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LESSON SM3.1

ECOSYSTEM MODELLING



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1. INTRODUCTION

This course is based on the notes in

A.M. De Roos, Modeling Population Dynamics, an introductory course in mathematical modeling.

https://staff.fnwi.uva.nl/a.m.deroos/downloads/pdf_readers/syllabus.pdf

Other needed references are contained in the text.

ECOSYSTEMS

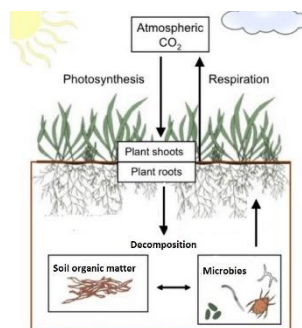
WHAT IS AN ECOSYSTEM?

An ecosystem is a community of living organisms (plants, animals, and microbes) existing in conjunction with the non-living components of their environment (air, water, and mineral soil), interacting as a system. These biotic and abiotic components are linked together through nutrient cycles and energy flows. As the network of interactions among organisms, or between organisms and their environment defines ecosystems, they can be of any size.

GRAPHICAL REPRESENTATION

The network of interactions can be represented graphically.

Example. The dynamics of soil organic carbon.



The carbon balance within the soil is controlled by carbon inputs from photosynthesis and carbon losses by respiration. SOC is the organic carbon that remains in the soil after decomposition of soil organic matter. The part that leaves the soil is due to the respiration of bacteria and released to the atmosphere as CO₂. Then it enters again into the soil recaptured by plants through photosynthesis.

A graphical representation that takes into account only the soil organic matter (Cs) and the microbial biomass (Cb) and their interaction with the environment is given by

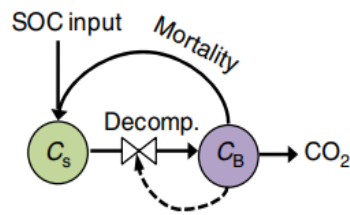


Figure from Georgiou, K., Abramoff, R. Z., Harte, J., Riley, W. J., & Torn, M. S. (2017). Microbial community-level regulation explains soil carbon responses to long-term litter manipulations. *Nature Communications*, 8(1), 1-10.

BIOMES

Although it is tempting to see the earth as a single ecosystem, it can clearly be divided into a number of distinct zones, each with their own climate and characteristic populations of living organisms. These zones are called biomes, but each one is capable of being subdivided further.

A biome is a large area characterized by its vegetation, soil, climate, and wildlife. There biomes: aquatic, grassland, forest, desert, and tundra, though some of these biomes can be further divided into more specific categories, such as freshwater, marine, savanna, tropical rainforest, temperate rainforest, and taiga.

Aquatic biomes include both freshwater and marine biomes. Freshwater biomes are bodies of water surrounded by land—such as ponds, rivers, and lakes—that have a salt content of less than one percent. Marine biomes cover close to three-quarters of Earth’s surface. Marine biomes include the ocean, coral reefs, and estuaries.

Grasslands are open regions that are dominated by grass and have a warm, dry climate. There are two types of grasslands: tropical grasslands (sometimes called savannas) and temperate grasslands.

Forests are dominated by trees, and cover about one-third of the Earth. Forests contain much of the world’s terrestrial biodiversity, including insects, birds, and mammals. The three major forest biomes are temperate forests, tropical forests, and boreal forests (also known as the taiga).

Deserts are dry areas where rainfall is less than 50 centimeters per year. They cover around 20 percent of Earth’s surface. Deserts can be either cold or hot, although most of them are found in subtropical areas. Because of their extreme conditions, there is not as much biodiversity found in deserts as in other biomes. Deserts can fall into four categories according to their geographic location or climatic conditions: hot and dry, semiarid, coastal, and cold.

A tundra has extremely inhospitable conditions, with the lowest measured temperatures of any of the five major biomes with average yearly temperatures ranging from -34 to 12 degrees Celsius. They also have a low amount of precipitation, just 15–25 centimeters per year, as well as poor quality soil nutrients and short summers. There are two types of tundra: arctic and alpine. The tundra does not have much biodiversity and vegetation is simple, including shrubs, grasses, mosses, and lichens. This is partly due to a frozen layer under the soil surface, called permafrost. The arctic tundra is found north of boreal forests and the alpine tundra is found on mountains where the altitude is too high for trees to survive. Any wildlife inhabiting the tundra must be adapted to its extreme conditions to survive.

From: *The Five Major Types of Biomes* | National Geographic Society:
<https://www.nationalgeographic.org/article/five-major-types-biomes/>



INTERNAL AND EXTERNAL CONTROLLING FACTORS

Ecosystems are dynamic entities controlled both by external and internal factors. External factors, such as climate and the parent material that forms the soil, control the overall structure of an ecosystem and the way things work within it, but are not themselves influenced by the ecosystem. While external processes generally control the resource inputs, the availability of these resources within the ecosystem is controlled by internal factors such as decomposition, root competition, or shading. Other internal factors include disturbance, succession, and the types of species present. From one year to another, ecosystems experience variation in their biotic and abiotic environments. A drought, an especially cold winter, and a pest outbreak all constitute short-term variability in environmental conditions. Animal populations vary from year to year, building up during resource-rich periods, but crashing as the food supply becomes scarce.

RESISTENCE, RESILIENCE AND REACTIVITY

In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. Resistance is the ability of an ecosystem to remain at equilibrium despite disturbances. Resilience is the speed at which an ecosystem recovers to equilibrium after being disturbed. Humans may impact the nature of an ecosystem to such a degree that the ecosystem can lose its resilience entirely. In these cases, external human influences can lead to the complete destruction or irreversible altering of the ecosystem equilibrium.

However, real ecosystems typically do not complete their response to a perturbation before the next occurs. Instead, they are buffeted by a more-or-less continual series of perturbations. The instantaneous response to perturbations can take the system dramatically far from stable equilibria, even if all perturbations will eventually die out. Neubert and Caswell (1997) firstly introduced to ecology the concept of reactivity, which quantifies the maximum amplification rate of perturbations. For reactive equilibria, some perturbations will immediately grow in magnitude before eventually decaying. Conversely, if all small perturbations decay immediately, such equilibria are non-reactive. As such, reactivity is defined as the maximal initial amplification rate.

Neubert, M. G., & Caswell, H. (1997). Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology, 78(3), 653-665.



2. ECOSYSTEM DYNAMICS

NATIVE SPECIES AND ECOSYSTEMS

Ecosystem management requires the knowledge of the species living in the ecosystems and the analysis of biotic and abiotic factors limiting their growth.

Native species are organisms including a plants or animals whose presence in given ecosystem is the result of only natural processes with no human intervention. Native species normally live and thrive in a particular ecosystem. Given adequate resources, (native) populations in their ecosystem (including humans) increase at rapid rates. The environmental conditions that a population is exposed influence its dynamics and usually sets the limits for its development. Environmental conditions can pertain to both biotic and abiotic factors of an ecosystem, for example, quantity of light and water, range of temperatures, and soil composition, humidity, the number of fellows members, predators or competitors around. Lack of resources and adequate environmental conditions, limit the growth of populations in specific niches in the ecosystem. Hence, describing populations in their ecosystems means to: 1) describe population dynamics (i.e. changes of population abundance) 2) investigate the impact on dynamics of growth limiting factors

POPULATION DYNAMICS

The population abundance changes over time. Any changes in the number of individuals within a population in a given ecosystem comes about by reproduction, death or migration of individual organisms.

BALANCE EQUATIONS

Population balance equation: changes in population abundance are a balance between processes that decrease this abundance (e.g. death and emigration) and processes that increase the abundance (e.g. reproduction and immigration). Population for which immigration and emigration can be neglected are usually referred to as closed populations or closed systems, as opposed to open populations or open systems, that are open to migration.

DISCRETE MODELS

More formally, consider $N(t)$ and $N(t + \Delta t)$ the population abundances at time t and at $t + \Delta t$.

$$N(t + \Delta t) - N(t) = \text{Births} + \text{Immigration} - \text{Deaths} - \text{Emigration}$$

It is calculated by adding the number of births plus immigration (the number of individuals coming into an area during Δt) and subtracting the number of deaths and emigration (the number of individuals leaving an area during Δt). Discrete time models only determine the state of the modelled population at specific points in time and do not tell what happens in between.

Example. Model for an annual plant.

A model for a population of annual plants. If reproduction only occurs once a year (or once a season) we could simply choose to specify the changes in the population state from year to year without specifying how the number of individuals in the population changes within a year. As annual plants reproduce by producing seeds, which overwinter and germinate in the next year. We could model this population by observing the number of plants present at the beginning of a growing season, say May 1st of every year. $N(t)$ would in this case be the

number of plants in one year and $N(t + \Delta t)$ the number in the year after, while Δt equals exactly 1 year. Specifying the number of deaths during Δt ($= 1 \text{ year}$) is straightforward, as all plants are annual and hence die before the next census time at $t + \Delta t$. The modeling of the dynamics in this case would boil down to specifying how the number of plants in a specific year (at time $t + \Delta t$) is related to the number of plants in the year before (at time t). This involves specifying the relationship between the number of seeds produced by a population of size $N(t)$, the probability that a seed germinates into a seedling and the probability that this seedling grows into a new plant. The essence is that the model only describes what the state of the population is at May 1st of each year. Two different species might show the same population dynamics (when censused at May 1st of each year), while the one species flowers only in May with all plants dying before the end of June and the other flowers all summer and plants die only during winter.

CONTINUOUS MODELS

ORDINARY DIFFERENTIAL EQUATIONS (ODES)

A continuous-time version of the balance equation can be derived by dividing both sides of the equation by Δt :

$$\frac{N(t+\Delta t)-N(t)}{\Delta t} = \frac{\text{Number of births during } \Delta t}{\Delta t} - \frac{\text{Number of deaths during } \Delta t}{\Delta t}$$

By taking the limit for Δt tending to 0, the left-hand side of this equation becomes the derivative of $N(t)$ with respect to time t , while the right-hand side becomes the population rate $f(N)$ i.e. the difference between the rate with which individuals are born into the population and the rate with which individuals disappear from the population due to death.

The continuous-time population balance equation can be given in the whole time horizon as

$$\frac{dN}{dt} = f(N) = B(N) - D(N)$$

The above equation is an ordinary differential equation or ODE for short. In this balance equation, the birth and death rate $B(N)$ and $D(N)$, respectively, as explicit function of the total number of individuals N to indicate that the number of individuals present in the population determine the number of births and deaths that do occur during a certain time period. The ODE does not specify a complete population dynamic model yet, as it only determines how the population abundance is going to change over time. We therefore still have to specify from what value it is going to change to start with. In other words, we have to specify an initial state of our population. Usually, this is done by specifying the number of individuals present at some particular point in time, which then simultaneously is chosen to equal the start of our times ($t = 0$): $N(0) = N_0$. In this initial state equation, the quantity N_0 is a known value from which the population dynamics is going to develop.

Here the model is specified by a single ODE, but they may also occur as systems of ODEs in more complex situations, for example, when we want to model more than a single population.

Example. Soil organic carbon model

SOC is the organic carbon that remains in the soil after decomposition of soil organic matter. The part that leaves the soil is due to the respiration of bacteria and released to the atmosphere as CO_2 . Then it enters again into the soil recaptured by plants through photosynthesis.

If we assume that the process is governed by the non linear interaction between only two pools (the soil organic matter represented by the variable C_s and microbial biomass by the variable C_b and between these pools and

the environment then the differential equations corresponding to the graphical representation here given, form a non-linear, autonomous, two-dimensional ODE system.

$$\begin{aligned}\frac{dC_s}{dt} &= I - \frac{\alpha C_b C_s}{\beta + C_s} + k_b C_b \\ \frac{dC_b}{dt} &= \varepsilon \frac{\alpha C_b C_s}{\beta + C_s} - k_b C_b\end{aligned}$$

PDES

ODEs models assume that N is uniformly distributed in space so that N depends only on time variable t i.e. $N = N(t)$.

Partial differential models are a flexible method for modeling the spread of a species. They can cope with coefficient values changing through space and time as well as various types of dispersal dynamics. In models described by Partial Differential Equations (PDEs), the abundance N is defined over a spatial region, whose boundary is identified. Then N may change according both the space x and the time t i.e. $N = N(x, t)$.

REACTION-DIFFUSION EQUATION FOR SPECIES DISPERSAL

The canonical reaction-diffusion equation for species dispersal (Okubo & Levin 2001) which include advection is given by

$$\frac{\partial N}{\partial t} - D \nabla^2 N + \mathbf{v} \cdot \nabla N = r N \left(1 - \frac{N}{K}\right)$$

The equation for the invasive species abundance, $N(x, t)$, at position x and time t is defined over a region, whose boundary is identified. The first term on the right-hand side is a diffusive term, which describes collective motion of randomly moving individuals throughout a landscape (Murray 2002). The coefficient D is the diffusivity, which governs how quickly the species disperses. The second term is advection, which is controlled by the coefficient \mathbf{v} . This allows for dispersal to be biased in a certain direction, which is important for modeling dispersal that is influenced by external forces, such as currents or winds. The third term is a logistic population growth term, where the coefficient r is the intrinsic growth rate of the population and K is the carrying capacity.

Okubo, A., & Levin, S. A. (2001). *Diffusion and ecological problems: modern perspectives* (Vol. 14, pp. xx+467). New York: Springer.

Murray, J. D. (2002). *Mathematical biology: I. An introduction. Interdisciplinary applied mathematics. Mathematical Biology, Springer. Example. Dynamics of an invasive plant.*

Example. The spread of invasive Hieracium Aurantiacum in Victorian Alpine National Park

Hieracium Aurantiacum, a native European plant, was introduced to the Bogong High Planes (within the Victorian Alpine National Park) in the 1980s. H. A. spreads via both runners and seeds, meaning that it will spread in all directions, which is modeled with diffusion $D = 50$, as well as with the prevailing winds $\mathbf{v} = [0.25, 0.75]$ (km/year) on the Bogong High Planes, which is in a south-easterly direction.

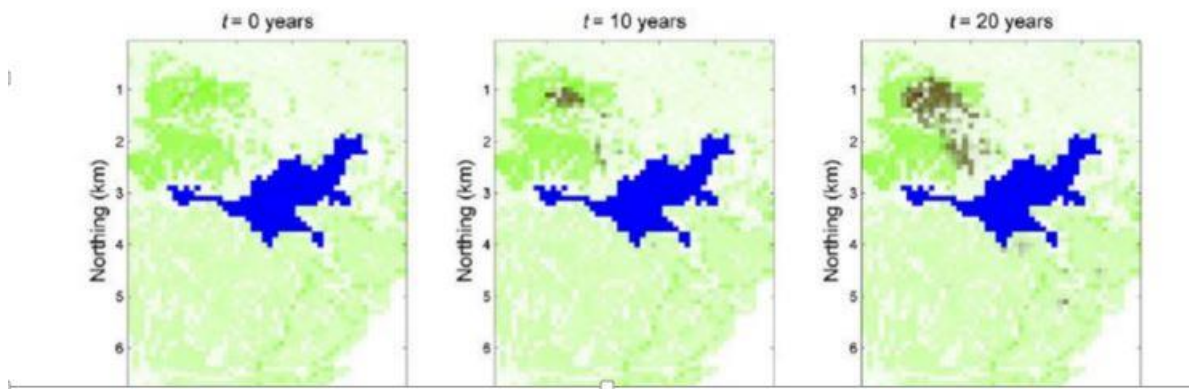


Figure 3 The spread of *H. aurantiacum* through the Bogong High Plains as predicted by the model over a 20-year period. Brown areas show the presence of *H. aurantiacum*, with the darker shading indicating high density. The green shading is the habitat suitability, where dark green is high suitability and white is unsuitable. The blue region is a lake. *H. aurantiacum* spread starts from a single site in the north-west of the region. The long-distance dispersal events allow *H. aurantiacum* to establish colonies on the south-east of the lake.

Baker, C. M. (2017). Target the source: optimal spatiotemporal resource allocation for invasive species control. *Conservation Letters*, 10(1), 41-48.

POPULATION GROWTH FUNCTION

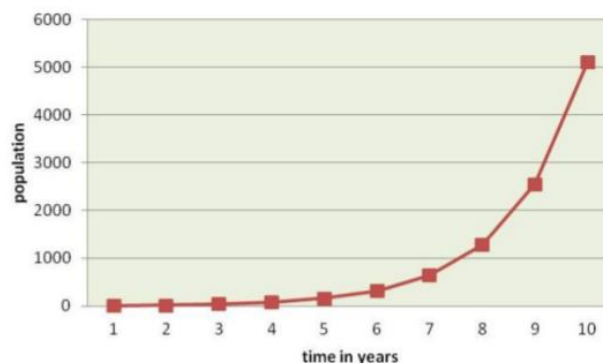
The population rate $f(N)$ is given by the difference between the rate with which the number of individuals increase and the rate with which the number of individuals decreases

$$f(N) = (f_b(N) - f_d(N)) N$$

The so-called per capita birth rate $f_b(N)$ and per capita death rate $f_d(N)$ have formal interpretations as the probability per unit time of an individual to born and to die, respectively.

EXPONENTIAL GROWTH

Exponential growth: this type of growth assumes that there is unlimited food, water, space, nesting sites, etc. available and that the population will continue to increase (with more births and immigration than deaths and emigration) until the end of time.



The per capita rates which are not influenced by any aspect of the population are model by means of constants, so that : $f_b(N) = \beta$, $f_d(N) = \delta \rightarrow f(N) = r N$ with $r = \beta - \delta$

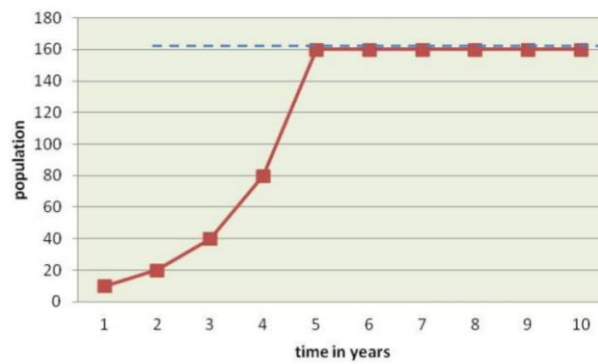
$$f(N) = r N$$

Depending on the values of the birth and death rates $f(N)$ is either a linearly increasing, strictly positive or a linearly decreasing, strictly negative function of N (or null for all values of N , when $r = 0$).

For positive values of $f(N)$ the population abundance will increase, while for negative values the abundance will decrease

LOGISTIC GROWTH

Logistic growth. It assumes that population growth is limited by several factors such as space, food, and water availability, nesting sites, weather, predators, competition, etc. The point where the line levels out is considered the carrying capacity K .



The per capita rates of a logistic growth model are defined as $f_b(N) = \beta \left(1 - \frac{N}{K}\right)$, $f_d(N) = \delta$

$$f(N) = r N \left(1 - \frac{N}{K}\right)$$

with $r = \beta - \delta$, $K = \frac{\beta - \delta}{\delta}$. The parameter r is actually the per capita birth rate at very low population abundances N . With increasing values of the population abundance it is assumed to decrease linearly with N to reach a value of 0 at carrying capacity $N = K$. If the initial population abundance would be either $N(0) = 0$ or $N(0) = K$ the abundance would remain 0 and K for all times. Such a value for the population abundance is referred to as a steady state or equilibrium.

The carrying capacity is the (maximum) size of a population that can be maintained within an ecosystem.

CARRYING CAPACITY

The carrying capacity is not a set number. Populations do not reach the carrying capacity and just stop. In fact, it is natural for populations to fluctuate over time, increasing some times and decreasing at other times. A population that is increasing has a positive population growth, while a population that is decreasing has a negative population growth. The carrying capacity is an estimated number that lies somewhere in the middle of these population fluctuations as it represents a growth rate of zero. There are many factors (besides limiting factors) that can cause population fluctuations. These include things like droughts, hurricanes, wildfires, mild winters, wet summers, etc. In some cases (such as droughts, hurricanes, and wildfires), you would expect the populations to drop. In other cases (such as mild winters or wet summers), you might expect an increase in the population. Having access to extra water during the summer or having mild winters might increase the chances

of offspring surviving to become sexually mature. Over the long term, many populations remain fairly stable in size and hover around their carrying capacity based limiting factors, but short term fluctuations may occur due to other events.

The carrying capacity can be kept artificially low or boosted to be artificially high. For example, hunting can keep the carrying capacity low. Should hunting be removed as a factor, the population may increase until it reaches its true carrying capacity of the environment. You can keep populations artificially high as well by providing food or water or nesting sites that normally would not occur. For example, if you feed the birds, provide them with nesting boxes, and give them water, you can keep the carrying capacity artificially high.

SUITABILITY FUNCTION

In PDE models we can introduce the suitability function $0 < \rho(x) < 1$ to weight the carrying capacity accordingly to the different point in the space. In a diffusion-reaction equation with logistic growth it can be introduced as follows

$$\frac{\partial N}{\partial t} - D \nabla^2 N + \mathbf{v} \cdot \nabla N = r N \left(\rho(x) - \frac{N}{K} \right)$$

Example. A plant population in a parking area

In this spatial area the vegetation was cut down and the owners covered the soil by gravel to use the zone as parking area; in this way, they made the spatial domain less suitable for vegetation growing. However, we observed in subsequent years the advancement of the front of vegetation spreading along edges and corners, which correspond to the parts that are not easily reachable by cars in the parking.



The spatial area is simplified as a triangular domain. We suppose that the parking area is represented by an ellipses inside the whole space. To model a different carrying capacity outside and inside the part reachable by cars, a suitability function is introduced (with values between 0 and 1). A lower value was set at zone occupied by car i.e. inside the ellipses while a higher outside where the soil is sealed by gravel. Simulations show that the diffusive dynamics reach the equilibrium at maximum carrying capacity scaled by suitability function.

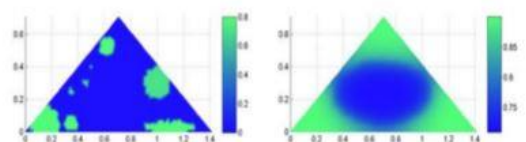


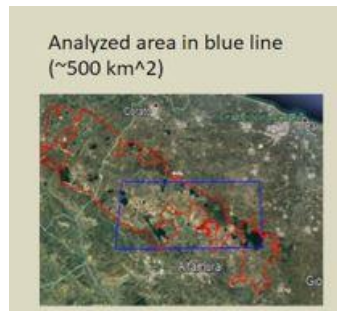
FIGURE 3 On the left side: values of initial distribution defined as $n_0(x, y) = a_i$ if $\left(\frac{x-h}{b}\right)^2 + \left(\frac{y-k}{h}\right)^2 < 1$, for $i = 1 \dots 8$. Parameters are chosen as $a_i = 0.8$ for $i = 1, 2, 3, 5$, and $a_i = 0.7$ for $i = 4, 6, 7, 8$, $X = [0.15, 0.35, 1.1, 1, 0.62, 0.5, 0.45, 0.35]$, $Y = [0.05, 0.05, 0.05, 0.3, 0.52, 0.4, 0.3, 0.25]$, $a = [0.11, 0.05, 0.2, 0.1, 0.06, 0.02, 0.02, 0.02]$, $b = [0.11, 0.05, 0.04, 0.1, 0.06, 0.02, 0.02, 0.02]$. On the right side: density distribution evaluated at $T = 20$ without control, that is, setting $E = 0$ everywhere

Baker, C. M., Diele, F., Marangi, C., Martiradonna, A., & Ragni, S. (2018). Optimal spatiotemporal effort allocation for invasive species removal incorporating a removal handling time and budget. *Natural Resource Modeling*, 31(4), e12190.

HOW ESTIMATING THE SUITABILITY FUNCTION

In the following we give an example about how estimating the suitability function.

The habitat suitability function was used also in modelling the invasion of *Ailanthus Altissima* in the Alta Murgia natural park.



We started from the species distribution and the land cover map produced in 2012 in the FAO-LCCS taxonomy.



The HSI corresponding to each LandCover class was calculated as proportional to the frequency of occurrence of that LC class in the surrounding of each pixel where the presence of *A. altissima* was detected. The rationale behind, is that the more LC class appears nearby an *A. altissima* tree, the more it is suitable to host the invasive species.

Habitat suitability index	
42 land classes (LCCS)	$\rho(x)$
Simple non-irrigated arable land	1
Natural pastures, grassland, uncultivated	0.81
Orchards and small fruit farms	0.21
Olive groves	0.24
Coniferous forest	0.09
...	...
Airports and heliports	0

ALLEE EFFECT

Warder Clyde Allee (1938) observed a fact that in a small population there may be also the extinction of the species. This observation related to the initial density of the population. Allee concluded that there is a critical point $N = A$ in which if the initial density of the population is below this critical point then the population vanishes and if it is above this critical point then the population has a positive growth phase

$$f(N) = r N \left(1 - \frac{N}{K}\right) \left(\frac{N}{A} - 1\right)$$

More generally, the phrase Allee effect is used to indicate a situation in which individuals at very low density are actually performing worse than at slightly higher densities.

Allee, W. C. (1938). Social life of animals.

Example. Wild boar colonization of Alta Murgia Park

This kind of growth function for modelling the wild boar colonization of the Alta Murgia Park. This colonization started with a restocking program and occurred more slowly in the initial stages of the reintroduction, probably due to stress factors related to the transportation as well as to the disruption of the social organization of animals removed from the wild. Thereafter, wild boars spread faster and the population growth was fostered by the hunting ban introduction in 2004. Based on the above considerations, an Allee growth for wild boar population with the Allee threshold A was estimated taking into account the amount of animals necessary to start the colonization of the Park.

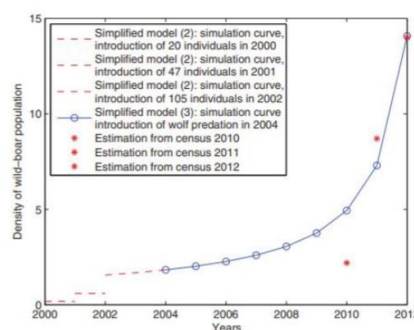


Fig. 2. Simulated wild boar dynamics corresponding to the optimal value for $r=0.0484$ with the simplified Eq. (2) in the interval [2000, 2004] and Eq. (3) in the interval [2004, 2012].

Lacitignola, D., Diele, F., & Marangi, C. (2015). Dynamical scenarios from a two-patch predator-prey system with human control—Implications for the conservation of the wolf in the Alta Murgia National Park. Ecological modelling, 316, 28-40.



LIMITING FACTORS TO POPULATION GROWTH

DISEASE

Impact depends on its lethality and its ability to spread.

Example. *Xylella fastidiosa* in olive trees, Covid 19 in human population

EPIDEMIC MODEL

The dynamics of the disease in a population is classically described by the SEIR model

$S = S(t)$ represents susceptible individuals at time t , $I = I(t)$ represents infectious individuals at time t , $R = R(t)$ represents recovered (immune) individuals at time t .

$N = S(t) + E(t) + I(t) + R(t)$ is the total number of individuals in the population

The model allows for an incubation period for the disease inside its host where an infected individual remains latent for some time before becoming infectious, creating an exposed class

$E = E(t)$ is the number of exposed or latent individuals at time t

$$\frac{dS}{dt} = \Lambda - \mu S - \beta I S$$

$$\frac{dE}{dt} = \beta I S - \sigma E - \mu E$$

$$\frac{dI}{dt} = \sigma E - \alpha I - \mu I - k I$$

$$\frac{dR}{dt} = k I - \mu R$$

Λ is the recruitment rate, μ is the natural death rate, β is the transmission rate, $1/\sigma$ the incubation period, α is the disease-related death-rate, k is the cure rate.

Lenhart, Suzanne, and John T. Workman. Optimal control applied to biological models. Chapman and Hall/CRC, 2007.

COMPETITION

Competition can occur between individuals of the same species and individuals of different species. This competition can be over resources such as water, food, nesting sites, space, etc. In the case of individuals of the same species, it can even be over mates.

Competition may be between individuals of the same species, in which case we call it intraspecific competition, or of different species, in which case it is called interspecific competition. Moreover competition may be direct or indirect. An example of direct or interference competition is when two individuals fight for the same piece of food that one of them has just caught. Also competition for sexual partners is usually a form of interference competition. On the other hand, indirect competition, which is also referred to as exploitation competition does not involve direct contact among the competitors. The most obvious example is when individuals feed on a

shared food source: the food eaten by one individual is unavailable to the others and hence there is a competitive interaction

Theory about competition for shared resources between different consumer species has been mainly developed by Tilman (1980) on the basis of competition experiments with different algal species in chemostat.

Tilman, David. "Resources: a graphical-mechanistic approach to competition and predation." The American Naturalist 116.3 (1980): 362-393.

ONE CONSUMER AND ONE RESOURCE

The basis of the theory is the interaction between consumer species and abiotic resources. Algae that use nutrients like phosphate and silicate for their growth are species to which the theory applies best and which hence have been used extensively to test and show the validity of the theory. The basic set of equations that is used to model this consumer-resource interaction is

$$\begin{aligned}\frac{dN}{dt} &= \alpha g(R) N - \mu N \\ \frac{dR}{dt} &= F(S - R) - Q \alpha g(R) N\end{aligned}$$

In the above equations the state variable N represents the abundance of consumers. It is assumed that the growth of the consumers is limited by a single resource, of which the actual concentration is denoted by R . The parameter S represents the maximum nutrient concentration that is possible in the habitat, which in a chemostat is identical to the inflow nutrient concentration of resource. The parameter F is the flow or supply rate of resource. The parameter Q indicates the amount of resource that is needed to produce a single consumer individual. Its inverse $1/Q$ is often referred to as the yield, since it represents the number of consumer individuals that a single unit of resource can yield. α represents the maximum population growth rate and μ the per capita mortality or death rate of consumers

$$g(R) = \frac{R}{\gamma + R} \text{ Michaelis-Menten equation}$$

γ is referred to as the half-saturation constant because $g(\gamma) = 1/2$

Possible outcomes:

1. the consumer population cannot persist;
2. the habitat is sufficiently productive and the consumers can establish a stable population.

TWO CONSUMERS AND ONE RESOURCE

$$\begin{aligned}\frac{dN_1}{dt} &= \alpha_1 \frac{R}{\gamma_1 + R} N_1 - \mu_1 N_1 \\ \frac{dN_2}{dt} &= \alpha_2 \frac{R}{\gamma_2 + R} N_2 - \mu_2 N_2 \\ \frac{dR}{dt} &= F(S - R) - Q_1 \alpha_1 \frac{R}{\gamma_1 + R} N_1 - Q_2 \alpha_2 \frac{R}{\gamma_2 + R} N_2\end{aligned}$$

There can be 2 outcomes.

In the first scenario, species 1 (or individual 1) outcompetes species 2 (or individual 2) for a resource, and species 2 (or individual 2) either leaves the area, dies, or has a reduction in its population and the resulting adjustment to its carrying capacity.

In the second scenario, species 2 (or individual 2) outcompetes species 1 (or individual 1) for a resource, and species 1 (or individual 1) either leaves the area, dies, or has a reduction in its population and the resulting adjustment to its carrying capacity.

In the first case, species 1 can sustain a stable population at a resource level that is too low for species 2 to persist. Hence, species 2 will go extinct. In the second case, the opposite occurs that species 2 drives species 1 to extinction due to its ability to persist at lower resource concentrations. In other words, it is the species with the lowest value of R^* that outcompetes the other consumers and drives to extinction.

The above equation do not allows the description of a third scenario: species 1 (or individual 1) and species 2 (or individual 2) end up sharing a resource, and therefore both species (and both individuals) coexist. For example, two species of fish live in the same pond. Species one lives in the shallow area while species 2 lives in the deeper area. Another example would be lions and elephants that need access to the same watering hole. The lions may visit in the morning, while the elephants may visit in the evening.

LOTKA-VOLTERRA COMPETITION MODEL

In the Lotka-Volterra model the competition between two species is represented without any reference to resources. For a particular species the presence of a competitor is simply assumed to reduce its growth.

$$\frac{dN_1}{dt} = f_1(N_1) - g_1(N_1)N_2$$

$$\frac{dN_2}{dt} = f_2(N_2) - g_2(N_2)N_1$$

Logistic growth rate for species N_1 : $f_1(N_1) = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right)$

Logistic growth rate for species N_2 : $f_2(N_2) = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right)$

Holling I: N_1 functional response $g_1(N_1) = r_1 \frac{\beta_{12}}{K_1} N_1$

Holling I: N_2 functional response $g_2(N_2) = r_2 \frac{\beta_{21}}{K_2} N_2$.

The following outcomes of the competition between species 1 and 2:

Case I: Species 2 outcompetes species 1 $\left(\max\left(\beta_{21}, 1/\beta_{12}\right) < \frac{K_2}{K_1}\right)$,

Case II: Species 1 outcompetes species 2 $\left(\min\left(\beta_{21}, 1/\beta_{12}\right) > \frac{K_2}{K_1}\right)$,

Case III: The outcome depends on the initial condition. $\left(1/\beta_{12} < \frac{K_2}{K_1} < \beta_{21}\right)$,

(If the two carrying capacities are equal $K_1 = K_2$ the condition simplifies to $\beta_{21} > 1$ and $\beta_{12} > 1$)



Case IV: Species 1 and 2 coexist when $\beta_{21} < \frac{K_2}{K_1} < 1/\beta_{12}$

.(If the two carrying capacities are equal $K_1 = K_2$ the condition simplifies to $\beta_{21} < 1$ and $\beta_{12} < 1$.)

Hence, only in Case IV both species can coexist, but they will do so at abundances below their carrying capacity. In all other cases, one species will outcompete the other.

For case IV to occur, the interspecific competition parameters β_{12}/K_1 and β_{21}/K_2 cannot be large i.e.

$$\frac{\beta_{12}}{K_1} < \frac{1}{K_2} \text{ and } \frac{\beta_{21}}{K_2} < \frac{1}{K_1}$$

which states that the interspecific competitions $\frac{\beta_{12}}{K_1}$ and $\frac{\beta_{21}}{K_2}$ are both less intense than the intraspecifics $\frac{1}{K_2}$ and $\frac{1}{K_1}$ respectively. If in any way, one interspecific competition is stronger than intraspecific competition, that is one of the species is more aggressively competing with the other than with its conspecifics, we falls in one of the previous case (I, II, III) and one of the two species will be excluded.

PREDATION

Predation can also occur between individuals of the same species and individuals of different species. The term applies to animals that eat other animals or animals that eat plants. It is important to remember that predators come in all different sizes. The impact of predation depends on the population number. For example, if you have 1 fox and 1000 rabbits, the fox can only eat so many rabbits, so predation will not have much of an impact on the rabbit population. However, if you have 100 foxes and 1000 rabbits, predation will have a larger impact on the rabbit population. In areas where predators and prey have coexisted for thousands of years, each develop certain strategies to either help it eat well (predator) or to avoid being eaten (prey). This is an important concept to remember as we discuss yet one more factor that affects the population size.



3. MODELLING PREDATOR-PREY INTERACTION

Volterra (1920) developed his model independently from Lotka (1910) and used it to explain why the percentage of predatory fish caught in the Adriatic Sea had increased during the years of World War I (1914–18) due to the reduced fishing effort during the war years. The model was later extended to include density-dependent prey growth and a functional response of the form developed by C. S. Holling; a model that has become known as the Rosenzweig–MacArthur model (1963). Both the Lotka–Volterra and Rosenzweig–MacArthur models have been used to explain the dynamics of natural populations of predators and prey, such as the lynx and snowshoe hare data of the Hudson’s Bay Company and the moose and wolf populations in Isle Royale National Park.

V. Volterra, *Variazioni e fluttuazioni del numero di individui in specie animali conviventi*, Mem. Acc. Lincei 2 (1926) 31–113.

Rosenzweig, M. L., & MacArthur, R. H. (1963). Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist*, 97(895), 209–223.

THE GENERAL DIFFUSIVE PREDATOR-PREY MODEL

Let $N = N(t)$ the prey population and $P = P(t)$ the predator population:

$$\frac{dN}{dt} - D \nabla^2 N = f(N) - g(N) P$$

$$\frac{dP}{dt} - D \nabla^2 P = \epsilon g(N) P - \mu P$$

FUNCTIONAL RESPONSES

Holling I: functional response assumes a linear increase in intake rate with food density, either for all food densities, or only for food densities up to a maximum, beyond which the intake rate is constant. The linear increase assumes that the time needed by the consumer to process a food item is negligible, or that consuming food does not interfere with searching for food:

$$g(N) = a N$$

Holling II: functional response is characterized by a decelerating intake rate, which follows from the assumption that the consumer is limited by its capacity to process food. The equation is

$$g(N) = \frac{a N}{1 + a h N}$$

The rate at which the consumer encounters food items per unit of food density is called the attack rate, a . The average time spent on processing a food item is called the handling time h

The Holling type II functional response is mathematically identical to the Michaelis-Menten equation that was used to model the nutrient uptake by bacteria, which was used in Tilman’s competition model.

LOTKA-VOLTERRA DIFFUSIVE PREDATOR-PREY MODEL

Exponential growth rate for prey $f(N) = rN$

Holling I predator functional response $g(N) = aN$

$$\frac{\partial N}{\partial t} - D \nabla^2 N = rN - aNP$$

$$\frac{\partial P}{\partial t} - D \nabla^2 P = \varepsilon aNP - \mu P$$

ROSENZWEIG-MACARTHUR MODEL

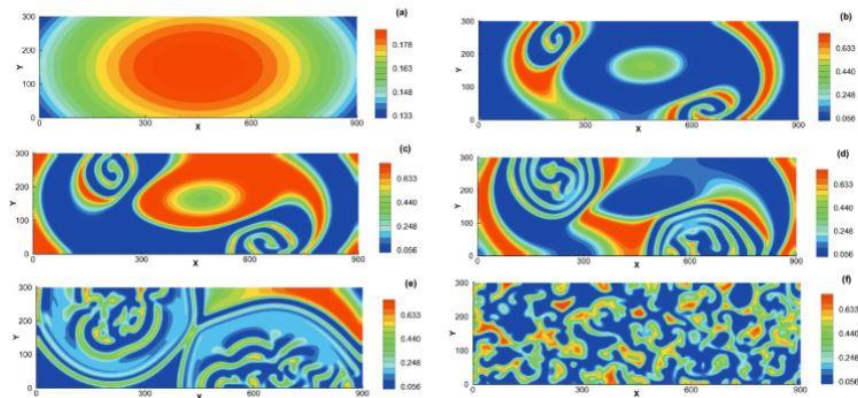
Logistic growth rate for prey $f(N) = rN \left(1 - \frac{N}{K}\right)$

Holling II predator functional response $g(N) = \frac{aN}{1 + ahN}$

$$\frac{\partial N}{\partial t} - D \nabla^2 N = rN \left(1 - \frac{N}{K}\right) - \frac{aN}{1 + ahN} P$$

$$\frac{\partial P}{\partial t} - D \nabla^2 P = \varepsilon \frac{aN}{1 + ahN} P - \mu P$$

Example. Phytoplankton-zooplankton system.



The system is affected by spatio-temporal chaos. Spiral patterns appear together with irregular patches that spread over the whole domain. Spatial distribution of prey (phytoplankton) for (a) $t = 0$, (b) $t = 120$, (c) $t = 160$, (d) $t = 300$, (e) $t = 400$, (f) $t = 1200$.

Medvinsky, A. B., Petrovskii, S. V., Tikhonova, I. A., Malchow, H., & Li, B. L. (2002). *Spatiotemporal complexity of plankton and fish dynamics*. *SIAM review*, 44(3), 311-370.

TWO PATCHES, TWO PREDATORS, TWO TIME SCALES

Here we give an example of modelling the interactions of two populations living in two different patches. Populations can migrate through corridors at a time scale, faster than the reproduction time.

Example. Wild-boar population in Alta Murgia Park

The Alta Murgia area extension and vegetation type appears to be unsuited for hosting a viable and stable population of wolves. Instead, the wild boar population exploded in recent years, especially because hunting



Fig. 1. Representation of the two areas (Alta Murgia and Monti Dauni) and of the three possible corridors that represent, from top to bottom, three alternative hypotheses of wolf colonization of the Alta Murgia from Monti Dauni: (top) the hypothesis that they have crossed the river Ofanto; (middle) the hypothesis of the shortest path; (bottom) the hypothesis of the path of natural areas (Pennacchioni, 2010). In our modeling framework, the two areas are razionalized as two patches.

activities were banned after the inclusion in the Natura 2000 network. It is known that wolves reached Alta Murgia from a nearby protected area, Monti Dauni, through ecological corridors. National legal obligations bind the managing Alta Murgia authorities to set up conservation policies for the protected species of wolves.

Figure from Lacitignola, D., Diele, F., & Marangi, C. (2015). *Dynamical scenarios from a two-patch predator–prey system with human control–Implications for the conservation of the wolf in the Alta Murgia National Park. Ecological modelling*, 316, 28-40.

Model assumptions:

1. Logistic growth rate with Allee effect for wild-boar $f(N) = r N \left(\frac{N}{A} - 1 \right) \left(1 - \frac{N}{K} \right)$
2. Holling I functional response of wolves in patch 1 (Alta Murgia) $g_1(N) = a_1 N$ (plus emigration and immigration)
3. Only wolf emigration and immigration in patch 2 (Monti Dauni)
4. Two-time scales: the fast part of the model at the fast τ scale only describes the migration of wolves between the two patches whereas, the evolution of the wild boar and wolf populations holds at slow time scale $t := \varepsilon \tau$ scale, with $\varepsilon \ll 1$

The resulting model is given by

$$\frac{dN}{d\tau} = \epsilon \left[r N \left(\frac{N}{A} - 1 \right) \left(1 - \frac{N}{k} \right) - a_1 N P_1 \right]$$

$$\frac{dP_1}{d\tau} = \epsilon (e a_1 N P_1 - \mu P_1) + d_2 P_2 - d_1 P_1$$

$$\frac{dP_2}{d\tau} = -\epsilon \mu P_2 + d_1 P_1 - d_2 P_2$$

THE AGGREGATION METHOD.

The presence of two different timescales (years/day) gave the chance to benefit from the general theoretical approach known as aggregation method (Auger et al., 2007).

This allowed for the reduction of the dimension of the two-patch model through a reduced one-patch system describing the dynamics of a smaller number of global variables. We defined $P = P_1 + P_2$ as the total amount of wolves and $d = \frac{d_2}{d_1 + d_2}$. Then

$$\frac{dN}{dt} = r N \left(\frac{N}{A} - 1 \right) \left(1 - \frac{N}{k} \right) - a_1 d N P$$

$$\frac{dP}{dt} = e a_1 d N P - \mu P$$

As the system is structurally stable and the parameter ϵ is small enough, the dynamics of the aggregated model is a good approximation of the dynamics of the global variables in the full system.

Auger, P., Bravo de la Parra, R., Poggiale, J., Sanchez, E., Nguyen Huu, T., 2007. Aggregation of variables and applications to population dynamics. In: Lecture Notes in Mathematics. Mathematical Biosciences Subseries, vol. 1936., pp. 209–264