Ecological Models for populations of interacting species

The basic idea is that we will let the variables be the density (concentration) of a given species in a patch of the environment & then allow them to interact using the laws of mass-action. This lets us derive ODEs for the evolution of their totals.

$X + Y \xrightarrow{r} pX + qY$ (eg if X eats Y, then $q=0$, $p>1$)

Rate $= r X \cdot Y$, and at each interaction, X, Y are "consumed" & produce $pX + qY$, so

$\frac{dX}{dt} = (p-1)$ Rate, $\frac{dY}{dt} = (q-1)$ Rate

$\frac{dX}{dt} = r(p-1)XY$, $\frac{dY}{dt} = r(q-1)XY$

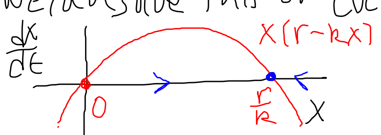
<u>EXAMPLE 1</u> $X \xrightarrow{r} 2X$ (spontaneous generation!)

$\frac{dX}{dt} = r(2-1)X = rX \Rightarrow X = X(0)e^{rt} \Rightarrow$ exponential growth

<u>EXAMPLE 2</u> $X \xrightarrow{r} 2X$, $X+X \xrightarrow{k} X$ (crowding effect)

$\frac{dX}{dt} = (2-1)rX + k(1-2)X^2 = X[r - kX]$

We can solve this or even easier, just plot the phase line:

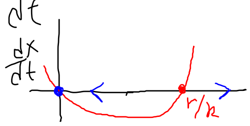


We see that if $X(0) > 0$, then $X(t) \to \frac{r}{k}$ as $t \to \infty$

We can actually solve this in closed form (exercise #1)

<u>EXAMPLE 3</u> $X \xrightarrow{r} *$, $X+X \xrightarrow{k} 3X$ (death + mating)

$\frac{dX}{dt} = -rX + kX^2 = X(-r+kX)$ If $X(0) > \frac{r}{k}$, $X(t) \to \infty$ "threshold" to blowup



Can add "threes a crowd" to make it stable (Ex#2)

Two-species interactions

Example 4 (Lotka-Volterra)

$X \xrightarrow{a} 2X$, $X+Y \xrightarrow{b} (1+p)Y$, $Y \xrightarrow{c} *$

growth of X, predation by Y, death of Y

$\dot{x} = ax - bxy$, $\dot{y} = -cy + pbxy \equiv -cy + dxy$

$\dot{x} = x(a-by)$, $\dot{y} = y(-c+dx)$

ASIDE $\dot{x} = f(x)$, $x \in \mathbb{R}^n$, $x(0)=x_0$, $f \in C^1(\mathbb{R}^n)$

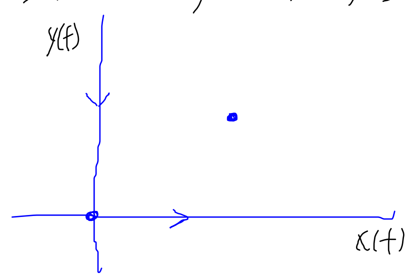
$\Rightarrow$ for $t \in (-a, a)$ there exists a unique solution $x(t)$ st $x(0)=x_0$.

END OF ASIDE

4 simple solutions: $x(t)=y(t)=0$ $\forall t$, $x(t)=0$, $y(t)=y_0e^{-ct}$, $x(t)=\frac{c}{d}$, $y(t)=\frac{a}{b}$

$y(t)=0$, $x(t)=x(0)e^{at}$.

Two are equilibria $(0,0)$ $\left(\frac{c}{d}, \frac{a}{b}\right)$



ASIDE $\dot{x} = F(x)$, $x \in \mathbb{R}^n$, $F \in C^1(\mathbb{R}^n)$

$\bar{x}$ is equilibrium if $F(\bar{x})=0$. Let $A = D_x F(\bar{x})$

If at least one eigenvalue of A has a positive real part, then $\bar{x}$ is an unstable equilibrium. If all eigenvalues of A have negative real parts, then $\bar{x}$ is an asymptotically stable equilibrium. If some eigenvalues have zero real part, cannot conclude much

END ASIDE For the LV model,

$$A = \begin{bmatrix} a-by & -bx \\ dy & -c+dx \end{bmatrix} \quad A_{(0,0)} = \begin{bmatrix} a & 0 \\ 0 & -c \end{bmatrix} \quad A_{\left[\frac{c}{d},\frac{a}{b}\right]} = \begin{bmatrix} 0 & -\frac{bc}{d} \\ \frac{ad}{b} & 0 \end{bmatrix}$$

unstable! $\pm i\sqrt{ac}$

Analysis of LV model

$\frac{dx}{dt} = x(a-by)$, $\frac{dy}{dt} = y(-c+dx)$

$\frac{dx}{dy} = \frac{x}{-c+dx} \cdot \frac{a-by}{y} \Rightarrow \frac{-c+dx}{x}\,dx = \frac{a-by}{y}\,dy \Rightarrow$

$\int\left(\frac{a}{y}-b\right)dy + \int\left(\frac{c}{x}-d\right)dx = K \Rightarrow (c\ln x - dx) + (a\ln y - by) = C$

Recalling $\bar{x} = \frac{c}{d}$, $\bar{y} = \frac{a}{b}$, we rewrite this as

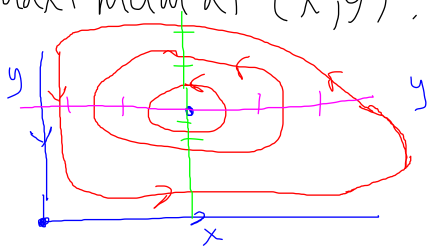
$V(x,y) = d\,H(x) + b\,G(y)$, $H(x) = \bar{x}\ln x - x$, $G(y) = \bar{y}\ln y - y$

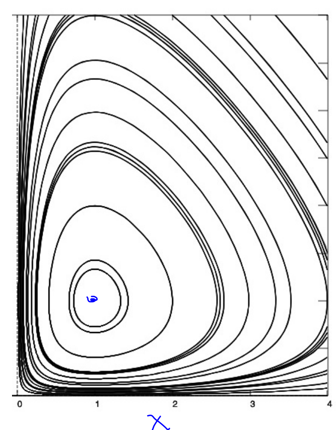
$\frac{d}{dt}V(x,y) = 0$, since $V(x,y) = $ constant along solutions.

$\frac{dH}{dx} = \frac{\bar{x}}{x} - 1$, $\frac{dG}{dy} = \frac{\bar{y}}{y} - 1 \Rightarrow H\,(G)$ has a maximum at $\bar{x}\,(\bar{y})$ so

$V(x,y)$ takes its maximum at $(\bar{x},\bar{y})$. Contours of $V=$ const

are solutions:





Example 5 Each has competition within the pop (crowding)

$\frac{dx}{dt} = x(a-ex-by)$, $\frac{dy}{dt} = y(-c+dx-fy)$, $e>0$, $f\geq 0$, $(x(0),y(0))\geq 0$

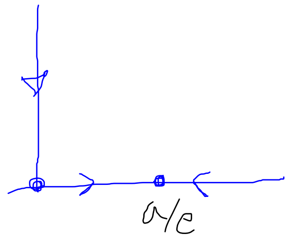
The orthant $x\geq 0, y\geq 0$ is invariant and if $x(0)>0$, $y(0)>0$, then $x(t)>0$, $y(t)>0$ for all finite t (Ex 3). Define $\mathbb{R}^2_+ = \{x>0, y>0\}$

The solutions on the boundary are $(0,0)$, $(0,\tilde{y}(t))$ + $(\tilde{x}(t),0)$

where $\dot{\tilde{x}} = \tilde{x}(a-e\tilde{x})$, $\dot{\tilde{y}} = \tilde{y}(-c-f\tilde{y})$

$\tilde{x} \to \frac{a}{e}$ as $t\to\infty$, $\tilde{y}\to 0$ as $t\to\infty$

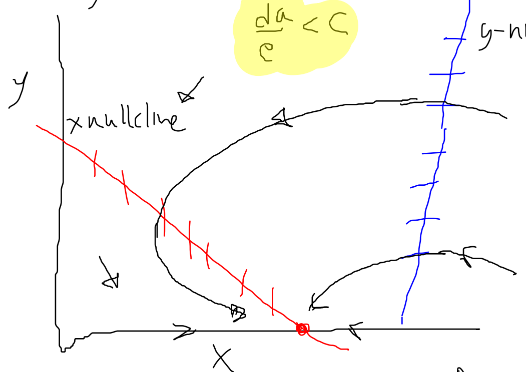
LV + competition ctd

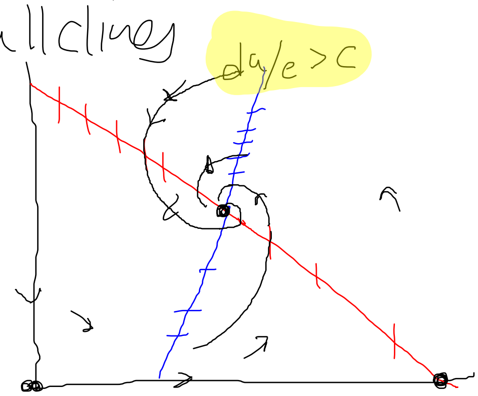


$(0,0)$ + $(\frac{a}{e}, 0)$

Are there any interior equilibria?

$a = ex + by$, $c = dx - fy$. Depending on parameters, these lines may or may not intersect in the interior. Indeed, they are the x- and y-nullclines





$$A = \begin{bmatrix} a-2ex-by & -bx \\ dy & -c+dx-2fy \end{bmatrix}$$

$A_{(0,0)} = \begin{bmatrix} a & 0 \\ 0 & -c \end{bmatrix}$ unstable

$A_{(\frac{a}{e},0)} = \begin{bmatrix} -a & -\frac{ba}{e} \\ 0 & -c+\frac{da}{e} \end{bmatrix}$ Stable iff $\frac{da}{e} < c$

$A_{(\bar{x},\bar{y})} = \begin{bmatrix} -e\bar{x} & -b\bar{x} \\ d\bar{y} & -2f\bar{y} \end{bmatrix}$ $\Rightarrow$ if $(\bar{x},\bar{y})$ are positive $\Rightarrow$ $Tr < 0$, $\det > 0$

$\Rightarrow$ A.S. (if $e > 0$ or $f > 0$)

<u>ASIDE</u>: $\omega(x) = \{y \in \mathbb{R}^n \mid x(t_n) \to y \text{ for some } t_n \to +\infty\}$ is called the ω-limit set of x. It can be empty or all of $\mathbb{R}^n$. $\omega(x)$ is closed, and invariant. Equilibria + periodic orbits are their own ω-limit sets.

<u>Theorem</u> Let $\dot{x} = f(x)$ be defined on some subset, G of $\mathbb{R}^n$ & let $V: G \to \mathbb{R}$ be ctsly diff. We define $\dot{V}(t) = \frac{\partial V}{\partial x} \cdot \dot{x}$. If for some solution $x(t)$, $\dot{V} \geq 0$ (or $\dot{V} \leq 0$) then $\omega(x) \cap G$ (and $\alpha(x) \cap G$) is contained in the set $\{x \in G \mid \dot{V}(x) = 0\}$

<u>Theorem</u> Suppose $V: \mathbb{R}^n \to \mathbb{R}$ satisfies the following in some open set G containing $\bar{x}$, $f(\bar{x}) = 0$, $\dot{x} = f(x)$ is our ODE:
(i) $V(\bar{x}) = 0$ (ii) $V(y) > 0$ for $y \in G$, $y \neq x$, (iii) $\dot{V} \leq 0$ in G with $\dot{V} = 0$ only at $\bar{x}$. Then if $x(0) \in G$, then $x(t) \to \bar{x}$ as $t \to \infty$. V is called a Liapunov function.

<u>END ASIDE</u>

Let $(\bar{x}, \bar{y})$ be an interior equilibrium of our PP system (case da > ec)
Let $V(x,y) = -dH(x) - bG(y) + dH(\bar{x}) + bG(\bar{y})$, $H(x) = \bar{x} \ln x - x$, $G(y) = \bar{y} \ln(y) - y$
Note $V(x,y)$ is positive definite since $(\bar{x}, \bar{y})$ is the global minimum
$\dot{V}(x,y) = \frac{\partial V}{\partial x} \dot{x} + \frac{\partial V}{\partial y} \dot{y} = -d\left(\frac{\bar{x}}{x} - 1\right) x(a - by - ex) - b\left(\frac{\bar{y}}{y} - 1\right) y(-c + dx - fy)$. we replace
$a = e\bar{x} + b\bar{y}$, $c = d\bar{x} - f\bar{y}$, + get
$\dot{V} = -de(x - \bar{x})^2 - bf(y - \bar{y})^2 \leq 0 \Rightarrow (\bar{x}, \bar{y})$ is the ω-limit set of the entire positive orthant!!
There are only periodic orbits when $e = f = 0$

<u>EXAMPLE 6</u> Competition $X \xrightarrow{a} 2X$, $2X \xrightarrow{b} X$, $Y \xrightarrow{d} 2Y$, $2Y \xrightarrow{f} Y$
$X + Y \xrightarrow{r} pX + qY$, $0 \leq p, q < 1$. Let $-c = r(p-1)$, $-e = r(q-1)$
$\dot{x} = x(a - bx - cy)$, $\dot{y} = y(d - ex - fy)$ $a - f > 0$. Competition equation
Three border solutions, $(0,0)$ $(x(t), 0)$, $(0, y(t))$, the last two of which tend to $(x_1, 0) = \frac{a}{b}$, $(0, y_1) = \frac{d}{f}$.
There will be an interior equilibrium if
$A\binom{x}{y} = \begin{pmatrix} b & c \\ e & f \end{pmatrix} \binom{x}{y} = \binom{a}{d}$ has a solution in $\mathbb{R}^2_+$. Unless $\det A = 0$, this equilibrium will be unique.

competition ctd

The linearization matrix is

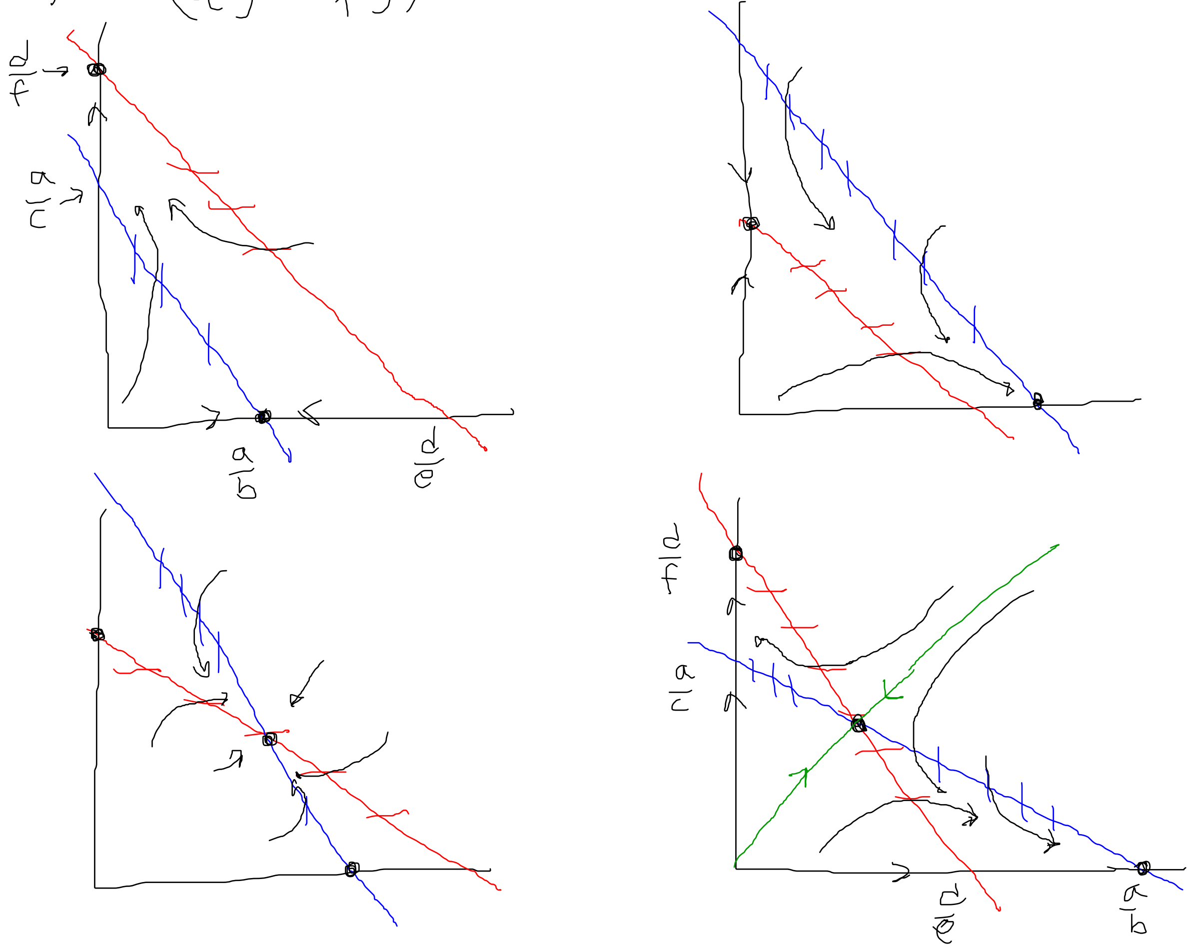
$$J = \begin{pmatrix} a-2bx-cy & -cx \\ -ey & d-2fy-ex \end{pmatrix}$$

$J_{(0,0)} = \begin{pmatrix} a & 0 \\ 0 & d \end{pmatrix} \rightarrow$ unstable node

$J_{(\frac{a}{b},0)} = \begin{pmatrix} -a & -\frac{ca}{b} \\ 0 & d-\frac{ea}{b} \end{pmatrix} \Rightarrow$ stable iff $bd < ea$

$J_{(0,\frac{d}{f})} = \begin{pmatrix} a-\frac{cd}{f} & 0 \\ -\frac{ed}{f} & -d \end{pmatrix} \Rightarrow$ stable iff $af < cd$

$J_{(\bar{x},\bar{y})} = \begin{pmatrix} -b\bar{x} & -c\bar{x} \\ -e\bar{y} & -f\bar{y} \end{pmatrix} \Rightarrow$ stable iff $\det(A) > 0$ $\left(\begin{matrix}\text{assuming} \\ (\bar{x},\bar{y}) \in \mathbb{R}_+^2\end{matrix}\right)$



Are L.C. possible?

ASIDE Let $\dot{x} = f(x)$ be an ODE defined on an open set $G \subseteq \mathbb{R}^2$. Let $\omega(x)$ be a nonempty compact ω-limit set. If $\omega(x)$ contains no equilibria, it must be a periodic orbit [POINCARÉ–BENDIXSON]

Let $B(x_1,x_2)$ be a positive function defined on G & write $\dot{x}_1 = f_1(x_1,x_2)$, $\dot{x}_2 = f_2(x_1,x_2)$ as our planar ODE

If $\frac{\partial Bf_1}{\partial x_1} + \frac{\partial Bf_2}{\partial x_2}$ is of fixed sign in G, then G can contain no limit cycles.

Proof Consider $\frac{dx_1}{dt} = f_1$, $\frac{dx_2}{dt} = f_2$

write $\frac{dx_1}{dx_2} = \frac{Bf_1}{Bf_2} \Rightarrow Bf_2\,dx_1 - Bf_1\,dx_2 = 0$

$$\Rightarrow \oint_{LC} Bf_2\,dx_1 - Bf_1\,dx_2 = 0 \Rightarrow \iint \frac{\partial}{\partial x_1}Bf_1 + \frac{\partial}{\partial x_2}Bf_2 \, dx_1 dx_2 = 0$$

divergence Thm

But quantity in $\iint$ is of one sign $\Rightarrow$ #

Note that if $\frac{\partial Bf_1}{\partial x_1} + \frac{\partial Bf_2}{\partial x_2} \equiv 0 \Rightarrow$

$\exists\, H$ st $Bf_1 = \frac{\partial H}{\partial x_2}$, $Bf_2 = -\frac{\partial H}{\partial x_1} \Rightarrow$

$\frac{dH}{dt} = 0$ along trajectories of $\dot{x}_1 = Bf_1$, $\dot{x}_2 = Bf_2$

But trajectories of $\dot{x}_1 = f_1$, $\dot{x}_2 = f_2$ are same as those of $\dot{x}_1 = Bf_1$, $\dot{x}_2 = Bf_2$

So get H = constant along trajectories of $\dot{x} = f(x)$

END ASIDE !!

LV-2D ⇒ NO LC!

Theorem $\dot{x} = \underbrace{x(a+bx+cy)}_{P(x,y)}, \quad \dot{y} = \underbrace{y(d+ex+fy)}_{Q(x,y)}$
admits no isolated periodic orbits.

Proof (Note that there can be periodic orbits but they will be nested like the classic LV model.)

Let γ be a periodic orbit. There must necessarily be an interior equilibrium point (PBT), so the two lines
$a+bx+cy=0$, $d+ex+fy=0$ must intersect in a unique pt in the interior of $\mathbb{R}^2_+$. $\Rightarrow \Delta = bf - ce \neq 0$ $\begin{pmatrix} -b & -c \\ -e & -f \end{pmatrix}\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} = \begin{pmatrix} a \\ b \end{pmatrix}$

We will choose $B(x,y) = x^{\alpha-1}y^{\beta-1}$ and apply Dulac Theorem

$\frac{\partial}{\partial x}(BP) + \frac{\partial}{\partial y}(BQ) =$

$\frac{\partial}{\partial x}\left[x^{\alpha}y^{\beta-1}(a+bx+cy)\right] + \frac{\partial}{\partial y}\left[x^{\alpha-1}y^{\beta}(d+ex+fy)\right]$

$= \alpha x^{\alpha-1}y^{\beta-1}(a+bx+cy) + x^{\alpha}y^{\beta-1}b + \beta x^{\alpha-1}y^{\beta-1}(d+ex+fy) + x^{\alpha-1}y^{\beta}f$

$= B\left[\alpha(a+bx+cy) + bx + \beta(d+ex+fy) + fy\right]$

$= B\left[(\alpha b + b + \beta e)x + (\alpha c + f + \beta f)y + \alpha a + \beta d\right]$

Choose α, β to kill x, y terms $\Rightarrow$

$\begin{pmatrix} b & e \\ c & f \end{pmatrix}\begin{pmatrix} \alpha \\ \beta \end{pmatrix} = \begin{bmatrix} -b \\ -f \end{bmatrix}$ iff $bf - ec \neq 0$!!

$\Rightarrow \frac{\partial BP}{\partial x} + \frac{\partial BQ}{\partial y} = B[\alpha a + \beta d]$ which is either identically zero or of fixed sign.

If fixed sign $\Rightarrow$ NO LC

If $\equiv 0 \Rightarrow$ integrable + $H \equiv C$ on trajectories $\square$

Let me clarify the last part: $\dot{x} = P, \dot{y} = Q \Rightarrow Q\,dx - P\,dy = 0$
B is an integrating factor! $\Rightarrow (BQ)\,dx - (BP)\,dy = 0$
$\exists\, V(x,y)$ st $dV = \frac{\partial V}{\partial x}dx + \frac{\partial V}{\partial y}dy = 0$ (exact) $\Rightarrow$
$\frac{\partial V}{\partial x} = BQ, \quad \frac{\partial V}{\partial y} = -BP$