Modelling Complex Ecological Dynamics

Part 5:
Differential equations with interesting properties
Preface

We present suggestions for differential equations which can be used to demonstrate specific properties of continuous dynamical systems. Examples outlined in MCED and beyond are listed and explained. The equations can be used in modelling exercises to get a feeling for the different types of dynamics in self-implemented model applications.

The content was based on lecture material developed (among others) for the Course “Systems Analysis” in the Master of Science Programme “International Studies in Aquatic Tropical Ecology” at the University of Bremen during the years 1999 – 2011

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Differential Equations

for modelling exercises
Technical backgrounds

• The models suggested here for simulation exercises can be integrated in almost any simulation software which can handle differential equations. To get reasonably precise results it is recommended not to use Euler integration but Runge Kutta 4th order integration (or an even better integration method).

• In our courses we have worked with the POPULUS Interaction Engine for simple equations and SIMILE for more complex applications.

Constant rate of increase or decrease

\[ \frac{dN}{dt} = C \quad \frac{dN}{dt} = -C \]

- This is the most simplistic differential equation. It represents a constant change over time. If the constant is positive, the variable N increases, if it is negative, the variable decreases. \( C = 0 \) separates the domains of increase and decrease representing a state where no change occurs.

See *MCED* page 69
Exponential increase and decay

\[ \frac{dN}{dt} = c \cdot N \quad \text{and} \quad \frac{dN}{dt} = -c \cdot N \]

- Depending on the size of the parameter C the variable either grows to infinity with increasing speed (if positive) – or it collapses towards zero (if negative). Exponential growth increases in a constant proportion to the variable. If the latter grows, then the absolute increase accelerates. The increase becomes so fast that within limited time spans the storage capacity for a variable becomes exceeded. The time span for which exponential growth is simulated must therefore been chosen with care (and for test purposes sufficiently small).

See *MCED* page 70
Circular oscillation

\[
\frac{dN_1}{dt} = c_1 \cdot N_2
\]
\[
\frac{dN_2}{dt} = -c_2 \cdot N_1
\]

Initial Conditions
- N1 = 1.0
- N2 = 2.0

Parameter
- c1 = 3.0
- c2 = 4.0

• If the change of a variable equals the size of another one – and the other one changes negative to the size of the latter, a sinusoid oscillation results (a circle, if the size of one variable is drawn over the other). The oscillation becomes ellipsoid if constants c1 and c2 have different positive values.

See *MCED* page 71
Two coupled oscillators

In this case, coupling two oscillators can lead to complex quasi-ergodic pattern as can be obtained by the overlay of different frequencies and can yield an “area filling” trajectory which by the time approximates any point of a given part of the state space.

\[
\begin{align*}
\frac{dx_1}{dt} &= y_1 + a \cdot x_2 \\
\frac{dy_1}{dt} &= -x_1 \\
\frac{dx_2}{dt} &= b \cdot y_2 \\
\frac{dy_2}{dt} &= -b \cdot x_2 + c \cdot y_1
\end{align*}
\]

Initial Conditions
- \(x_1 = 1.0\)
- \(y_1 = 1.0\)
- \(x_2 = 5.0\)
- \(y_2 = 2.0\)

Parameter
- \(a = 0.8\)
- \(b = 0.4\)
- \(c = 0.02\)
Two coupled oscillators

\[
\begin{align*}
\frac{dx_1}{dt} &= y_1 + a \cdot x_2 \\
\frac{dy_1}{dt} &= -x_1 \\
\frac{dx_2}{dt} &= b \cdot y_2 \\
\frac{dy_2}{dt} &= -b \cdot x_2 + c \cdot y_1
\end{align*}
\]

Initial Conditions
- \(x_1 = 1.0\)
- \(y_1 = 1.0\)
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- \(y_2 = 2.0\)

Parameter
- \(a = 0.8\)
- \(b = 0.4\)
- \(c = 0.02\)

\(x_2\) drawn over \(x_1\),
1000 steps,
display interval 0.1,
Integration: Runge Kutta 4th order.
The longer the model runs the more dense the area will be filled.
Logistic growth

\[ \frac{dN}{dt} = C1 \times N - C2 \times N^2 \]

- This formula, found by Verhulst in 1838 combines exponential growth with quadratic decay. It is still one of the most frequently used growth terms in ecological modelling. With positive constants C1 and C2 and a positive initial value for N the growth is stable and approximates a value of C1 / C2 for N as an equilibrium.

See *MCED* page 72
The Lotka-Volterra model

\[ \frac{d\text{Prey}}{dt} = C_1 \times \text{Prey} - C_2 \times \text{Prey} \times \text{Pred} \]
\[ \frac{d\text{Pred}}{dt} = C_2 \times b \times \text{Prey} \times \text{Pred} - C_3 \times \text{Pred} \]

- This is the basic starting point for population modelling using differential equation. The importance of the model derives from the possibility to modify and extend the basic structure, which is in itself biologically not too realistic. You can observe an interesting simulation artefact employing the Euler integration method. Instead of cycles you observe spirals (if displaying predator over prey) or increasing oscillations (if displaying the variables over time. Using Runge Kutta 4th order integration improves the results.

Initial Conditions
- Prey = 100
- Pred = 100

Parameter
- \( C_1 = 0.1 \)
- \( C_2 = 0.001 \)
- \( b = 0.1 \)
- \( C_3 = 0.1 \)

See *MCED* page 73
Lotka Volterra model with logistic extension

\[
\frac{d \text{Prey}}{dt} = C1 \times \text{Prey} \frac{(K - \text{Prey})}{K} - C2 \times \text{Prey} \times \text{Pred}
\]

\[
\frac{d \text{Pred}}{dt} = C2 \times b \times \text{Prey} \times \text{Pred} - C3 \times \text{Pred}
\]

- In this model, the constant C1 of the plain Lotka Volterra model was replaced (extended) by a logistic term. The marginally stable equilibrium of the original model changes its character. The equilibrium point now is a globally stable attracting point.

Initial Conditions
- Prey = 400
- Pred = 100

Parameter
- C1 = 0.1
- C2 = 0.001
- b = 0.7
- C3 = 0.1
- K = 2000

See \textit{MCED} page 79
Lotka Volterra model with saturation extension

\[
\frac{d\text{Prey}}{dt} = \left( C_1 + \left( \frac{C_{11} \times \text{Prey}}{C_S + \text{Prey}} \right) \times \text{Prey} \right) - C_2 \times \text{Pred} \times \text{Prey}
\]

\[
\frac{d\text{Pred}}{dt} = C_2 \times b \times \text{Prey} \times \text{Pred} - C_3 \times \text{Pred}
\]

- In this model, the constant $C_1$ of the original Lotka Volterra model was replaced by a saturation term in analogy to the form of the Michaelis-Menten equation. In a population context it means, that the rate of increase of the population raises with the growth of the population up to a saturation level where maximal reproduction is reached. The marginally stable equilibrium of the original model changes its character and becomes unstable. Oscillations increase in amplitude.

Initial Conditions
- Prey = 1000
- Pred = 152

Parameter
- $C_1 = 0.1$
- $C_{11} = 0.1$
- $C_S = 1000$
- $C_2 = 0.001$
- $b = 0.7$
- $C_3 = 0.1$

See MCED page 80
Modelling Complex Ecological Dynamics

Lotka Volterra model with a limit cycle

\[
\frac{dN_1}{dt} = \left(C_1 + \frac{C_{11} * N_1}{C_S + N_1}\right) * N_1 * \left(\frac{K - N_1}{K}\right) - \frac{(C_2 * N_1 * N_2)}{(A + N_1) / N_1}
\]

\[
\frac{dN_2}{dt} = \frac{(b * C_2 * N_1 * N_2)}{(A + N_1) / N_1} - C_3 * N_2
\]

- A limit cycle is a stable oscillation. Deviations from a specific frequency and amplitude decay over time. i.e. larger oscillations are damped, smaller oscillations increase. In a modified Lotka Volterra model we can obtain such a behaviour by combining a logistic term with a saturation term together with an additional effect which mimics the effect of a refuge for the prey which has a small capacity, which decreases predation rate for small prey populations. The constant A marks the prey population size where predation success decreases by 50%.

Initial Conditions
Prey = 1000
Pred = 152

Parameter
C1 = 0.1
C11=0.2
CS=1000
K = 10000
C2 = 0.001
A = 50
b = 0.1
C3 = 0.1

See MCED page 81, 82
Lotka Volterra model with a limit cycle

\[ \frac{dN_1}{dt} = \left(C_1 + \left(\frac{C_1 \times N_1}{C_s + N_1}\right) \times \left(\frac{K - N_1}{K}\right)\right) - \left(\frac{C_2 \times N_1 \times N_2}{N_1}\right) \]

\[ \frac{dN_2}{dt} = \left(\frac{b \times C_2 \times N_1 \times N_2}{N_1}\right) - C_3 \times N_2 \]

- In this model, the existence of a limit cycle depends on the choice of the parameter. The predator mortality parameter C3 can be used to demonstrate the transition. For C3 = 0.01 a stable equilibrium can be observed. Successively increasing C3 leads to a bifurcation where the stable point vanishes and gives rise to a limit cycle. When C3 is increased further towards 0.4 the limit cycle vanishes and another equilibrium point occurs.

See *MCED* page 89/90
Lorenz Attractor

\[
\begin{align*}
\frac{dX}{dt} &= a*(Y - X) \\
\frac{dY}{dt} &= X(b - Z) - Y \\
\frac{dZ}{dt} &= X*Y - c*Z
\end{align*}
\]

Initial conditions:
\(x = 1.0, \ y = 1.0, \ z = 1.0\)

Parameter:
\(a = 10, \ b = 28, \ c = 8/3\)

- The attractor was found by E.N. Lorenz. It was the first for which a chaotic dynamic was described. The equations can be integrated with Runge Kutta 4\(^{th}\) order integration but requires small step size. See also http://en.wikipedia.org/wiki/Lorenz_attractor
Rössler Attractor

\[
\begin{align*}
\frac{dy}{dt} &= x + ay \\
\frac{dz}{dt} &= b + z(x - c) \\
\frac{dx}{dt} &= -y - z
\end{align*}
\]

- The equation was found by O.E. Rössler. It is structurally simpler than the Lorenz attractor and exhibits a different shape of chaotic dynamics. See also [link](http://en.wikipedia.org/wiki/Rössler_attractor)

Initial Conditions

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>0.1</td>
</tr>
<tr>
<td>b</td>
<td>0.1</td>
</tr>
<tr>
<td>c</td>
<td>14.0</td>
</tr>
</tbody>
</table>

Initial Conditions

<table>
<thead>
<tr>
<th>x₀</th>
<th>y₀</th>
<th>z₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>-5.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>
The Gilpin Equations

\[
\begin{align*}
\frac{dN_1}{dt} &= N_1(r_1 - a_{11} \cdot N_1 - a_{12} \cdot N_2 - c_1 \cdot N_3) \\
\frac{dN_2}{dt} &= N_2(r_2 - a_{21} \cdot N_1 - a_{22} \cdot N_2 - c_2 \cdot N_3) \\
\frac{dN_3}{dt} &= N_3(b(c_1 \cdot N_1 + c_2 \cdot N_2) - d)
\end{align*}
\]


Initial Conditions
N₁=N₂=N₃ = 50

Parameter
- r₁ = r₂ = 1.0
- a₁₁ = 0.001
- a₁₂ = 0.001
- a₂₁ = 0.0015
- a₂₂ = 0.001
- c₁ = 0.01
- c₂ = 0.001
- b = 0.5
- d = 1.0

[See MCED page 83](#)
### Hysteresis

\[
\begin{align*}
\frac{dN1}{dt} &= (A * (- P3 * N1^3 + P2 * N1^2 - P1 * N1 + P01) + P02) * N1 - N1 * N2 \\
\frac{dN2}{dt} &= N1 * N2 - b * N2^2
\end{align*}
\]

- In a hysteresis model, a critical parameter is successively changed, here starting with 1.0 and step-wise increasing up to 3.0. It can be observed, that the variables approximate an equilibrium value near \(N1 = N2 = 0.18\). When \(b\) increases beyond a certain threshold, the equilibrium vanishes and a new equilibrium is approximated (near \(N1=0.8, N2 = 0.2\)). Starting the simulation close to this equilibrium it can be observed that the parameter \(b\) must be decreased much further than previously observed until the lower equilibrium is approximated again.

Initial Conditions
\(N1=N2= 0.10\)

Parameter
\[
\begin{align*}
A &= 2.0 \\
P3 &= 4.0 \\
P2 &= 6.0 \\
P1 &= 2.5 \\
P01 &= P02 = 0.25 \\
b &= 1.0 \ldots 3.0
\end{align*}
\]

See \textit{MCED} page 86/87
Complex hysteresis pattern

\[
\frac{dN_1}{dt} = N_1^2 (A + P_4 N_1^4 - P_3 N_1^3 + P_2 N_1^2 - P_1 N_1 + P_0) - N_1 N_2
\]

\[
\frac{dN_2}{dt} = N_1 N_2 - b N_2^2
\]

- Depending on the parameter, various types of transitions between different equilibria can occur. This is to illustrate, that more than two equilibria can be involved.
- The initial conditions can be freely chosen if only one equilibrium exists. In case of alternative equilibria, the one will be approximated in which domain of attraction the system is started. Initial conditions should be chosen not too far away from the equilibria – otherwise the integration may fail due to numeric artefacts.

See *MCED* page 87/88
Complex hysteresis pattern

Parameter $A = 2.0$
$P4 = 10.0$
$P3 = 38.0975$
$P2 = 68.585$
$P1 = 58.0725$
$P0 = 18.585$
Critical parameter $b = 0.5 \ldots 2.0$

Parameter $A = 1.2$
$P4 = 11.5$
$P3 = 51.38$
$P2 = 110.636$
$P1 = 113.604$
$P0 = 43.848$
Critical parameter $b = 0.5 \ldots 3.0$

Parameter $A = 3.5$
$P4 = 10.0$
$P3 = 38.99$
$P2 = 73.94$
$P1 = 67.89$
$P0 = 23.94$
Critical parameter $b = 0.5 \ldots 3.0$

C: To approximate the equilibrium at $N1=N2=2.0$ use $N1=N2=2.04$ as initial condition
A student’s simulation experiment

\[
\begin{align*}
\frac{dx_1}{dt} &= x_1 - x_1 y_1 - c y_1 x_1 y_2 \\
\frac{dy_1}{dt} &= y_1 x_1 - y_1 + c x_2 y_1 \\
\frac{dx_2}{dt} &= x_2 - x_2 y_2 - c x_2 y_1 \\
\frac{dy_2}{dt} &= x_2 y_2 - y_2 + c x_1 y_2 
\end{align*}
\]

- As a result of course groupwork, the above equations were suggested by two students in 2008. The model structure was derived from coupling two Lotka Volterra models (two prey and two predators feeding on both prey). The parameter c represents the coupling intensity.

Any idea what the dynamics might look like?

Initial Conditions
\begin{align*}
x_1 &= 3 \\
y_1 &= 1 \\
x_2 &= 5 \\
y_2 &= 1 
\end{align*}

Parameter
\begin{align*}
c &= 0.2 
\end{align*}
A student’s simulation experiment

- ... somehow up and down. Any idea what kind of dynamic this could be?
  
  **Left:** x1, x2, y1, y2 over time for 200 simulation steps
  
  **Right:** y2 over x1 is shown, running the simulation for 500 time steps.
  
  Run settings: Runge Kutta 4th order integration, adaptive error limit 1e-5, time step 0.05

*Looks dynamic, doesn’t it? …*
The coupling parameter was changed from 0.2 to 0.3 and the logarithm of the population sizes displayed. 

**Left:** log(x1), log(x2), log(y1) and log(y2) over time for 200 simulation steps.

**Right:** log(x2) over log(x1) is shown, running the simulation for 1000 time steps.

Simulation specification: Runge Kutta 4th order integration, adaptive error limit 1e-5, time step 0.05.

You can also try two different coupling parameter c1 and c2 (instead of c).

Looks even more dynamic.

Remember, it was a deterministic system.

Wasn’t it? …
Good luck for your own modelling exercises...

- The student’s simulation experiment, y2 over y1 on a logarithmic scale
That was it for now, have a nice time