<u>Stability and complexity in model ecosystems</u>

by Alejandro Stawsky

For this project we used the Lotka-Volterra Model (LVM) described in the prompt:

$$\frac{dn_i}{dt} = r_i(1 - \sum_{j=1}^{N} a_{ij}n_j)n_i \quad \forall i = 1 : N \quad \text{or} \quad \frac{dn_i}{dt} = -k_{extinction}n_i \quad \text{if} \quad n > \text{extinction-threshold}$$

where N is the number of species, r_i is the growth rate for species i, and $a_{i,j}$ are the elements of the interaction matrix A.

Assumptions and model explanation

For this model to show ecologically significant results we needed to make a few assumptions. There are four kinds of species: a prey, a predator, a predator-leaning hybrid, and a prey-leaning hybrid. Furthermore there are only three things one specie can do when confronted with another: ignore, compete for resources, eat the other, or be eaten by the other. There is always one winner and one loser in a predatoric interaction and the winner always consumes the loser for energy in a way that positively affects its species' population. A prey is a species that can only compete for resources and be eaten and a predator is a species that can only eat other species and be eaten itself. The other two species need to be defined because, as will be explained soon, the value of the growth rate r_i depends on how much of a predator or prey one species is with respect to the community it's living in.

Looking at the analysis to recreate the classical two species LVM we can see that, while our formulation and the original 2 species LVM are equivalent, we absolutely need at least one negative growth rate value, r_i, to express the same dynamics:

$$\begin{bmatrix}\partial_t n_1\\ \partial_t n_2\end{bmatrix} = \begin{bmatrix}r_1\\ r_2\end{bmatrix} * \begin{bmatrix}n_1\\ n_2\end{bmatrix} * \left(\begin{bmatrix}1\\ 1\end{bmatrix} - \begin{bmatrix}a_{11} & a_{12}\\ a_{21} & a_{22}\end{bmatrix} * \begin{bmatrix}n_1\\ n_2\end{bmatrix}\right) \equiv \begin{bmatrix}\frac{dx}{dt} = \alpha x(1 - \frac{\beta}{\alpha}y)\\ \frac{dy}{dt} = -\gamma y(1 - \frac{\delta}{\gamma}x)\end{bmatrix}_{\alpha,\beta,\delta,\gamma>0} = \text{Classical predator-prey, 2-species LVM}$$

$$\iff a_{1,1} = a_{22} = 0, \quad n_1 = x, \quad n_2 = y, \quad r_1 = \alpha, \quad r_2 = -\gamma, \quad a_{1,2} = \frac{\beta}{\alpha}, \quad a_{2,1} = \frac{\delta}{\gamma}$$

In the case of few or weak interactions, the summing term $\sum_{j=1}^{N} a_{ij}n_j$ is smaller than 1 and the sign of r_i dictates the weather the population of species i grows or declines. It would therefore make sense to assign the species that have negative growth rates, r_i, as predators since predators require interaction with prey to survive and can't feed on the resources around them. On the other hand, in the same sparse interaction environment, a prey would grow till its carrying capacity and be perfectly content without any interaction, because interaction to a prey can only mean competition or death since it survives only on the resources around it. Again, this contextual significance leads us to deduce that species with a positive growth rate, r_i, are prey.

So what about the other two specie types, predator-leaning hybrid and prey-leaning hybrid? Well, we took into account the possibility that some species can feed on a certain personal diet that consists of both available resources in the environment and eating other species when they interact with them. However these hybrids, when presented with a situation that has very little, weak interaction, will either generally decrease or increase in population size depending on the value of r_i and the ratio of positive to negative values in the species' interaction row $A_{i,j}\ \forall j$ (if the values of its interactions with each species are not too far apart, ie. small span in $A_{i,j} \, \forall j$). Therefore, whether r_i is positive or negative is what differentiates a prey-leaning hybrid from a predator-leaning hybrid.

The making of interaction matrix A

To avoid feedback loops we first create a random matrix with certain sparsity, then decide randomly for every specie whether it is a prey, a predator, a predator-leaning hybrid, or a prey-leaning hybrid, then hard code a set of symmetrical safeguards with respect to the interactions in matrix A and keeping in mind the sign of r_i for each specie kind. An example of one of these safeguards is that all values in a prey's interaction row, $A_{i,j} \, \forall j$, must be positive or equal to zero; Another example is that if predator i interacts with predator j, then signs of $A_{i,j}$ and $A_{j,i}$ must be opposite or both equal to zero, since in every interaction either they ignore each other or predator i eats predator j or vice-versa (in which case ones' population is therefore positively affected while the others' negatively affected). In order for species i to have an interaction value of zero with species j, species j must have an interaction value of zero with i as well (ie. $A_{i,j} = A_{j,i} = 0$, they must both not have any effect on each other to really ignore each other).

In general interpreting the interaction values depends on the signs of the species' respective r values, namely:

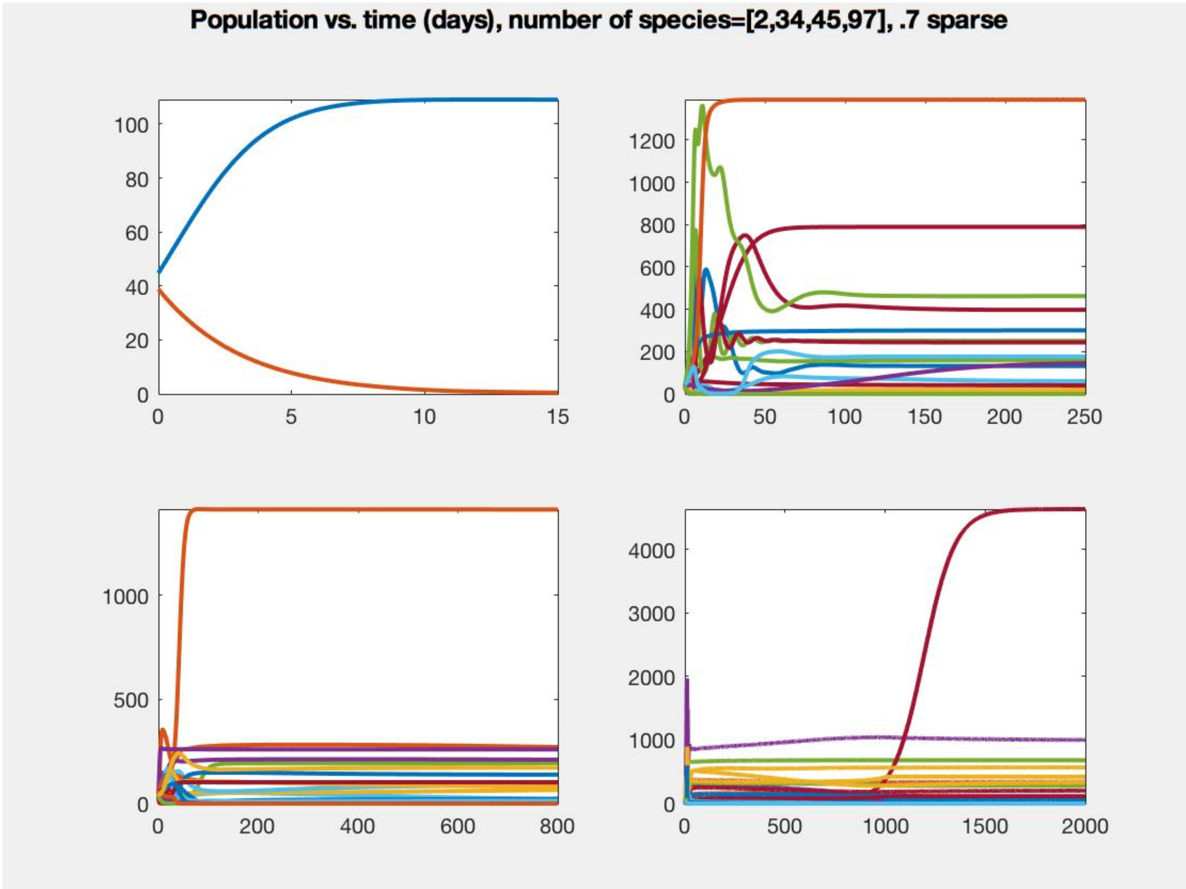
$$\text{if} \quad r > 0, \quad A_{i,j} > 0 \rightarrow \text{hinders growth}, \quad A_{i,j} < 0 \rightarrow \text{encourages growth}$$

$$\text{if} \quad r < 0, \quad A_{i,j} < 0 \rightarrow \text{hinders growth}, \quad A_{i,j} > 0 \rightarrow \text{encourages growth}$$

The full list of safeguards with comments can be found in the section of the code under the name %%% NO FEEDBACK LOOPS, INPUT LOGIC. It should also be noted that the interaction matrix must be relatively weak for stability to occur, ie. the entries of A must be below a certain threshold because, if not, the results of a single interaction over a small amount of time could cause decay or growth too sudden to be realistically meaningful or even too sudden for the ode solver in MATLAB to calculate. The magnitude of the entries of A should also be positively correlated to its sparsity to achieve stability (ie. the less entries in A, the more those entries can afford to differ in range and magnitude). This is mainly because of the second-order dependency of the term $n_i \sum_{j=1}^{N} a_{ij} n_j$.

Results

A) Here we will see how the ecosystem stability depends on the number of species. We take as examples four square interaction matrices of dimension size 2, 7, 15, and 20, both 70% sparse with a extinction-threshold of 1 and $k_{extinction} = .1$ (which we will be using in each simulation from now on).



We deduce a couple things from these graphs about how the system generally behaves as the number of species increases. We can see fast and oscillatory dynamics occur at the begging of the simulation, followed by slower dynamics which take increasingly more time to stabilize as the number of species increases. Also notice that the species populations increase, making the dynamical system more prone to unstable changes.

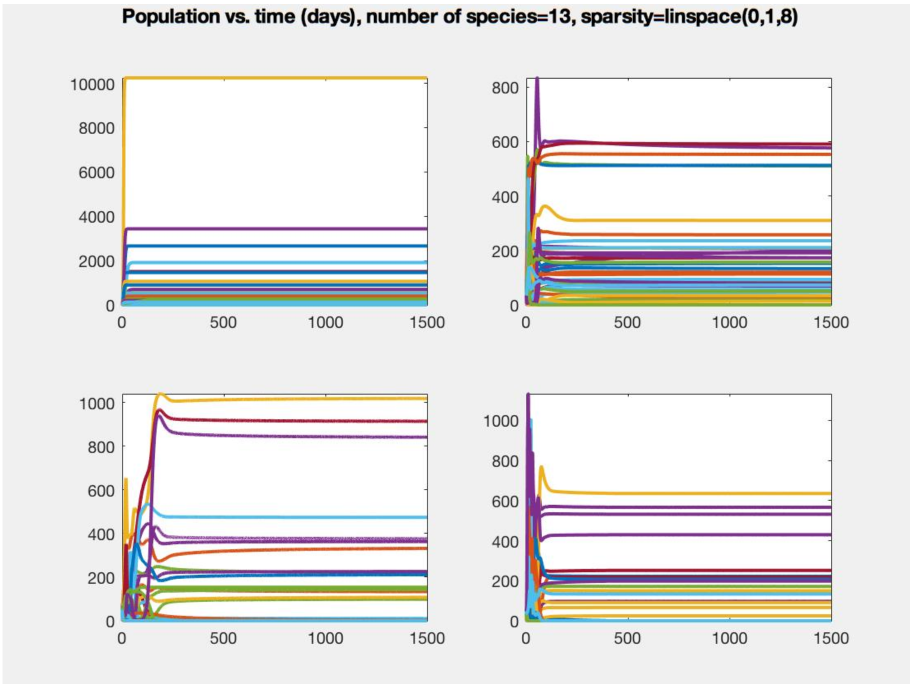
We also took a look at the survival ratio of the 4 types of species at the end of each simulation and found that the most "robust" type of specie is the prey-leaning hybrid:

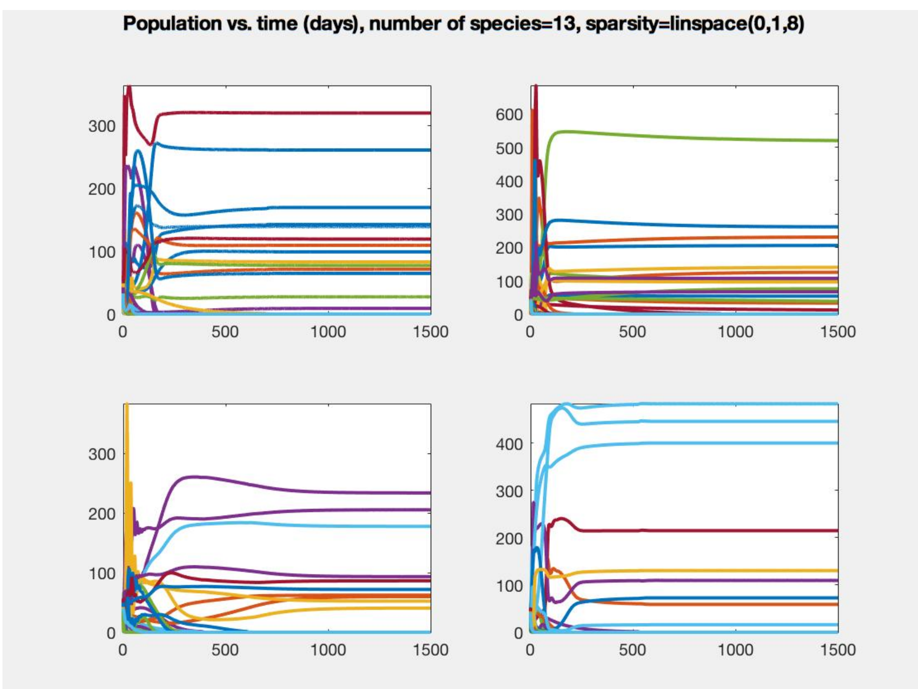
	Prey	Predator	PreyLeaningHybrid	PredatorLeaningHybrid
2 species	"0/0"	"0/0"	"1/1"	"0/1"
34 species	"3/7"	"4/11"	"7/11"	"0/5"
45 species	"3/9"	"2/9"	"11/16"	"0/11"
97 species	"2/26"	"3/23"	"7/28"	"1/20"

At first sight these results could be attributed to the amount of prey-leaning hybrid species at the beginning of the simulation being always bigger than the beginning amount of the other species, since the attribution of the type of specie to each specie is done using a random number generator and 97 species aren't enough for the law of large numbers to have much of an effect. However, if we take into account that our matrix is deliberately created sparse and weak in interactions, then it makes perfect sense that, the lower the amount of species in the environment, the more likely a prey or a prey-leaning hybrid would thrive in given such an environment. Since predators and predator-leaning hybrids thrive solely/mainly off of interaction, we would expect that, if we keep the entries of A between the same range and don't normalize them with respect to the number of species, these two type of species will increase in survival ratio. It also makes sense that the survival ratios of prey and prey-leaning hybrids are negatively correlated to the survival ratios of predators and predator-leaning hybrids. To test this we ran simulations for up to 400 species over a much longer amount of time and found those results to coincide with this analysis/trend.

In conclusion, the more species an ecosystem has the greater the survival rates of predators and predator-leaning hybrids, the less the survival rates of prey and prey-leaning hybrids and, if we don't renormalize the interaction matrix, the longer the system takes to stabilize and the higher the populations rise, making the whole system less stable.

B) Now we will take a random interaction matrix of dimension size 97 and see how the change of sparsity changes the outcome of the simulations and stability. A note: in order to prevent a specie from growing exponentially we decided to always have some value in the diagonal elements and therefore have that value determine the carrying-capacity of the specie. Below are the graphs for the simulations of linearly increasing values of sparsity in the interaction matrix (the top-left graph of the first figure has only elements in the diagonal, while the bottom right graph of the second figure has all the entries of the interaction matrix filled up):





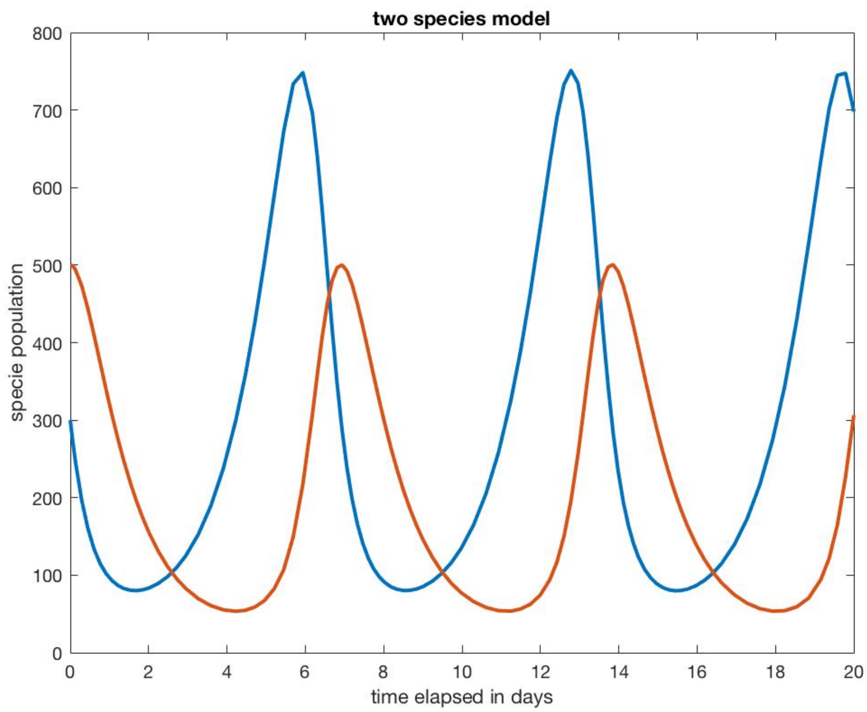
With the exception of the bottom right graph in the first figure, the population dynamics generally take longer to stabilize as A gets less and less sparse. The populations also generally tend to stabilize around smaller values as A gets less and less sparse. This is because the complexity of the model increases the more connective the interaction matrix is and, by the last graph, every change in one specie has some effect on all the others, which creates a domino effect that could take a long time to wear off. Another quantitative trend can be observed by looking at the table below containing the survival ratios:

	Prey	Predators	PreyLeaningHybrids	PredatorLeaningHybrids
sparcity=0	"21/21=1.000000"	"1/24=0.041667"	"26/26=1.000000"	"0/26=0.000000"
sparcity=0.14	"7/23=0.304348"	"7/24=0.291667"	"15/21=0.714286"	"4/29=0.137931"
sparcity=0.28	"4/25=0.160000"	"5/20=0.250000"	"9/22=0.409091"	"0/30=0.000000"
sparcity=0.42	"1/20=0.050000"	"9/32=0.281250"	"7/26=0.269231"	"0/19=0.000000"
sparcity=0.57	"1/22=0.045455"	"3/27=0.111111"	"7/19=0.368421"	"3/29=0.103448"
sparcity=0.71	"1/17=0.058824"	"5/34=0.147059"	"9/29=0.310345"	"0/17=0.000000"
sparcity=0.85	"0/24=0.000000"	"2/22=0.090909"	"8/25=0.320000"	"0/26=0.000000"
sparcity=1	"1/27=0.037037"	"2/20=0.100000"	"5/28=0.178571"	"1/22=0.045455"

As the sparcity increases the survival ratio of all types of species decreases, though we can see a much steeper drop in the prey and prey-leaning hybrids. As explained in the previous section, prey or prey-leaning hybrid are negatively affected by any interaction while for predators and predator-leaning hybrids interactions can either benefit or detriment their populations. This is why prey-leaning hybrids always fare better than any other type of specie and why predator-leaning hybrids almost always go extinct. Looking at the predators column, we can see that the best environment for predators is one which contains enough interactions to have a chance to feed but not too many so that there are not enough prey to feed on or too many predators eating each other. An interaction matrix with a low to middle sparsity value seems optimal for total specie survival.

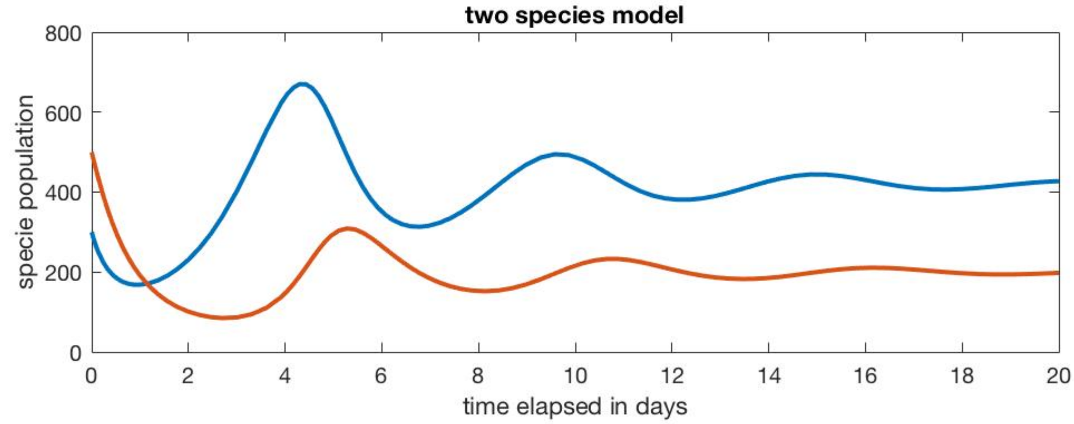
We now use the classic two-species predator-prey system to show what happens if we make the interaction matrix less sparse. We simulate the system $A = \begin{bmatrix} 0 & 1/200 \\ 1/300 & 0 \end{bmatrix}$,

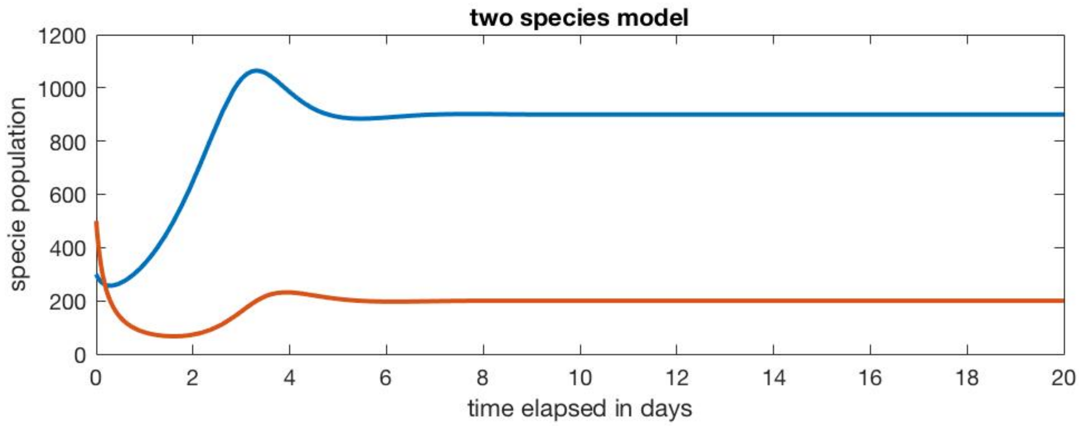
$r = [1, -1]$ to get the familiar oscillatory pattern:



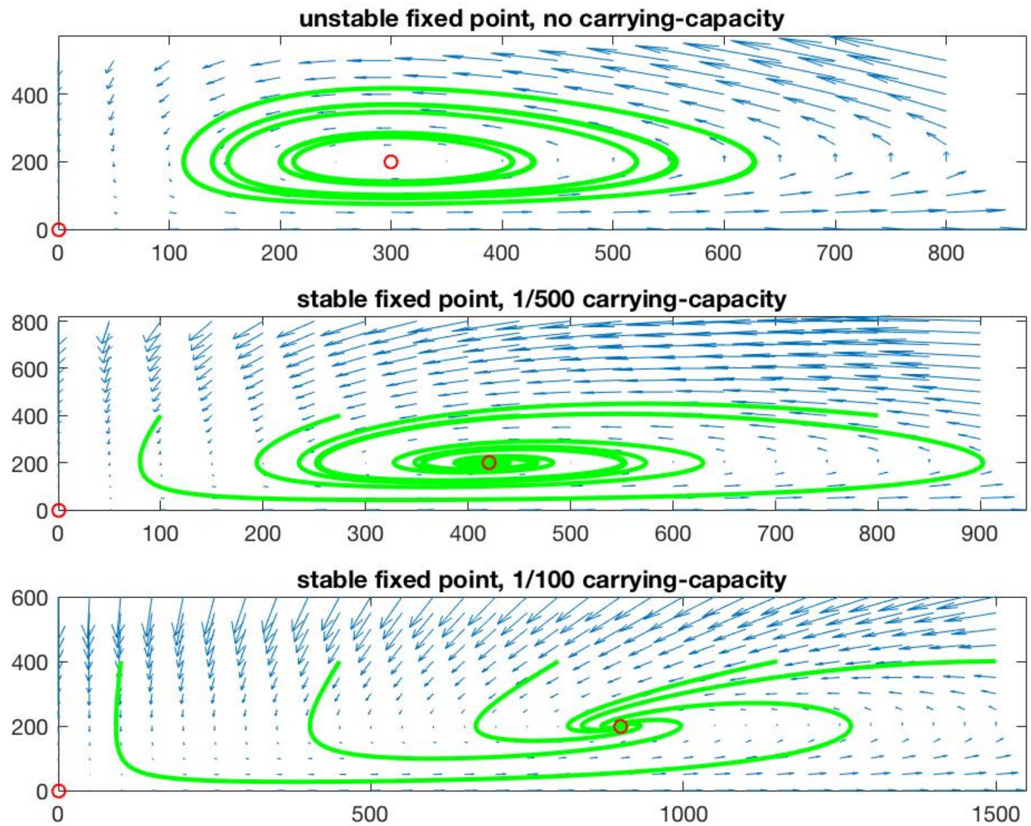
Notice that because there are no diagonal entries the predator and the prey depend solely on the others' population to keep alive, and disregard their own population, meaning there is no carrying capacity. We then experiment by adding two different carrying capacities to the predator population, with the matrices $A = \begin{bmatrix} 0 & 1/200 \\ 1/300 & -1/500 \end{bmatrix}$ and $A = \begin{bmatrix} 0 & 1/200 \\ 1/300 & -1/100 \end{bmatrix}$

shown in the graphs above and below, respectively.



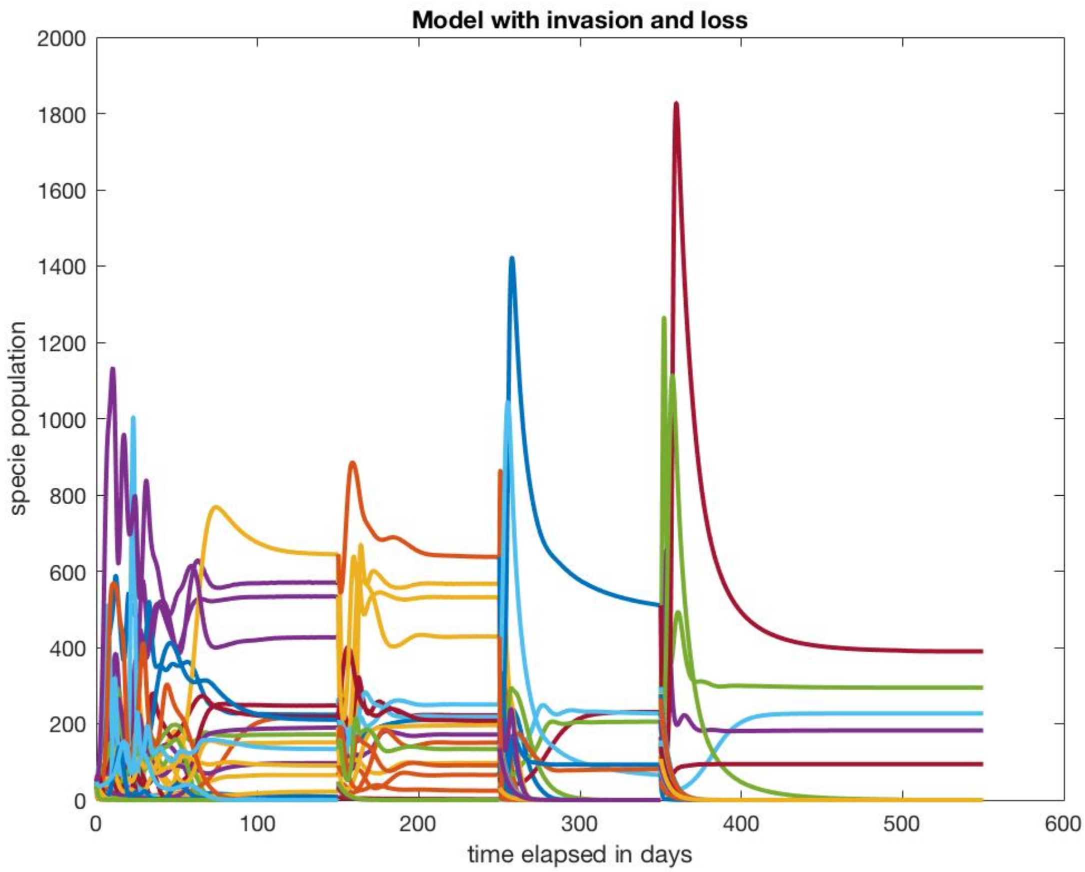


Therefore in this system, less sparsity means more stability, and the stronger this self regulation term is, the faster the system stabilizes. This goes contrary to the analysis shown before, but only because the analysis shown before had a carrying capacity for all the species in its system. In conclusion, the diagonal entries representing carrying capacity stabilize any system, since without them all systems just oscillate somewhat periodically. However, in the presence of a system with carrying capacities, if not calibrated properly, a non-sparse interaction matrix with strong entries leads to extinction across all specie types. The phase plots for all three matrices also gives a clear intuition for how the carrying-capacity values and their magnitude affect the stability of a system's fixed points:

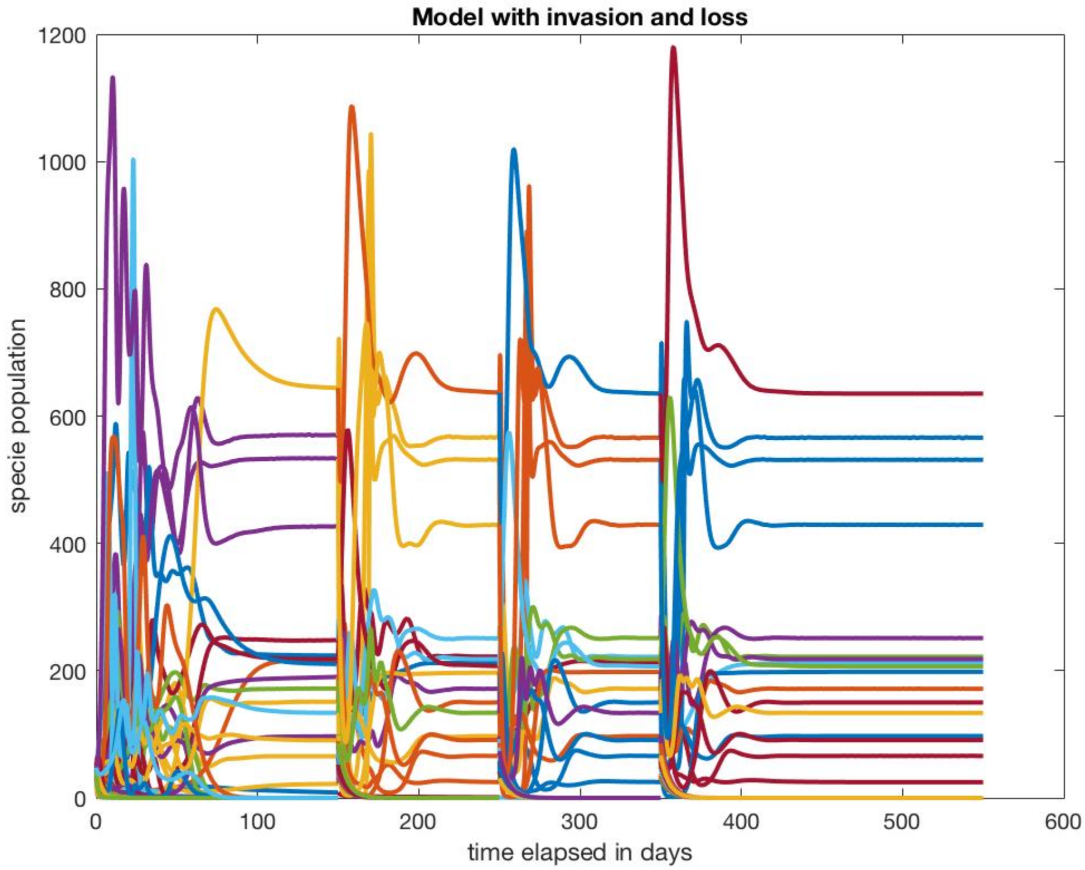


Notice how the top graph never has a solution reach the actual fixed point unless the initial populations of the simulations start exactly at the fixed point. Notice how the bottom two graphs have all their solutions reach the fixed point, making it stable, and how lowest graph takes less a much more direct path to the fixed point compared to the middle one, meaning it does not oscillate around the fixed point as much.

C) Finally we take a system of 97 species, sparsity of 0.42 and run it to equilibrium, simulate invasion or loss by changing the extinct species with invading species of populations between 30 and 50, 50, 200, 300:



And the same expect with invading species of rising populations between 30 and 100:



The survival statistics for the first and second set of four invasions/loss simulations are:

```
survival_rates =
  4×4 table
```

	Prey	Predators	PreyLeaningHybrids	PredatorLeaningHybrids
first simulation	"2/20=0.100000"	"9/32=0.281250"	"7/26=0.269231"	"0/19=0.000000"
second simulation	"2/26=0.076923"	"9/32=0.281250"	"7/22=0.318182"	"0/17=0.000000"
third simulation	"0/18=0.000000"	"2/29=0.068966"	"5/25=0.200000"	"0/25=0.000000"
fourth simulation	"0/23=0.000000"	"1/27=0.037037"	"4/25=0.160000"	"0/22=0.000000"

```
survival_rates =
  4×4 table
```

	Prey	Predators	PreyLeaningHybrids	PredatorLeaningHybrids
first simulation	"2/20=0.100000"	"9/32=0.281250"	"7/26=0.269231"	"0/19=0.000000"
second simulation	"2/26=0.076923"	"9/32=0.281250"	"7/22=0.318182"	"0/17=0.000000"
third simulation	"1/18=0.055556"	"9/29=0.310345"	"7/25=0.280000"	"0/25=0.000000"
fourth simulation	"1/21=0.047619"	"9/32=0.281250"	"7/23=0.304348"	"0/21=0.000000"

From these graphs we can tell that invading species tend to destabilize systems, that is to say cause species to go extinct, no matter what the invading species' populations are. Moreover, if the species are similar in range, we find that the solutions even look the same!