

Universität Osnabrück

Studienprojekt

Betreut durch

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Wintersemester 2023

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Host-Parasitoid Interactions

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Abgegeben am December 5, 2023

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# 1 Introduction

The Earth's biodiversity is made up of around 1.7 million recorded species. Of these, about 57% are insects, 25% plants, fungi and microorganisms and 20% vertebrates and other animals. Therefore there are nearly 1 million different insect species. (El-Kholy et al., 1992, S. 35ff) About 10% of all described insect species are parasitoids (Eggleton and Belshaw, 1997), which corresponds to about 100 thousand species. This leads to the conclusion that parasitism is a really common thing to expect in a natural environment. For this reason Thompson developed the first host-parasitoid models in the beginning of the 20th century, motivated by the possibility of regulating agricultural pests through the controlled use of parasitoids. These models were very simple and their predictions rather divorced from the often complex behavior found in the field. Therefore numerous other models have been developed. But as today as then, research faces a number of challenges. Although the data has grown over the years there is still a lack of mechanistic understanding of the interactions and complex dynamics that can occur in such a real life system or corresponding model.

When such highly non-linear behavior occurs, analytical mathematic's quickly reaches it's limits. However, thanks to the rapid development of computer technology and numerical algorithms for investigating such complex system behavior, it is now possible to gain insights into such models. This report is intended to show how efficient and convincing these algorithms have become and what results can be expected and achieved. For this purpose, we use cutting-edge algorithms developed in the Julia programming language.

## 2 Model and Methods

### 2.1 The Model

The modeling of host-parasitoid interactions has a long history. Since insects often have separate generations, discrete-time models are suitable. In general all our models base on the following assumptions:

$$\begin{aligned} N_{t+1} &= g(N_t)f(N_t, P_t) \\ P_{t+1} &= cN_t[1 - f(N_t, P_t)] \end{aligned} \tag{1}$$

Given this equations  $g(N_t)$  describes the growth of the hosts,  $f(N_t, P_t)$  the proportion of hosts that is not infested by parasites and  $c$  indicates the average number of parasites that emerge from a parasitized host.

Previos research often build on the assumption that the growth of host following the Ricker map given by:

$$g(N_t) = N_t e^{r(1-N_t)} \tag{2}$$

About this Ricker Model is known that in respect to the intrinsic growth rate  $r$  the behavior changes from stable, over period doubling to chaos. However we want to

reduce this impact, therefore we use the Beverton-Holt map as a also well known model. This model is also a discrete-time equivalent to logistic growth, which shows stable behavior and approaches the carrying capacity in every permitted parameter set.

The Beverton-Holt Model ist given by the following equation

$$g(N_t) = \frac{\lambda N_t}{1 + \frac{(\lambda-1)N_t}{K}} \quad (3)$$

with  $\lambda > 0$  as the intrinsic growth rate and  $K > 0$  as the capacity.

Assuming that the interaction between host and parasitoid is density-dependent with a Holling type III results:

$$f(N_t, P_t) = 1 - e^{-\frac{N_t a c}{N_t}} = 1 - e^{\left[ -\frac{a T N_t P_t}{1 + c N_t + a T_h N_t^2} \right]} \quad (4)$$

with the total time per generation  $T$ , the handling time  $T_h$  and the parasitization rate  $a$ .

Through dedimensionalization with

$$n_t = \frac{N_t}{K} \quad p_t = \frac{P_t}{bK} \quad \alpha = abTK^2 \quad \mu = aT_hK^2 \quad (5)$$

one receives:

$$\begin{aligned} n_{t+1} &= \frac{\lambda n_t}{1 + (\lambda - 1)n_t} e^{\frac{-\alpha n_t p_t}{1 - \mu n_t^2}} \\ p_{t+1} &= n_t \left( 1 - e^{\frac{-\alpha n_t p_t}{1 + \mu n_t^2}} \right) \end{aligned} \quad (6)$$

with the scaled growth rate  $\lambda > 0$ , the scaled parasitization rate  $\alpha > 0$  and the scaled handling time  $\mu > 0$

## 2.2 The Algorithms

The project was implemented in Julia<sup>1</sup> and uses the DrWatson package. To reproduce the results look at README.md on github.com<sup>2</sup>

Because of the complex behavior the existance and stability of an Attractor is hardly analytical shown. Therefore we investigate this behavior by using a few numerical methods. We choose the Julia programming Language because many required functionalities are already implemented, with easy readable code and great performance.

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<sup>1</sup><https://docs.julialang.org/en/v1/>

<sup>2</sup><https://github.com/relias96/Studienprojekt>

### 2.2.1 Orbit-diagramm

An orbit-diagramm is often mistakenly called bifurcation-diagramm. One thing in common is that a parameter is varied over a range, but while an orbit-diagramm only shows attracting equilibria/cycles or possible locations of chaos, a bifurcation diagram in contrast plots all attracting and repelling periodic points (Ross and Sorensen, 2000).

While the computation of the bifurcation diagram can be very complex and time-consuming, the computation of an orbit diagram is relatively simple. Since an orbit diagram is sufficient, we will use it in the following. Because there are co-existing attractors, we implement a algorithm in the following manner:

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#### Algorithm 1 Orbitdiagram

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```

1: function TIMESERIES(system, n, m)
2:   evolve system m times
3:   ts  $\leftarrow$  evolve system n times
4:   return ts
5: function INIT(system, i)
6:   system.initialState  $\leftarrow$  i
7: procedure MYPROCEDURE(system, p_values, period_limit)
8:   m  $\leftarrow$  transient time
9:   n  $\leftarrow$  tracked steps
10:  for all p  $\in$  p_values do
11:    repeat
12:      INIT(system, random)
13:      attractor  $\leftarrow$  Set(TIMESERIES(system, n, m))
14:      if length(attractor) < period_limit then
15:        PLOT(p, attractor) as dots
16:      else
17:        PLOT(p, attractor) as blurred dots
18:    until n > 10

```

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### 2.2.2 Basin of attraction

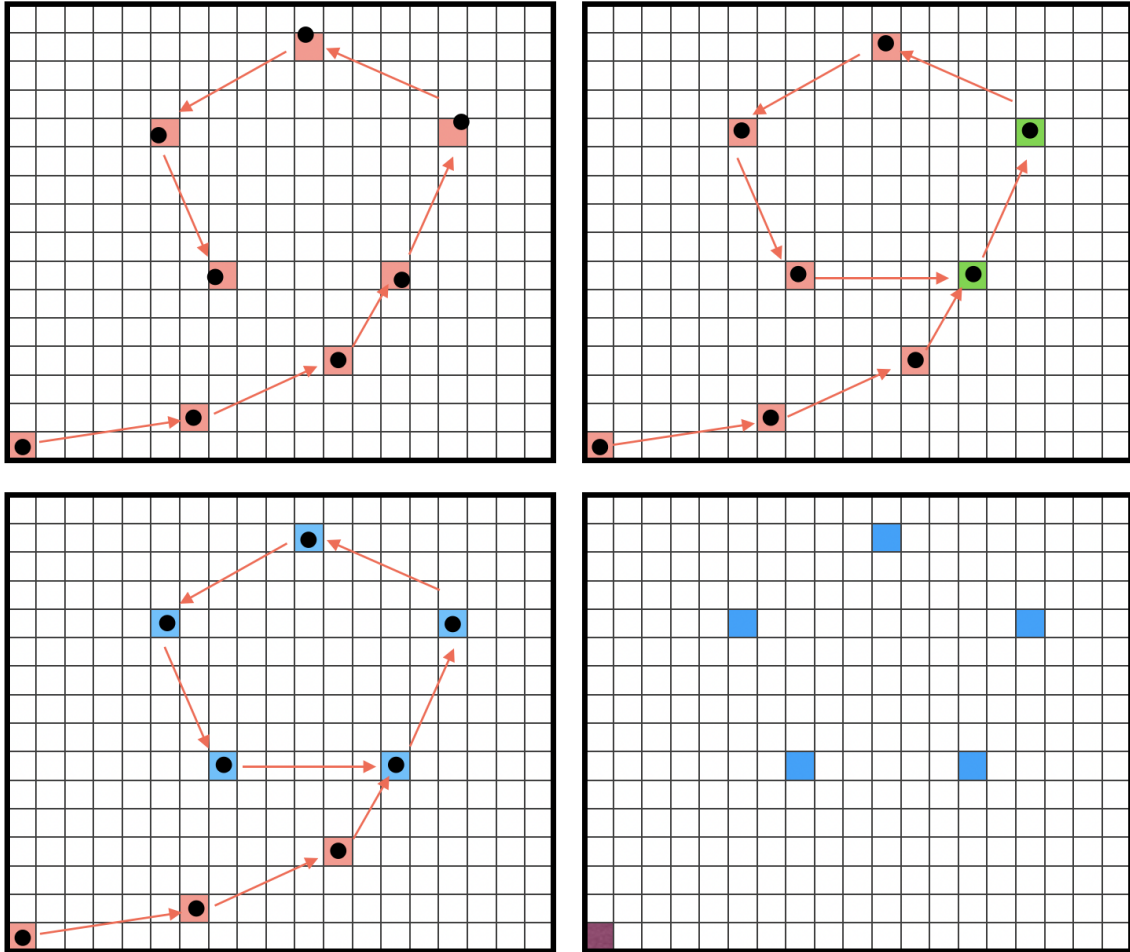


Figure 1: Basin of Attraction

Figure 1 shows the algorithm behind the function `basins_of_attraction` which relies on a method described in Chapter 7 of (Nusse and Yorke, 2012). To get the basin of attraction we use a finite state machine. The state space is divided into a discrete grid initialized with a value `unvisited`. For each initial condition we track the trajectory of the System by using the mapper `AttractorsViaRecurrences` which numerically evolves the given System using the `trajectory` function from the `DynamicalSystems` library and tracks its path in the Statespace. Once an Attractor hits a cell the value changes to `visited` (upper left of Fig:1). When the trajectory hits consecutive times previous `visited` cells an Attractor is detected (upper right of Fig:1). In the following Step the new found Attractor is tracked over `n` time iteration (lower left of Fig:1). In the last Step the initial condition is mapped to the Attractor. Following this algorithm each initial conditions can be matched with one of the Attractors to retrieve the basin of attraction.

For a more detailed description see ‘Effortless estimation of basin of attraction’ by Datseris (Datseris and Wagemakers, 2022).

### 3 Results

By the fact, that we use De-dimensionalized Equations and that we do not have a real life scenario to fit this for, our goal is to gain a qualitative understanding of the Model. Kaitala, Ylikarjula and Heino have shown that their Host-Parasitoid Model, under the assumption of Host growth following a Ricker map, behaves in some strange ways. Due to the behavior of the Ricker map, which shows Chaos at some parameter values, we choose the Beverton-Holt map with its stable Behavior over all parameters to eliminate this destabilizing impacts on the overall behavior. Never the less our Model is highly nonlinear and has some interesting features.

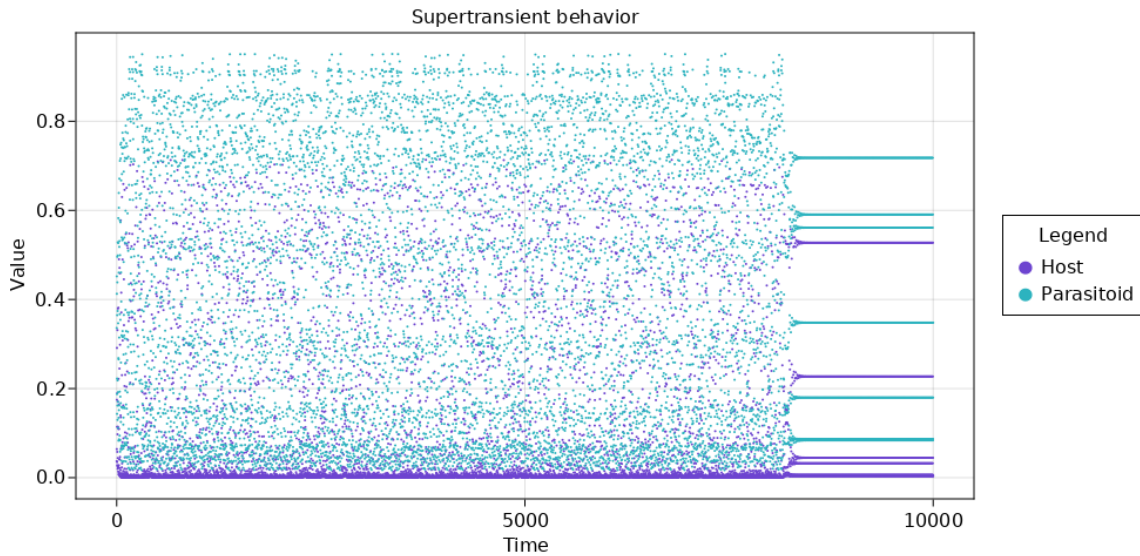
#### 3.1 Overview

The model shows the following complex behavior:

- Supertransient behavior
- Intermittency
- Non-unique dynamics, which mean coexisting attractors
- Basin of attraction

#### 3.2 Transient behavior

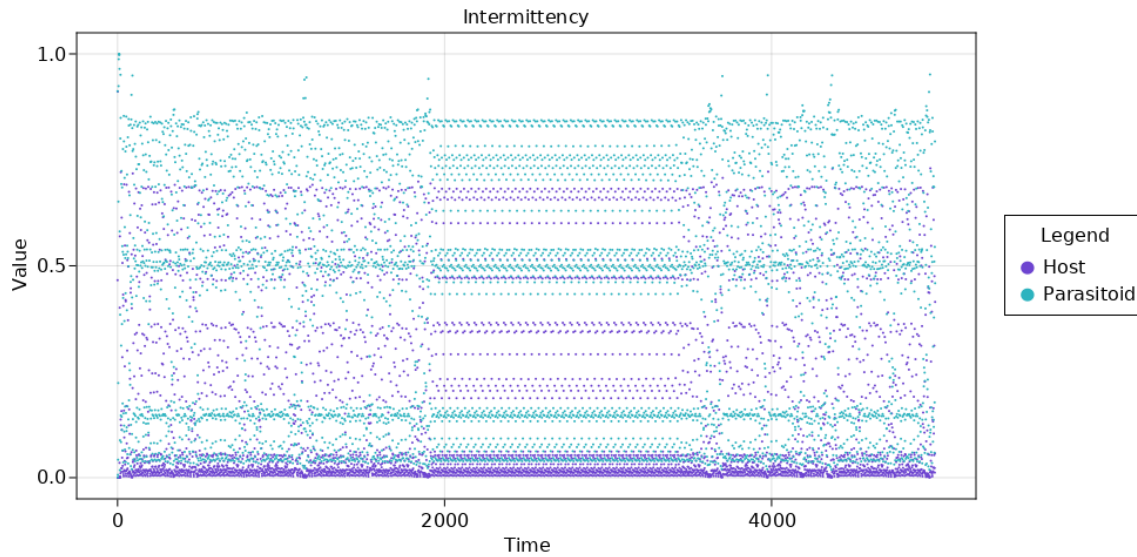
At first we discovered long transient phases before the Model reaches its final state. This means that it takes a unexpected long time of inconclusive behavior before the behavior settles to a state. In Figure 2 the Model ( $\lambda = 2.5$ ;  $\alpha = 17.23$ ;  $\mu = 0.1$ ) reaches it's Equilibrium after 8000 generations.



**Figure 2:** Supertransient behavior

### 3.3 Intermittency

For some parameter combination intermittency occurs in our Model. This means that a equilibrium is no longer stable, but instead randomly switches between states. It is rare to find in this model, but it is possible. In figure 3 the timeseries for the parameters  $\lambda = 6.5$ ;  $\alpha = 21.411$ ;  $\mu = 0.1$  is plotted.



**Figure 3:** intermittency

### 3.4 Non-unique Dynamics

To explore the dynamics we make use of the orbitdiagram to track all attractors given for a parameter combination and plots them in the given way (see Figure: 4).



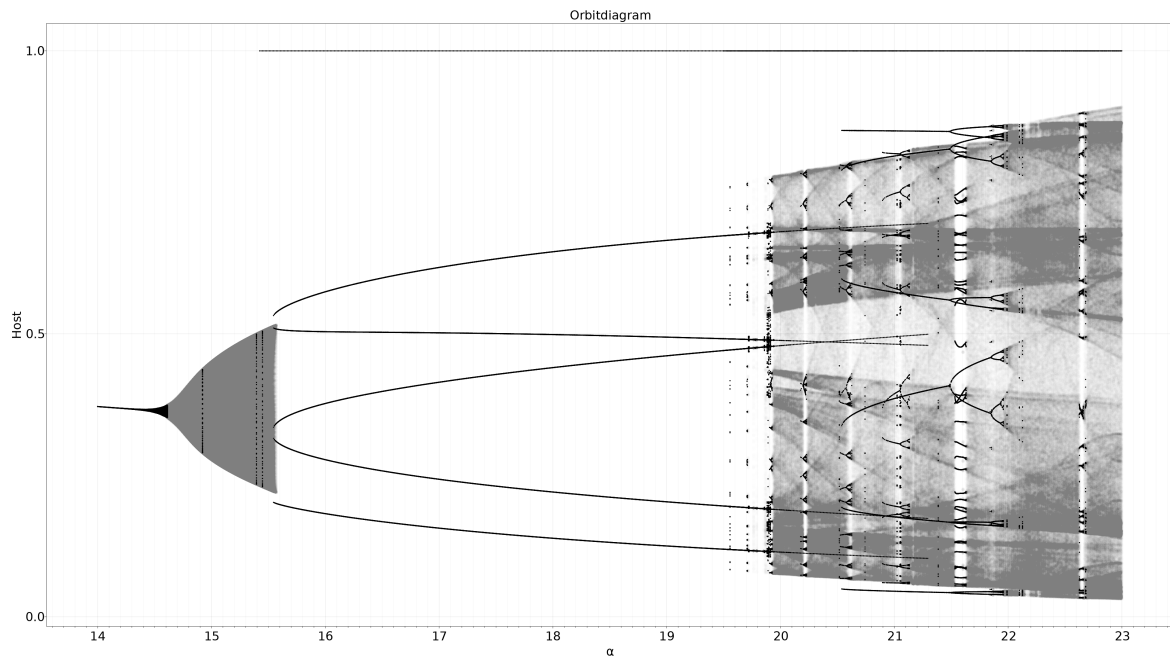


Figure 4: Orbitdiagram

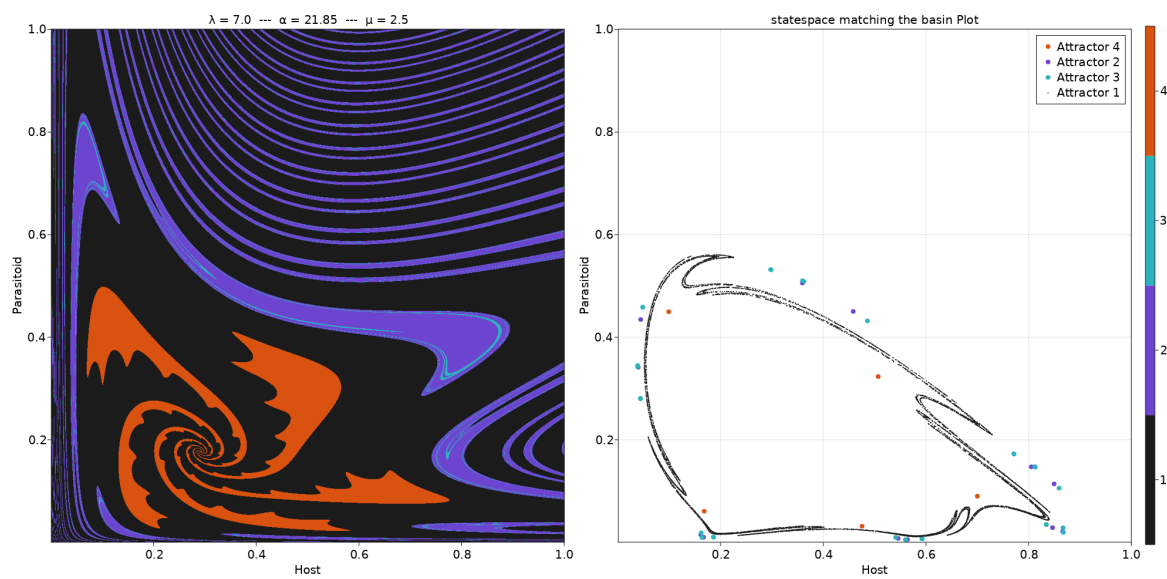
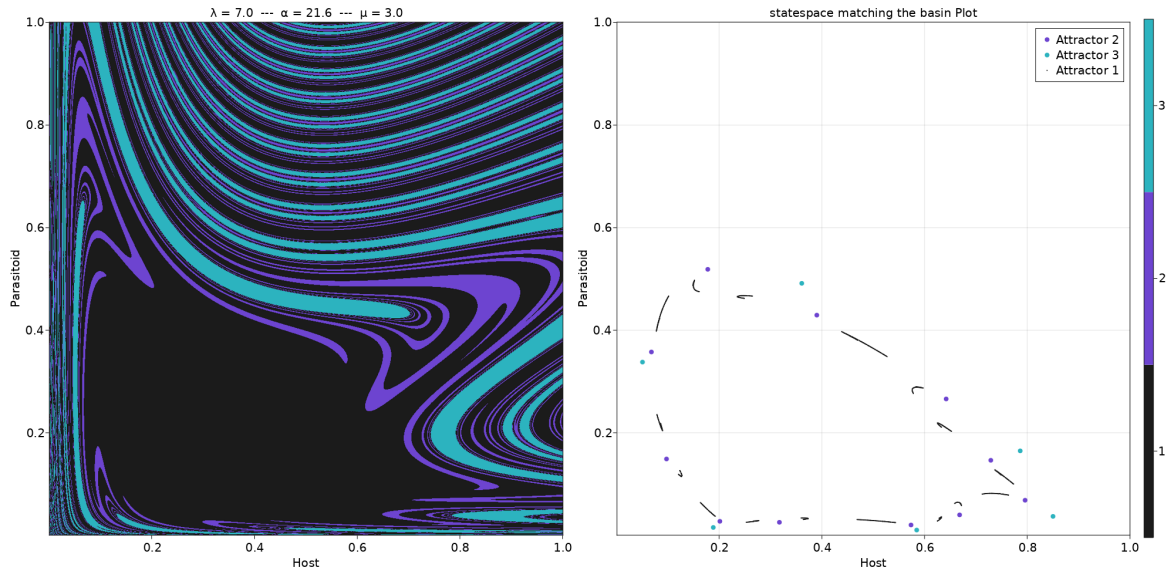


Figure 5: Basin of attraction: Coexisting attractors



**Figure 6:** Basin of attraction: Piece Chaos

## 4 Diskursion

The given System is a fully deterministic Model. Therefore fractal properties do not directly influence the stability of an Attractor. But under respect of random fluctuations, mixed up basins with close proximaty of different Attractors may disturb the System. A metric on the basin based on the neighborhood could quantify this insecurity.

sad(Yu et al., 2009) asdaf(El-Kholy et al., 1992) asgs(Hassell, 2000)

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