Thresholds, Dynamics, and Bifurcations

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Objectives

- Introduce in-host models (Mathematical Immunology)
- Introduce intraguild predation models (Mathematical Ecology)
- Introduce relevant bifurcation theory (Dynamical Systems)

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Is Mathematical Biology a branch of applied maths?

What is Mathematical Biology?

Classic In-host infection model

susceptible host cell: $$\frac{dT}{dt} = \lambda - \mu T - \beta TV$$

infected host cell: $$\frac{dI}{dt} = \beta TV - \delta I$$

free virus: $$\frac{dV}{dt} = pI - cV - \beta_v TV$$

- Nowak and May, 2000, *Virus dynamics: mathematical principles of immunology and virology*, Oxford University Press
- Bonhoeffer et al., 1997, *Virus dynamics and drug therapy*, PNAS

Classic In-host infection model: life-cycle

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Classic In-host infection model: equilibria

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free virus: $$\frac{dV}{dt} = pI - cV - \beta_v TV$$

- Infection-free equilibrium:

- Coexistence equilibrium:

Classic In-host infection model: stability and invasion

resident: $x = (T)$ $$\frac{dx}{dt} = f(x,y) = \lambda - \mu T - \beta TV$$

invader: $y = \begin{pmatrix} I \\ V \end{pmatrix}$ $$\frac{dy}{dt} = g(x,y) = \begin{pmatrix} \beta TV - \delta I \\ pI - cV - \beta_v TV \end{pmatrix}$$

Classic Immune Model

cellular immunity

susceptible host cell: $$\frac{dT}{dt} = \lambda - \mu T - \beta T V$$

infected host cell: $$\frac{dI}{dt} = \beta T V - \delta I - pIB$$

free virus: $$\frac{dV}{dt} = N\delta I - cV - pVB$$

immune cells: $$\frac{dB}{dt} = (a^* I + aV)B - bB$$

immune cell recruitment

humoral immunity

- Ciupe and Heffernan, 2017, *In-Host Modeling*, Infectious Disease Modelling
- Murase et al., 2005, J. Math. Biol.

Classic Lotka-Volterra Predator Prey Model

- LV1 Prey grow exponentially at per capita rate r in absence of the predator.
- LV2 Prey are killed at a constant per capita rate a per predator.
- LV3 Each prey killed due to predation gives rise to c predators.
- LV4 Predator death is at a constant per capita rate m.

The model consists of a pair of differential equations. Here N and P are the prey and predator densities, respectively.

$$\frac{dN}{dt} = rN - aNP, \tag{1}$$

$$\frac{dP}{dt} = caNP - mP. \tag{2}$$

The Volterra Model

In 1931, Volterra published an analysis of a predator-prey model with a prey carrying capacity:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - aNP, \tag{3}$$

$$\frac{dP}{dt} = caNP - mP. \tag{4}$$

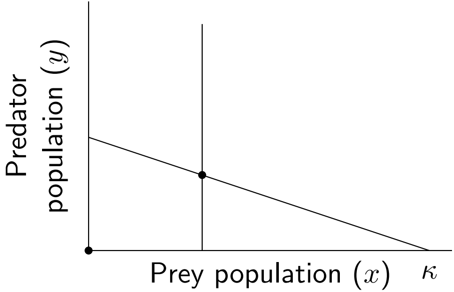
The model can be rescaled to yield

$$x' = x\left(1 - \frac{x}{\kappa}\right) - xy, \tag{5}$$

$$y' = \mu y(x - 1). \tag{6}$$

The Volterra Model State Space

These equations represent a similar vector field to the original Lotka-Volterra model. The x nullcline is no longer horizontal, but has the equation $y = 1 - x/\kappa$.



Computations show the interior equilibrium to be stable, the trivial equilibrium to be a saddle, and the solutions are oscillations decaying to the interior equilibrium.

The Rosenzweig-MacArthur Model

Rosenweig and MacArthur (1963) are credited with the addition of a hyperbolic functional response to the classic predator-prey model.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{aNP}{1+bN}, \tag{7a}$$

$$\frac{dP}{dt} = c\frac{aNP}{1+bN} - mP. \tag{7b}$$

The Functional Response

Turchin (2003) provides an excellent discussion of the various responses of predators to changes in prey populations.

$$\frac{dN}{dt} = NF(N) - H(N,P)P,$$
$$\frac{dP}{dt} = G(N,P)P - mP.$$

The three functions are usually referred to as

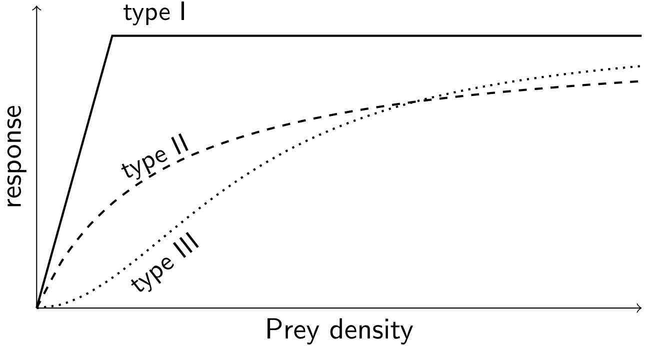
- the net per capita growth rate F, which is assumed independent of predation,
- the *functional response* H, which is the rate individual predators kill prey, and
- the *numerical response* G, which models the dependence of the per capita predator growth rate on population densities.

Predator-prey relationships include

- Consumer-resource
- Plant-herbivoire
- susceptible-infectivee
- host-pathogen
- host-parasite

The Functional Response

Holling (1959) introduced a simple classification of functional responses of predators into type I, II, or III. Mathematically, type I and II are similar, and represent a saturating response.



The Rosenzweig-MacArthur Model: equilibria

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{aNP}{1+bN}, \tag{8a}$$

$$\frac{dP}{dt} = c\frac{aNP}{1+bN} - mP. \tag{8b}$$

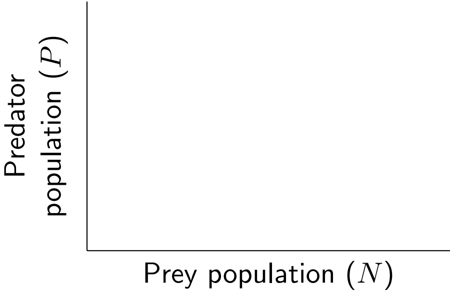
- trivial equilibrium: $(0,0)$
- predator-free equilibrium: $(0,K)$
- coexistence equilibrium: $(\bar{N},\bar{P})$, if $0 < \frac{m}{ca-mb} < K$

$$\bar{N} = \frac{m}{ca-mb},$$

$$\bar{P} = r\bar{N}(1+b\bar{N})\left(1 - \frac{\bar{N}}{K}\right).$$

The Rosenzweig-MacArthur Model: state-space

$$
\begin{aligned}
\frac{dN}{dt} = 0 \qquad & r\left(1 - \frac{N}{K}\right) - \frac{aP}{1 + bN} = 0, \\
\frac{dP}{dt} = 0 \qquad & c\frac{aN}{1 + bN} - m = 0.
\end{aligned}
$$



The Rosenzweig-MacArthur Model: Hopf-bifurcations

A stability analysis of the interior fixed point is simplified by writing the system in the *Kolmogorov form*

$$\frac{dN}{dt} = Nf(N), \tag{9a}$$

$$\frac{dP}{dt} = Pg(P), \tag{9b}$$

where

$$f(N,P) = r\left(1 - \frac{N}{K}\right) - \frac{aP}{1+bN}, \qquad g(N,P) = c\frac{aN}{1+bN} - m.$$

The interior equilibrium satisfies $f(\bar{N}) = g(\bar{P}) = 0$.

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The interior equilibrium satisfies $f(\bar{N}) = g(\bar{P}) = 0$.
The Jacobian at $(\bar{N},\bar{P})$ is

$$\begin{pmatrix} \bar{N}\bar{f}_N & \bar{N}\bar{f}_P \\ \bar{P}\bar{g}_N & \bar{P}\bar{g}_P \end{pmatrix}$$

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- $f(\bar{N}) = g(\bar{P}) = 0.$
- $\bar{g}_P = 0,\ \bar{f}_P < 0,\ \bar{g}_N > 0$

The Rosenzweig-MacArthur Model: Hopf-bifurcations

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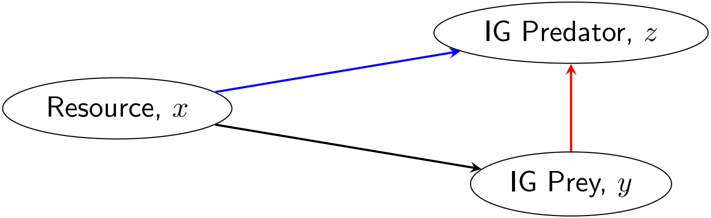
- $f(\bar{N}) = g(\bar{P}) = 0.$
- $\bar{g}_P = 0,\ \bar{f}_P < 0,\ \bar{g}_N > 0$
- The Hopf Birfurcation Theorem implies $(\bar{N},\bar{P})$ changes from a stable to unstable focus as $\bar{f}_N$ changes from positive to negative.
- a stable limit cycle bifurcates from the equilibrium as the trace increases through zero.

A Simple Intraguild Predation Model



$$\dot{x} = x(1-x) - xy - \alpha_2 xz,$$

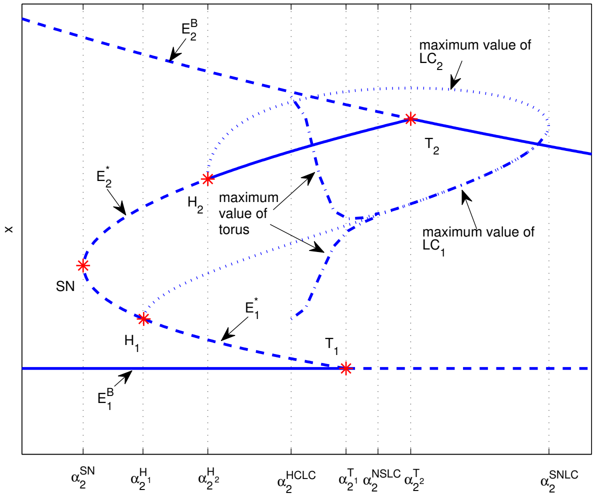
$$\dot{y} = \sigma_1 xy - \frac{yz}{1+\beta_3 y} - \mu_1 y,$$

$$\dot{z} = \frac{\sigma_2\alpha_2 xz}{1+\beta_2 x} + \frac{\sigma_3 yz}{1+\beta_3 y} - \mu_2 z.$$

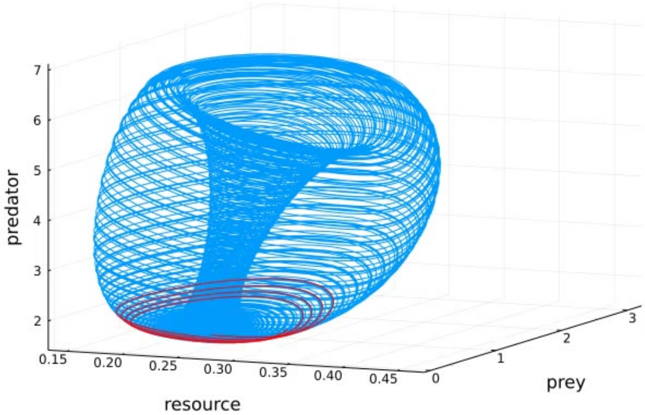
- Type II interaction between IG prey and IG predator (β_3)
- Saturating numerical response of IG predator to resource (α_2, β_2)

Xi Hu, 2014, PhD Thesis

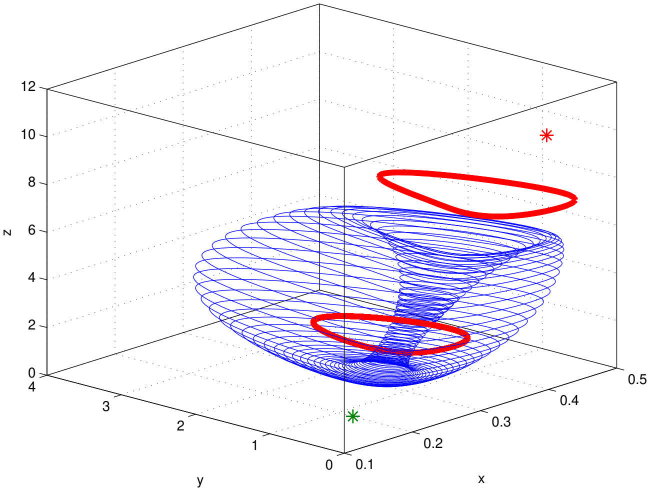
Intraguild Predation: bifurcation diagram

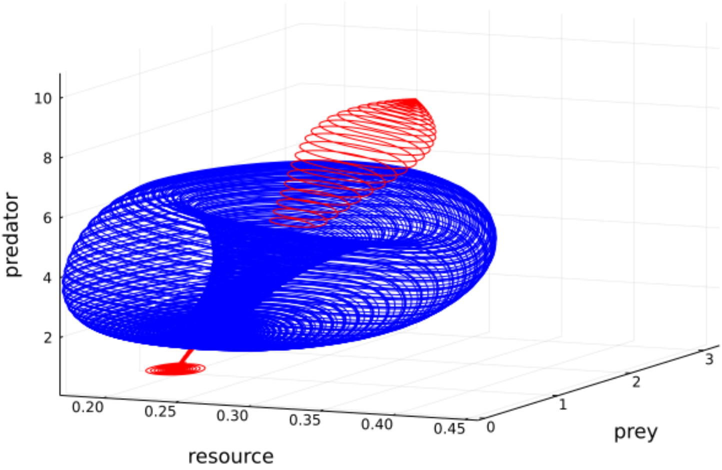


The Stable Torus



Tristability with an Attracting Torus




predator
10
8
6
4
2
0.20
0.25
0.30
0.35
0.40
0.45
resource
0
1
2
3
prey

Poincaré section through torus