Differential Equations Model of Mutualism between Two Species

Ecosystem Modelling [I0P65A]

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1 Introduction

During the course of Ecosystem Modelling we have used models of the type of Lotka-Volterra and Verhulst in order to understand and interpret the interaction between two species within an ecosystem. Such models have been also applied along the course to resource-consumer systems.

The prey-predator system is probably the most common example of application of Lotka-Volterra and Verhulst models. In such systems, the growth of one species has a negative effect on the growth of the other, in the same way as an increase number of predators undermine the population of their preys. In contrast, in this report the focus lies on investigating beneficial rather than negative interactions between different species, i.e. mutualism.

Mutualistic interaction are very common in nature and can unfold in different ways depending on the situation. The benefit that one species can bring to a different one is usually classified as a form of resource or service. Some examples are:

- Resource-resource mutualism: rhizobia bacteria fix nitrogen that become available to be used by leguminous plants, that in turn provide sugars to the rhizobia.
- Service-resource: many animals disperse seeds or pollen in return of food.
- Service-service: sea anemones provide protection to anemone fish, and anemone fish protect sea anemones against butterflyfish, that eat anemones.

In this report, a model of mutualism between two species developed by Graves et al. (2006) is explained and several relevant outcomes arising from the model are analyzed. Moreover, a sensitivity analysis is performed, that is to say, a study of how sensitive the solutions of the system are to variations of the parameters.

2 The model

2.1 First approach: a mutualism model with potentially unlimited growth rate

First, we consider a model of mutualism according to the following assumptions:

1. The individual dynamics of each species in the absence of the other follows a logistic behavior.

2. Mutualism implies that the presence and growth per capita of one species has a positive effect on the growth per capita of the other one.

3. The benefits obtained by each species from the mutualistic interaction are proportional to the size of the other species' population.

Mathematically, assumption 1 can be expressed as:

$$
\begin{aligned}
\frac{dx_1}{dt} &= R_1(x_2)\, x_1 - a_1\, x_1^2 \\
\frac{dx_2}{dt} &= R_2(x_1)\, x_2 - a_2\, x_2^2
\end{aligned}
\tag{1}
$$

Where $R_i(x_j) > 0\, (i, j = 1, 2; i \neq j)$ expresses the positive effect of the interaction on the growth rate of populations.

From the first assumption $a_i > 0$, and from the third $R_i(x_j) = b_i\, x_j + c_i\, (b_i > 0; i, j = 1, 2; i \neq j)$. Then, the system of equations 1 can be written as:

$$
\begin{aligned}
\frac{dx_1}{dt} &= (b_1\, x_2 + c_1)\, x_1 - a_1\, x_1^2 \\
\frac{dx_2}{dt} &= (b_2\, x_1 + c_2)\, x_2 - a_2\, x_2^2
\end{aligned}
\tag{2}
$$

Hence, under the above-mentioned assumptions, we can obtain a system of equations 2 that resemble those of Lotka-Volterra model. Indeed, in the absence of interaction ($b_i = 0$), the system directly transforms in a Verhulst model where c_i represents the natural reproduction rate of species i and c_i/a_i the carrying capacity.

2.2 The limited growth rate mutualism model

In the model developed above, there are no limitations on the benefits that one species is able to provide to the other, since $R_i(x_j)$ is linearly dependent on x_j (assumption 3). This situation may lead to an unbounded growth rate of the species, which might not be a realistic description of the population dynamics within an ecosystem (at least not in the long run). Instead, it seems reasonable to think that, as the two species enjoy the benefits of the symbiosis, they asymptotically approach to a saturation point with regard to the benefits that they can reciprocally supply to the other. This is the assumption made by Graves et al. (2006) in order to derive their model: the limited growth rate mutualism model.

Hence, a new model can be derived from the first two above-stated assumptions in the previous model, plus a third assumption that incorporates the limitations to the potential benefits of mutualism. In summary, the assumptions made in the limited growth rate mutualism model are the following:

1. The individual dynamics of each species in the absence of the other follows a logistic behavior.
2. Mutualism implies that the presence and growth per capita of one species has a positive effect on the growth per capita of the other one.
3. The benefit obtained by each species from mutualism exponentially decreases when approaching to the maximum attainable benefit.

Mathematically, new assumption 3 can be expressed as:

$$\begin{aligned} R_1(x_2) &= c_1 + (m_1 - c_1)\,(1 - e^{-d_1 x_2}) \\ R_2(x_1) &= c_2 + (m_2 - c_2)\,(1 - e^{-d_2 x_1}) \end{aligned} \tag{3}$$

Where the introduced parameters $m_i (i = 1, 2)$ stand for the maximum attainable benefit for population i. The parameters $d_i (i = 1, 2)$ control the exponential decrease of benefits from symbiosis when the reciprocal population grows.

Hence, from the system of equations 1, we obtain the system of equations of the limited growth rate mutualism model:

$$\begin{aligned} \frac{dx_1}{dt} &= \Big(c_1 + (m_1 - c_1)\,(1 - e^{-d_1 x_2})\Big)\, x_1 - a_1\, x_1^2 \\ \frac{dx_2}{dt} &= \Big(c_2 + (m_2 - c_2)\,(1 - e^{-d_2 x_1})\Big)\, x_2 - a_2\, x_2^2 \end{aligned} \tag{4}$$

Analogously to the first model of potentially unlimited growth rate, in the limit of no interaction ($m_i \approx c_i$) the species' growth rate behaves as individual populations in a Verhulst model. On the other hand, in contrast to the first model of potentially unlimited growth rate, in this one populations' growth is restricted. The maximum benefit that population $x_1(x_2)$ can obtain from population $x_2(x_1)$ is attained when $(x_1\,(x_2) \to \infty)$. Under such conditions population 1 (population 2) behaves again as in a Verhulst model, but with natural reproduction rate m_1 (m_2) and carrying capacity $m_1/a_1(m_2/a_2)$.

3 The simulations

In this section the output of the simulations from the models developed in the previous section are shown. The implementation of the models in R and the set of parameters used in each simulation are shown in the Appendix files.

3.1 Model of mutualism with potentially unlimited growth rate

In Figure 1 we can see a simulation from Equations 2 when $b_1 b_2 < a_1 a_2$. This regime is called *weak mutualism* because the self limitation of each species (expressed by the negative term in Equations 2) dominates over the mutualistic

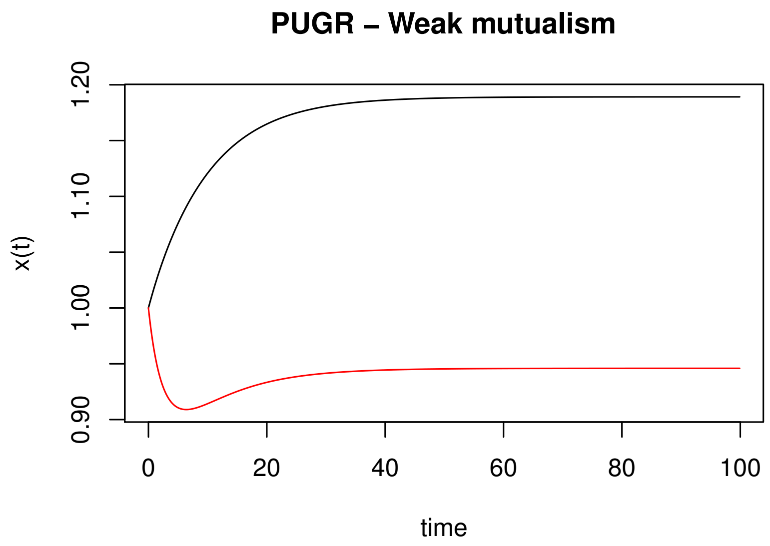

Figure 1: Simulation of the model with potentially unlimited growth rate (PUGR, Equations 2), in the regime of weak mutualism ($b_1 b_2 < a_1 a_2$). The black line corresponds to $x_1(t)$ and the red line to $x_2(t)$.

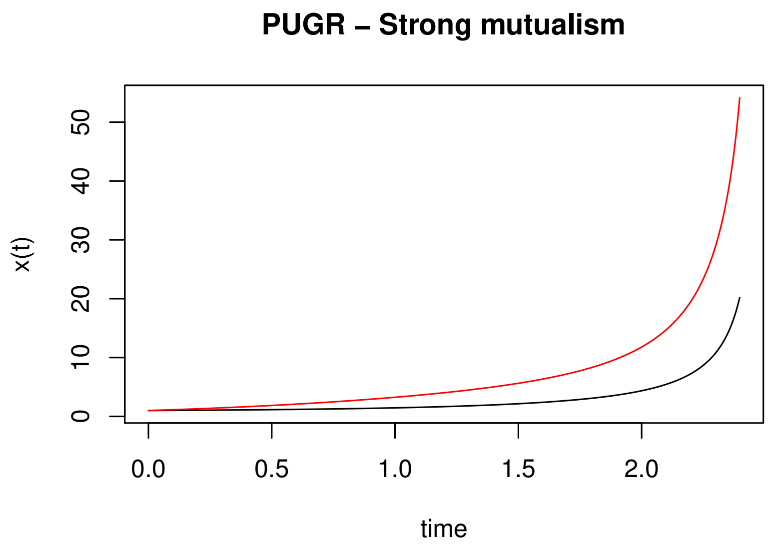

Figure 2: Simulation of the model with potentially unlimited growth rate (PUGR, Equations 2), in the regime of strong mutualism ($b_1 b_2 > a_1 a_2$). The black line corresponds to $x_1(t)$ and the red line to $x_2(t)$.

positive feedback and prevents the populations to grow indefinitely. Indeed, in this regime the populations remain bounded and they asymptotically approach to certain carrying capacity that is higher than the carrying capacity of the species considered individually.

In Figure 2 we can see a simulation from Equations 2 when $b_1 b_2 > a_1 a_2$. This regime is called *strong mutualism*. In contrast to the previous simulations, this regime is characterized by unbounded growth of the populations.

3.2 Model of mutualism with limited growth rate

In Figure 3 a simulation from Equations 4 with $m_1 d_1 m_2 d_2 < a_1 a_2$ is shown. Again, in this regime there is weak mutualistic interaction. The populations tend towards certain carrying capacity in the long term.

In Figure 4 a simulation from Equations 4 with $m_1 d_1 m_2 d_2 > a_1 a_2$ is shown. In this regime we have again strong mutualism but, in contrast to the strong mutualism regime in the first model, in this model the growth rate is bounded by definition. However, the populations are clearly benefited from the stronger reciprocal interaction and they tend towards values higher than in the regime of weak interaction.

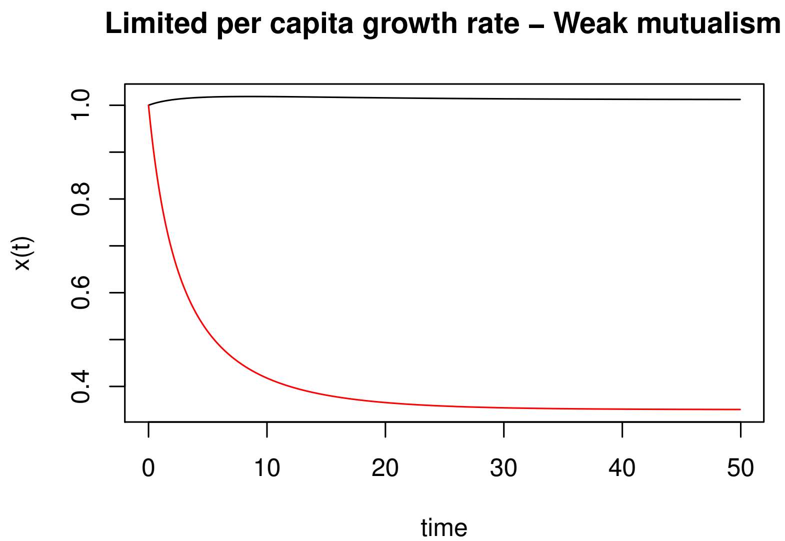

Figure 3: Simulation of the model with limited growth rate (LGR, Equations 4), in the regime of weak mutualism ($m_1 d_1 m_2 d_2 < a_1 a_2$). The black line corresponds to $x_1(t)$ and the red line to $x_2(t)$.

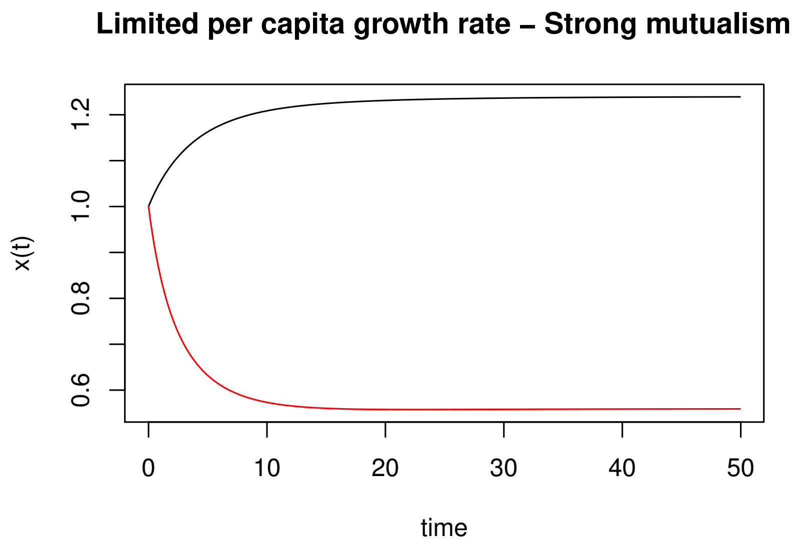

Figure 4: Simulation of the model with limited growth rate (LGR, Equations 4), in the regime of strong mutualism ($m_1 d_1 m_2 d_2 > a_1 a_2$). The black line corresponds to $x_1(t)$ and the red line to $x_2(t)$.

4 Sensitivity analysis

In this section we perform a sensitivity analysis of the parameters used in the model of potentially unlimited growth rate (PUGR) with weak interaction. As can be seen in Equations 2, there are 6 parameters in the model: $a_i, b_i, c_i;\ i = 1, 2$. There are different approaches to assess the sensitivity of the parameters in a model. Given the simplicity of our PUGR model, we can use the more rigorous analytical approach. For instance, the sensitivity of $x_i(t)$ to the parameter a_i is defined as $\frac{\partial x_i(t)}{\partial a_i}$. Although this partial derivative cannot be directly calculated because $x_i(t)$ is not known a priori, it can be incorporated as a new variable in a new equation within the system of equations 2, as explain in the Chapter *Systems Ecology* in the course notes. This new system of equations can be solved in R as a usual Ordinary Differential Equation. The solution of the sensitivity of $x_i(t)$ to each of the parameters $a_i, b_i, c_i;\ i = 1, 2$ for the PUGR model with weak mutualism can be found in the file *sensdata.csv*.

Once the sensitivity for each parameter is known, it is possible to calculate the maximum error Δx_i attainable in the solutions given certain uncertainty in the parameters' estimation:

$$\Delta x_i = \sum_{j=1}^{j=2} \Big(\frac{\partial x_i(t)}{\partial a_j} \Delta a_j + \frac{\partial x_i(t)}{\partial b_j} \Delta b_j + \frac{\partial x_i(t)}{\partial c_j} \Delta c_j \Big);\ \ i = 1, 2 \qquad (5)$$

In Figure 5 we show the solutions when we incorporate the maximum error from Equation 5 and we use a parameters' uncertainty $\Delta\alpha = 0.1\%$. Despite the small $\Delta\alpha$ used, we can see that the solutions are very sensitive to the employed parameters.

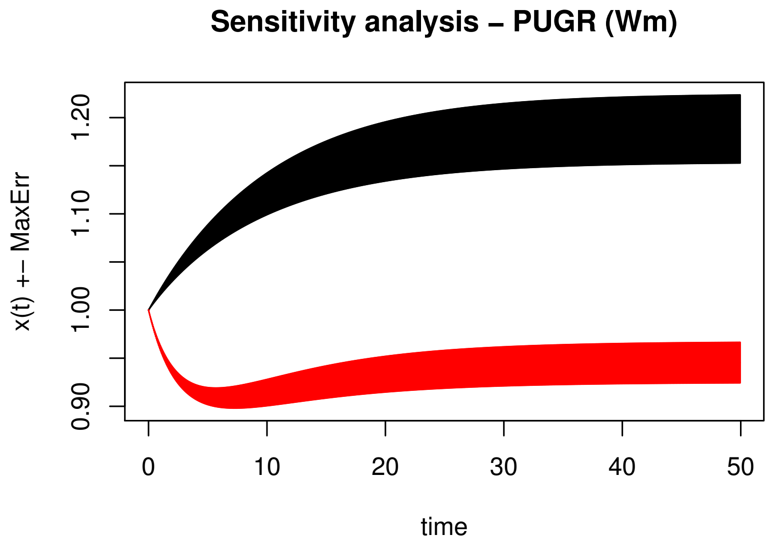

Figure 5: Simulation of the PUGR model with weak mutualism, incorporating the maximum error that arises from an uncertainty in the parameters' estimation $\Delta\alpha = 0.1\%$. The black and red bands represent $x_1(t)$ and $x_2(t)$, plus-minus their respective maximum errors.

5 Conclusions

In this report different models of mutualism between two species have been analyzed, based on the model developed by Graves et al. (2006) of limited growth rate (LGR). We have shown that when strong interaction is present, an assumption of linear benefits obtained by the species would lead to rapid and unbounded growth of the populations. This situation does not seem realistic for most situations. In contrast, the constraints imposed in the LGR model to the benefits that species can obtain from strong interactions may lead to a better description of real phenomena (particular examples are out of the scope of this report).

In addition, the analysis of sensitivity in the PUGR model has shown that the solutions are very sensitive to uncertainties in the set of parameters. Therefore, any application of this type of model must take into account that the precision of the parameters' estimation must be extremely high in order to obtain reliable predictions.

References

W.G. Graves, B. Peckham, and J. Pastor. A bifurcation analysis of a differential equations model for mutualism. *Bulletin of Mathematical Biology*, 68(8):1851–1872, 2006. doi: 10.1007/s11538-006-9070-3.

A Appendix: reference to files

The following files are relevant for this assignment:

- Implementation of the model in R: *Mutualism.R*
- Set of parameters:
  - *Params_PUGR-Wm.R* (PUGR, weak interaction)
  - *Params_PUGR-Sm.R* (PUGR, strong interaction)
  - *Params_LGR-Wm.R* (LGR, weak interaction)
  - *Params_LGR-Sm.R* (LGR, strong interaction)
  - *Params_Sens.R* (sensitivity analysis based on the model PUGR, weak interaction)
- Sensitivity functions of time for every parameter: *sensdata.csv*