Tutorial: non-linear dynamics

Winter School on Quantitative Systems Biology:
Quantitative Approaches in Ecosystem Ecology

Leonardo Pacciani-Mori (University of Padua, Italy)
November 30th and December 1st, 2020

The Abdus Salam
International Centre
for Theoretical Physics

Structure of the tutorial

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- Introduction: why is non-linearity interesting?
  - $\rightarrow$ Examples of non-linearity in ecology

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Important

The aim of these tutorials is also to encourage discussion: ***please* don't hesitate to interrupt me and ask questions** if you have them!!!

Introduction

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$$\dot{x}^2 = xy \qquad \dot{y} = \frac{x}{y} \tag{2b}$$

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Why are nLDE important?

Every interesting and/or non-trivial phenomenon is described by nLDE.

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4. Lotka-Volterra equations:

$$\dot{x} = \alpha x - \beta xy \tag{6a}$$

$$\dot{y} = \delta xy - \gamma y \tag{6b}$$

where:
$x > 0 \rightarrow$ prey's population, $y > 0 \rightarrow$ predator's population; $\alpha > 0 \rightarrow$ prey's growth rate, $\beta > 0 \rightarrow$ predation rate, $\delta > 0$ $\rightarrow$ predator's growth rate, $\gamma > 0 \rightarrow$ predator's death rate.
If written as $\dot{\vec{z}} = f(\vec{z})$, with $\vec{z} = (x, y)$, $f(\vec{z})$ is non-linear.

Equilibria

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- An equilibrium x^* is said to be ***unstable*** if there are solutions $x(t)$ with $x_0 = x(0)$ "close enough" to x^* which go "away" from x^*

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Can we obtain some information on a non-linear system's ***equilibria*** (and their stability) without solving it analytically?

There are several ways we can do so. A very simple yet useful one is drawing ***stream plots***, i.e. drawing trajectories of the system in the state space.

Stream plots

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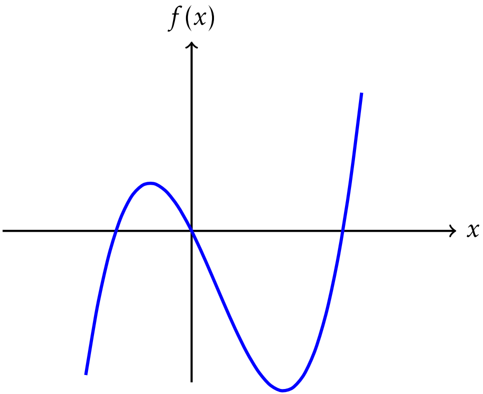

$$f(x) = x^3 - x^2 - 2x = x(x-2)(x+1) \tag{9a}$$

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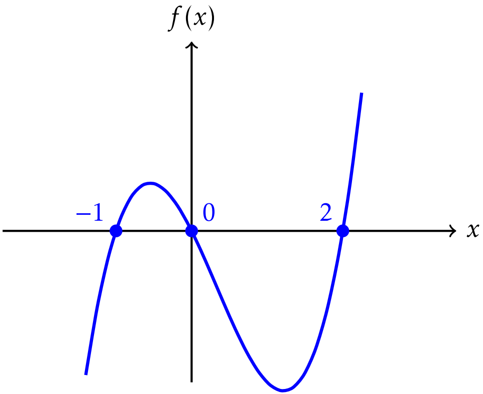

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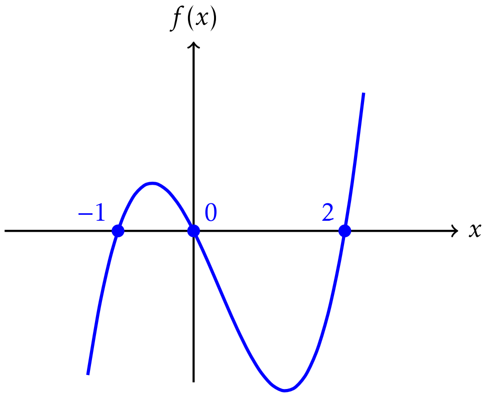

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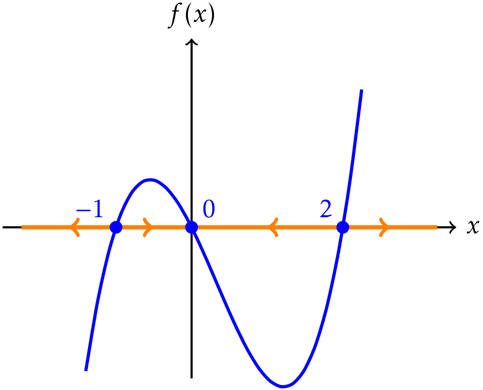

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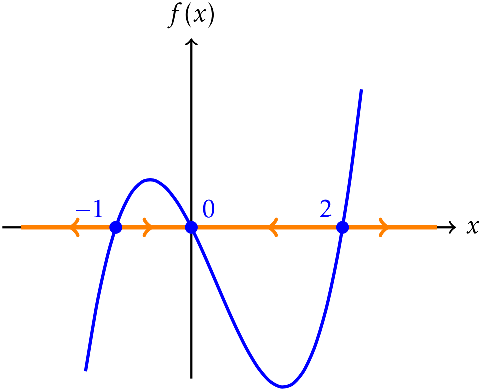

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When $f(x) > 0$, $\dot{x} > 0$ so x increases, and viceversa x decreases when $f(x) < 0$.

We can get a sense of which equilibria are stable and which are unstable:

$x^* = 0 \longrightarrow$ stable; $x^* = -1$, $x^* = 2 \longrightarrow$ unstable.

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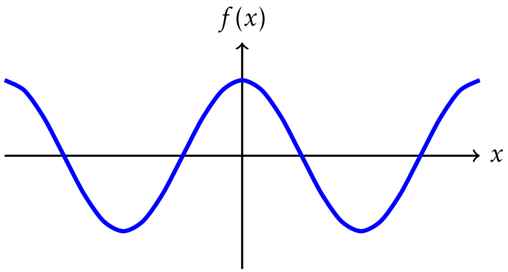

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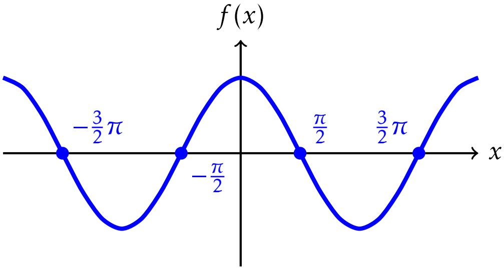

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$$x^* = \pm(2k+1)\frac{\pi}{2} \qquad k = 0, 1, 2, \dots \tag{11b}$$

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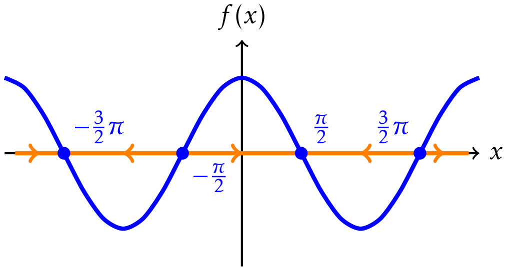

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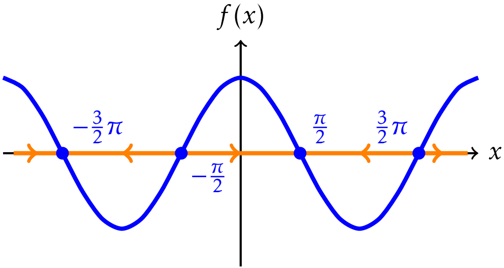

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k even and $x^* > 0$, or k odd and $x^* < 0 \rightarrow$ stable;
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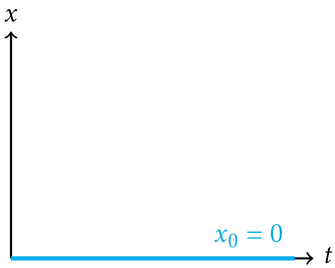

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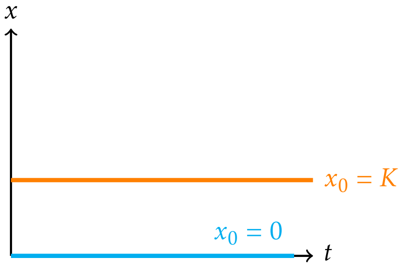

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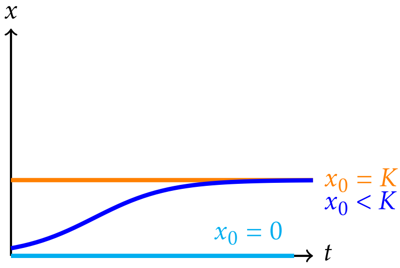

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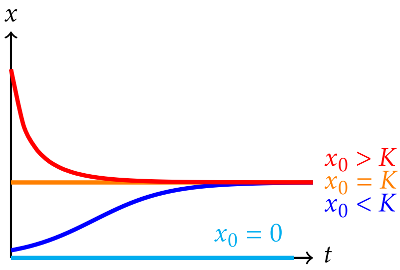

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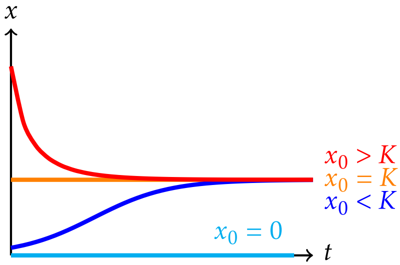

The maximal population that the system can sustain is K ($\rightarrow$ *carrying capacity*).

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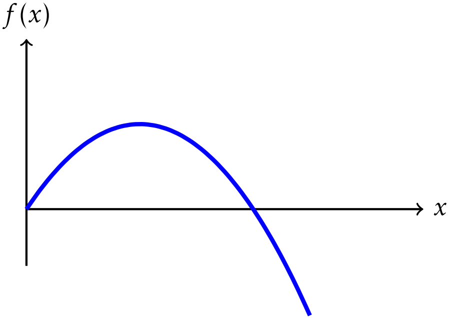

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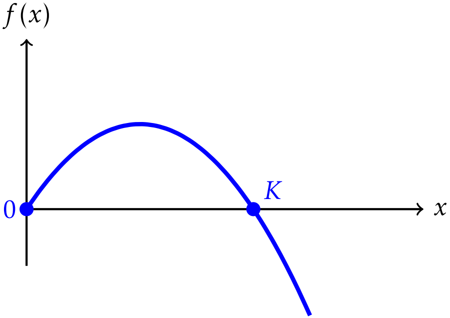

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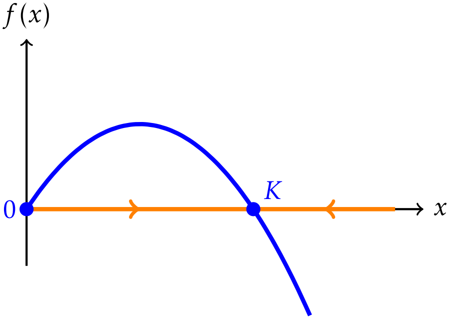

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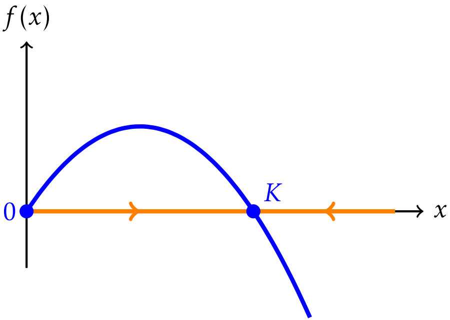

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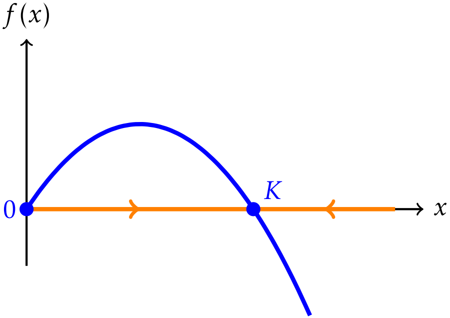

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Conclusion

We have indeed recovered the same behavior!

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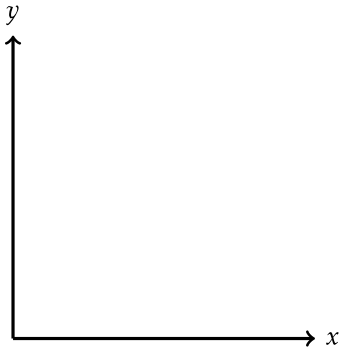
Let's apply the same principle to the Lotka-Volterra equations:

$$\begin{pmatrix}\dot{x}\\ \dot{y}\end{pmatrix} = \begin{pmatrix}\alpha x - \beta xy\\ \delta xy - \gamma y\end{pmatrix} := f\begin{pmatrix}x\\ y\end{pmatrix}, \qquad \begin{matrix} x, y > 0 \\ \alpha, \beta, \gamma, \delta > 0 \end{matrix} \tag{16}$$



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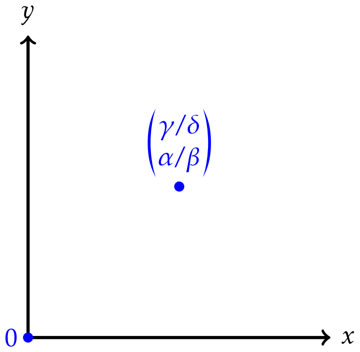

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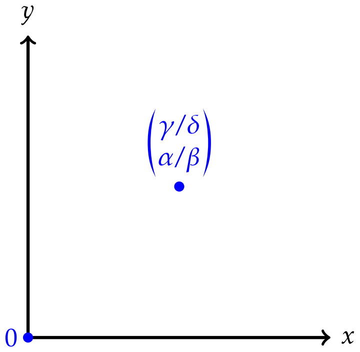

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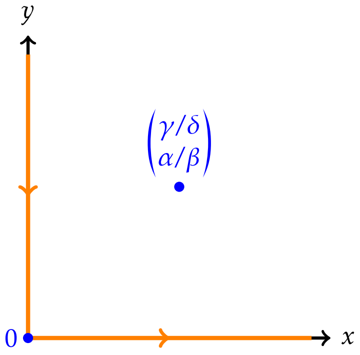

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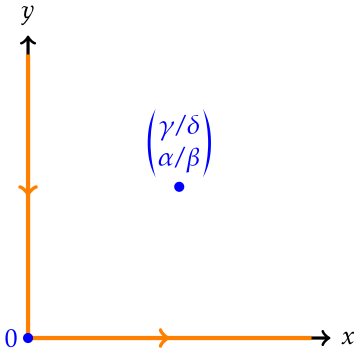

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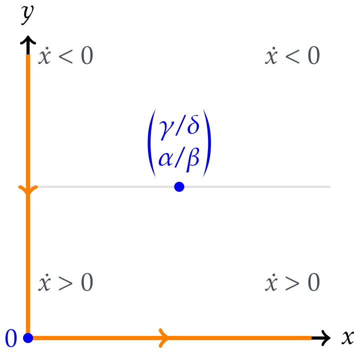

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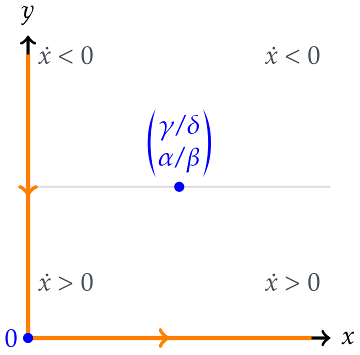

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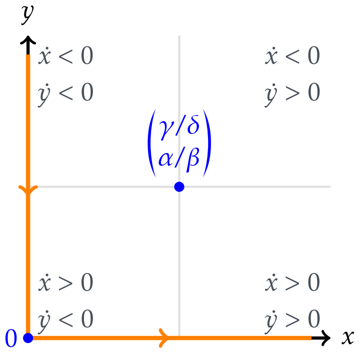

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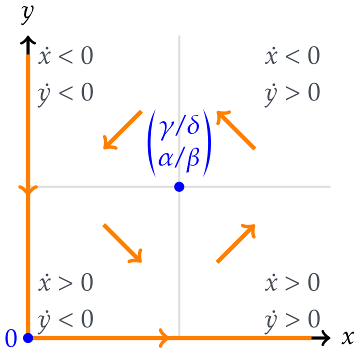

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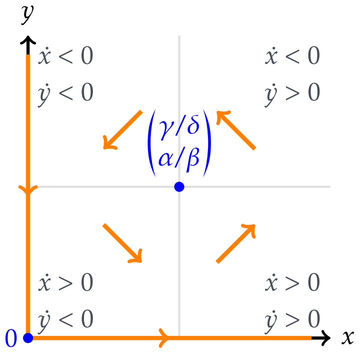

The trajectories oscillate around the equilibrium $(\gamma/\delta, \alpha/\beta)$!

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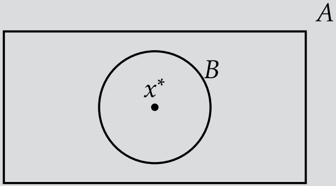

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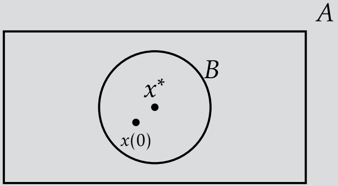

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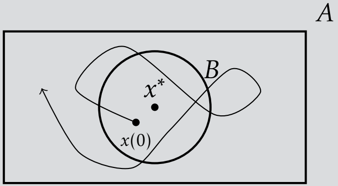

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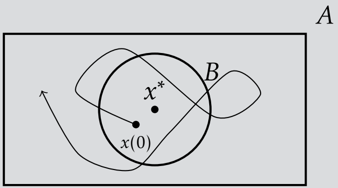

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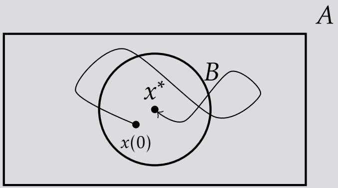

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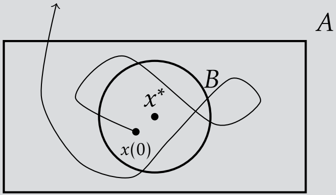

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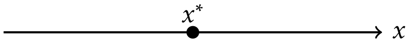

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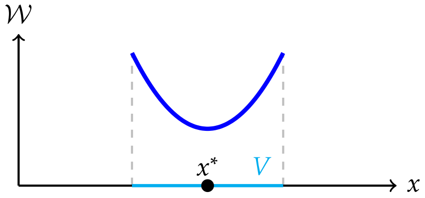

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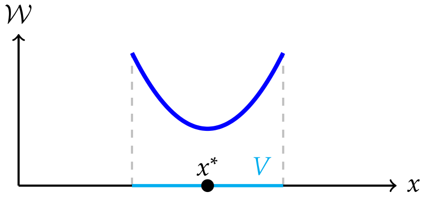

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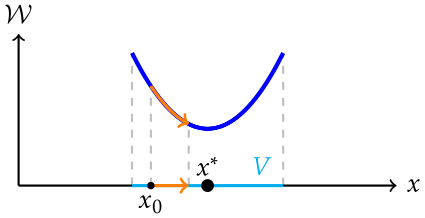
  - $\rightarrow$ if $\mathcal{W}(x(t))$ decreases, i.e. $\dot{\mathcal{W}} < 0$, $x(t)$ will move towards x^*, so x^* is asymptotically stable



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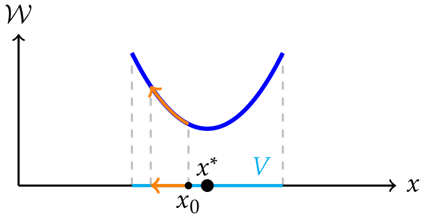
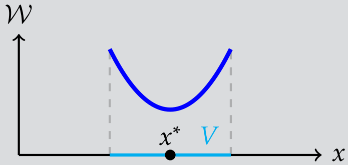
- Assume we can define a function $\mathcal{W} : V \to \mathbb{R}$ (with V neighborhood of x^*) that is differentiable and has a relative minimum in x^*
- Let's consider a solution $x(t)$ of the system, and calculate $\mathcal{W}(x(t))$. Then:
  - $\rightarrow$ if $\mathcal{W}(x(t))$ decreases, i.e. $\dot{\mathcal{W}} < 0$, $x(t)$ will move towards x^*, so x^* is asymptotically stable
  - $\rightarrow$ if $\mathcal{W}(x(t))$ increases, i.e. $\dot{\mathcal{W}} > 0$, then $x(t)$ will move away from x^*, and so x^* is unstable



Lyapunov functions

Lyapunov's second theorem

Let x^* be an equilibrium of the system $\dot{x} = f(x)$, V a neighborhood of x^* and $\mathcal{W} : V \to \mathbb{R}$ a differentiable function with a local minimum in x^*.



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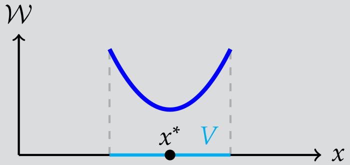

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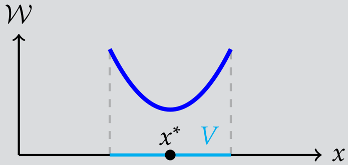

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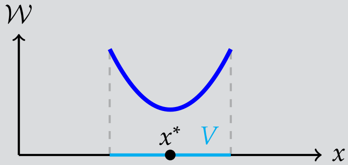

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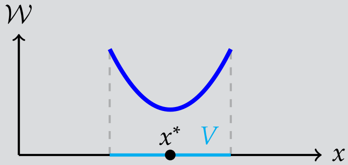

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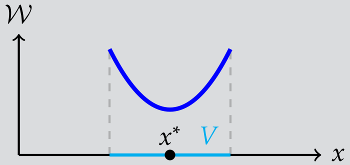

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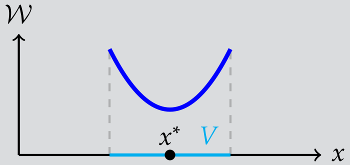

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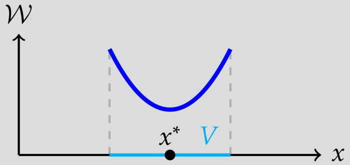

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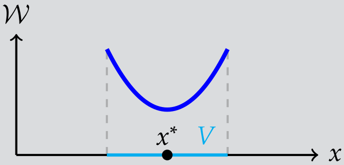

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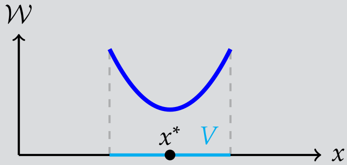

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- This method can give a lot of information on equilibria
- It only gives sufficient and not necessary conditions for (in)stability: an equilibrium can be (un)stable without having a Lyapunov function
- It is not always easy to find Lyapunov functions (exception: conserved quantities)

Lyapunov functions

Example

Let's see if we can find a Lyapunov functions for the Lotka-Volterra equations.

$$\frac{dx}{dt} = \alpha x - \beta xy \qquad \frac{dy}{dt} = \delta xy - \gamma y \tag{19}$$

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Important

There is no "general recipe" to find a system's Lyapunov function!

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Conclusion

The equilibrium $(\gamma/\delta, \alpha/\beta)$ of the Lotka-Volterra equations is ***stable at all times***.
We can't say anything on the equilibrium $(0, 0)$.

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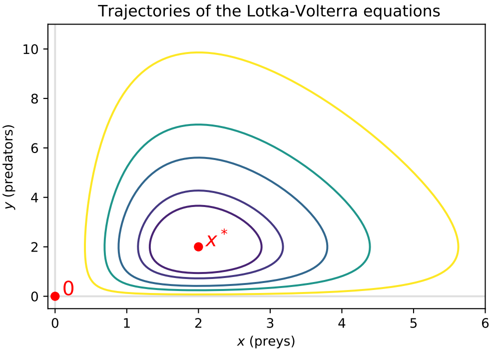

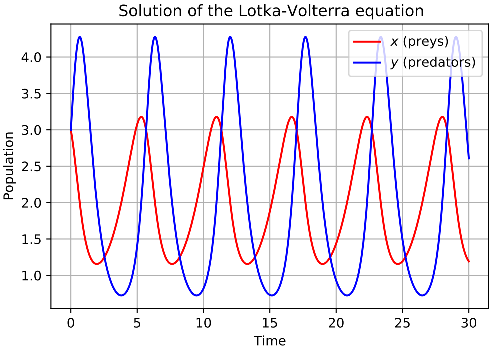

$$x_0 = y_0 = 3$$

Simulations with $\alpha = 2/3$, $\beta = 1/3$, $\gamma = 2$, $\delta = 1$.

Spectral analysis

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The eigenvalues of the jacobian matrix give us valuable information on the stability of x^*.

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- This approach can be used in *any* non-linear system
- The stability properties of a non-linear system are the same of its linearization

Spectral analysis

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Let x^* be an equilibrium of the non-linear system $\dot{x} = f(x)$, $x \in \mathbb{R}^n$. Then:

1. *All* eigenvalues of J have negative real part $\Rightarrow x^*$ is ***asymptotically stable***
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Pros and cons

- This approach can be used in *any* non-linear system
- The stability properties of a non-linear system are the same of its linearization
- If at least one of the eigenvalues has null real part (i.e., it's 0 or purely imaginary) and all others have negative real part, we can't say anything on x^* ($\rightarrow$ higher orders)

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3. *All* the eigenvalues of J are purely imaginary $\Rightarrow x^*$ is ***marginally stable***

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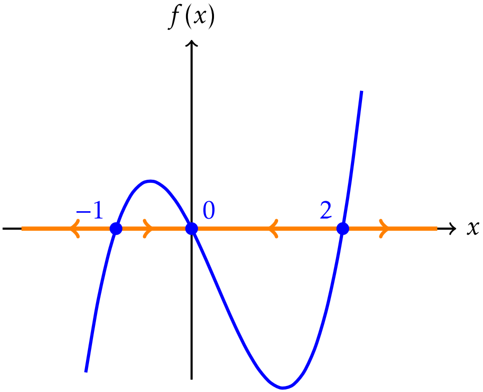

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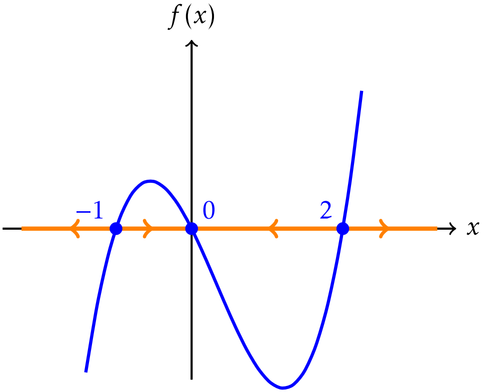

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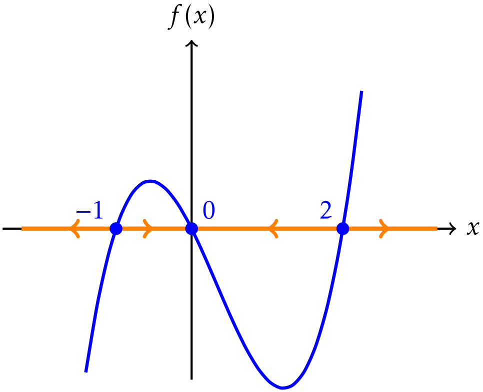

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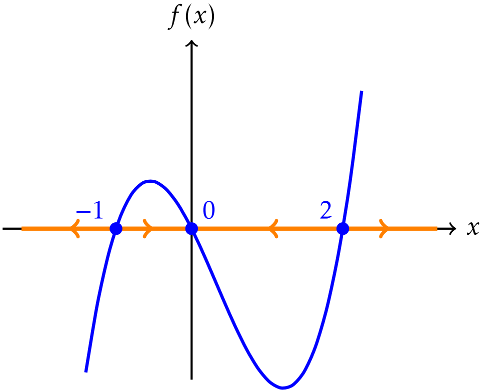

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Therefore:
$x^* = -1, x^* = 2 \longrightarrow$ unstable
$x^* = 0 \longrightarrow$ asymptotically stable

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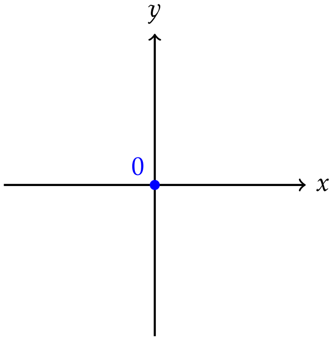

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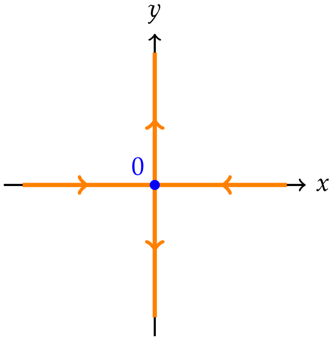

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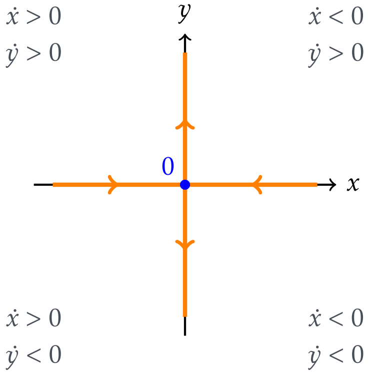

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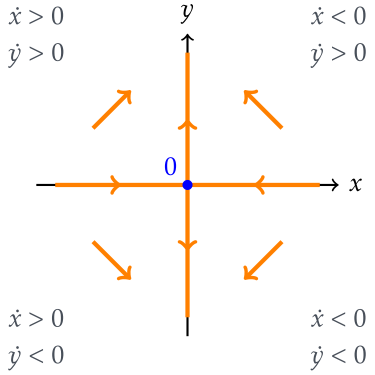

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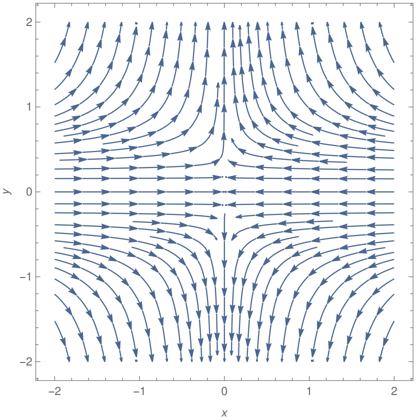

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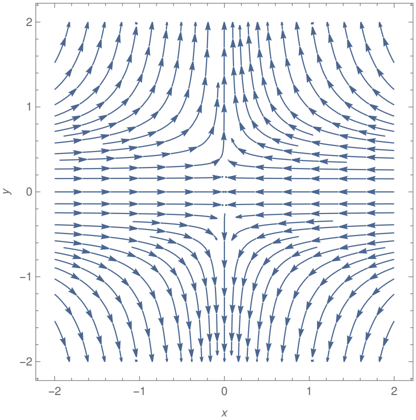

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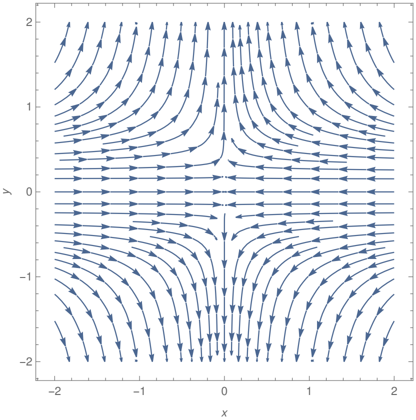

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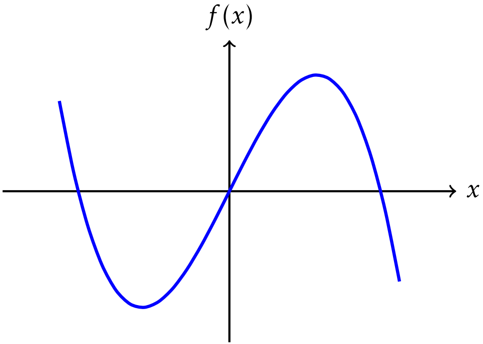

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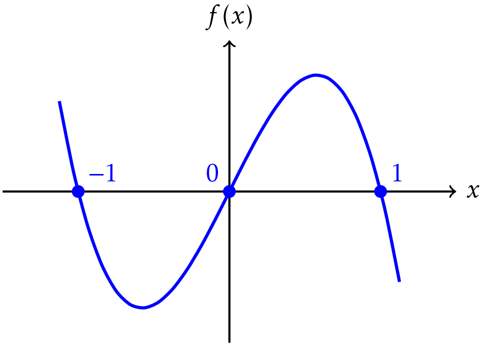

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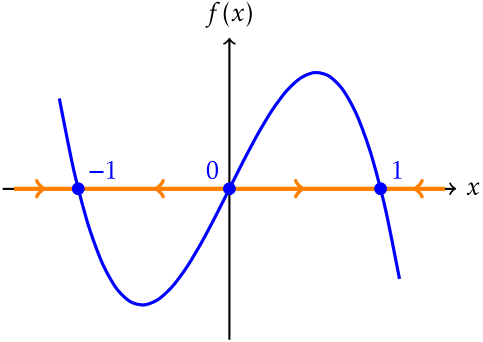

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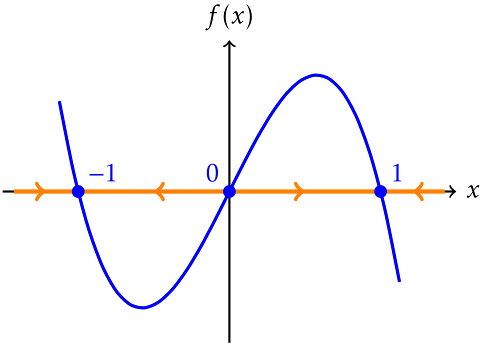

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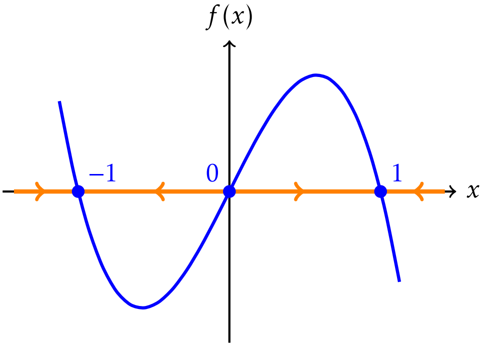

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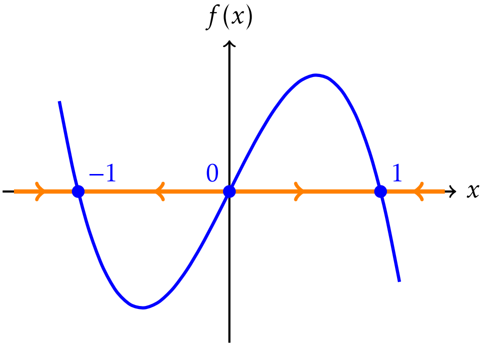

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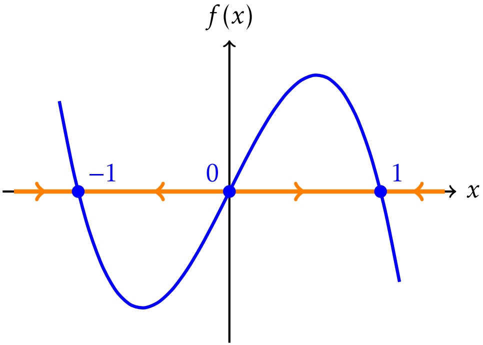

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Bistability

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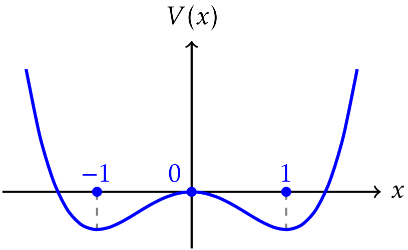

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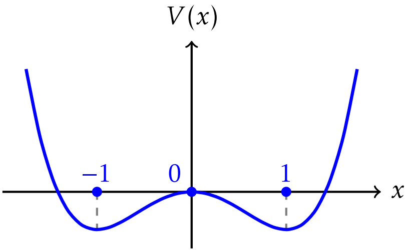

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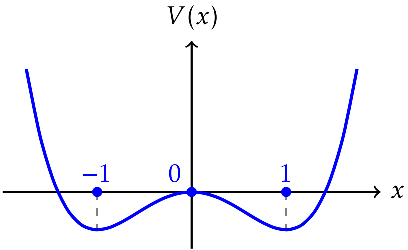

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External perturbations can move the system from one equilibrium to the other.

Timescale separation

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Notice

The validity of this approach depends on the system considered. We need some phenomenological knowledge on the system to justify this separation of timescales.

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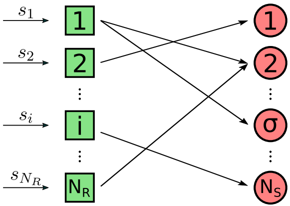

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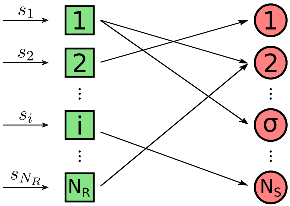

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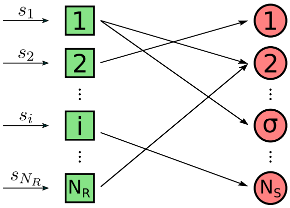

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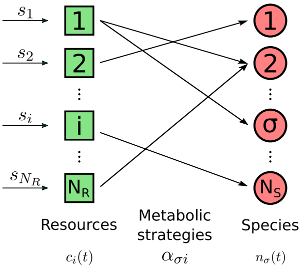

The equations of the model are:

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} r_i(c_i) - \delta_\sigma \right) \qquad \dot{c}_i = s_i - \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} r_i(c_i) \tag{41}$$

where:

$$r_i(c_i) = \frac{c_i}{c_i + K_i} \quad \text{and} \quad \sigma = 1, \dots, N_S \quad \text{and} \quad i = 1, \dots, N_R \tag{42}$$

How is the consumer-resource model built?

Timescale separation

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We can therefore describe the system using only the species' populations.

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$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} c_i - \delta_\sigma \right) \qquad \dot{c}_i = g_i c_i \left(1 - \frac{c_i}{Q_i} \right) - \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} c_i \tag{45}$$

If we apply again the separation of timescales so that c_i are the fast variables:

$$\dot{c}_i = 0 \quad \Rightarrow \quad c_i = Q_i \left(1 - \frac{1}{g_i} \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} \right) \tag{46}$$

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These are called ***generalized Lotka-Volterra equations***.

That’s all!

Questions?

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Backup slides

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Solution of the logistic equation

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Back to original slide

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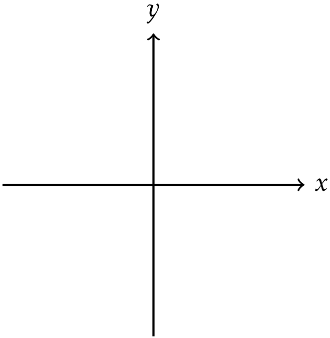

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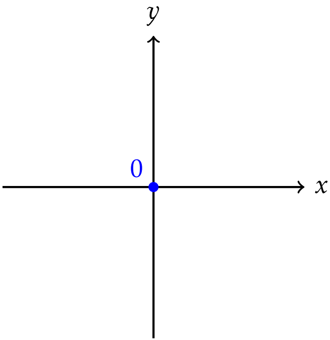

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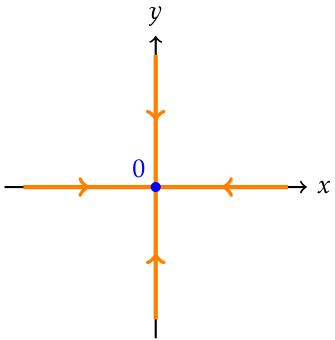

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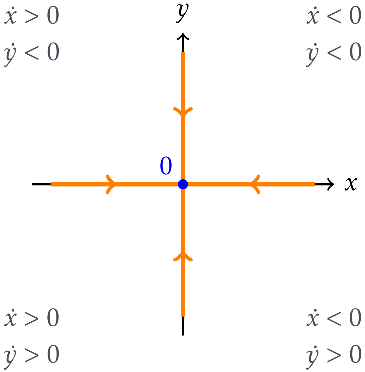

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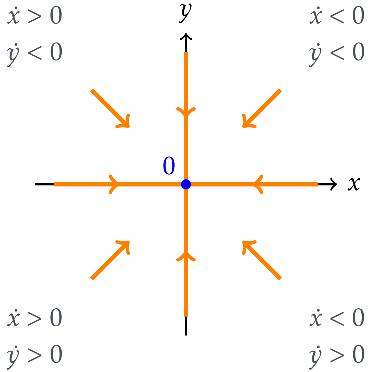

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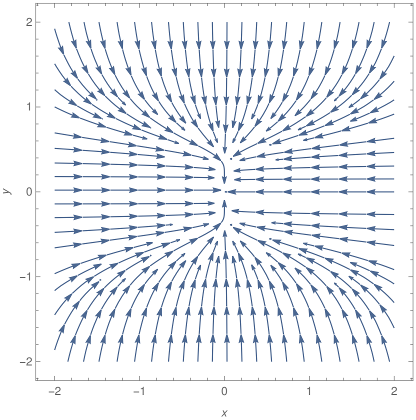

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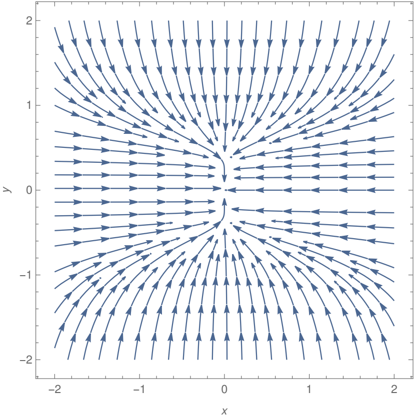

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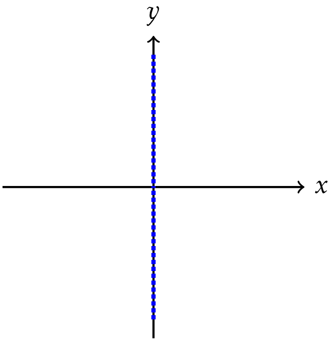

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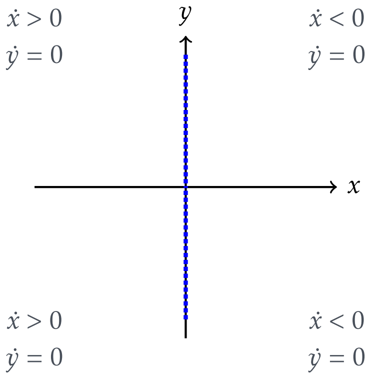

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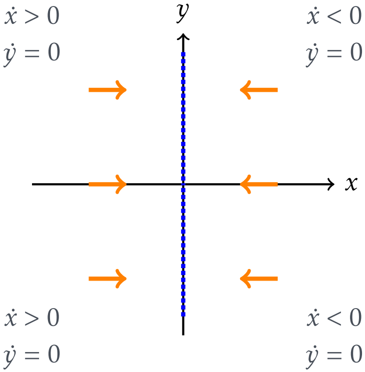

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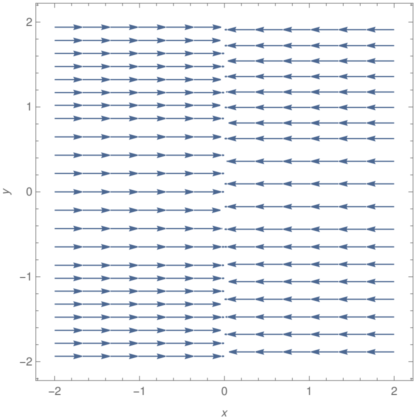

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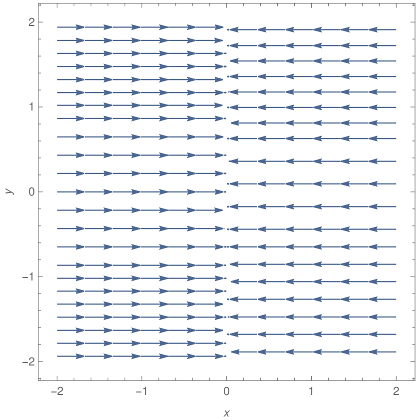

Back to original slide

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Therefore:

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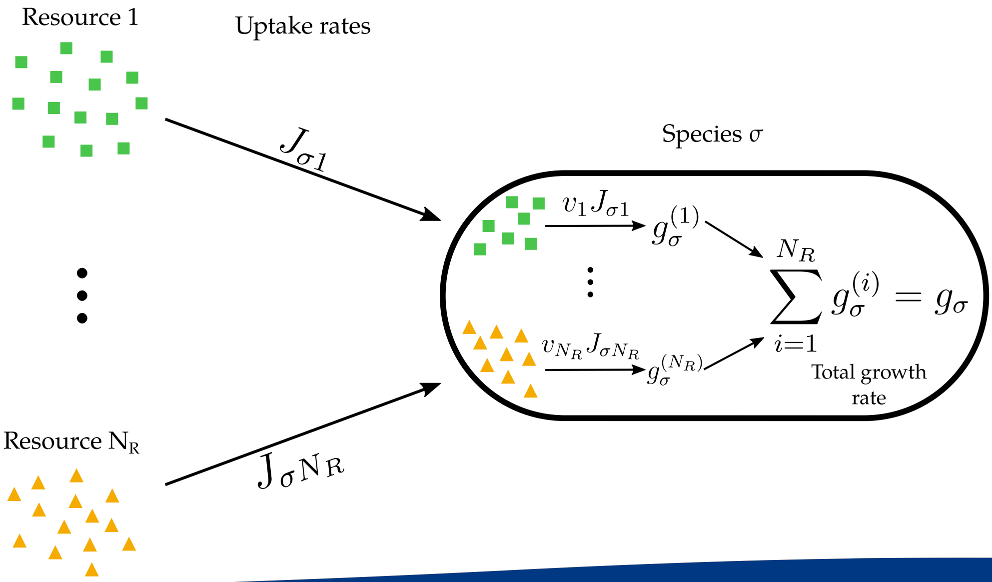

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$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} \frac{c}{c_i + K_i} - \delta_\sigma \right) \qquad \dot{c}_i = s_i - \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} \frac{c}{c_i + K_i}\,, \tag{57}$$

Alternatively, we can assume $J_{\sigma i} = \alpha_{\sigma i} c_i$, but we need a logistic term instead of s_i to limit the uptake rates:

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} c_i - \delta_\sigma \right) \qquad \dot{c}_i = g_i c_i \left(1 - \frac{c_i}{Q_i} \right) - \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} c_i\,, \tag{58}$$

Back to original slide

From C-R to generalized L-V

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} c_i - \delta_\sigma \right) \qquad \dot{c}_i = g_i c_i \left(1 - \frac{c_i}{Q_i} \right) - \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} c_i$$

$$\dot{c}_i = 0 \quad \Rightarrow \quad c_i = Q_i \left(1 - \frac{1}{g_i} \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} \right) \tag{59}$$

From C-R to generalized L-V

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$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} c_i - \delta_\sigma \right) \qquad \dot{c}_i = g_i c_i \left(1 - \frac{c_i}{Q_i} \right) - \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} c_i$$

$$\dot{c}_i = 0 \quad \Rightarrow \quad c_i = Q_i \left(1 - \frac{1}{g_i} \sum_{\sigma=1}^{N_S} n_\sigma \alpha_{\sigma i} \right) \tag{59}$$

Substituting in $\dot{n}_\sigma$:

$$\begin{aligned} \dot{n}_\sigma &= \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \sum_{i=1}^{N_R} v_i \alpha_{\sigma i} \frac{Q_i}{g_i} \sum_{\rho=1}^{N_S} n_\rho \alpha_{\rho i} - \delta_\sigma \right) = \\ &= n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma \right) \left(1 - \frac{1}{\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma} \sum_{\rho=1}^{N_S} n_\rho \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \right) \end{aligned} \tag{60}$$

From C-R to generalized L-V

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$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma \right) \left(1 - \frac{1}{\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma} \sum_{\rho=1}^{N_S} n_\rho \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \right) \tag{61}$$

From C-R to generalized L-V

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma \right) \left(1 - \frac{1}{\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma} \sum_{\rho=1}^{N_S} n_\rho \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \right) \tag{61}$$

Then:

$$\lambda_\sigma := \sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma$$

From C-R to generalized L-V

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma \right) \left(1 - \frac{1}{\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma} \sum_{\rho=1}^{N_S} n_\rho \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \right) \tag{61}$$

Then:

$$\lambda_\sigma := \sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma \qquad \Rightarrow \qquad \dot{n}_\sigma = n_\sigma \lambda_\sigma \left(1 - \frac{1}{\lambda_\sigma} \sum_{\rho=1}^{N_S} n_\rho \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \right) \tag{62}$$

From C-R to generalized L-V

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma \right) \left(1 - \frac{1}{\sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma} \sum_{\rho=1}^{N_S} n_\rho \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \right) \tag{61}$$

Then:

$$\lambda_\sigma := \sum_{i=1}^{N_R} v_i \alpha_{\sigma i} Q_i - \delta_\sigma \qquad \Rightarrow \qquad \dot{n}_\sigma = n_\sigma \lambda_\sigma \left(1 - \frac{1}{\lambda_\sigma} \sum_{\rho=1}^{N_S} n_\rho \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \right) \tag{62}$$

Finally:

$$\beta_{\rho\sigma} := \frac{1}{\lambda_\sigma} \sum_{i=1}^{N_S} v_i \frac{Q_i}{g_i} \alpha_{\sigma i} \alpha_{\rho i} \qquad \Rightarrow \qquad \dot{n}_\sigma = n_\sigma \lambda_\sigma \left(1 - \sum_{\rho=1}^{N_S} \beta_{\rho\sigma} n_\rho \right) \tag{63}$$

Back to original slide