INTERACING POPULATIONS IN A RESTRICTED HABITAT– MODELLING, SIMULATION AND MATHEMATICAL ANALYSIS IN CLASS

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This presentation will introduce an authentic modelling process for two interacting species which is well accessible to high school students. Based on an analysis of ecological systems, a simple conceptual model leads to simulation software tools and the derivation of a mathematical model. A wide range of systems, e.g. predator-prey, competition or parasitism can be investigated. The approach also allows independent modelling activities and in silico experimentation by students. As the presented modelling process builds on authentic research by Johannson and Sumpter (2003) it allows to give students an insight into current research of Theoretical Biology.

MODELLING

The importance of modelling in the teaching of mathematics is universally accepted. But often work with models in education consists only in the usage of formulas or the fitting of parameters. There is not much suitable teaching material about reality-based mathematical models. Some groundbreaking efforts were made by Sonar and Grahs (2001, 2002). Gotzen (2003) created well comprehensible, reality-based one-species-models for school use in his doctoral thesis. The two-species models presented in this paper are based on his work.

We will use the following modelling process:

1. Definition of the purpose of the model.
2. Analysis of the real situation.
3. Establish a conceptual model, from simplified description of the real situation.
4. Simulation software and mathematical model equations on the basis of the conceptual model.
5. Predictions and validation using the simulations and/or the mathematical models.

Except for some slight modifications these are the five modelling steps presented by Gotzen, Liebscher and Walcher (2008). See also earlier work of Schupp (1988). Results gained during the modelling process have to be compared to reality and the intention of modelling and thus must eventually be corrected. Hence the modelling process is rather a modelling-cycle as Blum and Leiß (2007) presented. Nevertheless the main idea of modelling will be comprehensible for students following the five steps.

We will introduce population models which are very suitable for educational use because of their relevance, authenticity and traceability for students.

- The models are relevant as they are built on current research of Theoretical Biology (Johannson & Sumpter, 2003).
- As the modelling process is based on capturing the most relevant features of a population development, observed on an ecological level, it ensures a strong biological foundation. This kind of modelling is called "bottom up" modelling. A detailed description of the advantages of "bottom-up" models and a separation from classical "top-down" models is given by Sumpter & Broomhead (2001).
- They are suitable for educational use because the whole modelling process is comprehensible with means of school education. Furthermore the models provide explanations of the observed phenomena and allow predictions.

The models are applicable in mathematical and biological classes in secondary school as well as in education at university (e.g. classes of Biomathematics).

The software and a workbook, which gives all necessary instructions and allows self-contained work of students, are allocated for free use in the internet (Roeckerath, 2008).

PURPOSE OF THE MODEL

We want to derive a bottom-up model of two interacting species which is capable to give information about their development over time. The model shall capture the main important ecological patterns and phenomena affecting the development of the species. Thus we are looking for a model, which gives the size of each population at every generation.

THE ECOLOGICAL SYSTEM

The basis of the modelling process must be an analysis of the ecological system in order to capture the main important structures concerning the development of both populations.

We look at two interacting species which share a restricted habitat. The populations have non-overlapping generations. This ecological phenomenon is common for insects and annual plants and means that at every time there is only one generation alive. Thus parents and children never live together. Parents distribute their offspring randomly over the entire habitat. The offspring is during the first development state (nearly) not able to move (eggs, larvae, seeds).

Individuals interact with individuals of their own as well as with individuals of the other species. These phenomena are called intra- respectively interspecific interactions and affect the individuals' ability of reproduction.

We want to include several kinds of intra- and interspecific interactions appearing in ecology. In the following we want to capture them in formulating interaction laws.

Intraspecific Interactions

Intraspecific interactions appear mostly as competition for resources like food, territory or sunlight. The availability of such resources is mainly responsible for the ability of an individual to reproduce itself. We want to distinguish two kinds of intraspecific competition: exploitation and interference competition, which Nicholson describes as “scramble” and “contest” (1954).

Exploitation competition can appear when individuals share a restricted quantity of resources. In this case a high density causes a lack of resources which prevents individuals from reproducing. Ecological examples of this phenomenon are weakness because of hunger or lacks of breeding or germination areas. We capture the main idea in the interspecific law

> **INTRA 1**. If there is a sufficiently high population density no individual will be able to reproduce.

In the case of interference competition individuals deal directly with each other. There is one dominant individual, which is able to gain enough resources and to reproduce, even if there is a high population density. Ecological examples are cainism, where cubs kill each other until only the strongest cub is still alive, or allelopathy, where plants spread poison into the ground in order to prevent other plants from growing. A simplified description of these phenomena gives the reproduction law

> **INTRA 2.** There is a dominant individual which is able to reproduce even if there is a high density.

More detailed biological background concerning intraspecific interactions and concrete biological examples can be found in the article of Gotzen, Walcher, Liebscher (2006).

Interspecific Interactions

Interactions between individuals of different species can have a positive, negative or no influence on their development. There are many ecological examples showing these kinds of influences. For example an individual of a predator-population needs prey. Thus an interaction with individuals of the prey species will cause positive effect on the predator’s reproduction. A suitable reproduction law for positive influence is

> **INTER +.** If an individual interacts with at least one individual of the other species, then it will be able to reproduce.

On the other hand interspecific interactions can also cause negative influence. A prey animal is only able to survive and reproduce if it will not be killed by a predator.

Also in the case of competition for resources between different species interspecific interactions have a negative influence on the reproduction. A simplified summary is the reproduction law

> **INTER -.** If an individual does not interact with any individual of the other species, then it will be able to reproduce.

In eco-systems there can be populations which share a habitat and interact but one species is not affected by the other. For example huge plants which take daylight from small plants. There is an interaction, but the huge plants are not affected by the small plants. This is captured in the reproduction law

> **INTER 0**. Individuals reproduce independently from the other species.

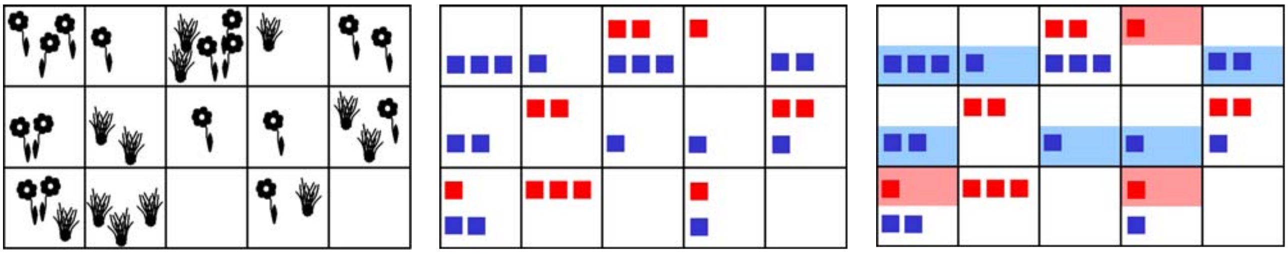
Using the specified interaction laws we will be able to describe a wide range of two interacting species. A concrete example is the following ecological system.

Example: Amensalism
There are two populations of plants which use the same resources. The first species shows the following dominant behaviour. It affects the second species negatively without any influence for it self. Thus it not affected by the second species. This ecological phenomenon is called amensalism. Within the species 1 obtains exploitation competition and within the species 2 interference competition. Using the interaction laws we can determine that species one follows **INTRA 1** and **INTER 0** and the species 2 follows the reproduction laws **INTRA 2** and **INTER-**.

FROM THE ECOLOGICAL SYSTEM TO THE CONCEPTUAL MODEL

After the ecological observations, we will now capture the main important structures affecting the populations' development in a conceptual model. A conceptual model is a (partly very strong) simplified description of the reality. The challenge is to distinguish the relevant and the irrelevant factors. The conceptual model is often only a caricature of the real system but it is clearly arranged and practicable.

The habitat is displayed on a field with a fixed number of sites. Each site represents an area of the habitat. As shown in figure 1(a) and 1(b) for each area the containing individuals are displayed by a dot in the corresponding site. To distinguish the different species the dots are differently coloured.



(a) (b) (c)

Figure 1: Conceptual model

Individuals displayed at the same site are close to each other und thus interact. Due to the non-overlapping generations the development of the real system can be described with discrete time-steps and it is only affected by the number of reproductions. A site provides enough resources for at most one reproduction per species. As parents deposit their offspring randomly somewhere in the habitat, for every new generation the concerning number of dots will be randomly distributed over the field.

Interaction laws

The sites provide a basis to comprise the concept of “high density” for the intraspecific, and the concept of “presence” for the interspecific interaction laws in the conceptual model.

We assume that we have a high density at a site, if it contains more then one individual. Using this understanding of density we can integrate the introduced interaction laws in our model.

> **INTRA 1.** At a site there will be a reproduction for a species, if it contains exactly one individual of the same species.
>
> **INTRA 2.** At a site there will be a reproduction for a species, if it contains at least one individual of the same species.

The concept of “presence” can easily be realized in the conceptual model. The other species is present, if there is at least one of its individuals. Thus we get the following interaction laws for the conceptual model.

> **INTER +.** At a site there will be a reproduction for a species, if it contains at least one individual of the other species.
>
> **INTER -.** At a site there will be a reproduction for a species, if it contains no individual of the same species.
>
> **INTER 0.** At a site there will be a reproduction for a species, if it contains any number of individuals of the other species.

Now the means to determine if there is a reproduction for a species at a site are available: If a species follows the interaction laws **INTRA** and **INTER** then there is a reproduction for this species at a site if and only if **INTRA** and **INTER** are both fulfilled at the site.

In order to get a species' population size of the next generation the reproduction laws must be applied at each site. Multiplying the resulting number of reproductions with the mean number of offspring per reproduction we get the population size of the next generation. The generation cycle repeats by spreading this number randomly over the field. On the basis of this conceptual model, software was created which simulates the development of the species.

Example: Amensalism

Species 1 follows **INTRA 1** and **INTER 0**

Species 1 will reproduce at a site, if and only if it contains exactly one individual of species 1 and an arbitrary number of individuals of species 2.

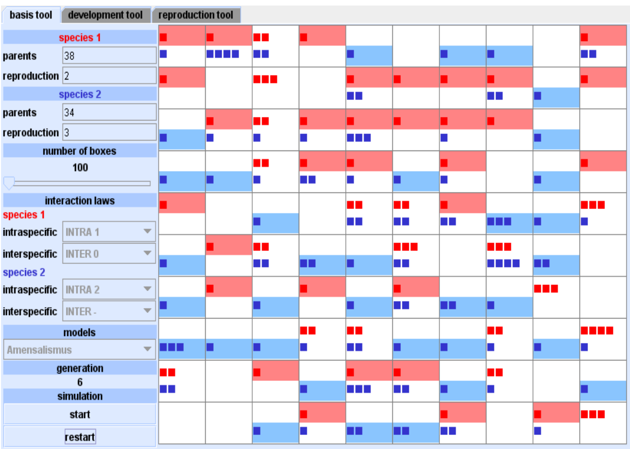
Species 2 follows **INTRA 2** and **INTER-**

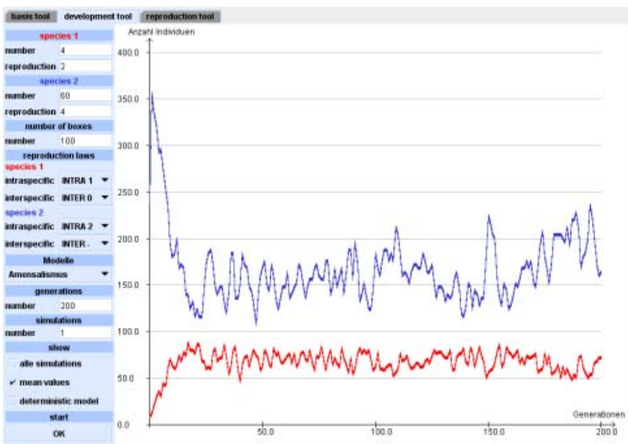
Species 2 will reproduce at a site if and only if the site contains at least one individual of species 2 and no individual of species 1.

Figure 1(c) shows the evaluation of the field concerning the reproduction laws of species 1 and 2. A light blue respectively a pink mark of a box represents a reproduction of the blue respectively the red species.

FROM THE CONCEPTUAL MODEL TO THE STOCHASTIC MODEL

The simulation tools provide excellent observation and exploration possibilities to students. Furthermore it should be mentioned that in silico investigations using simulations are very common in modern biological research.





(a) (b)

Figure 3: (a) The basic tool; (b) The development tool

Figure 3(a) depicts the graphical surface of the basic tool, which implements the simulation of the described generation-cycle. For each species students can enter the start sizes of the population, the mean number of offspring per reproduction and the intra- and interspecific interaction laws. Starting the first simulation the entered number of individuals will be spread randomly over the field. The program evaluates for each site and each species if there is a reproduction according to the selected interaction laws. Thus, the program computes the population sizes for the simulation of the next generation.

The development tool, pictured in figure 3(b), was created to get a better insight of the species' development. The tool simulates the development over a longer period of time and displays the resulting population sizes of each generation in a coordinate system. This offers a clear depiction of the long term development for both species.

Example: Amensalism
In figure 3(b) a simulation of the amensalism system (species 1: **INTRA 1** + **INTER 0**, species 2: **INTRA 2** + **INTER-**) is shown. In this case the two species are able to live in coexistence. Changing the parameters, students can determine values for the initial populations and the mean numbers of offspring per reproduction which cause an extinction of one species or which allows coexistence. Thus students are able to explore the biological role and of the parameters.

FROM THE CONCEPTUAL MODEL TO THE DETERMINISTIC MODEL

Using the conceptual model students are able to derivate a mathematical description of the systems. We define the number of individuals at a time t as $S_1(t)$ and $S_2(t)$. Due to non overlapping generations, the change of population size from generation t to generation $t+1$ exclusively depends on reproduction. The function of reproduction $R_1(S_1,S_2)$ respectively $R_2(S_1,S_2)$ indicates for species 1 respectively for species 2 how many individuals are able to reproduce, when S_1 individuals of species 1 and S_2 individuals of species 2 are randomly spread over the field. We define the number of mean offspring for each reproduction, as r_1 for species 1 and r_2 for species 2. Thus we get the following mathematical description of the population sizes.

$$S_1(t+1) = r_1 \cdot R_1(S_1(t), S_2(t))$$

$$S_2(t+1) = r_2 \cdot R_2(S_1(t), S_2(t))$$

To derive the whole mathematical description we need the reproduction functions. With the reproduction tool students can derivate reproduction functions via regression.

The reproduction tool, shown in figure 5(a), allows simulations of the functions $\mathrm{R}_{1,\mathrm{S}_2}(S_1)$, $\mathrm{R}_{2,\mathrm{S}_2}(S_1)$, $\mathrm{R}_{1,\mathrm{S}_1}(S_2)$ and $\mathrm{R}_{2,\mathrm{S}_1}(S_2)$, which determine the number of reproductions of one species depending on a fixed number of individuals of one species and a variable number of individuals of the other species.

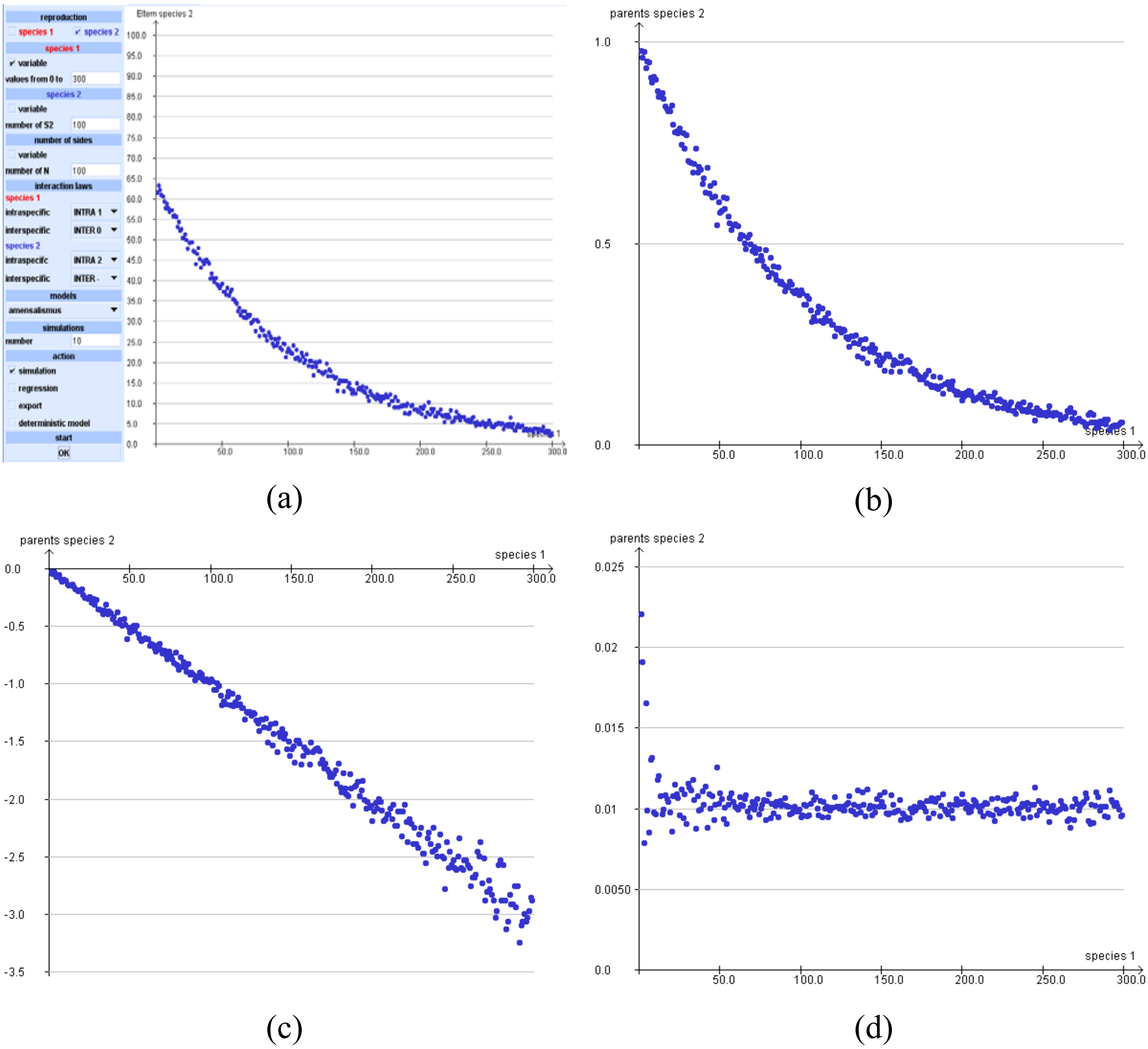


Figure 5: The reproduction tool: (a) Simulation of $\mathrm{R}_{2,S_2}(S_1)$ ($\tilde{R}(S_1)$ simulation values); (b) $\tilde{\mathrm{R}}^{(1)}(S_1) := \tilde{R}^{(2)}(S_1)/64$; (c) $\tilde{R}^{(2)}(S_1) := \log(\tilde{R}^{(1)}(S_1))$ can be approximated by a linear function; (d) $\tilde{R}^{(3)}(S_1) := -\tilde{R}^{(2)}(S_1)/S_1 \approx 0.01$

The tool provides the possibility to modify the simulated values in order to determine the reproduction functions. In the following $\mathrm{R}_2(S_1, S_2)$ of the amensalism system with $\mathrm{N} = 100$ will be derived.

Example: Amensalism
Simulating $\mathrm{R}_{2,S_2=100}(S_1)$ with the reproduction tool we get the graph $\tilde{R}(S_1)$ shown in figure 5(a). $\mathrm{R}_{2,S_2=100}(S_1) = M\,e^{-K S_1}$ seems to be a proper approach to approximate $\tilde{R}(S_1)$. With the software the simulation values can be linearized in order to check if a

certain function is suitable to approximate them. Figure 5(b) shows the resulting graph $\widetilde{R}^{(1)}(S_1)$ after dividing the simulation values by M, which is approximately 64. In the next step the logarithm will be applied to $\widetilde{R}^{(1)}(S_1)$. As it is shown in Figure 5(c) the resulting graph $\widetilde{R}^{(2)}(S_1)$ can be approximated by a linear function. This verifies that the approach is suitable. The constant $K = 0.01$ can be obtained by dividing $\widetilde{R}^{(2)}(S_1)$ by S_1, as it is shown in Figure 5(d).

In order to figure out how R_2 depends on S_2, it has to be checked how the remaining constants in $R_{2,S_2}(S_1) = M e^{-KS_1}$ depend on S_2. Determining $R_{2,S_2}(S_1)$ for different values of S_2, shows that M depends on S_2, while $K = 0.01$ remains constant. Thus, we obtain $R(S_1, S_2) = M(S_2)e^{-KS_1}$. If $S_1 = 0$, then $R_2(0, S_2) = M(S_2) = R_{2,S_1=0}(S_2)$. Using the tool $R_{2,S_1=0}(S_2) = L(1-e^{-KS_2})$ with $L = 100$ can be determined. Thus $R_2(S_1, S_2) = L(1-e^{-KS_2})e^{-KS_1}$ is the reproduction function of species 2. With the derivation of the reproduction function of species 1 we can determine the following model equations for the amensalism system:

$$S_1(t+1) = r_1 \cdot L \cdot S_1(t) \cdot e^{-KS_1(t)}$$
$$S_2(t+1) = r_2 \cdot L \cdot (1-e^{-KS_2(t)})e^{-KS_1(t)}$$

Detailed descriptions and instructions for many different systems can be found in the workbook (Roeckerath, 2008).

PREDICTIONS

A good model offers predictions for the real system. Many systems develop over time from different states into a relatively stable final state, the climax state, like coexistence of both species or extinction of one or both of them. They can also develop cyclic or even chaotic behaviour. As mentioned above for the amensalism system, students can use the development tool to explore which values of $r_1, r_2, S_1(0)$ and $S_2(0)$ yield to different kinds of systems' behaviours. Doing these kinds of predictions students are able to explore the ecological meaning of parameters.

As the derived models are dynamical systems in form of difference equations, next to the development tool students from a higher educational level can gain predictions with analytical or numerical investigations. A stable fixed point for example gives information about population developments which reach a climax state.

CLASSROOM USE

The models and tools offer various options for classroom use. They were tested successfully in a mathematics workshop for 12th grades students and a 13th grade biology class. During the workshop students worked independently with a workbook (Roeckerath, 2008). Most of them were able to derive the model equations for the modelled systems using the workbook. In the biology class the models were used to introduce population dynamics and to do some in silico experimentation. A derivation of the model equations was not part of the lessons.

The introduced models give a realistic insight into scientific research and real mathematical applications. Authentic modelling processes are always complex. The introduced models cannot be discovered by students autonomously. But they convey the basic processes of “real” modelling. A reasonable use of the introduced models in education requires that the teacher tries to find a proper balance between leading students in certain situations and encourage them to explore and experiment independently.

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