Funded by
European Union

Grant Agreement 952111
H2020 WIDESPREAD-05-2020 (Twinning)

Standard course – Modelling
Lesson SM3.1 – ECOSYSTEM MODELLING

Fasma Diele and Carmela Marangi – IAC-CNR

CERTH
CENTRE FOR
RESEARCH & TECHNOLOGY
HELLAS

CREAF

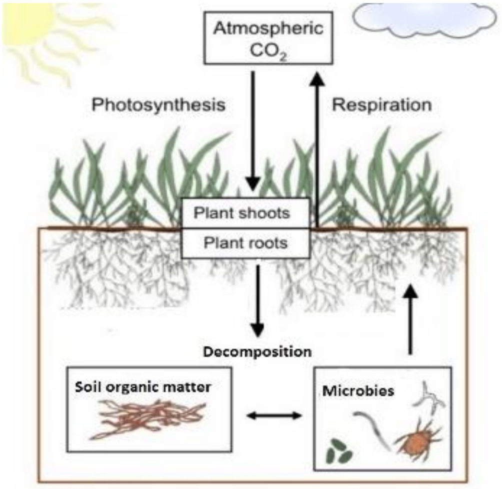
Consiglio Nazionale
delle Ricerche

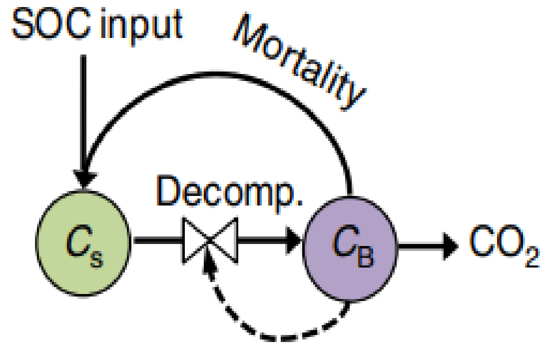
What is an ecosystem?

- An ecosystem is a community of living organisms existing in conjunction with the nonliving components of their environment, interacting as a system.
- These biotic and abiotic components are linked together through nutrient cycles and energy flows.
- Then ecosystems are defined by the network of interactions among organisms, or between organisms and their environment.
- Consequently, ecosystems tend to be very complex and governed by many intricate and usually non-linear mechanistic interactions

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. 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

Biomes

A biome is a large area characterized by its vegetation, soil, climate, and wildlife. There 5 main biomes:

- Aquatic
- Grasslands
- Forests
- Deserts
- Tundra

Some of these biomes can be further divided into more specific categories, such as freshwater, marine, savanna, tropical rainforest, temperate rainforest, and taiga.

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.
- Internal factors control the availability of input resources within the ecosystem: decomposition, root competition, or shading. Other internal factors include disturbance, succession, and the types of species present.

Resistence, resilience and reactivity

- 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.

- Reactivity is defined as the maximal initial amplification rate.

Native species and ecosystems

- 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.
- 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 native species in specific niches in the ecosystem.

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: 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).

Discrete models

Discrete time models only determine the state of the modelled population at specific points in time and do not tell what happens in between.

- $N(t)$ the population abundances at time t
- $N(t + \Delta t)$ the population abundances at time t + Δt.

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

Continuous models: ODEs

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

- Divide both sides of the discrete model by Δt:

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

- Take the limit for Δt tending to 0 to obtain an ordinary differential equation (ODE)

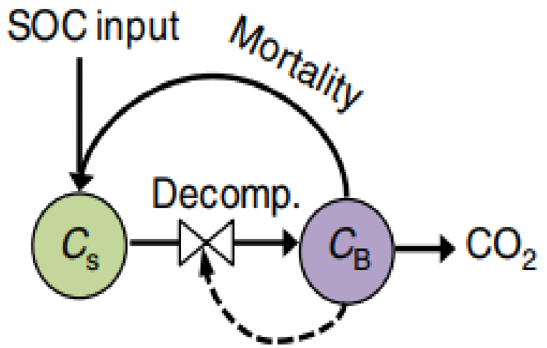
$$\frac{dN}{dt} = f(N), \qquad f(N) = B(N) - D(N)$$

$B(N)$ represents the birth rate, $D(N)$ represents the death rate

- Specify an initial state (t=0) of population i.e. $N(0) = N_0$

Example: SOC model

- Two pools model: the process is governed by the non linear interaction between the soil organic matter represented by the variable Cs and microbial biomass by the variable Cb and between these pools and the environment



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

The graphical representation corresponds to a non-linear, autonomous, two-dimensional ODE system.

Partial differential equations (PDEs)

In PDEs models 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-advection equation for species dispersal

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

- $D\,\nabla^2 N$ is a diffusive term, which describes collective motion of randomly moving individuals throughout a landscape. The coefficient D is the diffusivity, which governs how quickly the species disperses.
- $\boldsymbol{\nu} \cdot \nabla N$ is the advection, which is controlled by the coefficient $\boldsymbol{\nu}$. 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.
- $r\,N\left(1 - \frac{N}{K}\right)$ is the reaction described by is a logistic population growth term, where the coefficientr is the intrinsic growth rate of the population and K is the carrying capacity.

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

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

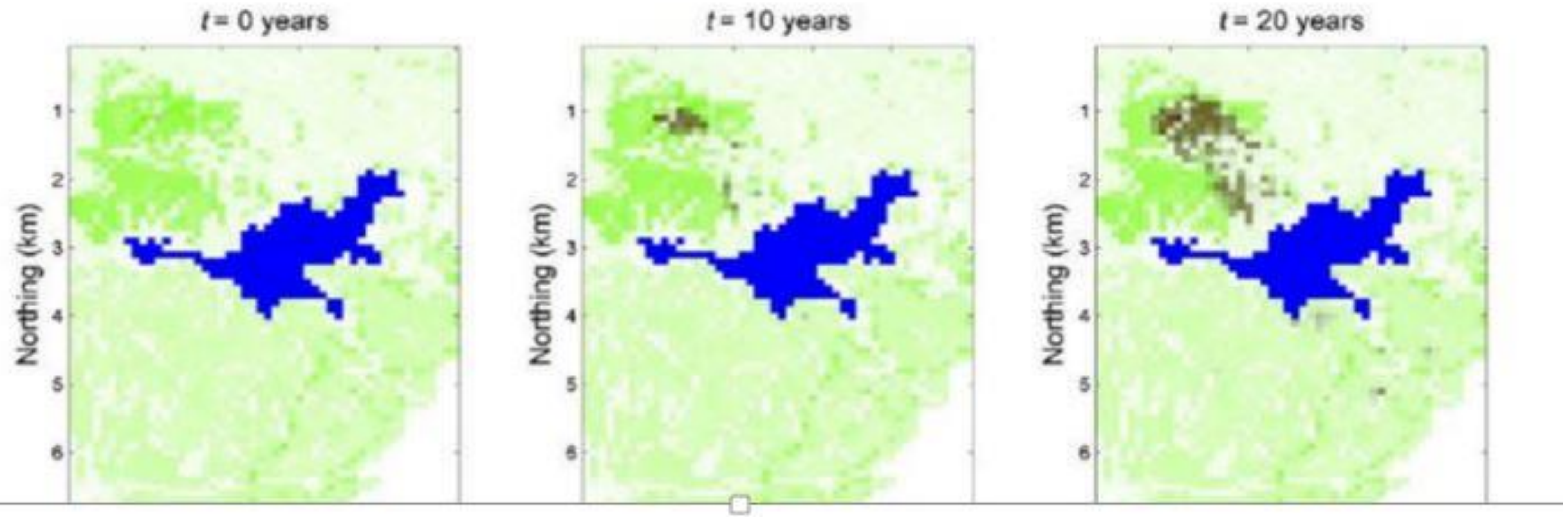


Figure 3 The spread of *H. aurantiacum* through the Bogong High Planes as predicted by the model over a 20-year period. Brown areas show the presence of *H. aurantiacum*, with the darker shading indicating high density. The green shading is the habitat suitability, where dark green is high suitability 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.

Population growth functions

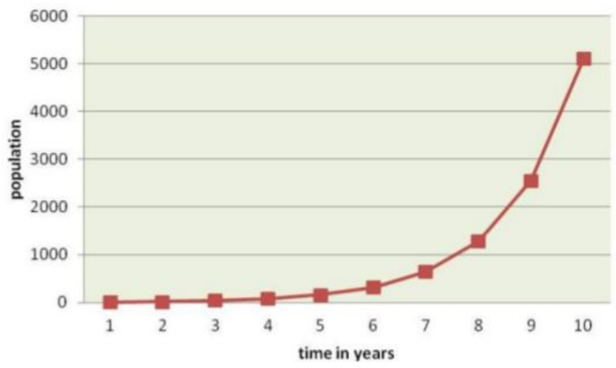
- The population rate $f(N)$ is given by the difference between the rate with which the number of individuals increase and the rate with which the number of individuals decreases

$$f(N) = \left(f_b(N) - f_d(N)\right) N$$

- The 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 assumes that there is unlimited resources available and that the population will continue to increase until the end of time

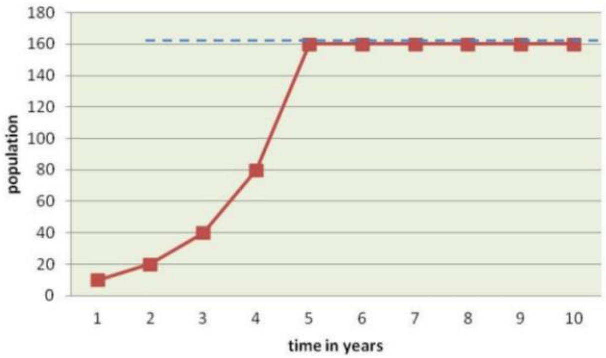


- $f_b(N) = \beta$, $f_d(N) = \delta$, $r = \beta - \delta$

$$f(N) = r\,N$$

Logistic growth

- Logistic growth assumes that population growth is limited by several factors The point where the line levels out is considered the carrying capacity K.



- $f_b(N) = \beta\left(1 - \frac{N}{\gamma}\right),\ f_d(N) = \delta, r = \beta - \delta,\ K = \frac{\beta - \delta}{\beta}$

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

Grant Agreement 952111, H2020 WIDESPREAD-05-2020 (Twinning)

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. 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.
- 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.

Suitability function

In PDE models we introduce the suitability function

$$0 < \rho(x) < 1$$

to weight the carrying capacity accordingly to the different point in the space.

- A reaction-diffusion-advection equation with logistic growth and suitability function

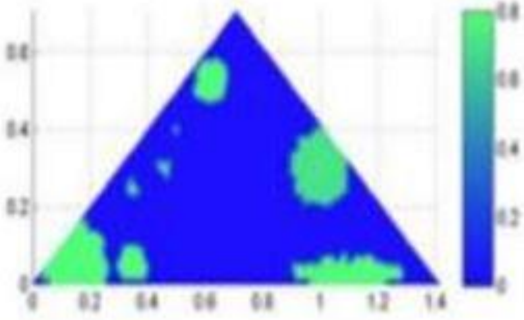
$$\frac{\partial N}{\partial t} - D\,\nabla^2 N + \boldsymbol{\nu} \cdot \nabla N = r\,N\left(\rho(x) - \frac{N}{K}\right)$$

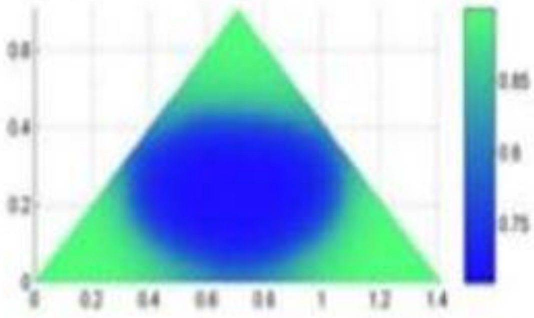
Example. A plant population in a parking area

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.

- 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.

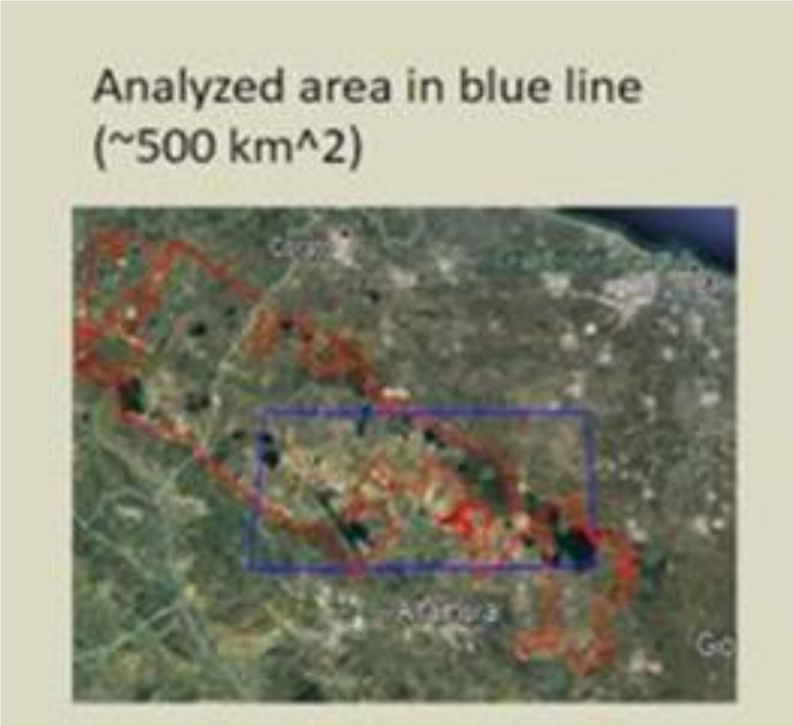
- The spatial area is simplified as a triangular domain and the parking area is represented by an ellipses inside the whole space.
- A different carrying capacity outside and inside the part reachable by car: a lower value was set at zone occupied by car i.e. inside the ellipses while an higher outside where the soil is sealed by gravel.
- Simulations show that the diffusive dynamics reach the equilibrium at maximum carrying capacity scaled by suitability function





How estimating the suitability function

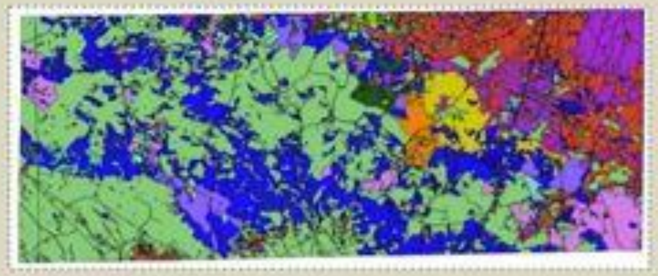
Spread of Ailanthus Altissima in the Alta Murgia Natural Park (Apulia region, south of Italy)



How estimating the suitability function

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

Land cover map - Regione Puglia Repository



Presence of Ailanthus

- The Habitat Suitability Index (HIS) 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.

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

- When there is a critical point $N = A$ such that 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 then we refer to as Allee effect

- The population growth function is given by

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

- 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.

Example. Wild boar colonization of Alta Murgia Park

- The wild boar colonization of the Alta Murgia Park started with a restocking program and occurred more slowly in the initial stages of the reintroduction
- 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.

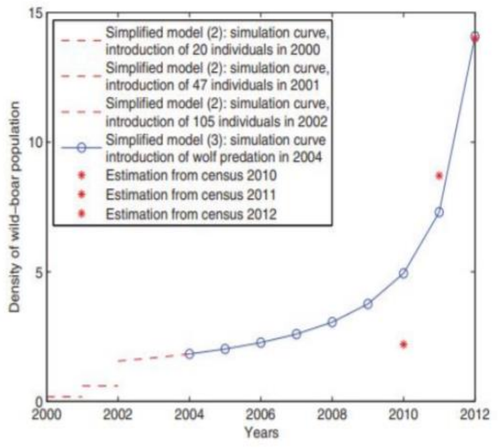


Fig. 2. Simulated wild boar dynamics corresponding to the optimal value for $r = 0.0484$ with the simplified Eq. (2) in the interval [2000, 2004] and Eq. (3) in the interval [2004, 2012].

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
- Competition
- Predation

Disease

Examples. Xylella fastidiosa in olive trees, Covid 19 in human population

EPIDEMIC MODEL

SEIR model

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

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

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

Competition

Theory about competition for shared resources between different consumer species has been mainly developed by

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

Competition can occur 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.

- Intraspecific competition: competition is between individuals of the same species,
- Intraspecific competition: competition is between individuals of different species
- Direct competition: 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.
- Indirect competition: (or exploitation competition) does not involve direct contact among the competitors. An 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

One consumer and one resource

$$\frac{dN}{dt} = \alpha\, g\,(R)\, N - \mu\, N$$

$$\frac{dR}{dt} = F(S - R) - Q\, \alpha\, g\,(R) N$$

- N abundance of consumers.
- Rconcentration of a single resource.
- S maximum nutrient concentration that is possible in the habitat
- F is the flow or supply rate of resource.
- Q the amount of resource that is needed to produce a single consumer individual. $1/\,Q$ is often referred to as the yield, since it represents the number of consumer individuals that a single unit of resource can yield.
- α maximum population growth rate.
- μ per capita mortality or death rate of consumers.

Michaelis-Menten functional response

$$g\ (R) = \frac{R}{\gamma + R}$$

γ is the half-saturation constant ($g\ (\gamma)\ =\ ½$)

Possible outcomes:

1. The equilibrium value R* for the resource concentration is too large i.e. R* > S, the consumer population cannot persist.
2. If R* < S. i.e. if habitat is sufficiently productive the consumers can establish a stable population and control the resource concentration in the habitat at the concentration equal to R*

Two consumers and one resource

$$\frac{dN_1}{dt} = \alpha_1 \frac{R}{\gamma_1 + R} N_1 - \mu_1 N_1$$

$$\frac{dN_2}{dt} = \alpha_2 \frac{R}{\gamma_2 + R} N_2 - \mu_2 N_2$$

$$\frac{dR}{dt} = F(S - R) - Q_1 \alpha_1 \frac{R}{\gamma_1 + R} N_1 - Q_2 \alpha_2 \frac{R}{\gamma_2 + R} N_2$$

Outcome: one species outcompetes the other consumer

Lotka-Volterra competition model

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

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

- Logistic growth rates f_1, f_2
- Holling I functional responses g_1, g_2

Possible outcomes:

1. Case I: Species 2 outcompetes species 1,
2. Case II: Species 1 outcompetes species 2,
3. Case III: Species 1 can outcompete species 2, but species 2 can also outcompete species 1. The outcome depends on the initial condition.

Coexistence scenario

Case IV: Species 1 and 2 coexist when

$$^{K_2}/_{\beta_{21}} > K_1 \; and \; ^{K_1}/_{\beta_{12}} > K_2$$

If $K_1 = K_2$ the condition on the interspecific parameters simplifies to

$$\beta_{21} < 1 \quad \text{and} \quad \beta_{12} < 1$$

- The Lotka-Volterra competition model allows the description of a coexistence scenario: species 1 and species 2 end up sharing a resource, and therefore both species coexist.

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.
- The impact of predation depends on the population number.
- 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).

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

$N = N(t)$ the prey population

$P = P(t)$ the predator population

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

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

- $f(N)$ growth function
- $g(N)$ functional response

Holling type functional responses

- Holling I: functional response assumes a linear increase in intake rate with food density. 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

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

- a is the attack rate i.e. the rate at which the consumer encounters food items per unit of food density
- h is the handling time i.e. the average time spent on processing a food

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 for prey $f\ (N) = r\ N$
- Holling I predator functional response $g\ (N) = a\ N$

$$\frac{\partial N}{\partial t} - D\ \nabla^2 N = r\ N - a\ N\ P$$

$$\frac{\partial P}{\partial t} - D\ \nabla^2 P = \mathcal{E}\ a\ N\ P - \mu\ P$$

Rosenzweig-MacArthur model

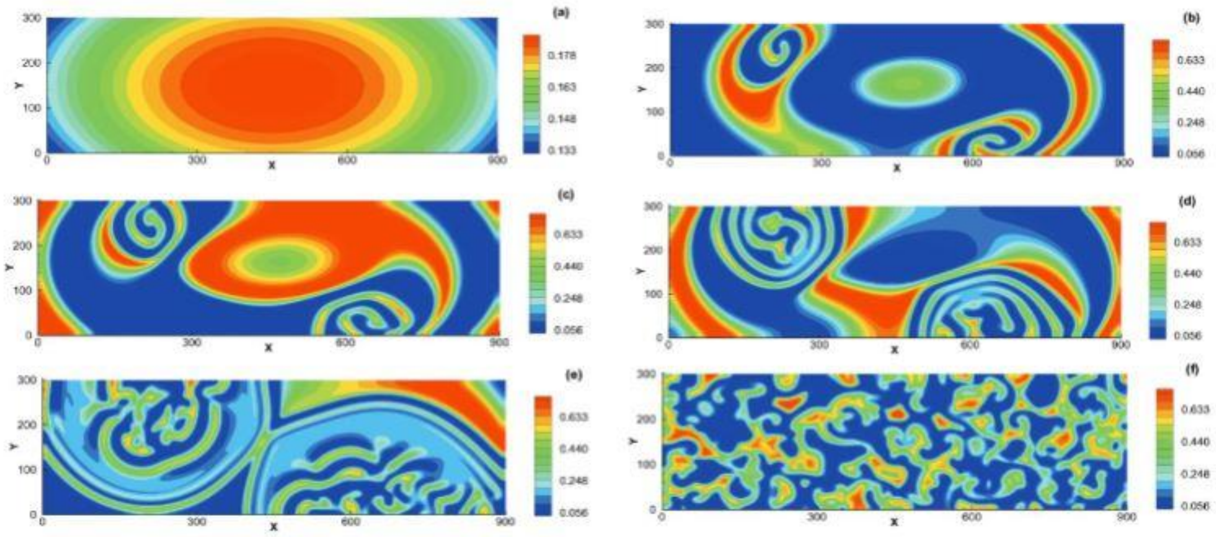
- Logistic growth for prey $f(N) = r\,N\left(1 - \frac{N}{K}\right)$
- Holling II predator functional response $g\,(N) = \frac{a\,N}{1+a\,h\,N}$

$$\frac{\partial N}{\partial t} - D\,\nabla^2 N = r\,N\left(1 - \frac{N}{K}\right) - \frac{a\,N}{1 + a\,h\,N}\,P$$

$$\frac{\partial P}{\partial t} - D\,\nabla^2 P = \varepsilon\,\frac{a\,N}{1 + a\,h\,N}\,P - \mu\,P$$

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

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 because hunting activities were banned after the inclusion of Alta Murgia Park in the Natura 2000 network.
- Wolves reach 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.

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.

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

- Logistic growth rate with Allee effect for wild-boar

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

- Holling I functional response of wolves in patch 1 (Alta Murgia)

$g_1\,(N) = a_1\,N$ (plus emigration and immigration)

- Only wolf emigration and immigration in patch 2 (Monti Dauni)

- Two-time scales: the fast part of the model at the fast τ scale (daily 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 (yearly scale) $t = \varepsilon\,\tau$ scale, with $\varepsilon \ll 1$

The model

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

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

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

Aggregation method $\longrightarrow$

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

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

Reduction of the dimension of the two-patch model to one-patch system by defining $P = P_1 + P_2$ as the total amount of wolves and $d = \frac{d_2}{d_1 + d_2}$.

As the system is structurally stable and the parameter Ɛ 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