Fitting ecological models to time series data when component functions are misspecified

Hannes Erbis

Systems Science study project - Winter semester 2019/20
Supervisor: Matthew Adamson, PhD

Osnabrück University
Institute of Environmental Systems Research
School of Mathematics/Computer Science

Abstract

When doing research on ecological systems the assumed model may be improperly defined regarding its component functions. One specific exemplary case, which serves as the foundation of this project, is the Rosenzweig-MacArthur predator-prey model in a situation where multiple almost congruent functional responses result in vastly different system responses. The goal of this project is to find out if we can get a correct understanding of the ecosystem even when a component function has been misspecified. Our approach to this problem is to fit an incorrectly defined model to the time series of the supposedly correct model.

The results of this project suggest it may be possible for the Rosenzweig-MacArthur model to decently describe the behaviour and development over time for the predator and prey population, using a functional response that previously gave an improper prediction. This can be realised by using the method of least squares to find appropriate parameters for the incorrect model. However, the resulting parameters may alter the functional response to a degree it's quite distinctive to the actual one which suggests the fitted model doesn't quite grasp the underlying food intake of the predator, decreasing its credibility and applicability. Therefore a correct understanding over an ecosystem is best accomplished by a correct structural specification rather than parameter estimation using misspecified components.

1. Introduction

Sensitivity to the choice of model parameters is a commonly known characteristic of a dynamical system. What's probably less well known but certainly just as critical, is that the behaviour of the system can also be highly sensitive to the precise choice of the component functions. This aspect is even more interesting if said component functions are nearly indistinguishable from another.

In this project we consider an ecological model in the form a predator-prey system where the usage of different almost congruent resource uptake functions results in drastically different system dynamics. Due to the similarity of those functions, one might incorrectly specify this important ecological aspect when finding a model that predicts the dynamics of the ecosystem. The goal of this project is to find out if we can get a correct understanding over the behaviour of an ecological system, even if the model is at least partially incorrectly defined regarding its component functions. We try to tackle this problem by using principles of Statistical Learning in order to find parameters for which an incorrect assumptions leads to a correct prediction of the systems behaviour.

The ecological model we shall consider here is the Rosenzweig-MacArthur (**R-M**) predator-prey model which describes the relationship and development of a prey population x and a predator population y in an ecosystem over time as follows: [1]

$$\frac{dx}{dt} = g(x) - f(x)y \tag{1}$$

$$\frac{dy}{dt} = \epsilon f(x)y - my. \tag{2}$$

The function $g(x)$ describes the growth of the prey population. For this research we assume logistic growth, meaning

$$g(x) = rx(1 - \frac{x}{K}). \tag{3}$$

The parameter r serves as the growth rate and K as the carrying capacity of the prey population. The predator population shrinks in size according to the mortality rate m while the conversion efficiency parameter ϵ describes how effectively a predator can convert the food, i.e. the prey, into usable body energy. To ensure consistency with previous research works, we will assume $\epsilon = 1$ from now on.

1.1. Functional Responses

The functional response (or resource uptake function) $f(x)$ describes how the predator consumes its prey. The prey population shrinks while the predator population grows according to the functional response. In this project we are only concerned with non-linear resource uptake functions opposed to linear functions like it is the case in a Lotka-Volterra system.[2]

Previous research by G. F. Fussmann and B. Blasius (2005) highlights the importance of a proper specification of a functional response and suggests that the dynamics of an ecological model can be highly sensitive to the specific choice of this component function, even when the choices themselves are very similar to each

other. To show this they used the following three different functional responses in the otherwise same R-M-model to compare the impact of increased enrichment.

$$f_H(x) = a_H \frac{x}{1 + b_H x} \tag{4}$$

$$f_I(x) = a_I(1 - exp(-b_I x)) \tag{5}$$

$$f_T(x) = a_T tanh(b_T x) \tag{6}$$

Between the three functional response, (4) is probably the most well known way to describe how the predator hunts and consumes its prey. It is called a Holling Type 2 function and it tries to translate the inability of a predator to search and consume food at the same time.[3] Another widely used functional response is the so called Ivlev function, (5), while other examples like trigonometric functions, (6), are also possible options to describe the underlying situation. The parameters of these functions can be adjusted such that they look very similar to each other.[4]

Figure 1 shows just how similar those functions can be with a specific set of parameters. If not otherwise stated we will continue using these parameters for the functional response. Furthermore we set $r = 1$ and $m = 0.1$ and call the resulting parameter sets **default parameters**.
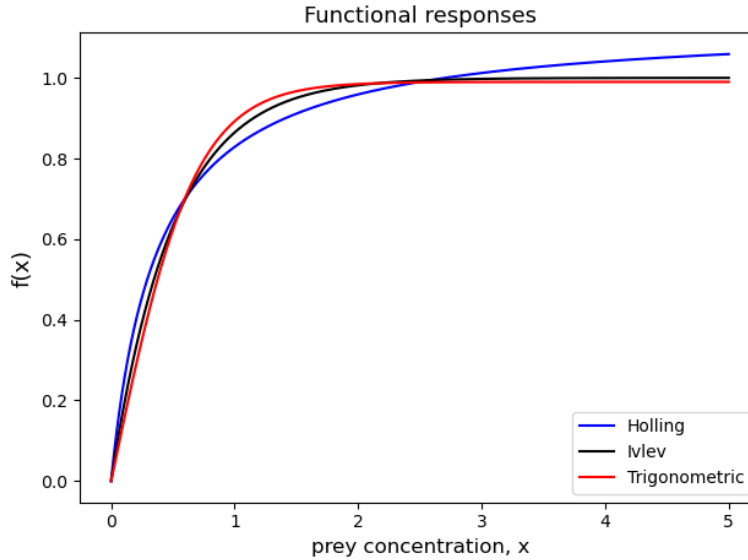

Figure 1: Different functional responses as functions of the prey concentration, x.
Parameters : $a_H = 3.05, b_H = 2.68, \ a_I = 1, b_I = 2, \ a_T = 0.99, b_T = 1.48$
Source: Own illustration based on Fussmann/Blasius (2005)

3

1.2. Nullclines and stability

Although the mentioned functions look very much alike the resulting stability of the equilibria can be quite different. To research this we can take a look at the phase planes of those models. To do so, we need to find the nullclines, i.e. the values for which there is no change in the population size over time. Therefore in a first step we need to set

$$\frac{dx}{dt} = 0 \tag{7}$$

and

$$\frac{dy}{dt} = 0. \tag{8}$$

from *(7)* follows:

$$g(x) - f(x)y = 0 \quad \Leftrightarrow \quad y^{Null} = \frac{g(x)}{f(x)} \tag{9}$$

which is the y-nullcline. To find the other nullcline we have to insert the specific expressions for $f(x)$ and solve for x. Without further prove we attain the following three x-nullclines for the three respective functional responses:

$$x_H^{Null} = \frac{m}{a_H - mb_H}, \quad x_I^{Null} = -\frac{ln(1 - \frac{m}{a_I})}{b_I}, \quad x_T^{Null} = \frac{tanh^{-1}(\frac{m}{a_T})}{b_T} \tag{10}$$

At this point we recognize that the x-nullclines are mere constant values, so to find the equilibria of the systems we only need to look at the point where the y-nullcline takes on those constants. To determine the stability of those equilibria we can and will use the Routh-Hurwitz Criterion (See Appendix A).

The nullclines, equilibria and their respective stability are visualized for $K = 1$ and $K = 4$ in Figure 2. We can clearly see the stability of the populations is sensitive to the choice of the functional response used in that model.

The changing stability properties for different variations of K also offer an alternative explanation as to why real world experiments often fail to replicate the paradox of enrichment, i.e. the destabilisation of populations when more resources are available. K can be thought of a way to simulate enrichment because it increases the available food for predators. An explanation as to why this paradox doesn't always occur, even when the model would predict so, could be that the functional response was misspecified (e.g. a Holling function was used in the model while a trigonometric function would have been more appropriate, which would mean the model would predict a destabilisation of the population for much lower values of K than actually is the case).[4]

Figure 3 gives an overview over when the respective systems destabilise for increasing values of K. Therefore the response to enrichment in the R-M model is sensitive to the model structure. As an additional side note, we won't be concerned with the multi-stability mentioned in the table.
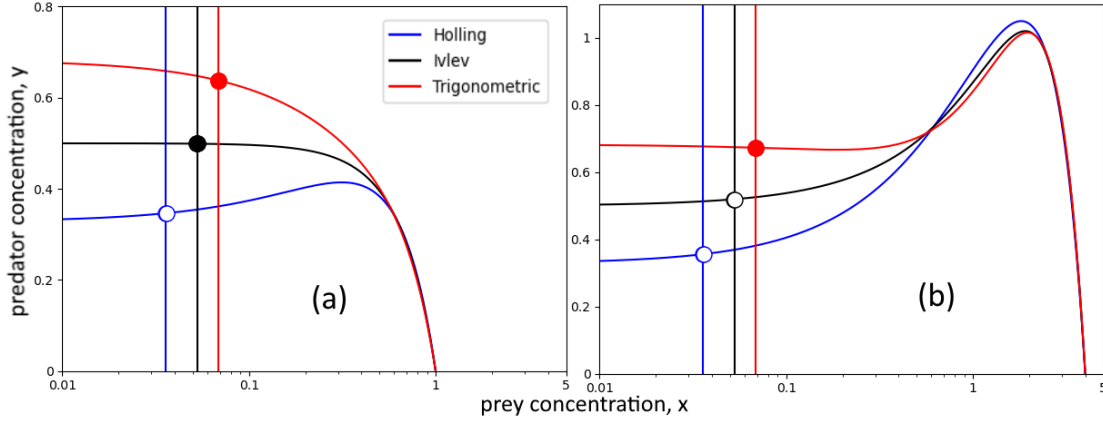
4

Figure 2: Nullclines and equilibria of the R-M model using the three functional responses respectively for **(a)** $K = 1$ and **(b)** $K = 4$. Stable equilibria are illustrated by filled circles; unstable equilbria with open circles.
Source: Own illustration based on Fussmann/Blasius (2005)

level of enrichment	Holling $f_H(x) = a_H x/(1 + b_H x)$	Ivlev $f_I(x) = a_I(1 - \exp(-b_I x))$	trigonometric $f_T(x) = a_T \tanh(b_T x)$
$K < 0.45$	stable	stable	stable
$0.45 < K < 1.08$	unstable	stable	stable
$1.08 < K < 2.65$	unstable	unstable	stable
$2.65 < K < 10.12$	unstable	unstable	multi-stable[a]
$K > 10.12$	unstable	unstable	unstable

[a] Initial conditions determine whether dynamics are oscillatory or settle on equilibria.

Figure 3: Impact of increased enrichment on the stability of the R-M model using the three functional responses.
Source: Fussmann, G. F., Blasius, B. (2005). Community response to enrichment is highly sensitive to model structure

1.3. Time series

To understand how the predator and prey stocks change over time, we have to integrate the given differential equations that describe the two populations. If not otherwise stated we shall consider the initial values $[x_0, y_0] = [0.1, 1]$. The choice of the initial values doesn't have too much of an impact on the dynamics of the Holling and Ivlev system but may cause the trigonometric system to destabilise for specific values of K. Our particular choice of initial conditions causes the trigonometric system to be stable for both $K = 1$ and $K = 4$. Figure 4 illustrates the resulting time series. We notice limit cycles arise just as we would expect from looking at the phase plane in Figure 2.
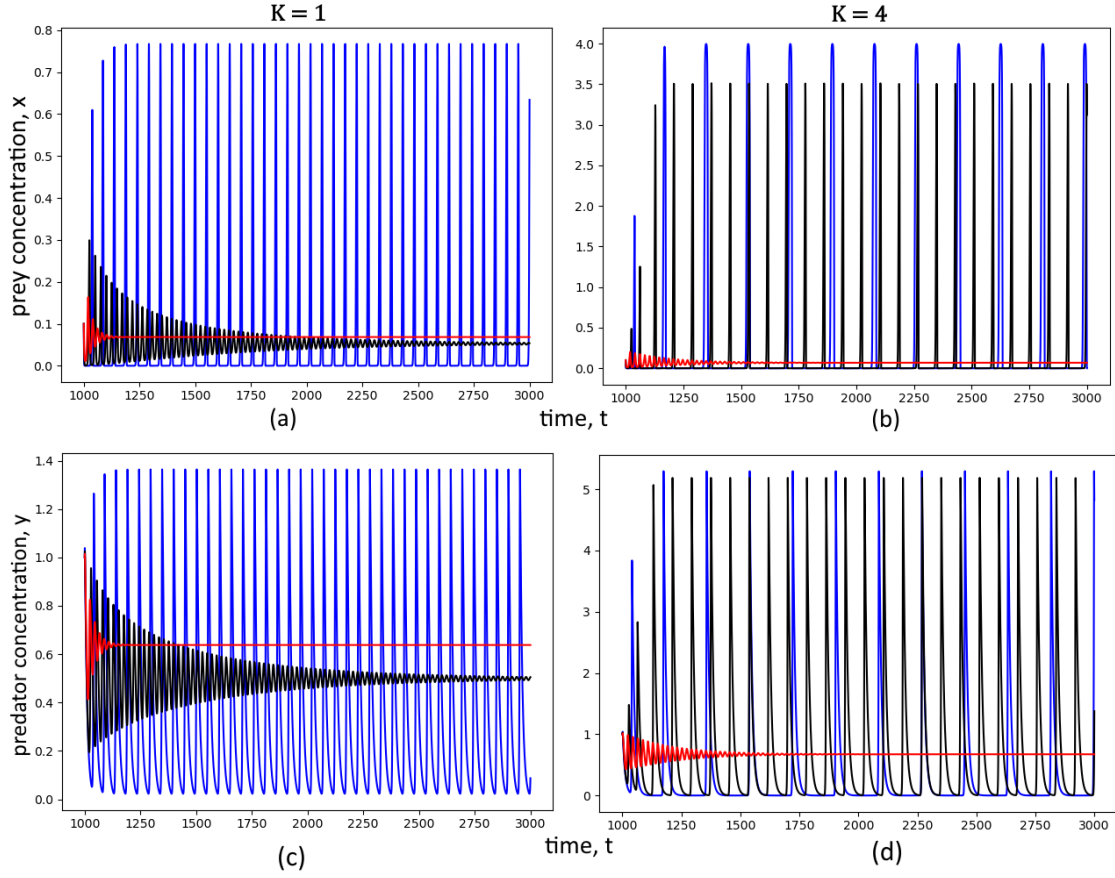
Figure 4: Time series for the prey and predator population for $K = 1$ (**(a)** / **(c)**) and $K = 4$ (**(b)** / **(d)**) for $t = [1000; 3000]$ and Initial values $= [0.1, 1]$. Holling, blue; Ivlev, black; Trigonometric, red

We've seen the stability properties of ecological models may be sensitive to the choice of the function response used and a misspecification of said model component could result in a bad prediction and understanding of the system dynamics. Coming back to the research problem, we want to find out if we can still get a correct understanding from an incorrect model, i.e. a model containing misspecified functions. To tackle this problem we try to use model fitting to see if we can get a correct prediction.

6

2. Model fitting

To find out if we can get a correct understanding using an incorrect model, we want to change the parameters in a way the dynamics match reality. Our approach will be to compare the time series, that the incorrect model produces, to the actual time series of the population and iteratively adjust the model parameters until the time series are as similar as possible to each other. This process is also called *model fitting* and our goal is to *fit* the incorrect model to the actual time series data.

In this project we will consider R-M models with two different functional responses, mentioned in (4), (5) and (6); one as the incorrect and one as the correct model. This serves the purpose of simulating a misspecification of the functional response.

To fit the model to the data, we use the method of least squares, meaning we minimise the squared error between the prediction and the data. Since our models produce two time series maps, i.e. one for the predator and one for the prey population, it's best to consider both in our fit, even though using only one data set might be sufficient for a good fit. In other words, we will minimise

$$\sum_{X,Y} ((x - \hat{x})^2 + (y - \hat{y})^2). \tag{11}$$

X and Y are the prey and predator time series data sets; x and y are actual data points with $x \; \epsilon \; X$ and $y \; \epsilon \; Y$, while $\hat{x}$ and $\hat{y}$ are the predictions of the respective data points. Usually we would divide this sum by the number of data points, n, to obtain the mean squared error but since n stays constant in our implementation across all models and data sets, we can safely ignore it since it has no influence on the argument (parameters) that minimise the error.

We can calculate this error with all combinations of different data and fitting models but for this paper we shall mainly consider the following the scenario:
We want to research the behaviour of two population that are in a predator-prey relationship and we want to use an R-M model to understand the dynamics. We define the functional response based on our idea about the food intake of the predator using the Holling type 2 or the Ivlev function. We define the parameters a and b such that the resulting functional response resembles our previous knowledge and believes as accurately as possible. The other model parameters are defined in a similar fashion. At this point we are ready to simulate the temporal behaviour and dynamics of the populations. Later we notice our model doesn't respond to enrichment the same way the actual populations do. Our model was fine at predicting the population for a specific degree of enrichment, i.e. a specific value of K, but fails to describe the systems response to an increase of it. For example we could have used the Holling function and $K = 0.4$ in our model which would predict the populations to be stable but if enrichment would increase, let's say K

increases to 4, they would be unstable according to the model (see Figure 3) while real world data might show the population remains stable for said K. We now know that our model was incorrectly defined.

Let's assume the populations can be accurately described by using the trigonometric functional response (6) with the given default parameters but we are not aware of it. At this point we might ask ourselves if we can change the parameters of our model so it correctly explains the response to enrichment and therefore the system dynamics. This is were model fitting comes into play. We try to fit the models with the Holling or Ivlev functions to the actual time series data of the populations, which here is artificially created by the model with the trigonometric function.

Figure 5 shows the different nullclines and equilibria for K = 0.4. We notice that all systems have a stable limit cycle, so we might not notice a misspecification right away. Now if we increase the enrichment in the system by increasing the carrying capacity K we attain the phase plane in Figure 2 (b), where only the trigonometric model would predict a stable population size. We now try to change the parameters of the Holling and Ivlev systems, so their time series are as similar as possible to the ones of trigonometric system for K = 4, so we can use them to get a correct understanding of the population dynamics.
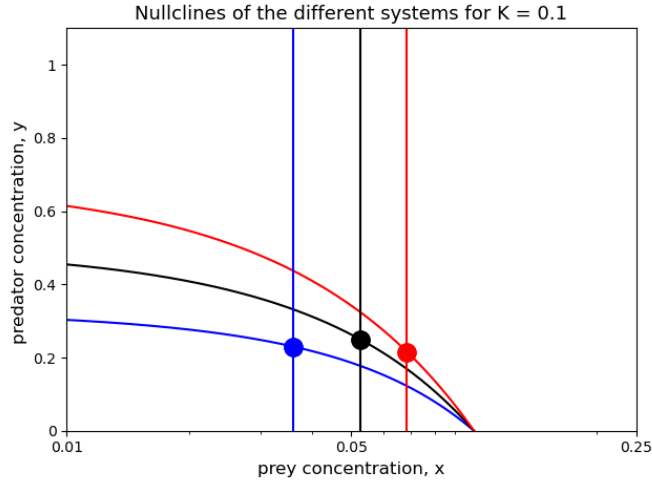

Figure 5: Nullclines and equilibria for the different systems; $K = 0.4$ Holling, blue; Ivlev, black; Trigonometric, red

For the fitting process we use a global minimisation algorithm called Basin-hopping, which makes it possible for the process to escape from local minima. As starting parameters we usually use the default parameters and the same K as used in the data model. Due to the nature of the chosen algorithm, the outcome shouldn't be sensitive to the choice of the starting parameters but it can have

quite an impact on the computing time. Furthermore we restrict our fitting model parameters to always be positive.

2.1. Parameter estimation

First let us understand how model fitting would work out if we restrict the algorithm to only consider the parameters of the functional response, i.e. a and b. This might be interesting for researchers because to validate the model, we can focus on examining if the fitted functional response is compatible with the observed feeding rate.

If we fit the Ivlev and the Holling system to the trigonometric one the fit will be surprisingly successful even when the parameters r, K and m are fixed. If we use other models in the process it might not be as successful though.

Figures 2 (b) and 4 (b) and (d) mark the starting points of the process. After some iterations the time series of the fitted models start to look similar to the data and with a look at the phase plane we notice that the equilibrium shifts towards the one of the data model. At the end of the fitting process we attain the following parameter sets (in the format [**a**, **b**, **r**, **K**, **m**]) for which the models produce time series that are as close as possible to data:

Holling:
$$[1.47335, \ 0.12232, \ 1, \ 4, \ 0.1] \tag{12}$$
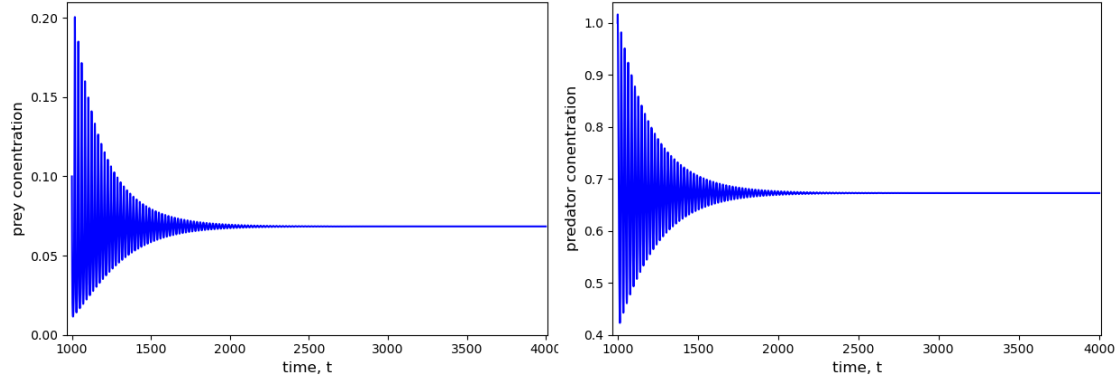
Ivlev:
$$[6.07528, \ 0.24252, \ 1, \ 4, \ 0.1] \tag{13}$$

Figure 5 illustrates the time series of the fitted Holling and Ivlev models using the parameters above. Figure 6 shows how the fitted and original equilibria practically overlap.

So it seems that it's easily possible to change the parameters of the functional response to get a good understanding of the underlying dynamics of the previously structurally sensitive model. We can also extend the scope of the fitting parameters to also include r, K and m. Interestingly the outcome will be mostly the same in our examples. All parameters will stay roughly the same, often only varying after three decimal places. The fitting error on the other hand can be slightly reduced when more parameters are being considered. For example we can achieve an estimation error of 0.037 instead of 0.05 if we fit the Ivlev system to the trigonometric time series from 1000 to 4000 time steps and use all five parameters in the fitting process. We could also find a middle ground by fixing K and changing the remaining parameters. This might be compelling because we get a marginally superior fitting result while still being able to compare the influence of increased enrichment in the three similar systems.
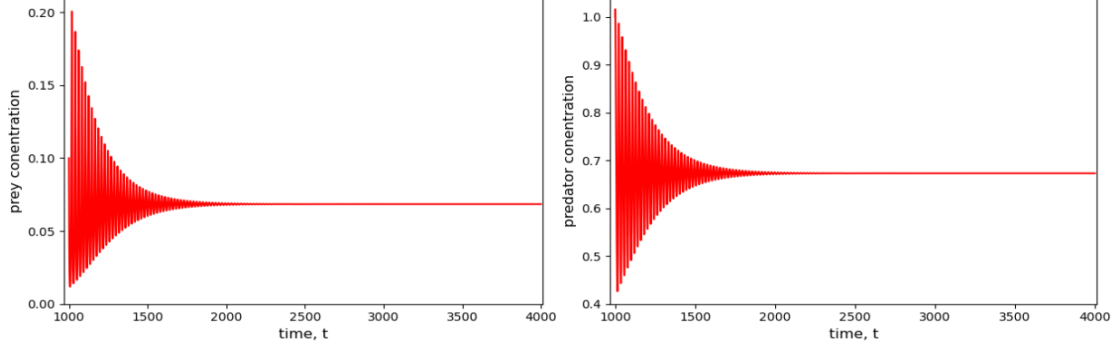
(a) Trigonometric time series using the default Parameters

(b) Holling fitted to trigonometric time series. Same parameters as in (12)
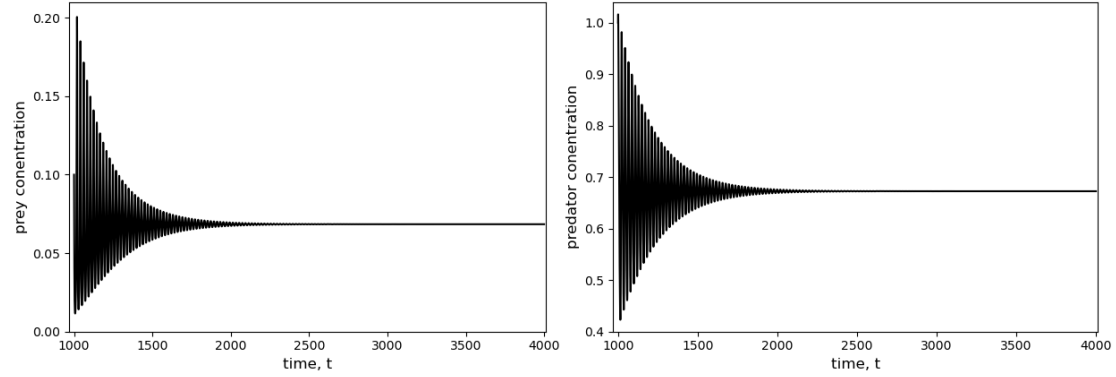
(c) Ivlev fitted to trigonometric time series. Same parameters as in (13)

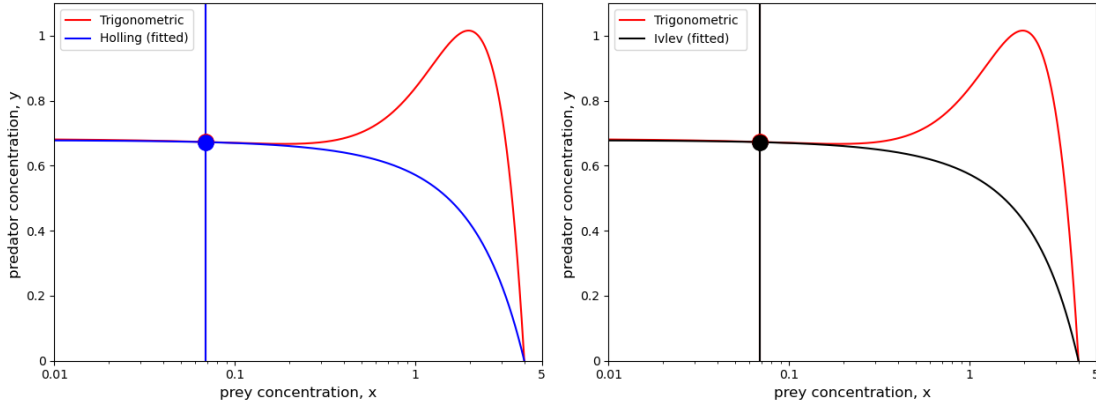Figure 5: Fitting results, Times series of the data *(a)* and the fitted Holling *(b)* and Ivlev *(c)* models.

Figure 6: Nullclines and equilibria of the fitted Holling *(left)* and Ivlev *(right)* models

Fixing a and b and only fitting r, K and m doesn't seem like a valid option because then the fitted model isn't even remotely capable of reproducing the data, resulting in a more than 100 times higher fitting error.

So for now it seems like a good idea to focus on the functional response and only consider a and b in the fit and put up with the slightly higher fitting error but be able to have a better comparison over the different results.

2.2. Measurement error

When doing real world measurements the data often isn't perfectly accurate, e.g. due to the limited precision of measurement devices or human errors. To simulate these circumstances we add a normally distributed noise term around every data point.

The normal (or Gaussian) distribution is a probability distribution that takes the mean, μ, and the variance, σ^2, of a random variable as parameters and outputs a bell curve that's centred around the mean value and whose exact shape is determined by the variance. If we want to model the noise we need to define a relatively realistic variance. For this project we model the noise with a standard deviation (σ) of 0.05, i.e. a variance of 0.05^2. Logically the mean has to be zero because we wouldn't expect the noise to lean towards one direction, meaning the measured value has the same probability to be higher than lower than the actual value. We can now say that after introducing the measurement error, the new data points are normally distributed around the old data point with the variance of the noise term. Figure 7 shows how the old data compares to the new noisy data. As we can see, the noisy data set looks very different than it would without noise.

So at first glance some might think that the algorithm will have a problem to properly fit the function to the underlying dynamics and instead focus too much on the noise, resulting in entirely different model parameters than before. Surprisingly, fitting to the data with added noise will give us parameters that are very close to
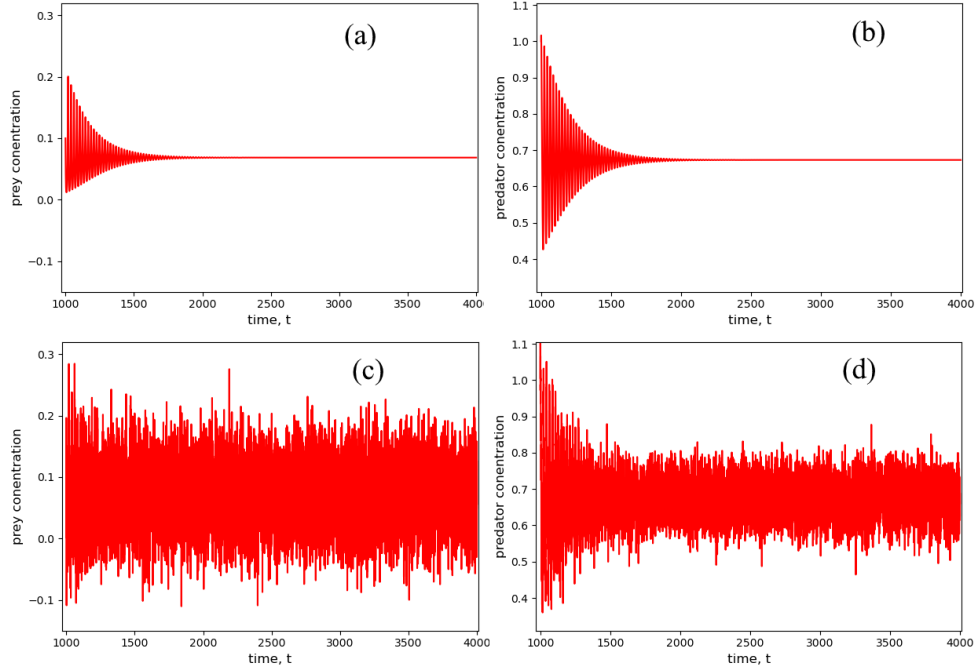
Figure 7: Trigonometric time series with (($\mathbf{c}$) / ($\mathbf{d}$)) and without (($\mathbf{a}$) / ($\mathbf{b}$)) noise ($\sigma = 0.05$).

the ones we got without considering any measurement error, often only varying after two to four decimal places. Note that the specific values are still slightly different for each run since the added noise is somewhat random. A reason for the similarity between the old and new parameter sets could be that the R-M model isn't complex enough for *overfitting* to be a problem, meaning that the model isn't capable of replicating the added noise.

2.3. Original vs. fitted functional response

One might wonder now if our results suggest that we can just interchange the functional responses as we please since the model isn't structurally sensitive regarding the new functional responses. If we take a look and compare the fitted Holling and Ivlev functional responses with the trigonometric one from the real model, we notice a big difference between the three (see figure 8).

So we now arrive at the exact opposite situation of where we started: We have three very different functional responses that produce almost the same system dynamics as opposed to three very similar functional response that produce very different dynamics. This fact comes with certain implications we need to address in the discussion.
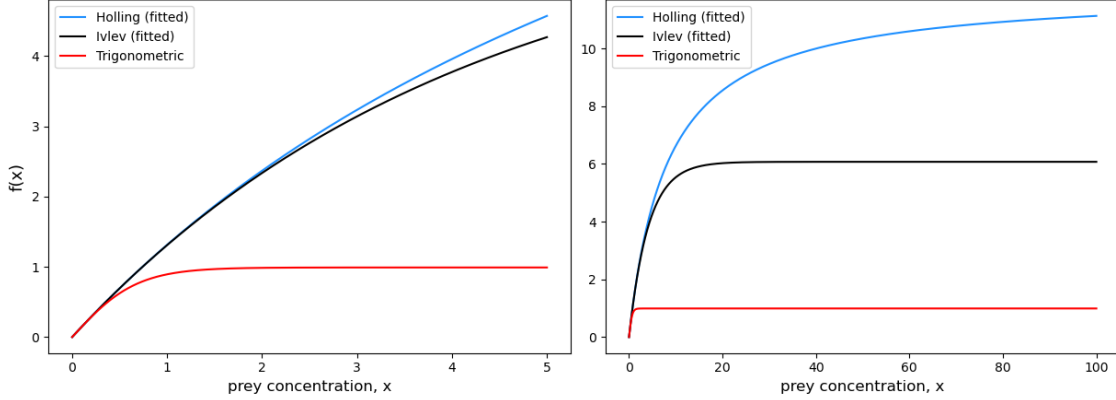
Figure 8: Functional responses in comparison; fitted Holling/Ivlev and trigonometric functional responses, Left: closer look ($x < 5$), Right: zoomed out ($x < 100$).

2.4. Response to enrichment

Now we want to compare the response to enrichment between the three systems. For this we increase K and look at how the system changes it's behaviour, i.e. it's stability. In the style of the works of Fussmann and Blasius, Table 1 illustrates how the stability changes with increased enrichment using the different (fitted) functional responses.

To find these critical values we iteratively increase K and look at the stability of the equilibrium. Due to the structure of the model we can assume that once there has been a regime shift for a specific value of K, increasing it further won't reverse the stability properties. So the first K for which the system is unstable marks the critical point for which every higher value also results in instability or at least multi-stability, which we won't be concerned about in this project. It certainly would be interesting for further research to find out if the new fitted systems are also multi stable for specific values of K like the trigonometric system is.

Looking at table 1 we notice the fitted systems are now considerably more robust to increased enrichment than they were with the old parameters (see figure 3). So the response to enrichment in the fitted systems look more akin to the original but still have noticeable differences.

Table 1: Critical enrichment values in the R-M model for original and the two fitted functional responses

Response to enrichment			
level of enrichment	Holling(fitted) $f_H(x) = 1.47 \frac{x}{1+0.12x}$	Ivlev(fitted) $f_I(x) = 6.08(1 - exp(-0.25x))$	trigonometric(data) $f_T(x) = 0.99 \cdot tanh(1.48x)$
$K < 8.38$	stable	stable	stable
$8.38 < K < 8.4$	unstable	stable	stable
$8.4 < K < 10.12$	unstable	unstable	stable
$K > 10.12$	unstable	unstable	unstable

13

3. Discussion

The results show us it's possible to decently fit mischosen systems to the data by changing it's parameters. In our case, where we fit the Holling and Ivlev systems to the trigonometric one, it seems like fixing r, K and m and only finding parameters for a and b is a very viable option, as an increased scope of parameters only marginally improves the quality of the fit.

Instead of our current example we could also look at what happens if we use other models in the fitting process. For instance it's just as plausible to look at a situation were we used the Holling function, when we should have used the Ivlev one. Fitting the trigonometric model to the data of another model looks to be a little problematic though, as the prediction error will be especially high. This means that the trigonometric model isn't flexible enough to produce time series that are similar to the ones of the other models.

One important note we need to make on the fitting process is that the fitting error seems to decrease when enrichment is lower. The fitting error will be significantly lower if we chose for example $K = 1$ or even $K = 0.4$ instead of $K = 4$ but will skyrocket for even higher values. This once again highlights the big difference in the response to enrichment of the different models as an increase in enrichment can have such a big impact that it is not even possible to change the parameters of the model to produce time series that are satisfyingly similar to ones of another model.

In this project we always used $[x_0, y_0] = [0.1, 1]$ as initial values because they cause the trigonometric system to be stable. We might as well choose any other set of initial values as long as the data model still has a stable limit cycle. For further research it might be interesting to find out how the initial values change the quality and properties of the fit.

3.1. Challenges

Throughout the project there were a few difficulties and complications. First of, our research depends on two computationally heavy tasks: model fitting and differential equation solving. This results in excessive computation time and hinders quick troubleshooting.

Another complication that needed some workarounds was the *stiffness* of some differential equations especially when using the Ivlev functional response. This problem causes some issues for the ODE solver unless we define a very low step size resulting in a considerably more time consuming solving process.[6] To keep the computation time in a relatively modest range it was important to use a solving method that's suited to deal with this problem.

As a quick side note on the response to increased enrichment in the different systems, as seen in figure 3 and table 1: presumably due to number rounding or usage of different methods in this project as opposed to the works of Fussmann

and Blasius, there are some very minor inconsistencies between the specific critical values of K. Our replication of the table in figure 3 underestimated the values by up to 0.03. So it seems probable that the values from table 1 would also vary by a comparable amount.

Last but not least, a quite interesting problem persisted when the data model had an unstable equilibrium. The minimisation algorithm couldn't handle the constant oscillating data when fitting a model to it, meaning that the algorithm wouldn't terminate with a remotely successful fit. Our explanation as to why this happens is that the spikes of the unstable cycle are extremely "sharp" and a prediction, that is also unstable, will cause a gigantic fitting error if it's just a little bit off. So the only way to get a good chance at finding a decent fit is if the algorithm already knows a set of parameters that result in an unstable equilibrium where the spikes almost completely overlap with the data. Otherwise the algorithm will just settle in a stable limit cycle that goes right through the middle of the oscillating data. This gets even more trivial if we use the method of least squares, which we usually do, because bigger mismatches between the prediction and the data will weigh in significantly harder than medium ones. So a straight line through the data seems like the only probable fitting outcome as it always has a mediocre estimation error throughout the entire data set. Unfortunately, minimising the absolute instead of the squared error wasn't met with great success either.

A possible solution could be that we design a new method which not only measures the mismatch between every point but also between the properties of the maps. Since unstable cycles can partially be described by wave characteristics like amplitude and wave length, we might as well consider it when defining a minimisation function. So possible alternatives to the function (11), that could potentially work for unstable cycles, could be:

$$\sum_{X,Y} ((x - \hat{x})^2 + (y - \hat{y})^2) + \omega |\mathcal{A} - \hat{\mathcal{A}}| \tag{14}$$

with $\mathcal{A}$ and $\hat{\mathcal{A}}$ being the amplitudes of the data and fitted time series. Or:

$$\sum_{X,Y} ((x - \hat{x})^2 + (y - \hat{y})^2) + \omega |\lambda - \hat{\lambda}| \tag{15}$$

with λ and $\hat{\lambda}$ being wave lengths of the data and fitted time series. ω would be a parameter that sets the weight on how much the additional condition influences the total error sum. To assure a good fit it would have to be carefully defined. Nonetheless, even after experimenting with different methods this problem remained unsolved in this project.

15

3.2. Interpretation

Now let us try to understand the importance and implications of the project results. As already mentioned it's possible to change the parameters of our model such that the produced time series match reality. Adding artificial noise doesn't seem to impact the fitting results too much but it adds another complexity layer that helps to realistically simulate actual ecological measurements.

If we take a look at figure 8 we notice quite a big discrepancy between the different functional responses, even though they are all responsible for producing very similar looking times series data. This means that the fitted model doesn't grasp all underlying system properties correctly. Therefore it is advisable for researchers to validate the fitted model by manually measuring certain processes. It's especially important for researchers to validate if the fitted functional response is at least approximately in line with reality. This could be done by manually measuring the intake rates of the predator and compare it with the prediction of the model. If we were to take such measurements in our example, we would notice a big difference between the real and predicted functional response, decreasing the applicability of the fitted model, since it fails to properly describe important ecological processes. At this point it might be a good idea to look for another functional response that appropriately describes the feeding rates as well as the dynamics over time. In our example a trigonometric function would be best suited for this. A decision on what specific structure should be used in an ecological model has to be made cautiously since a misspecification can have drastic consequences that might not be satisfyingly correctable just by changing the model parameters.

Appendix A. Theorem 1: Routh-Hurwitz Criterion for a two dimensional differential equation system

Let

$$J_{xy} = \begin{bmatrix} \frac{\partial \phi_x}{\partial x} & \frac{\partial \phi_x}{\partial y} \\ \\ \frac{\partial \phi_y}{\partial x} & \frac{\partial \phi_y}{\partial y} \end{bmatrix} \tag{A.1}$$

be the Jacobian matrix of the two functions (ϕ_x and ϕ_y) that make up the differential equations of two state variables (x and y). Furthermore let $tr(J_{xy})$ and $det(J_{xy})$ be the trace and determinant of the Jacobian matrix.

An equilibirium $[x^*, y^*]$ is stable if

$$tr(J_{xy}) < 0 \quad \wedge \quad det(J_{xy}) > 0 \quad [5] \tag{A.2}$$

The source code, figures and additional information are available for public view at `https://github.com/HannesOS`.

References

[1] Rosenzweig, M., MacArthur, R. (1963). Graphical Representation and Stability Conditions of Predator-Prey Interactions. The American Naturalist, 97(895), 209-223.
`https://doi.org/10.1086/282272`

[2] Bacaër N. (2011) Lotka, Volterra and the predator–prey system (1920–1926). In: A Short History of Mathematical Population Dynamics. Springer, London.
`https://doi.org/10.1007/978-0-85729-115-8_13`

[3] Holling, C. (1959). The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. The Canadian Entomologist, 91(5), 293-320. doi:10.4039/Ent91293-5

[4] Fussmann, G. F., Blasius, B. (2005). Community response to enrichment is highly sensitive to model structure. Biology letters, 1(1), 9–12.
`https://doi.org/10.1098/rsbl.2004.0246`

[5] Malchow, H. (2019). Gleichungsbasierte Modelle I, Skript zum Gebrauch neben der Vorlesung, Universität Osnabrück, Page 61, 99-100

[6] Moler, Cleve; (MathWorks) (2003). Stiff Differential Equations
`https://mathworks.com/company/newsletters/articles/`
`stiff-differential-equations.html`