Systems Biology: Mathematics for Biologists

Kirsten ten Tusscher, Theoretical Biology, UU

Limit cycles

The "classical" Lotka-Volterra model

Consider the classical Lotka-Volterra predator-prey model.

$$\begin{cases} \frac{dR}{dt} = aR - bNR \\ \frac{dN}{dt} = cNR - dN \end{cases}$$

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Note: no density-dependence, no saturation of predators.

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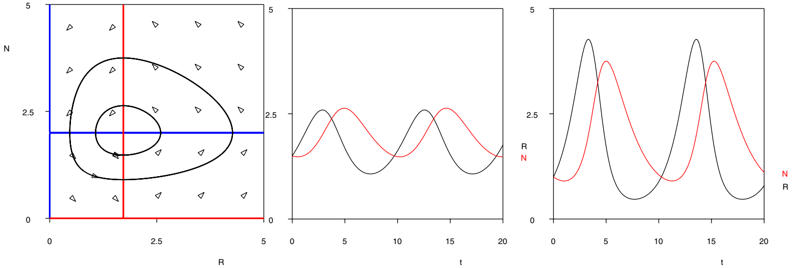

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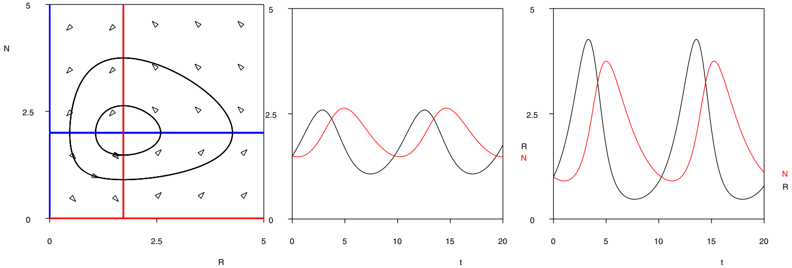

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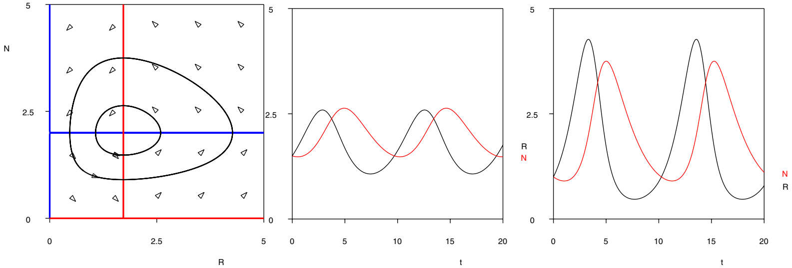

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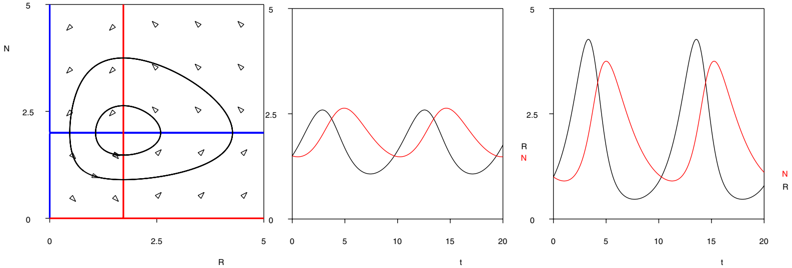

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Let us study this system for:

$b = 0.5$, $d = 0.43$, $h = 0.1$, $r = 1$ and different values of K.

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Finally this gives us: $N = \frac{r}{b}(1 - \frac{\frac{dh}{b-d}}{K})(h + \frac{dh}{b-d}) \approx 1.43(1 - \frac{0.61}{K})$

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Thus the equilibria are:
$(0,0)$, $(0,K)$,
$(\frac{dh}{b-d}, \frac{r}{b}(1 - \frac{\frac{dh}{b-d}}{K})(h + \frac{dh}{b-d})) \approx (0.61, 1.43(1 - \frac{0.61}{K})) \approx (0.61, 1.43 - \frac{0.88}{K})$

Null-clines of the realistic LV-model

Let us determine the null-clines of this system:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - \frac{R}{K}) - \frac{bNR}{h + R} = 0$$

null-cline 1: $R = 0$
null-cline 2: $N = \frac{r}{b}(1 - \frac{R}{K})(h + R) = (1 - \frac{R}{K})(0.2 + 2R)$ (parabola)
intersection points: $(K, 0)$ and $(-h, 0) = (-0.1, 0)$
location of top $R = \frac{-h+K}{2}$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{bNR}{h + R} - dN = 0$$

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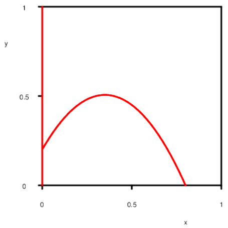

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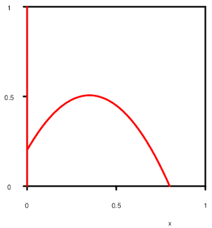

Determine the **prey** vectorfield relative to $N = (1 - \frac{R}{K})(0.2 + 2R)$:

- below it there are few predators so prey will increase: $\leftarrow$
- above it there are many predators so prey will decrease: $\rightarrow$

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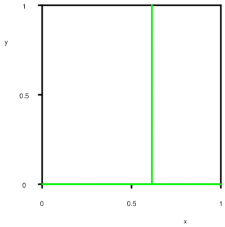

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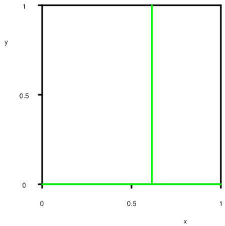

Determine the **predator** vectorfield relative to $R \approx 0.61$:
- left of it there are few prey so predators will decrease: $\downarrow$
- right of it there are many prey so predators will increase: $\uparrow$

Parameter change in LV-model

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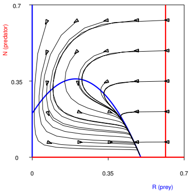

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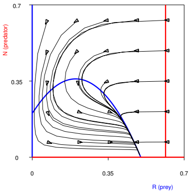

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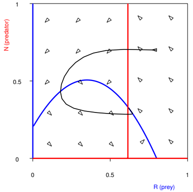

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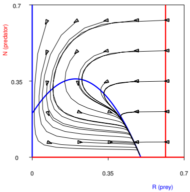

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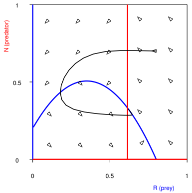

Non-trivial equilibrium.

But this is not the end of the story!

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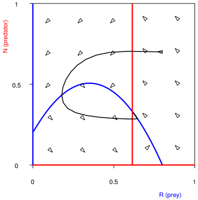

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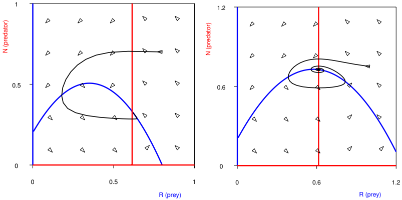
- For $1 < K < 1.333$ we have a stable spiral(right of top parabola)



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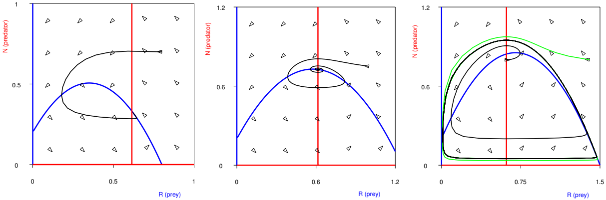
- For $K > 1.33$ we have an unstable spiral (left of top parabola).



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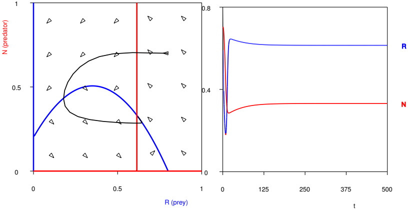

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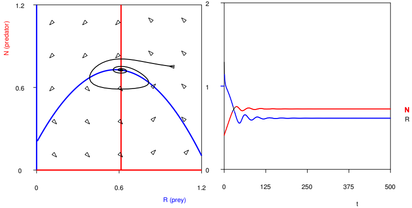

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Numerical solutions needed to tell apart spiral from node.

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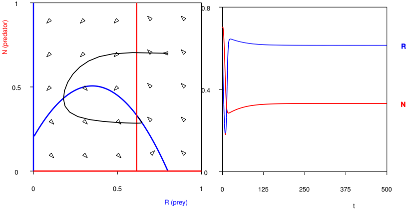

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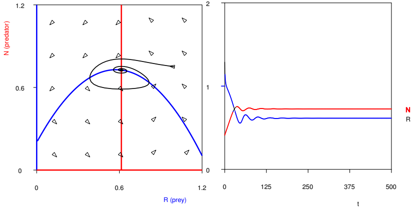

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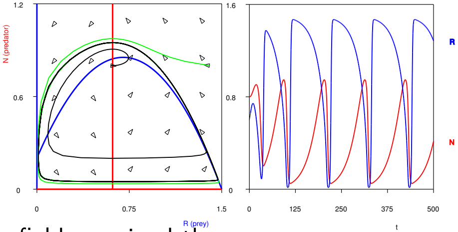
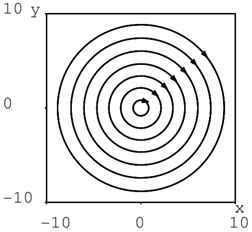
$K = 1.5$: unstable spiral, stable limit cycle



The **global** vectorfield remained the same.
The **local** vectorfield (self-feedback) became unstable.
Numerical solution needed to determine that it is a spiral.

Dynamics on closed loops

Let us reconsider center point equilibria



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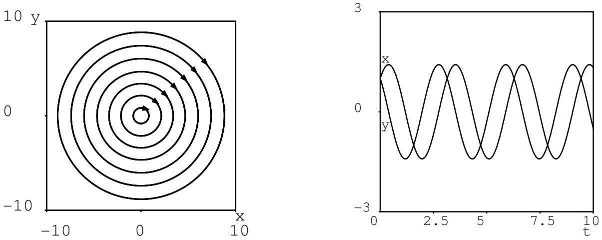

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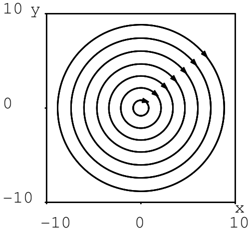

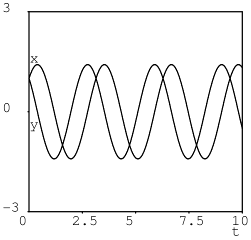

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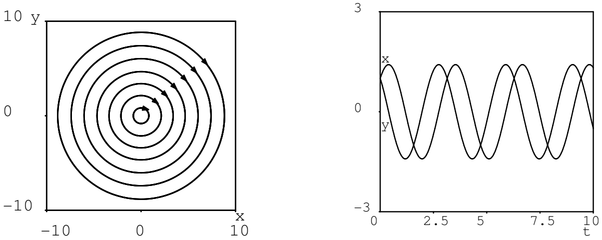

- A series of closed loops.
- Rotating dynamics in the phase plane.
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- Which loop is followed, depends on initial conditions.
- This also determines the amplitude of the oscillations.

Point and Cycle attractors

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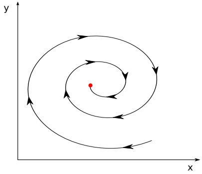

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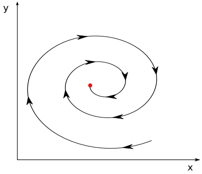
- It's a single (x, y) point in phase space.



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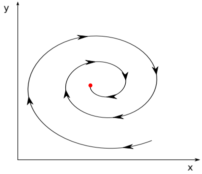

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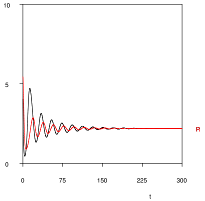

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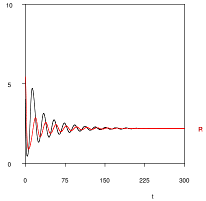

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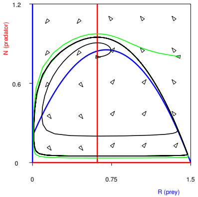

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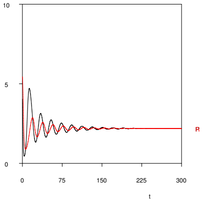

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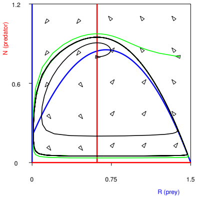

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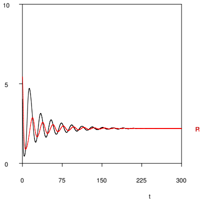

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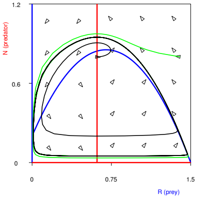

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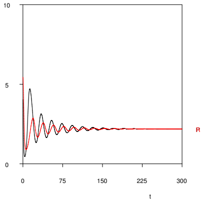

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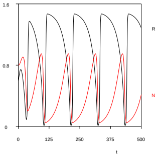
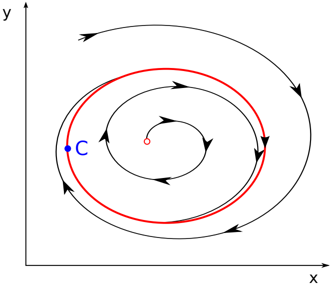


Dynamics

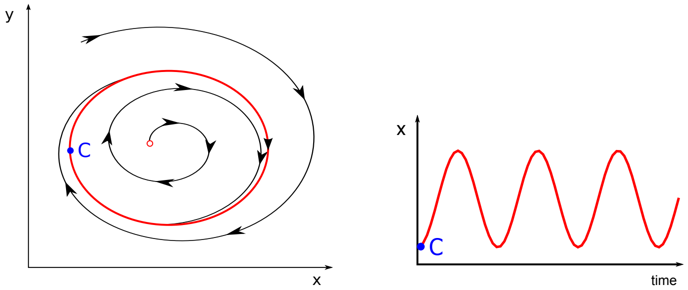
Limit cycle



- A single closed loop.

Dynamics

Limit cycle



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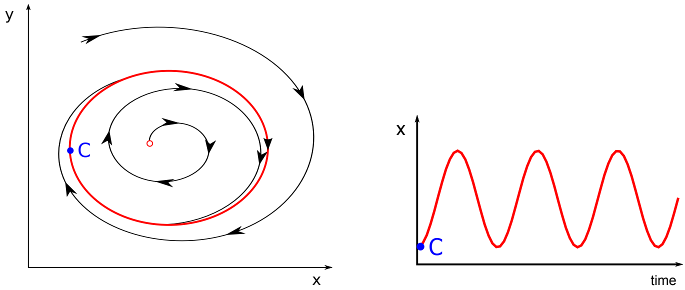
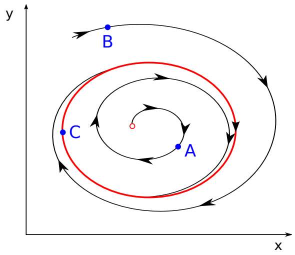


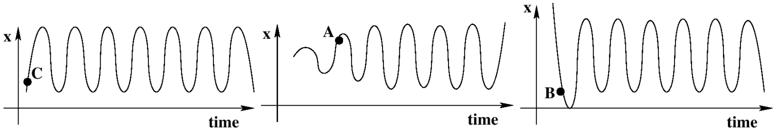
- A single closed loop.
- So there is only one single amplitude of oscillations.
- The vectorfield dictates the direction of rotation.

Stable limit cycle

A **stable limit cycle** is an **attractor**
It consists of a **closed loop of points**, rather than a single point:

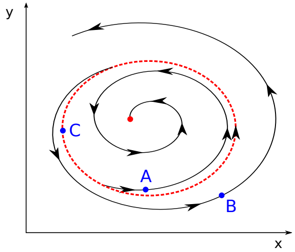


All trajectories converge to the closed loop formed by the limit cycle

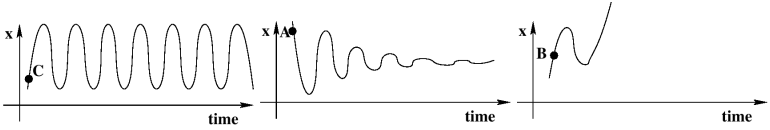


Unstable limit cycle

An **unstable limit cycle** is a **repellor**
It consists of a closed loop of points that acts as a **boundary** for the basin of attraction of the attractor that is often within the loop:



All trajectories diverge from the limitcycle.On what side of the limitcylce a trajectory starts determines where it goes.



Why and when do limit cycles occur?

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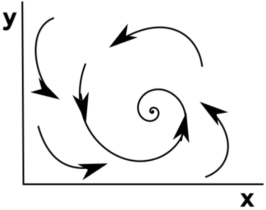
Globally the system **always** converges.



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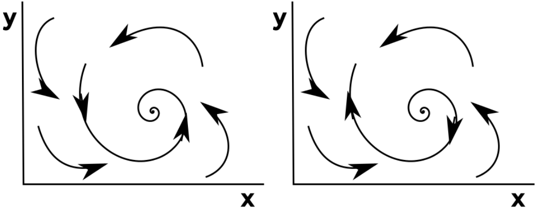
Locally dynamics are **for certain situations** unstable.



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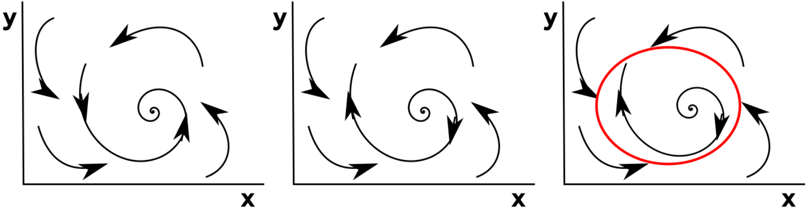

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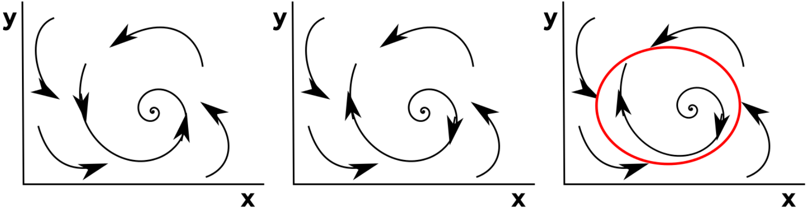

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The local change in stability is called a **Hopf bifurcation**.

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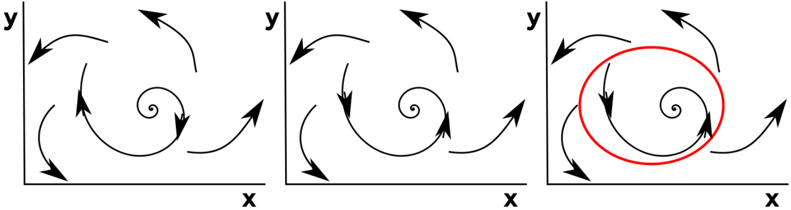

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Again, this local change in stability is called a **Hopf bifurcation**.

Why and when do limit cycles occur?

Note that it is either or:

Either
The system is globally stable
, and it needs a stable limitcycle if it becomes locally unstable (conflict)
and no limitcycle if system is globally and locally stable (no conflict)

Or
The system is globally unstable
, and it needs an unstable limitcycle if it becomes locally stable (conflict)
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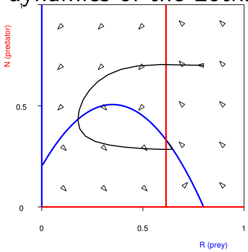
Why and when do limit cycles occur?

How do you know whether the global dynamics is stable or not?

Let us consider the global dynamics of the Lotka-Volterra model:



1. upper-right: prey $\leftarrow$ and predators $\uparrow$ pushing system to:
2. upper-left: prey $\leftarrow$ and predators $\downarrow$ pushing system to:
3. lower-left: prey $\rightarrow$ and predators $\downarrow$ pushing system to:
4. lower-left: prey $\rightarrow$ and predators $\uparrow$ pushing system to **1.**

System is **constrained**: can not blow up, suggesting global stability.

Imagine **inverse** vectorfield: upper-right prey $\rightarrow$ and predators $\downarrow$: prey can blow up: suggesting global instability

Example

The Holling-Tanner model for predator-prey interactions:

$$\begin{cases} dP/dt = rP(1-\frac{P}{K}) - \frac{aRP}{d+P} \\ dR/dt = bR(1-\frac{R}{P}) \qquad P > 0; R > 0 \end{cases}$$

We fix $a = 1$, $b = 0.2$, $r = 1$, $d = 1$ and vary K.

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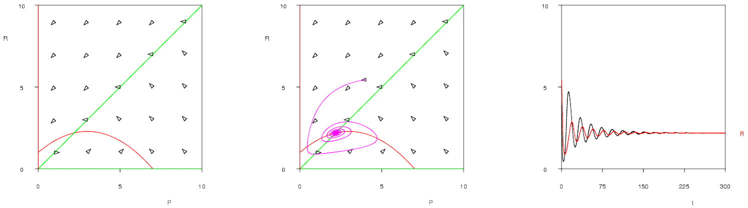
R null-clines:
$R = 0$ and $R = P$

Example

Null-clines and dynamics for $K = 7$:



A **stable spiral**, whole phase plane is basin of attraction.

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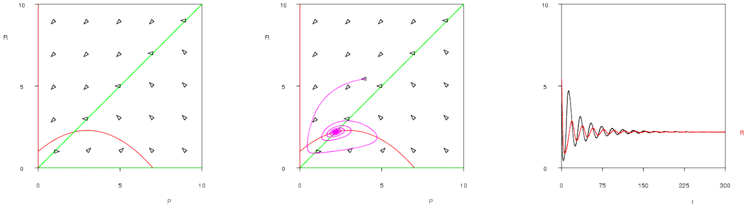

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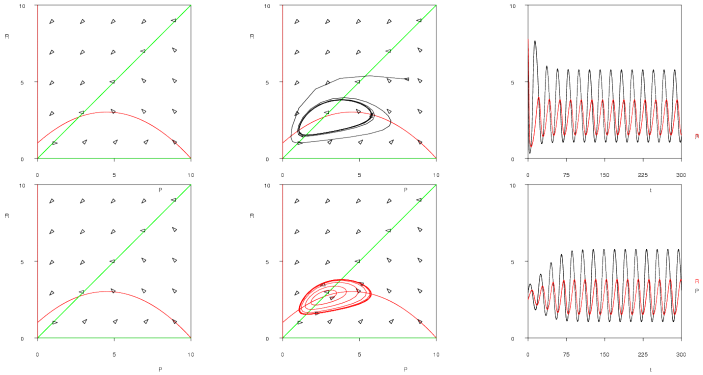
Global dynamics are stable

Example

Null-clines and dynamics for $K = 10$:



An **unstable spiral** and a **stable limit cycle**
Inside and outside trajectories converge to limit cycle.

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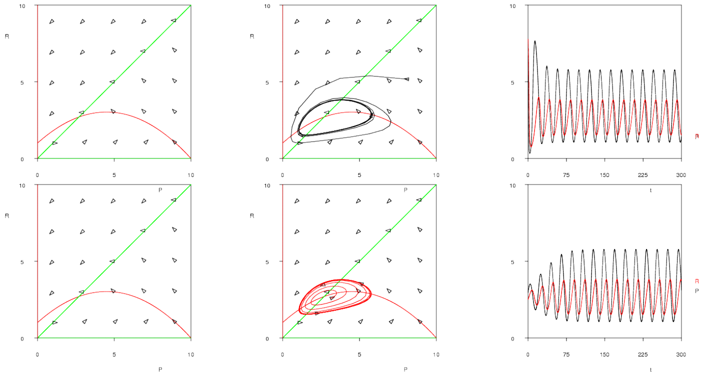
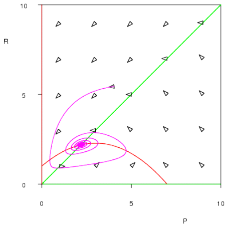
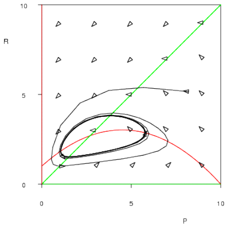


An **unstable spiral** and a **stable limit cycle**
Inside and outside trajectories converge to limit cycle.
Global dynamics still stable, local dynamics unstable

Example

Hopf bifurcation:





Intersection of the nullclines is left of the top in both cases!
Close to top: stable spiral (consistent with global dynamics)
Further away: unstable spiral + stable limit cycle (resolve conflict)

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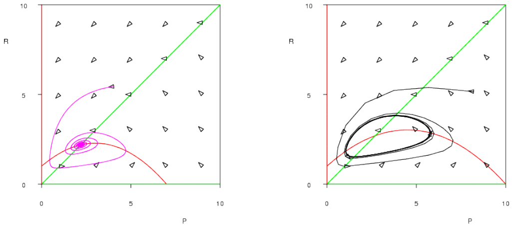

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Change is more subtle here:
LV model: transition from − and 0 to + and 0 self-feedback
HT model: both cases + x and − y self-feedback
Apparently balance changes from − to +!

Analysis of 2D systems

First look at the entire vectorfield:
is it clearly a stable node, unstable node, saddle?

YES: you are finished!

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Local stability change
If we have a globally rotating vectorfield
and a parameter change causes a local change in stability
a Hopf bifurcation occurs and a limitcycle appears

If global dynamics is stable, local instability requires stable limitcycle

If global dynamics is unstable, local stability requires unstable limitcycle