Nonlinear models of interaction

Two different populations and the analysis of their interactions

Preview

- We modeled single species populations (Malthusian/logistic growth model; linear in nature).
- We broke a single population into subgroups, such as by age or developmental stage (age-structured model- matrix and graphical method; linear models in nature).
- We treated it as if it is unaffected by the other species or populations with which it might share an environment.
- We now move our attentions to interactions between species or populations (Two difference equations with the nonlinear interaction terms).

Competition and Mutualism

- Most living things interact with many coinhabitants of their environment.
- Species may find themselves in competition for limited resources, whether food or space, so that growth in one population is detrimental to another.
- Mutualism, where several species interact in a way that benefits both, also occurs in nature.
- A real ecosystem may have hundreds or thousands of interacting populations, with all sorts of direct and indirect interactions between them.
- How can we understand the effects of these interactions without being lost in the complexity of it all?

Interactions between two populations

- We consider the Prey-Predator model.
- Understand the dynamics of only two interacting populations and a single type of interaction.
- How to modify the existing models that we have already looked into?
- For instance, what to add in the model to capture the interaction term?
- What behavior does a computer simulation of such a modelshow? Does one species disappear, and if so why?
- What are the dynamics?
  equilibrium, oscillate, or jump wildly etc…
- Can such a system of interacting populations show stability, and if so, under what circumstances?

Predator--Prey Model

- Two species, one of which the predator, say fox preys on the other, the prey, the rabbit.
- Predator--prey interaction between these species is the most important one for determining population sizes.
- The rabbits are the primary food source for the foxes.
- Foxes provide the primary limitation to the unchecked growth of the hare population.

Mathematical model of predator-prey interaction

- Letting P_t and Q_t denote the size of the prey and predator population respectively at time t

- The equations that govern the dynamics are

$$\Delta P = F(P,Q)$$
$$\Delta Q = G(P,Q)$$

- What will be the functions F and G on the right hand side?

Model…

- If no predators are around, the population would be described by the discrete logistic model:

$$\Delta P = r\, P\, (1 - P/K) \quad \text{(equation For Prey)}$$

(in the absence of predators)

- If we assume the predator's primary source of food is the prey, in the absence of it, population of predators to decline

$$\Delta Q = -uQ \quad \text{(equation for Predator)}$$

(in the absence of prey)

- What about the interaction term?

Interaction terms in the model

- Interaction between the species is given as the product PQ, a good candidate for describing interactions.
- It's a nonlinear term.
- For example, If both populations P and Q are small, so that we would expect little effect from the interaction, then PQ is small.
- If both P and Q are large, so that we would expect major effects from the interaction, then PQ is large.
- If either P or Q is small, and the other is large, then the product PQ will be intermediate.
- The product PQ, gives a good description of the amount of interaction we might expect between the populations.

Model representation including interactions

$$\Delta P = r P (1 - P/K) \boxed{- \ s PQ} \text{ (For Prey)}$$
$$\Delta Q = -u Q \boxed{+ \ v PQ} \text{ (For predator)}$$

- s and v both denote positive constants.
- The term "- sPQ" describes a detrimental effect of the predator--prey interaction on the prey
- The term “ + v PQ" describes a beneficial effect of the interaction on the predator.
- There is no reason to expect that the values of s and v need to be of the same size, since the predator may well benefit more than the prey is harmed, or the prey may be harmed more than the predator benefits.

Simulating the dynamics: Phase plane

$$P_{t+1} = P_t(1 + r(1 - P_t/K)) - sP_tQ_t,$$
$$Q_{t+1} = (1 - u)Q_t + vP_tQ_t.$$

with r, s, u, v, and K all positive constants, and $u < 1$.

The phase plane. To be concrete, consider the parameter values

$$K = 1,\ r = 1.3,\ s = .5,\ u = .7, \quad \text{and} \quad v = 1.6,$$

so that our model becomes

$$P_{t+1} = P_t(1 + 1.3(1 - P_t)) - .5P_tQ_t,$$
$$Q_{t+1} = .3Q_t + 1.6P_tQ_t.$$

Time series: P, Q as a function of time

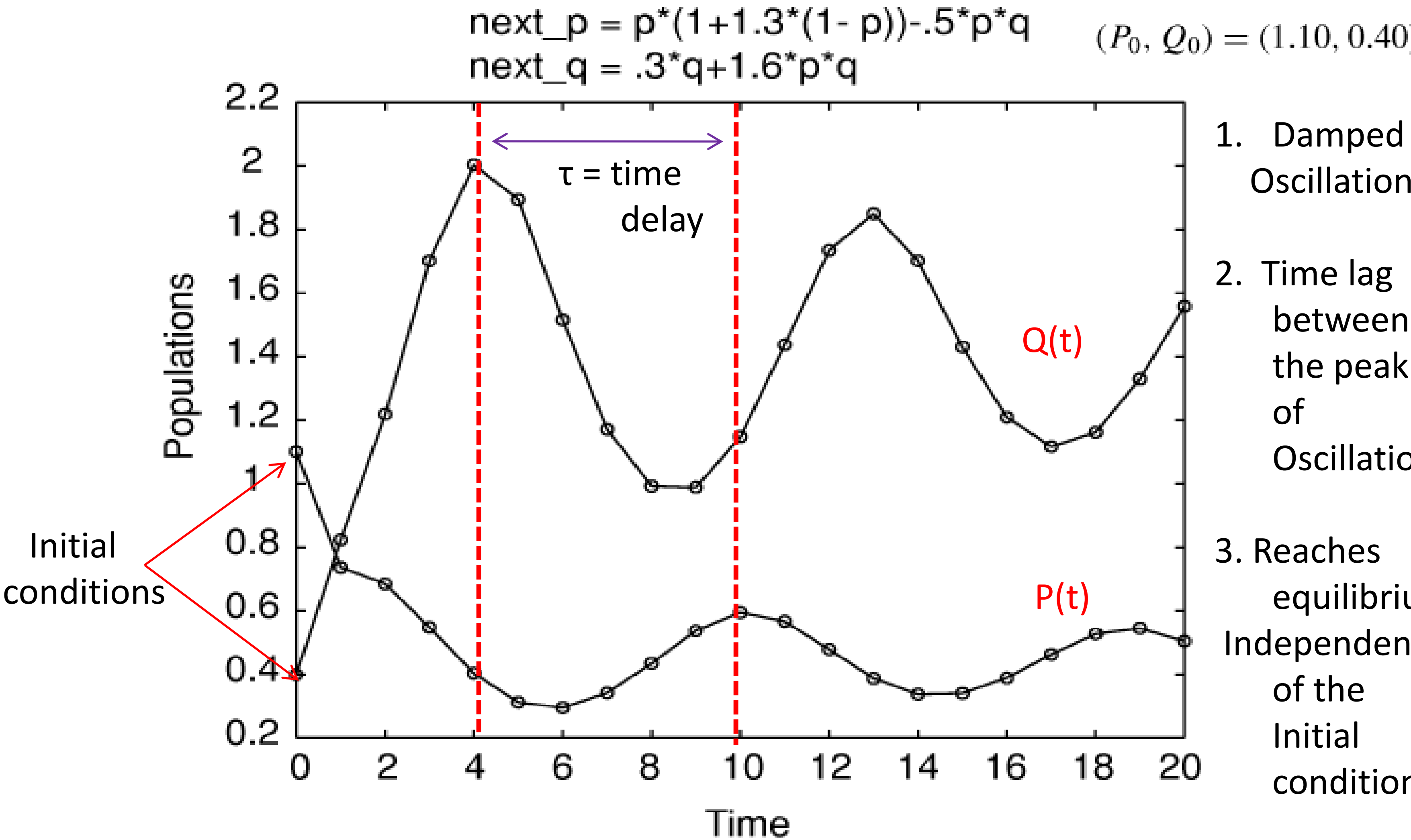


Figure 3.1. Predator–prey model time plot.

1. Damped Oscillations
2. Time lag between the peaking of Oscillations
3. Reaches equilibrium Independent of the Initial conditions

Phase plane plot and orbit

Consider axes P and Q, and put a dot at the point representing (P0, Q0).

Then put another dot at (P1, Q1) and draw a line from our first dot to it.

Then plot (P2, Q2) and connect it to its predecessor, and continue on connecting each consecutive pair of points representing the two population sizes.

The succession of points (P0, Q0), (P1, Q1), (P2, Q2),... is called the population orbit.

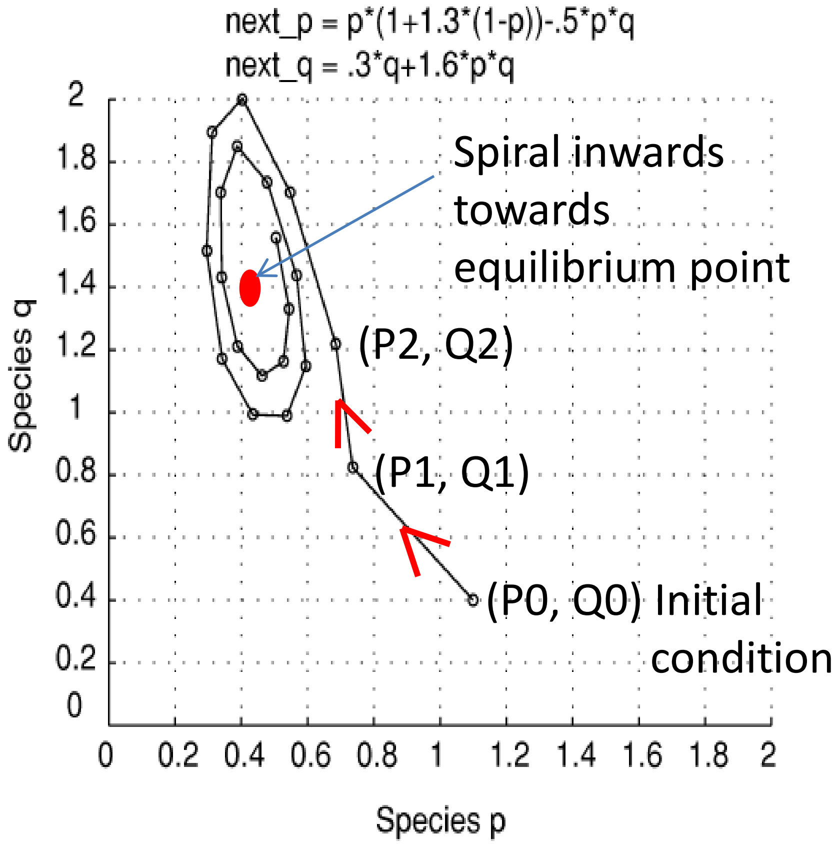


Figure 3.2. Predator–prey model phase plane plot; single orbit.

With many different initial conditions

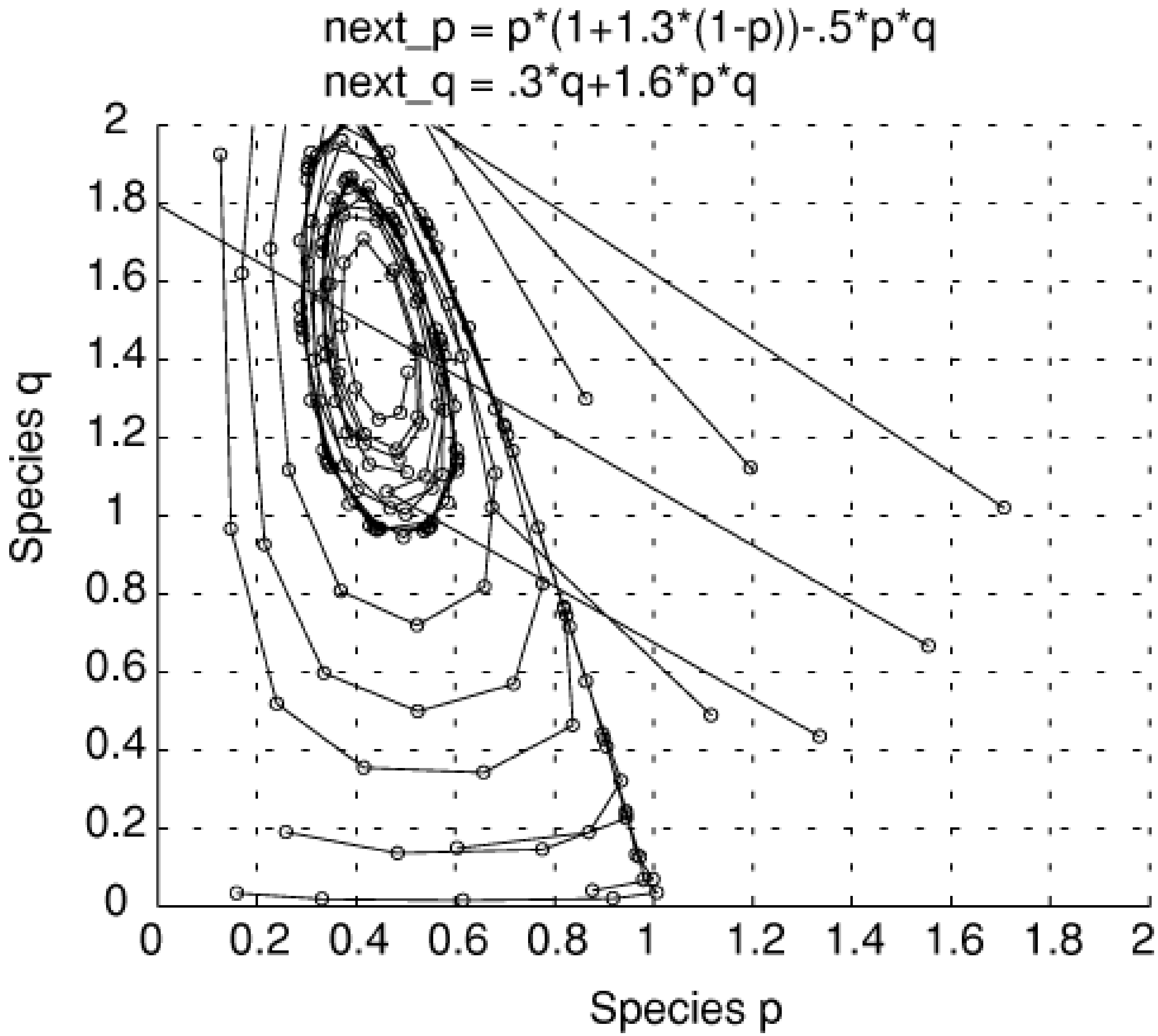


Figure 3.3. Predator–prey model phase plane plot; many orbits.

Network representation?

$\Delta P = r\,P\,(1 - P/K) - s\,PQ$ (For Prey)

$\Delta Q = -u\,Q + v\,PQ$ (For predator)

Production

$\longrightarrow A$

loss

$A \longrightarrow$

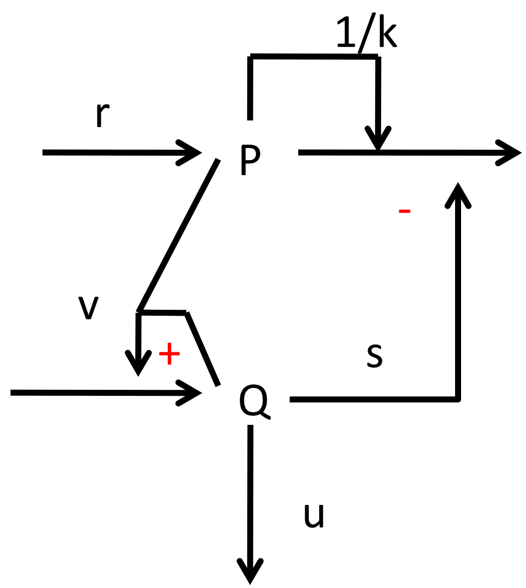
autocatalysis

$A + B \longrightarrow 2B$

complexation

$A + B \longrightarrow AB$

Network



Biochemical steps

$\xrightarrow{r} P$

$2P \xrightarrow{r/k} \phi$

$Q \xrightarrow{u} \phi$

$P + Q \xrightarrow{v/s} 2Q$

(autocatalytic
With respect to Q
and
Negative Feedback
with respect to P)

Equilibria of Multipopulation Models

Definition. For a model of two populations given by $P_{t+1} = F(P_t, Q_t)$ and $Q_{t+1} = G(P_t, Q_t)$, an *equilibrium* is a point (P^*, Q^*) with $P^* = F(P^*, Q^*)$ and $Q^* = G(P^*, Q^*)$. For a model given in the form $\Delta P = f(P, Q)$ and $\Delta Q = g(P, Q)$, it is a point (P^*, Q^*) with $f(P^*, Q^*) = 0$ and $g(P^*, Q^*) = 0$.

$$P_{t+1} = P_t(1 + 1.3(1 - P_t)) - .5P_tQ_t$$
$$Q_{t+1} = .3Q_t + 1.6P_tQ_t.$$

(Model)

(Condition for equilibrium)

$$P^* = P^*(1 + 1.3(1 - P^*)) - .5P^*Q^*,$$
$$Q^* = .3Q^* + 1.6P^*Q^*,$$

or

$$0 = P^*1.3(1 - P^*) - .5P^*Q^* = P^*(1.3 - 1.3P^* - .5Q^*),$$
$$0 = -.7Q^* + 1.6P^*Q^* = Q^*(-.7 + 1.6P^*).$$

From the factorization in the second equation, we see

$$\text{either} \quad Q^* = 0 \quad \text{or} \quad P^* = .7/1.6 = .4375.$$

If $Q^* = 0$, then the first equation says either $P^* = 0$ or $P^* = 1$, giving us the two equilibria $(0, 0)$ and $(1, 0)$. If $P^* = .4375$, on the other hand, then the first equation requires that $0 = 1.3 - 1.3(.4375) - .5Q^*$, so that $Q^* = 1.4625$. This means there is a third equilibrium at $(.4375, 1.4625)$.

(Three equilibrium points)

Nullcline analysis

Definition 8 *The x-null-cline (*Δx *= 0 null-cline) is the set of points satisfying the condition* $f(x,y) = 0$. *The y-null-cline (*Δy *= 0 null-cline) is the set of points satisfying the condition* $g(x,y) = 0$.

Nullclines and vectorfields

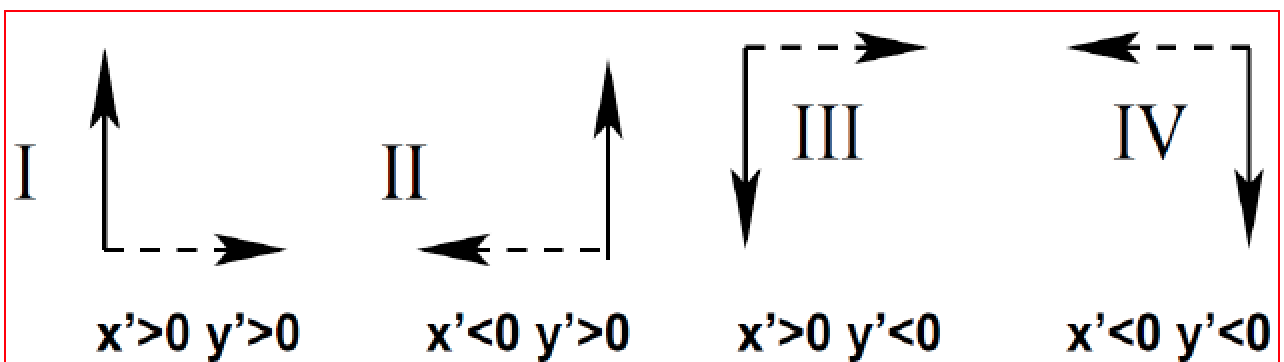
$$\left.\begin{aligned} \Delta x &= f(x,y) \\ \Delta y &= g(x,y) \end{aligned}\right\}$$

There are two vector components– x and y

- **Draw the vector field similar to 1D system and depends on whether derivatives are increasing or decreasing.**

- **In the 2D system vectors are drawn based on both the derivatives.**

FOUR CASES



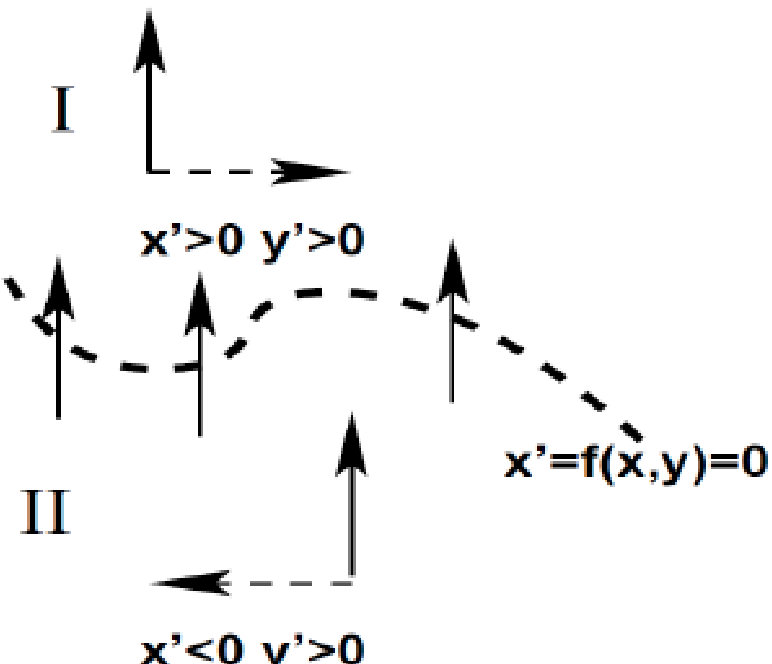
TAKE CASES - I and II

x’>0 y’>0 x’<0 y’>0

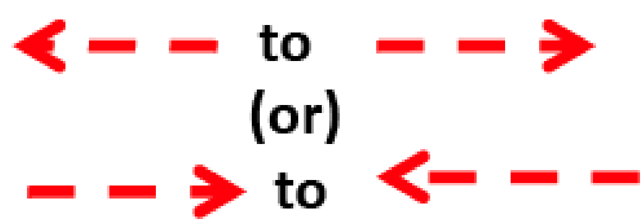
Note
Δx = x’
Δy= y’

These two cases are separated by a boundary Δx $= f(x,y)$ = 0

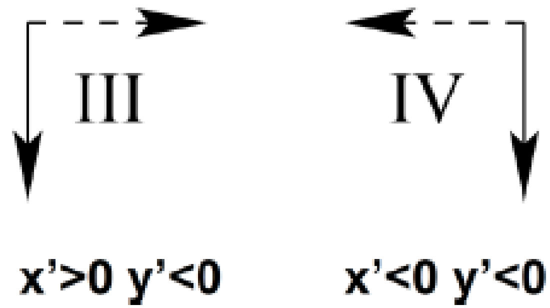
$$\boxed{f(x,y) = 0}$$



- Horizontal component = 0 and vertical component is present
- When crossing the boundary the horizontal component changes from



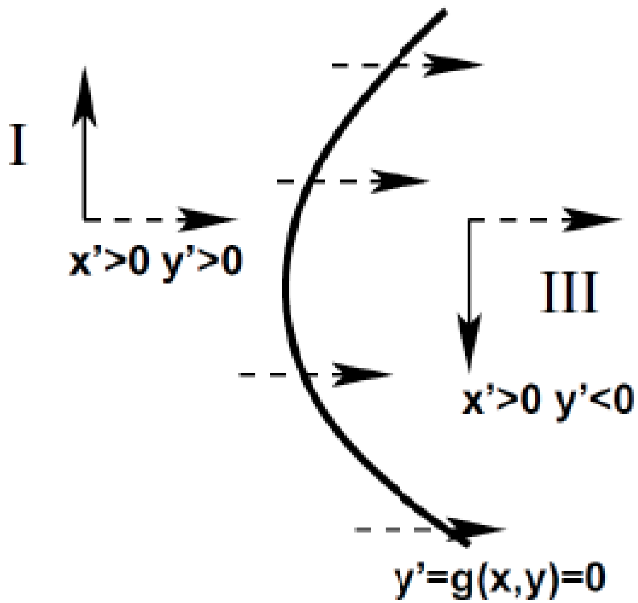
TAKE CASES - III and IV



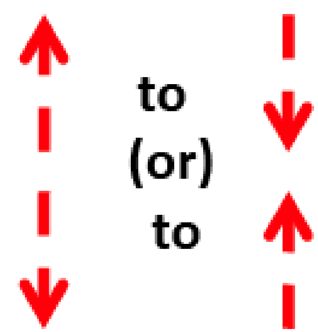
Note:
$\Delta x = x'$
$\Delta y = y'$

These two cases are separated by a boundary $\Delta y = g(x,y) = 0$

$$\boxed{g(x,y) = 0}$$



- Vertical component = 0 and horizontal component is present
- When crossing the boundary the vertical component changes from



Nullcline analysis—steps involved

- Draw the nullclines --- Δx = 0 and Δy = 0; i.e., plot f(x,y) = 0 and g(x,y) = 0. The x-component is f(x,y) and y-component is g(x,y).

- To distinguish x-component, denote by ---------- (dashed line) and
  To distinguish y-component, denote by __________ (Solid line)

- Choose any point in the x-y plane and find the x-y components of the vector field.

- If f(x,y) > 0 then draw the x-component directed as and
  if f(x,y) < 0, then draw the x-component directed as

- If g(x,y) > 0 then draw the y-component is directed as and
  if g(x,y) < 0, then draw the y-component is directed as

Change in vector field direction when transiting different regions

Dashed component changes i.e. g(x,y) or y-component is crossed

- Change the direction of the dashed component of the vector field if in order to get to the adjacent region you cross the dashed nullcline.

Solid component changes i.e. f(x,y) or x-component is crossed

- Change the direction of the solid component of the vector field if in order to get to the adjacent region you cross the solid nullcline.

- Show the direction of the vector field on the null-clines

Vector fields of different signs

	$f(x,y)>0$	$f(x,y)=0$	$f(x,y)<0$
$g(x,y)>0$	$\nearrow$	$\uparrow$	$\nwarrow$
$g(x,y)=0$	$\rightarrow$	$\circ$	$\leftarrow$
$g(x,y)<0$	$\searrow$	$\downarrow$	$\swarrow$

Example

$$P_{t+1} = P_t(1 + r(1 - P_t)) - s P_t Q_t,$$
$$Q_{t+1} = (1 - u)Q_t + v P_t Q_t.$$

Difference Equation (carrying capacity K=1)

The equilibrium equations are:

$$0 = P^*(r(1 - P^*)) - s P^* Q^* = P^*(r(1 - P^*) - s Q^*), \qquad (3.1)$$
$$0 = -u Q^* + v P^* Q^* = Q^*(-u + v P^*).$$

The factorizations of these equations mean equilibria are determined by at least one of the conditions

$$P^* = 0 \quad \text{or} \quad r(1 - P^*) - s Q^* = 0,$$

(P – nullclines)

and at least one of

$$Q^* = 0 \quad \text{or} \quad -u + v P^* = 0.$$

(Q– nullclines)

Therefore, if we graph the four lines

$$\underbrace{P = 0, \quad Q = \frac{r}{s}(1 - P),}_{\text{P - nullclines}} \quad \underbrace{Q = 0, \quad P = \frac{u}{v}}_{\text{Q - nullclines}}$$

There are 5 intersections

Equilibrium points (3)

Not an equilibrium point (2)

$$(0,0),\ (1,0),\quad \text{and}\quad \left(\frac{u}{v}, \frac{r}{s}\left(1-\frac{u}{v}\right)\right).$$

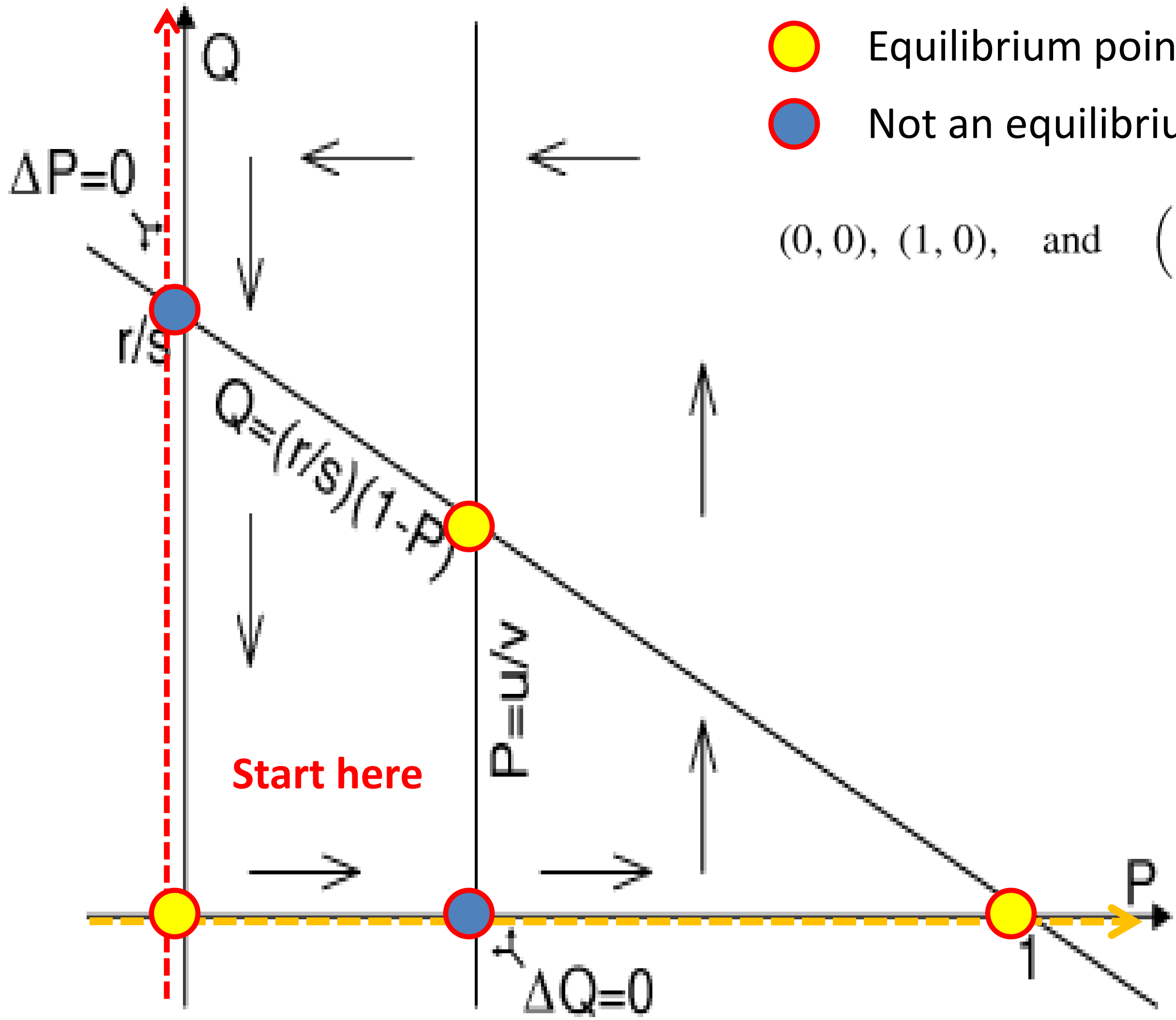


Figure 3.4. Nullclines, $\Delta P = 0$ and $\Delta Q = 0$, for the predator–prey model.

Linear stability analysis

To focus attention at the equilibrium, we let

$$P_t = P^* + p_t,$$
$$Q_t = Q^* + q_t,$$

where p_t and q_t represent small perturbations from the equilibrium. We are interested in seeing how these perturbations change over time. Do they grow or do they shrink?

For the model

$$P_{t+1} = P_t(1 + 1.3(1 - P_t)) - .5P_tQ_t,$$
$$Q_{t+1} = .3Q_t + 1.6P_tQ_t,$$

with equilibrium $(P^*, Q^*) = (.4375, 1.4625)$, substituting in the expressions for populations in terms of perturbations from equilibria, gives

$$\begin{aligned}.4375 + p_{t+1} &= (.4375 + p_t)(1 + 1.3(1 - (.4375 + p_t))) \\ &\quad - .5(.4375 + p_t)(1.4625 + q_t), \\ 1.4625 + q_{t+1} &= .3(1.4625 + q_t) + 1.6(.4375 + p_t)(1.4625 + q_t).\end{aligned}$$

Some rather messy algebra, which is nonetheless worth checking, gives us

$$p_{t+1} = .43125p_t - .21875q_t - 1.3p_t^2 - .5p_tq_t,$$
$$q_{t+1} = 2.34p_t + q_t + 1.6p_tq_t.$$

$$p_{t+1} \approx .43125 p_t - .21875 q_t,$$
$$q_{t+1} \approx 2.34 p_t + q_t.$$

Approximated to linear one

$$\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} .43125 & -.21875 \\ 2.34 & 1 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$$

In matrix form

we just need to compute the eigenvalues of the matrix. Using MATLAB to do this gives the two complex eigenvalues $\lambda = .7156 \pm .6565i$. Computing the absolute value of both eigenvalues yields $|\lambda| = \sqrt{.7156^2 + .6565^2} = .9711$. Since this number is less than 1, the perturbations from equilibrium must get smaller over time. Thus, the equilibrium really is stable as suspected.

3.3.7. (Calculus) Stability of equilibria can be determined through derivatives, as in Chapter 1, provided you understand partial derivatives. The *Jacobian matrix* of a model

$$P_{t+1} = F(P_t, Q_t),$$
$$Q_{t+1} = G(P_t, Q_t)$$

(Do it!)

is the matrix

$$\begin{pmatrix} \frac{\partial F}{\partial P_t} & \frac{\partial F}{\partial Q_t} \\ \frac{\partial G}{\partial P_t} & \frac{\partial G}{\partial Q_t} \end{pmatrix}.$$

General conditions for stability for 2 x 2 matrix

Denoting the two eigenvalues by $\lambda 1$ and $\lambda 2$, we might see several different types of behavior around the equilibrium, depending on the sizes of $\lambda 1$ and $\lambda 2$.

(i) If both $|\lambda 1| < 1$ and $|\lambda 2| < 1$, as was the case in our example, then all small perturbations from the **equilibrium shrink**. In this case, the **equilibrium is stable.**

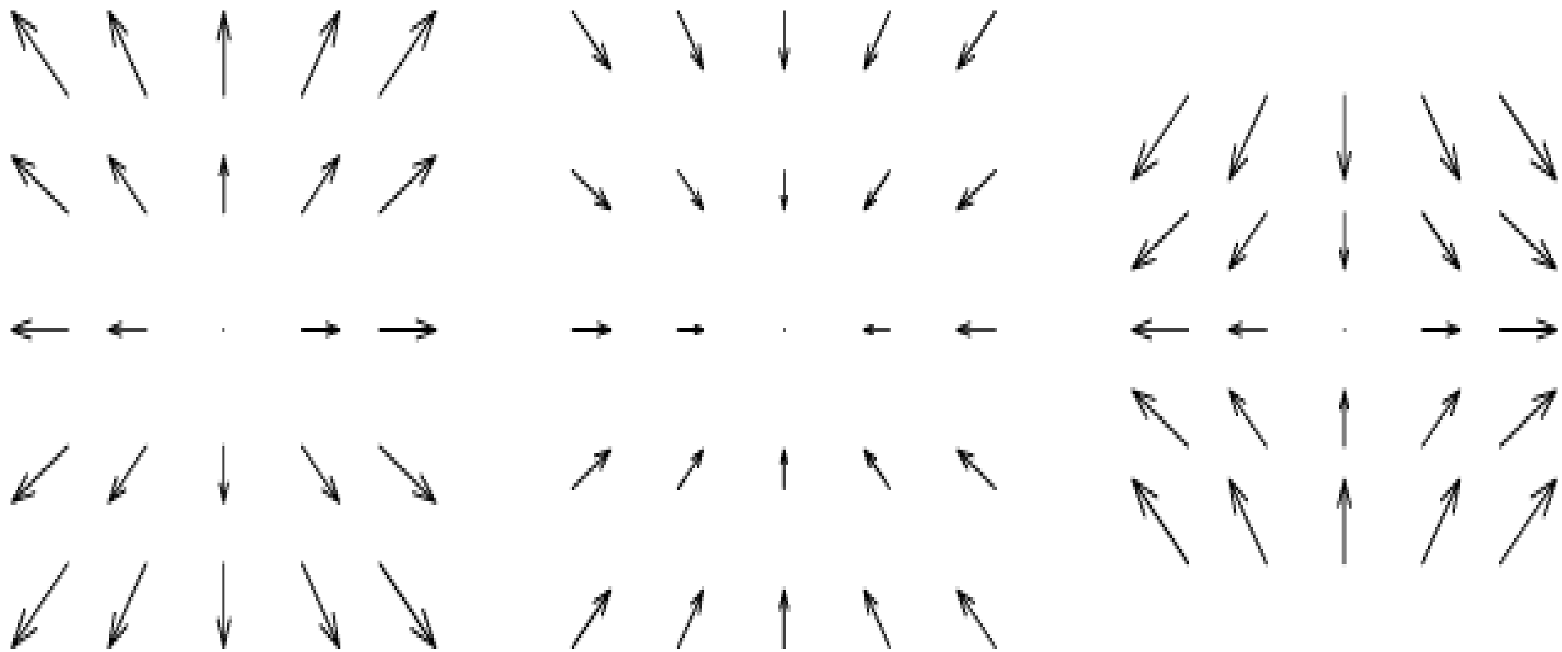
(ii) If both $|\lambda 1| > 1$ and $|\lambda 2| > 1$, then all small perturbations from **the equilibrium grow**, and so the **equilibrium is unstable**.

(iii) If $|\lambda 1| > 1$ and $|\lambda 2| < 1$, or vice versa, then different perturbations behave qualitatively differently.

A perturbation that is an eigenvector with eigen value $\lambda 1$ will grow, whereas one that is an eigenvector with eigenvalue $\lambda 2$ will shrink.

Most perturbations are some combination of these, and so will exhibit a combined behavior.

An equilibrium that exhibits this last type of behavior is a new sort that is often referred to as a **saddle equilibrium.**



$|\lambda_1|, |\lambda_2| > 1$ $\quad$ $|\lambda_1|, |\lambda_2| < 1$ $\quad$ $|\lambda_1| > 1, |\lambda_2| < 1$

Figure 3.5. Possible behaviors near equilibrium points.