



**Course title:** EOTIST Standard course

**Course subject:** Modelling

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## LESSON SM1.1

### HOW TO WRITE AN ECOLOGICAL MODEL



EOTIST project has received funding from the *European Union's Horizon 2020 research and innovation programme* under grant agreement No 952111

[H2020 WIDESPREAD-05-2020 (Twinning)]





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## 1. INTRODUCTION

The first step is to ask a specific question. There are no model that are good for everything. All models are wrong. But some are useful, depending upon context. So, ask a specific question.

Next, we need to determine what are the variables of interest: Population density, individuals, density of functional types, biomass, etc... The choice depends on the question that are posed.

Also, we have to decide whether we want a single variable for a given population, or whether we want to take into account the age/stage structure (i.e., density of population in a given age class).

Then, we have to decide whether we want to treat a homogeneous system (without spatial variability) or we want to include the description of space. In the former case, we use for example Ordinary Differential Equations (ODE), while in the latter case we use Partial Differential Equations (PDE). We also have to decide whether we want a description based on continuous variables (in time, space, and the dependent variable itself) or based on discrete variables. Discrete time may for example be useful for species that reproduce once in a given time period, for example once a year.

Once defined the model, we need to fix the parameters at values that are relevant for the problem at hand. Some parameters are clear, for others it may be more difficult to determine the reasonable values (for example, the preference of a predator for a given type of prey).

## DETERMINISTIC AND STOCHASTIC MODELS

The simplest ecological model is that leading to Malthusian (exponential) growth for a single species with infinite resources. The solution is exponential growth or decay depending on whether the reproduction rate  $r$  is larger or smaller than the death rate  $d$ .

The next step is to define a model for a single species with finite resources, leading to the so-called logistic equations. Here, growth is not infinite, but a given finite equilibrium value for the population density emerges: the “carrying capacity” of the ecosystem determined by the values of the model parameters.

The model can now become more complicated. We can consider two species, one is a “prey” and the other is a “predator”. The prey  $X$  grows exponentially but it is eaten by the predator  $Y$ . The predator, by itself, decays exponentially but it consumes the prey and can grow. It is the Lotka-Volterra system, which can give rise to self-sustained oscillations. However, this system is “conservative”, that is, its final state depends on the initial conditions, and it is not stable for perturbations of the form of the equations (structural instability).

To overcome some of the limitation of the Lotka-Volterra model, Rosenzweig and MacArthur used a “Holling type II” (or Michaelis-Menten) form for predation and a logistic form for the growth of the prey. This leads to a more stable, dissipative model, that can have both stable stationary equilibria and self-sustained oscillations (limit cycles).

The Holling type II form is appropriate when the consumer (predator) does not need to search for the nutrient (prey). If the predator spends time searching for prey, then another form can be used: Holling type III.

The simplest trophic chain is a Nutrient-Grazer-Predator system, especially useful for aquatic ecosystems. Here, it is called a Nutrient-Phytoplankton-Zooplankton model (NPZ), as detailed in the slides. The various terms are commented in the slides.



In aquatic ecosystems, the various components (N, P, Z) can be advected by a velocity field. Here we introduce the example of a horizontal (turbulent) advection field with velocities  $u$  and  $v$ . At the end, we show an example of phytoplankton advected by a horizontal 2D turbulent field, mimicking mesoscale oceanic turbulence. In the example, nutrients are injected in a stripe at the center of the domain and advection carries nutrients, phytoplankton and zooplankton around. They are advected and at the same time undergo the ecological prey-predator dynamics.

A final example concerns a model for a nutrient-poor (oligotrophic) lake ecosystem. We collected data from several lakes in the Gran Paradiso National Park, Italy, and developed a model for the lake ecosystem dynamics. The slides show the structure of the model, the parameters, and an example of the behavior.

Refer to slides SM1.1a.

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### MODELS FOR VEGETATION DYNAMICS

The second set of slides (SM1.1b) focuses on vegetation models. Here, we explore a simple model for savanna dynamics, including also the effect of stochastic fires, and a model for the insurgence of summer droughts at midlatitudes. For this part, a comment will play together with the slide show.

The model is an extension of the original Tilman's model, where the variables are the fraction of surface covered by a given type of vegetation. Clearly, Each of such variables varies between 0 and 1.

Each vegetation type has a different ability to colonize the landscape. Some species are faster to reach new areas, but others are better competitors for resources and they can displace the species that are worse competitors.

The model adopted here has trees, tree seedlings and grasses. Trees are generated by seedlings, and seedlings are generated by trees. Trees are the best competitor, and they can displace grass. However, grass is a better competitor than tree seedlings. This three-compartment model displays a rich dynamics, which includes mono-species situations, coexistence or bistability.

Finally, we explore a case with explicit spatial dynamics, where the models, now expressed in terms of Partial Differential Equations, describe the biomass as a function of spatial location and time, showing the emergence of vegetation patterns.

The slides are complemented by the original papers.