02-02-2012

Previous lecture we derived the predator-prey model

$$
(*)\quad \begin{cases} \dfrac{dn}{dt} = -\alpha x n + \gamma y \\ \dfrac{dx}{dt} = -\alpha x n + \gamma y + \delta(x_0 - x - y) \\ \dfrac{dy}{dt} = +\alpha x n - \beta y - \gamma y \end{cases}
$$

(See prev. lecture for interpretation).

This is a 3D system, and as such awkward to analyze.

<u>However</u>:

High-dimensional systems <u>often</u> can be split into a number of lower-dimensional systems if there are

- large differences in <u>population densities</u> of different kinds of individuals, and/or
- Large differences in the <u>reaction rates</u> of different i-level processes.

Such differences may result in different timescales on which different densities change.

Consider the model ⊛ on the previous page, and assume that the predator is rare compared to the prey, i.e., $\boxed{x_0, x, y \ll n}$

More precisely: assume that the ratio of pred. dens. to prey dens. is of order $\varepsilon > 0$, and define

$$\boxed{x_0^* := \frac{x_0}{\varepsilon}}, \quad \boxed{x^* := \frac{x}{\varepsilon}}, \quad \boxed{y^* := \frac{y}{\varepsilon}}$$

($\varepsilon > 0$ is a small dimensionless scaling parameter, our "microscope" if you will, that magnifies the predator density to the densities x_0^*, x^* and y^*, which are comparable in magnitude to the prey density n.)

Rewriting ⊛ in terms of n, x^* and y^* gives:

$$(**) \quad \begin{cases} \dfrac{dn}{dt} = -\varepsilon \alpha x^* n + \varepsilon \gamma y^* & \text{(slow)} \\[2ex] \dfrac{dx^*}{dt} = -\alpha x^* n + \gamma y^* + \delta (x_0^* - x^* - y^*) & \text{(fast)} \\[2ex] \dfrac{dy^*}{dt} = +\alpha x^* n - \gamma y^* - \beta y^* & \text{(fast)} \end{cases}$$

So, n changes slowly while x^* and y^* change fast.

Notice:

First the pred. and prey densities differed by an order $\varepsilon > 0$, but after rescaling pred. density by a factor ε^{-1}, the rate of change of the densities differ by an order $\varepsilon > 0$.

Singular perturbation theory tells us that the behavior of (**) for small $\varepsilon > 0$ is qualitatively (i.e, topologically) equivalent to that of the limiting case for $\varepsilon \to 0$.

Letting $\varepsilon \searrow 0$ in (**) we get

fast dyn.
$$\begin{cases} \dfrac{dn}{dt} = 0 \\ \dfrac{dx^*}{dt} = -\alpha x^* n + \gamma y^* + \delta(x_0^* - x^* - y^*) \\ \dfrac{dy^*}{dt} = +\alpha x^* n - \gamma y^* - \beta y^* \end{cases}$$

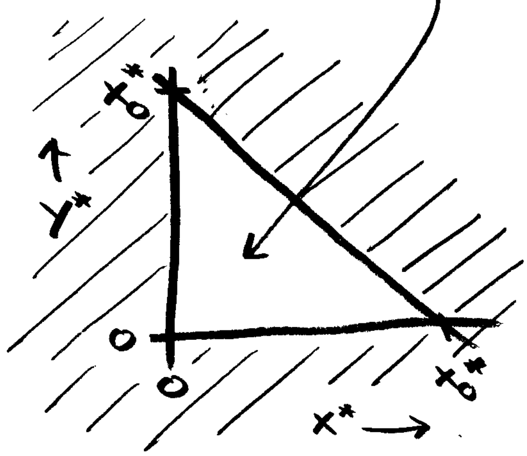
This is essentially a 2D system (because n is now constant) that we can analyze with the phase-plane method.

Phase-plane analysis fast dynamics:

Equilibrium calculation:

$$\begin{cases} \dfrac{dx^*}{dt} = 0 \\ \dfrac{dy^*}{dt} = 0 \end{cases} \iff \begin{cases} x^* = x_0^* \cdot \dfrac{(\beta+\gamma)\delta}{(\beta+\gamma)\delta + \alpha\beta n + \alpha\delta n} =: \bar{x}^* \\ y^* = x_0^* \cdot \dfrac{\alpha\delta n}{(\beta+\gamma)\delta + \alpha\beta n + \alpha\delta n} =: \bar{y}^* \end{cases}$$

allowable set of (x^*, y^*)-values:



Only white region can be interpreted. (why?)

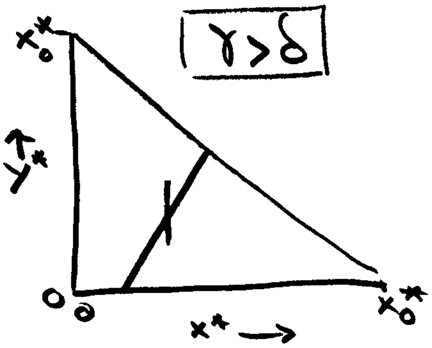
$0 \leq x^* \leq x_0^*$ & $0 \leq y^* \leq x_0^*$ & $x^* + y^* \leq x_0^*$

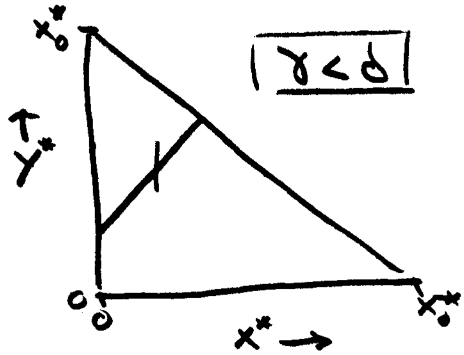
Notice that the equilibrium $(\bar{x}^*, \bar{y}^*)$ calculated above always exists (all rates are positive, and so is n) and always lies in the white region.

Is $(\bar{x}^*, \bar{y}^*)$ stable?

Zero cline of x^*.

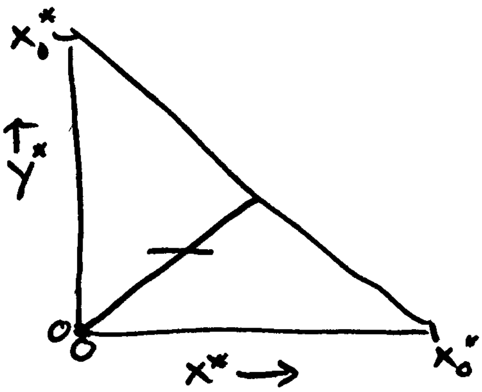
$$\frac{dx^*}{dt} = 0 \iff y^* = \frac{(\alpha n + \delta)x^* - \delta x_0^*}{\gamma - \delta}$$



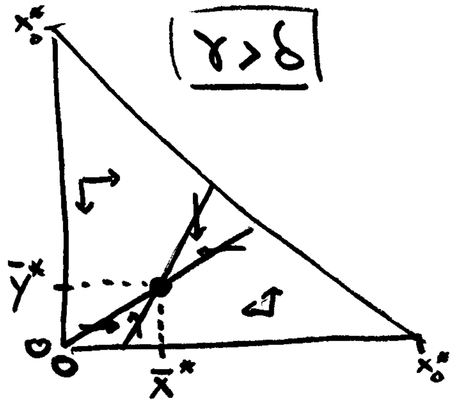


Zero cline of y^*

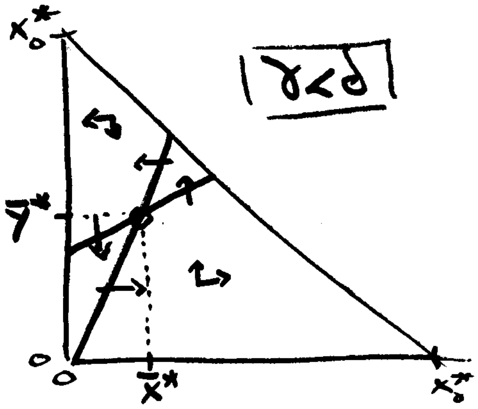
$$\frac{dy^*}{dt} = 0 \iff y^* = \frac{\alpha n x^*}{\beta + \gamma}$$



Super-position of the zeroclines of x^* and y^* (and knowing that they must intersect in the interior of the phase-plane), we get:



$(\bar{x}^*, \bar{y}^*)$ is globally attracting



We need more sophisticated tools to decide whether $(\bar{x}^*, \bar{y}^*)$ is stable or not.

We'll focus on this case

(The other case will come in a later lecture after we've done "linear stability analysis".)

Conclusion:

If $\gamma < d$, then the fast dynamics (page 22) converges to $(x^*, y^*) \to (\bar{x}^*, \bar{y}^*)$.

Let's go back to (**) on page 21:

For small $\varepsilon > 0$, the prey density n changes only slowly compared to the scaled pred. densities x^* and y^*.

To observe these slow changes, we have to look over a longer time.

Therefore, we introduce "slow time" $\boxed{t^* := \varepsilon t}$ and rewrite (**) in terms of changes in t^* time:

$$\frac{d}{dt^*} = \frac{d}{dt} \cdot \frac{dt}{dt^*} = \frac{d}{dt} \cdot \frac{1}{\varepsilon} \implies$$

$$(***) \quad \begin{cases} \dfrac{dn}{dt^*} = -\alpha x^* n + \gamma y^* \\[2ex] \varepsilon \dfrac{dx^*}{dt^*} = -\alpha x^* n + \gamma y^* + \delta(x_0^* - x^* - y^*) \\[2ex] \varepsilon \dfrac{dy^*}{dt^*} = +\alpha x^* n - \gamma y^* - \beta y^* \end{cases}$$

Letting $\varepsilon \searrow 0$ in ~~(***)~~ gives

slow dyn.
$$\begin{cases} \dfrac{dn}{dt^*} = -\alpha x^* n + \gamma y^* \\ 0 = -\alpha x^* n + \gamma y^* + \delta(x_0^* - x^* - y^*) \\ 0 = +\alpha x^* n - \gamma y^* - \beta y^* \end{cases}$$

Notice that the two last equations are the equilibrium equations of the fast dynamics and therefore give $(x^*, y^*) = (\bar{x}^*, \bar{y}^*)$. (see page 23).

The slow dynamics (above) shows how the slow variable n changes on a long time-scale (i.e. in t^* time) if the fast variables x^* and y^* are at their (fast) equilibrium.

We need the fast dynamics (page 22) to see whether $(\bar{x}^*, \bar{y}^*)$ is stable or not.

For the slow variable we thus get (after substitution of $(\bar{x}^*, \bar{y}^*)$ into the equation):

$$\boxed{\frac{dn}{dt^*} = -\frac{\alpha\beta\delta x_0 n}{(\beta+\gamma)\delta + \alpha(\beta+\delta)n}} \quad (\gamma > \delta)$$

Conclusion

By assuming vastly different population densities of the prey and the predator, we were able to split the 3D system ⊛ (page 20) into one 2D system (the fast dynamics; page 22) and one 1D equation (the slow dynamics; previous page), both of which are easy to analyze.

Different time-scales can also be the result of vastly different <u>rates</u> of i-level processes:

Consider the model introduced on page 10 of the lecture of 26/01. and analyzed on pages 12 – 14 of the lecture of 31/01:

$$(*)\quad \begin{cases} \dfrac{dx}{dt} = +\beta(n_0 - x)y - \mu x & \text{(site owner)} \\[2ex] \dfrac{dy}{dt} = -\beta(n_0 - x)y + \alpha x - \nu y & \text{(free indiv.)} \end{cases}$$

Suppose that the sites are difficult to find (<u>small β</u>), that sites give good protection (<u>small μ</u>), that sites contain many resources for fast reproduction (<u>large α</u>), and that life without a site is very risky (<u>large ν</u>)

More precisely, we assume that

$$\alpha = \alpha_0 \varepsilon^{-1}, \quad \nu = \nu_0 \varepsilon^{-1}, \quad \beta \in O(1), \quad \mu \in O(1)$$

for small $\varepsilon > 0$.

(ε is again a dim.less scaling param.)

Rewriting $\circledast$ with the above assumptions gives:

$$
(\ast\ast)\quad \begin{cases} \dfrac{dx}{dt} = +\beta(n_0 - x)y - \mu x & \text{(slow)} \\[2ex] \dfrac{dy}{dt} = -\beta(n_0 - x)y + \boxed{\dfrac{\alpha_0}{\varepsilon}x - \dfrac{\nu_0}{\varepsilon}y} & \text{(fast)} \end{cases}
$$

(it's these therms with ε^{-1} that make changes in y fast)

We cannot just let $\varepsilon \searrow 0$, because then $|dy/dt| \to \pm\infty$.

Instead we first introduce "fast time" $\boxed{t^* := \dfrac{t}{\varepsilon}}$ and rewrite $(\ast\ast)$ in terms of t^*:

$$
\frac{d}{dt^*} = \frac{d}{dt}\cdot\frac{dt}{dt^*} = \frac{d}{dt}\cdot\varepsilon \implies
$$

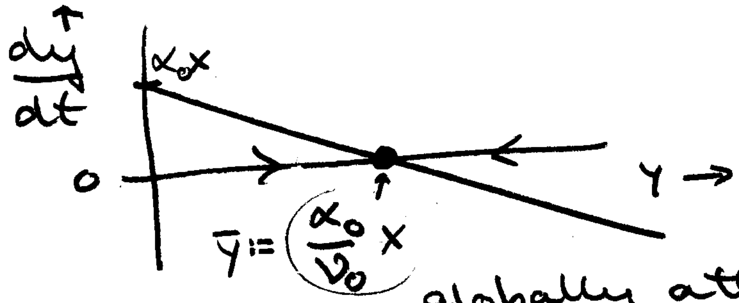
$$
\begin{cases} \dfrac{dx}{dt^*} = +\varepsilon\beta(n_0 - x)y - \varepsilon\mu x \\[2ex] \dfrac{dy}{dt^*} = -\varepsilon\beta(n_0 - x)y + \alpha_0 x - \nu_0 y \end{cases}
$$

Letting now $\varepsilon \searrow 0$ we get:

$\longrightarrow$

fast dyn.
$$\begin{cases} \dfrac{dx}{dt^*} = 0 \\[2ex] \dfrac{dy}{dt^*} = \alpha_0 x - \nu_0 y . \end{cases}$$

This is essentially a one-dim equation.



globally attracting equil.

Conclusion:

$$y \longrightarrow \bar{y} =: \frac{\alpha_0}{\nu_0} x \quad \text{in fast time } t^*.$$

To see what happens to the slow variable x in normal time t, rewrite (**) (prev. page) as

$$\begin{cases} \dfrac{dx}{dt} = +\beta(n_0 - x)y - \mu x \\[2ex] \varepsilon \dfrac{dy}{dt} = -\varepsilon\beta(n_0 - x)y + \alpha_0 x - \nu_0 y . \end{cases}$$

Letting $\varepsilon \searrow 0$ this gives $\longrightarrow$

slow dyn
$$\begin{cases} \dfrac{dx}{dt} = \beta(n_0 - x)y - \mu x \\ 0 = \alpha_0 x - \nu_0 y \end{cases}$$

Notice that the second equation is the equil. equation of the fast dynamics (prev. page) which gave $y = \frac{\alpha_0}{\nu_0} x =: \bar{y}$

Hence, for $\frac{dx}{dt}$ we find

$$\frac{dx}{dt} = \beta(n_0 - x)\bar{y} - \mu x$$

$$= \beta(n_0 - x)\frac{\alpha_0}{\nu_0} x - \mu x.$$

Which is the logistic equation

$$(***) \begin{cases} \dfrac{dx}{dt} = rx\left(1 - \dfrac{x}{K}\right) \\ \text{with} \\ r = \beta n_0 \dfrac{\alpha_0}{\nu_0} - \mu \\ K = n_0 - \dfrac{\mu}{\beta \frac{\alpha_0}{\nu_0}} \end{cases}$$

Note:

We've seen the logistic equation before, in lecture 26/01, page 9.

The population equation is the same as in $\cancel{xxx}$ (prev. page), but the interpretation of the r and the K is different because on the i-level totally different processes play a role.

In other words: we've now seen two different mechanistic underpinnings of the logistic equation.

This becomes important, e.g. when we start varying parameters: with the present underpinning r and K cannot vary independently, but with the former underpinning that would be possible.