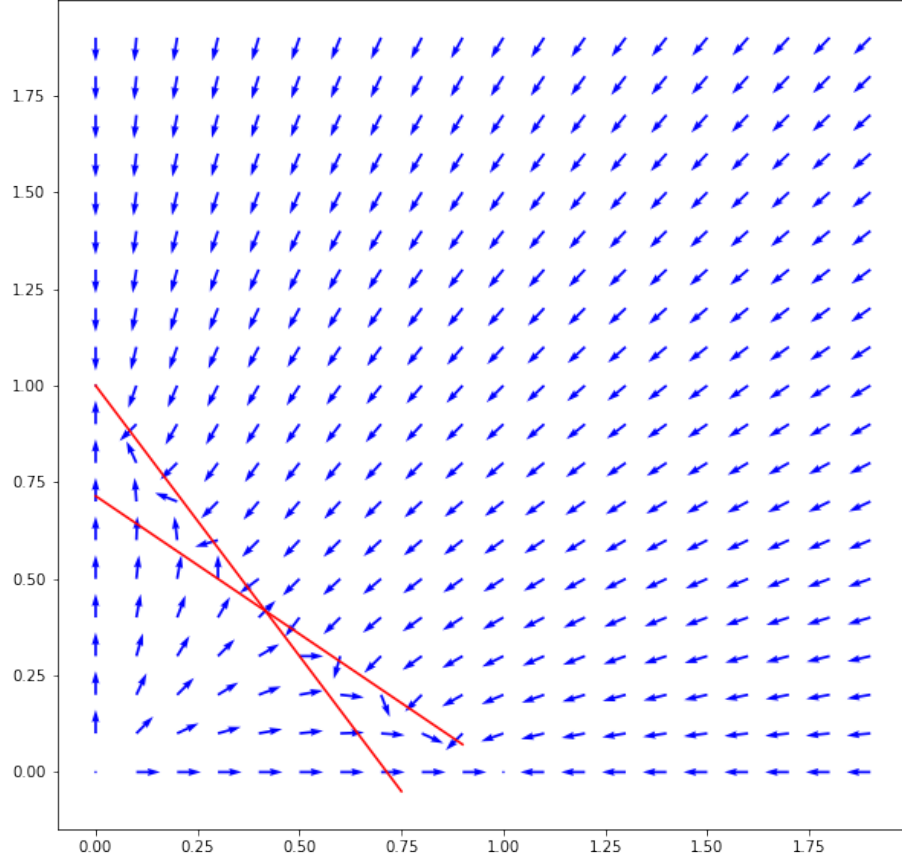


Figure 6: Case 2 with condition $a_{12} > 1, a_{21} > 1$. Here, $a_{12} = 0.5$ and $a_{21} = 0.5$

In this case we observe our positive critical point that used to be a stable point in the previous case is now unstable, as all trajectories near it tend away from it. Where do they go? We can see that they either tend towards $(0, 1)$ or $(1, 0)$, depending on the trajectory's initial value. Thus, these two points are stable steady states. We can infer that in this case, a population will "defeat" the other. One will eventually drive the other to extinction over time, and this depends on the initial values of the populations.

4.1.3 Case 3

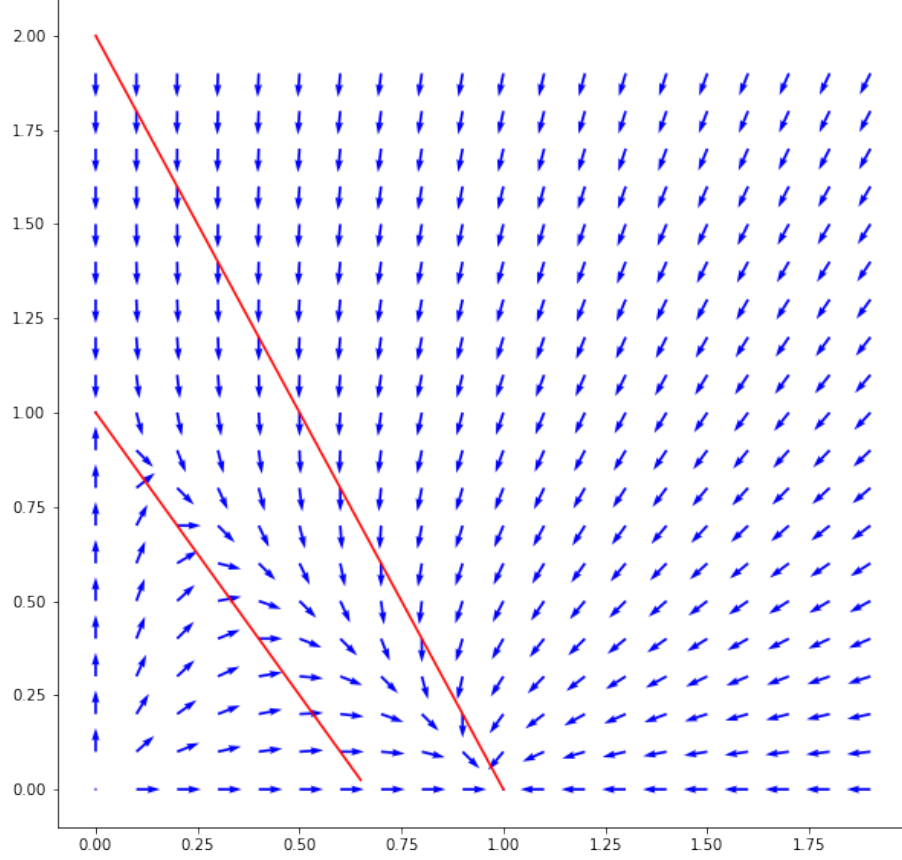


Figure 7: Case 3 with condition $a_{12} < 1, a_{21} > 1$. Here, $a_{12} = 0.5$ and $a_{21} = 1.5$

In this case we observe one stable steady state at $(1, 0)$. Most significantly, we can see that all trajectories tend towards this point, even trajectories that start near the other critical point, $(0, 1)$ (thus, this point is unstable). We can reason this behavior is due to the constants defined. Since a_{21} is based on b_{21} , which is defined as the competitive effect of population 1 on population 2, we can see that population 1 on the x-axis wins, no matter the initial values of both populations. This is expected behavior, since if population 1's competitive effect is so significant on population 2 then population 1 will defeat population 2. One can imagine a scenario where population 2 could be small, defenseless animals, and the other population are large and dominating, easily out competing the other population.

4.1.4 Case 4

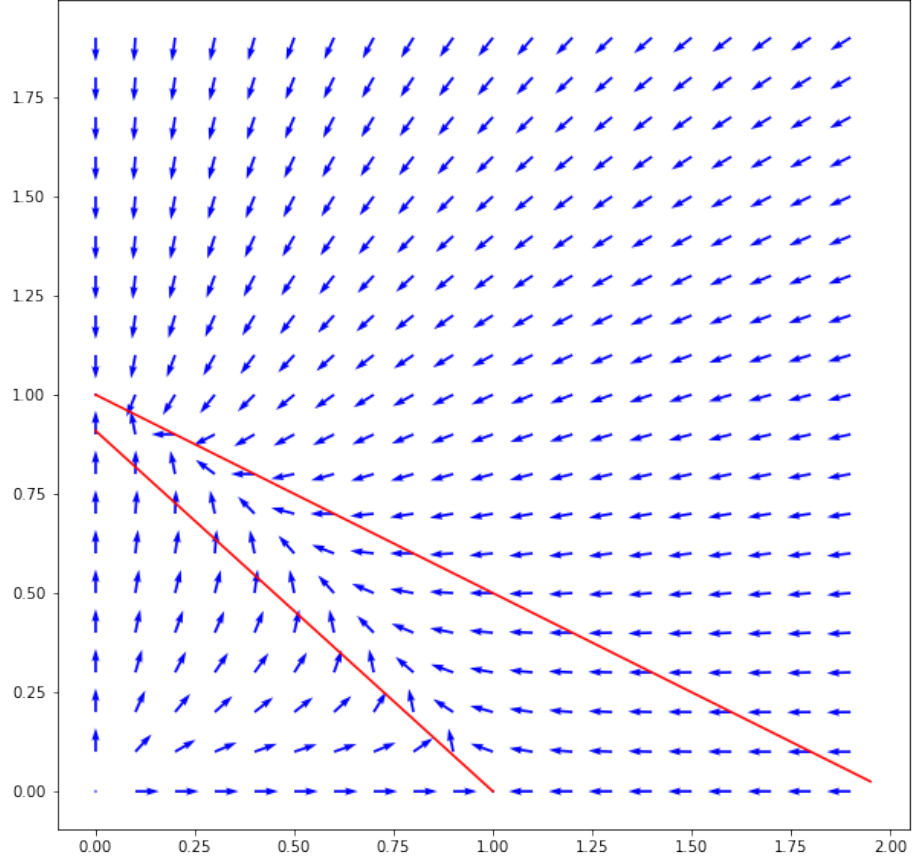


Figure 8: Case 4 with condition $a_{12} > 1, a_{21} < 1$. Here, $a_{12} = 1.1$ and $a_{21} = 0.5$

In this case we observed the steady state at $(0, 1)$. The most important thing to note is that the trajectories point towards that specific point no matter where they start from, which is very similar to Case 3 also being an unstable state. This case always leads to one of the populations becoming extinct, in this case population 2 could kill off population 1.

4.2 Findings

We can see that from the cases, we witness the "principle of competitive exclusion." Except for case 1, all cases result in one species going extinct. We can also see there is a contrast to Lotka-Volterra, which does not predict stable coexistence is possible. As the text puts it, case 2-4 "illustrate the competitive exclusion principle whereby 2 species competing for the same limited resource cannot in general coexist." Note also that $a_{12} = a_{21} = 1$ is a special case (not elaborated in the text) and also results in competitive exclusion. The results found are not surprising, and the book mentions several practical applications for this model, particularly with animals of significant differences in sizes (or lack of differences). Mentioned competition cases include squirrels, wolf-deer survival, and genetically engineered organisms.

5 Mutualism

In this scenario, interaction of two or more species is advantageous to all. It plays a role in promoting and maintaining a species, such as plant and seed dispersal. This particular behavior has not been as studied, in part because simple models like Lotka-Volterra give meaningless results. One such proper mutualism model that is simple like Lotka-Volterra is:

$$\frac{dN_1}{dt} = r_1 N_1 + a_1 N_1 N_2 \quad (12)$$

$$\frac{dN_2}{dt} = r_2 N_2 + a_2 N_2 N_1 \quad (13)$$

Where the r 's and a 's are positive constants, similar to the competition model. These differential equations grow unboundedly. It is defined that realistic models must show mutual benefit, as well as positive steady states or limit cycle oscillation. We can thus add limited carrying capacities for both species.

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + b_{12} \frac{N_2}{K_1} \right] \quad (14)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + b_{21} \frac{N_1}{K_2} \right] \quad (15)$$

One very significant thing to notice is that these equations are **extraordinarily similar to the competition model equations!** The only change is the sign of the b constants. We can infer that these change from representing competitive effect/aggression to quantifying the strength of mutual benefit, thus a positive change in population instead of negative. We again nondimensionalize with the same constants as before and achieve a very similar result (see competition section for definition of new constants):

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) \quad (16)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) \quad (17)$$

These equations are also very similar to the competition model, again with the only difference being a sign change. The definitions of the constants are also the same, so see previous section for definitions.

5.1 Stability and Visualizations

Much like the competition model, we have more than one case, but here we have two instead of four. These values also depend on a_{12}, a_{21} , yet they depend on the product of these values rather than the values themselves. And, again, we have three critical points at $(0, 0), (1, 0), (0, 1)$ and a fourth positive critical point for one particular case. Additionally, our growth rate ratio constant $\rho = 1$ as before. Nullclines are $1 - u_1 + a_{12}u_2 = 0$ and $1 - u_2 + a_{21}u_1 = 0$, represented in red.

5.1.1 Case 1

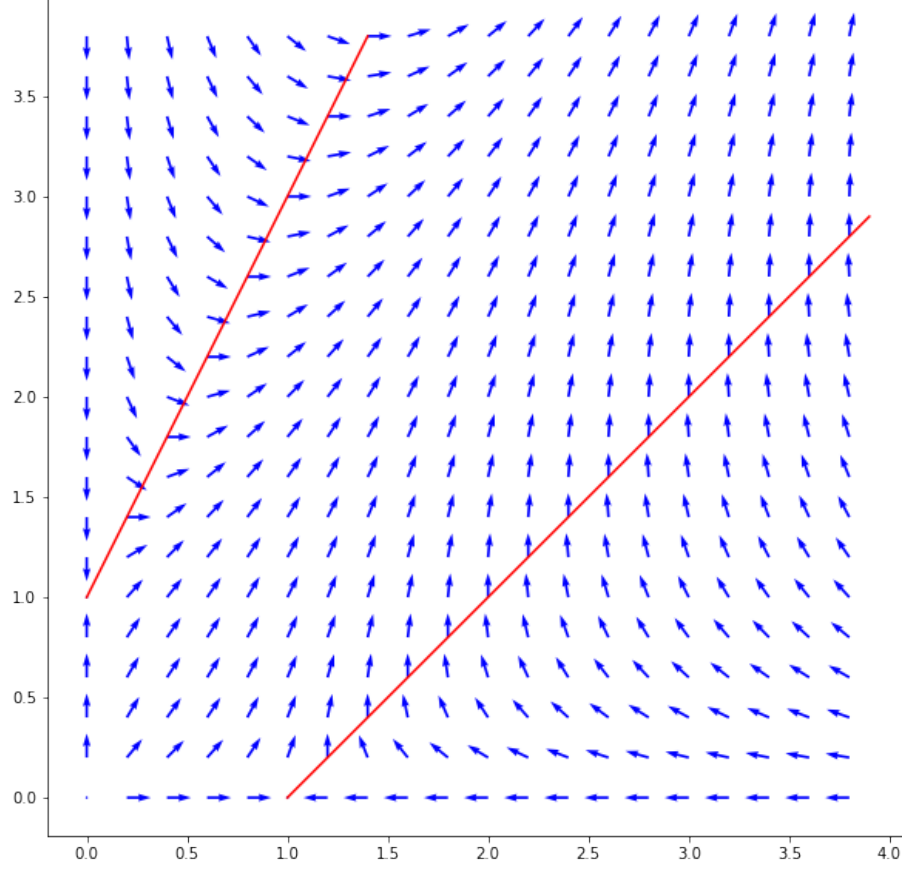


Figure 9: Case 1 with condition $a_{12}a_{21} > 1$. Here, $a_{12} = 1$ and $a_{21} = 2$

Here, we observe unbounded growth from any of the three critical points. The domain is bounded within the nullclines. Conceptually, this can be reasoned since a species with a significantly higher population than the other may begin to die out since there is not enough of the other population to sustain it, but as the other species grows, the species begins to grow as well. The species help each other out and thus having both populations equally supported by the other leads to growth. Thus we can see that as long as both populations are relatively the same, they are predicted to grow towards ∞ . Since this is the case where the a constants multiplied is greater than 1, we can see that the mutual benefit effect of at least one of the populations is so significant that both populations can easily grow.

5.1.2 Case 2

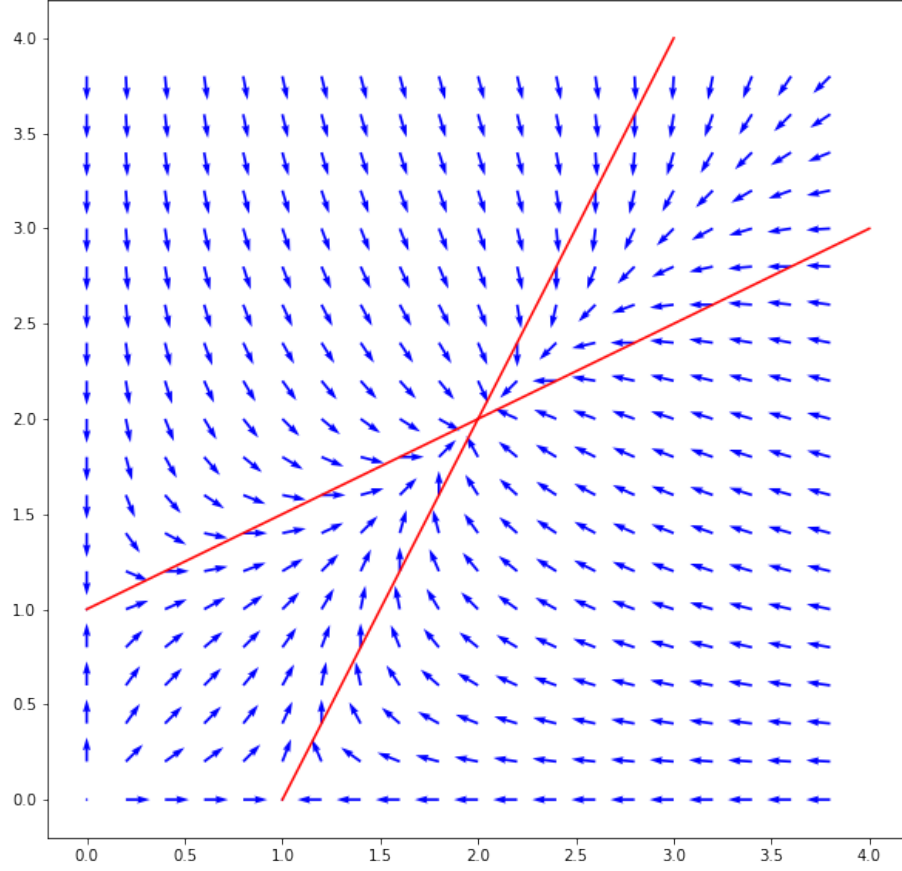


Figure 10: Case 1 with condition $a_{12}a_{21} < 1$. Here, $a_{12} = 0.5$ and $a_{21} = 0.5$

In this case, we see all trajectories tend towards a fourth positive steady state, with the other critical points also being unstable. We can see that there still exists a region of mutual benefit, with similar behavior as the previous case in the lower triangle half of the graph, but after a certain point the populations are bounded and go back towards the steady point. We can reason that the mutual benefit is not significant enough to support the increasing population of a certain species, and thus tends back down to the steady point where both species are comfortably supported by each other. The initial benefit is caused as the carrying capacity for each species is greater than if no interaction were present.

5.2 Findings

We find that this model effectively has the necessary attributes to be a somewhat realistic model: it shows mutual benefit (as witnessed by seeing the growth) as well as a positive steady state, though no limit cycle type oscillation. Thus, we can see that the drawbacks include the sensitivity between unbounded growth and a finite positive steady state. Unbounded growth is rarely if ever realistic, and it is caused when symbiosis of either species is too large. So, the sensitivity is caused due to the inequality that determines the cases of either unbounded growth, or a finite positive steady state. It would be of interest if this project was expanded to analyze a model that does not have these drawbacks. However, this model is indeed useful for analyzing mutual benefit populations, as this type of interaction in the vein of Lotka-Volterra simply give silly results. Thus, this model evokes the same spirit of simplicity to Lotka-Volterra while also realistically depicting the behaviors of a mutualistic system.

Also unrelated to the model but a significant difficulty is that **the equations on page 100 of the textbook is wrong**. They forgot to change the sign of the equations from the competition version, which was extremely frustrating when beginning analysis as our outputs would not align with the provided graphs. Very annoying. The equations included here are the *correct* ones.

6 Conclusion

We hope by exploring these models we see how Lotka-Volterra can be either improved on or used as inspiration to reflect different types of ecology. We can see that we have several notable models, each of which we explored and saw its behavior for how it can accurately reflect these systems. We were able to see how certain models are realistic in some regards, though of course some are still flawed. However, these models either improve or expand upon Lotka-Volterra's behavior and what it simulates, and in doing so we learn how exactly these different types of ecology behave and thus, what attributes the models require. In the future, it would be interesting to explore behaviors of more than just two species. It is mentioned in passing that chaos can be observed for certain models when using more than two models, so this would be topic that could easily be explored further.

All models, equations, and information are referenced, derived, and gathered from *Mathematical Biology I: An Introduction*, J.D. Murray.

Code for graphing phase portraits will be available on my github.
<https://github.com/eugene-y-mak>

Modeling different types of interacting populations (*From Mathematical Biology I, J.D. Murray*)

Eugene Mak and Jenna Riley

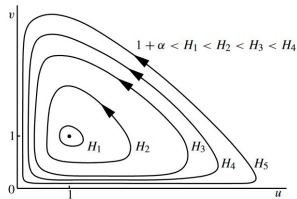
Lotka-Volterra

- A simple, but flawed model. Some reasons include the fact it is a conservative system, which are “of little use as models for real interacting populations,” and it allows negative or unbounded populations.
- We achieve a more realistic model by fixing these two flaws, seen below.
- Lotka-Volterra’s simplicity inspired our other models to be similarly simple, but realistic.

$$\frac{dN}{dt} = N(a - bP),$$

$$\frac{dP}{dt} = P(cN - d),$$

$$\frac{du}{d\tau} = u(1 - v), \quad \frac{dv}{d\tau} = \alpha v(u - 1).$$



Realistic Predator-Prey

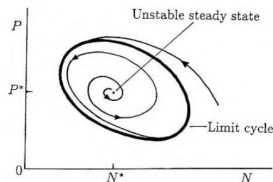
- There are MANY possible variations that are more realistic predator-prey models, specifically due to different possible predation and growth terms.
- Any of these variations should make growth rates depend on prey and predator densities (unlike LV, which is unbounded)
- Also depicts *stable limit cycle* oscillation, have bifurcation properties as parameters vary (steady state \rightarrow oscillation)

$$\frac{dN}{dt} = N \left[r \left(1 - \frac{N}{K} \right) - \frac{kP}{N + D} \right],$$

$$\frac{dP}{dt} = P \left[s \left(1 - \frac{P}{N} \right) \right],$$

$$\frac{du}{d\tau} = u(1 - u) - \frac{auv}{u + d}$$

$$\frac{dv}{d\tau} = bv \left(1 - \frac{v}{u} \right)$$

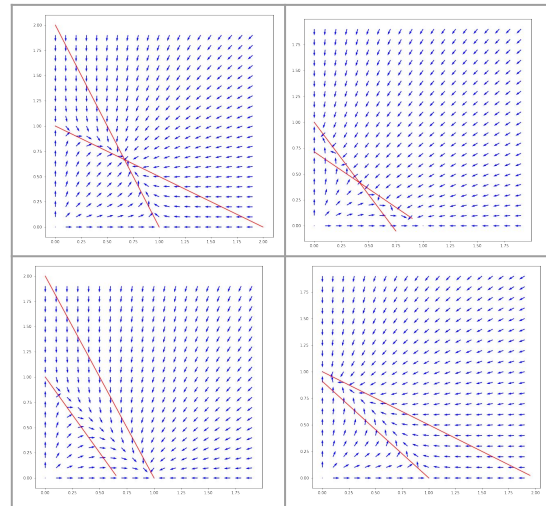


Competition

- Scenario where two species compete for same limited resource (food, territory). Lotka-Volterra CAN model this with logistic growth, but this is a simpler model that has the same properties, in addition to not being conservative.
- Predicts different cases of stability: one where species co-exist (II), one where either species can dominate (I), and two where one or the other species will ALWAYS dominate (III, IV). Most cases demonstrate competitive exclusion principle.

$$\frac{dN_1}{d\tau} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right],$$

$$\frac{dN_2}{d\tau} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right],$$

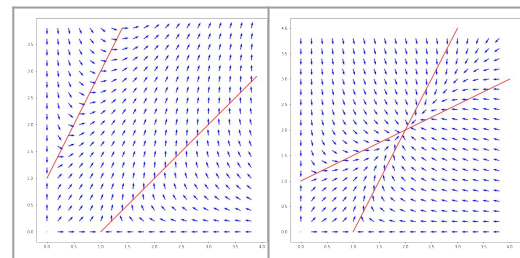


$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2),$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2).$$

Mutualism/Symbiosis

- Interaction between two species is advantageous to both (ex. Plant and seed dispersal). Not as widely studied, even though it is just as important, partly because simple models like LV fail. We use a model that is simple but effective (very similar to competition model).
- Two cases: one with unbounded growth of both species, other with a positive steady state. Unbounded growth is one of its main flaws.



$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12} \frac{N_2}{K_1} \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21} \frac{N_1}{K_2} \right),$$

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1)$$