Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion

Reaction-Diffusion Models and Bifurcation Theory Lecture 1: Basics and Examples from ODEs

Junping Shi

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Planar systems

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N-D ODE

Conclusion

Topic course in Fall 2007



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Conclusion

My visits to Taiwan: 2005, 2007, 2009, 2010, 2013



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Course F	Plan				

- Basics and Examples from ODEs
- Ø Diffusion, advection and cross-diffusion models
- Oelay, chemotaxis and nonlocal models
- Linear stability (ODE, reaction-diffusion models)
- Solution Linear stability (delay models)
- Numerical simulations
- Analytic bifurcation theory for stationary problems

- Turing bifurcation and pattern formation
- Iclobal bifurcation for stationary problems
- Hopf bifurcation

Scalar ODEs

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ODEs in Biology

Planar systems

N-D ODE

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Conclusion

Earliest Bifurcation: Buckling



(Left: Buckling due to glaze icing; Right: Buckling of rails)

In engineering, buckling is a failure mode characterized by a sudden failure of a structural member subjected to high compressive stresses, where the actual compressive stresses at failure are greater than the ultimate compressive stresses that the material is capable of withstanding. This mode of failure is also described as failure due to elastic instability.

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Euler Buckling Equation



(Left: buckling under different thrusts; Right: bifurcation diagram (λ, ϕ))

 $\phi'' + \lambda \sin \phi = 0, x \in (0, \pi), \phi(0) = \phi(\pi) = 0$

 $\phi(x)$ is the angle between the tangent to the column's axis and the y-axis, and λ is a parameter proportional to the thrust.

The word bifurcation is from the Latin *bifurcus*, which means two forks.

[Da Vinci, Codex Madrid, 1478-1519], [Euler, 1757], Galileo, Bernoulli

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Da Vinci's sketching showing buckling



Figure 4 Leonardo da Vinci: drawing to illustrate the bending of a column under a vertical weight [from Codex Madrid 1 [9], page 117].

Bifurcation in Natural World

Predator-prey interaction: Lotka-Volterra model Classical examples: Hudson company lynx-hare data in 1800s





Alfred Lotka Vito

Vito Volterra

$$\frac{du}{dt} = u(a - bu) - cuv, \quad \frac{dv}{dt} = -dv + fuv.$$





Planar systems

N-D ODE

Conclusion

Bifurcation to Oscillations



<u>Paradox of enrichment</u>: $\frac{dU}{ds} = \gamma U \left(1 - \frac{U}{K}\right) - \frac{CMUV}{A + U}$, $\frac{dV}{ds} = -DV + \frac{MUV}{A + U}$. Environment is enriched if *K* (carrying capacity) is larger, but when *K* is small, a coexistence equilibrium is stable; but when *K* is larger, the coexistence equilibrium is unstable, and a stable periodic orbit appears as a result of Hopf bifurcation.

[Rosenzweig, *Science* 1971] Paradox of enrichment: destabilization of exploitation ecosystems in ecological time.

[May, Science 1972] Limit cycles in predator-prey communities.

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Planet earth, global warming, critical transition

2013 is the year of Mathematics for Planet Earth. http://mpe2013.org

A sudden critical transition can bring catastrophic change to the earth ecosystem, thus it is important to predict and prevent it http://www.early-warning-signals.org

Critical Transitions in Nature and Society, by Marten Scheffer http://www.sparcs-center.org/about-us/staff-contacts/marten-scheffer.html



Rich Spatial Patterns in Diffusive Predator-Prey System



Patterns generated by diffusive predator-prey system

$$\begin{cases} u_t - d_1 \Delta u = u (1 - u) - \frac{muv}{u + a}, & x \in \Omega, \ t > 0, \\ v_t - d_2 \Delta v = -\theta v + \frac{muv}{u + a}, & x \in \Omega, \ t > 0, \\ \partial_{\nu} u = \partial_{\nu} v = 0, & x \in \partial\Omega, \ t > 0, \\ u(x, 0) = u_0(x) \ge 0, \ v(x, 0) = v_0(x) \ge 0, & x \in \Omega. \end{cases}$$

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Patchiness (spatial heterogeneity) of plankton distributions in phytoplankton-zooplankton interaction [Medvinsky, et.al., *SIAM Review* 2002] Spatiotemporal complexity of plankton and fish dynamics.

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Conclusion

Spatial Model: Bifurcation from Grassland to Desert



 $\begin{array}{l} \frac{\partial w}{\partial t}=a-w-wn^2+\gamma\frac{\partial w}{\partial x}, \quad \frac{\partial n}{\partial t}=wn^2-mn+\Delta n, \quad x\in\Omega.\\ w(x,y,t): \text{concentration of water; }n(x,y,t): \text{ concentration of plant,}\\ \Omega: a two-dimensional domain.\\ a>0: \text{ rainfall; }-w: \text{ evaporation; }-wn^2: \text{ water uptake by plants; water flows downhill}\\ at speed \gamma; wn^2: \text{ plant growth; }-mn: \text{ plant loss}\\ [Klausmeier, Science, 1999]\\ Regular and Irregular Patterns in Semiarid Vegetation.\\ [Rietkerk, et.al. Science, 2004]\\ Self-Organized Patchiness and Catastrophic Shifts in Ecosystems.\\ \end{array}$

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 Stability of a Steady State Solution
 Stability
 Stability

For a continuous-time evolution equation $\frac{du}{dt} = F(\lambda, u)$, where $u \in X$ (state space), $\lambda \in \mathbb{R}$, a steady state solution u_* is locally asymptotically stable (or just stable) if for any $\epsilon > 0$, then there exists $\delta > 0$ such that when $||u(0) - u_*||_X < \delta$, then $||u(t) - u_*||_X < \epsilon$ for all t > 0 and $\lim_{t \to \infty} ||u(t) - u_*||_X = 0$. Otherwise u_* is unstable.

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Basic Result: If all the eigenvalues of linearized operator $D_u F(\lambda, u_*)$ have negative real parts, then u_* is locally asymptotically stable.

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Bifurcation (change of stability): if when the parameter λ changes from $\lambda_* - \varepsilon$ to $\lambda_* + \varepsilon$, the steady state $u_*(\lambda)$ changes from stable to unstable; and other special solutions (steady states, periodic orbits) may emerge from the known solution $(\lambda, u_*(\lambda))$.

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Steady State Bifurcation (transcritical/pitchfolk): if 0 is an eigenvalue of $D_u F(\lambda_*, u_*)$. Hopf Bifurcation: if $\pm ki$ is a pair of eigenvalues of $D_u F(\lambda_*, u_*)$.

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The rate of change of a variable in the model may depend on the quantities of several independent variables.

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Possible characters x (independent variables other than time t):

- 1. space location (spatially-structured),
- 2. age, sex, size of individuals (physiologically-structured, or stage-structured)
- 3. genetic phenotype (genetically structured)

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variable (t or x) is a countable set ($\in \{1, 2, 3, 4, \dots\}$) or a continuum ($\in (0, T)$)

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3. discrete time and continuous space: integral projection model (IPM)

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- 3. discrete time and continuous space: integral projection model (IPM)
- 4. discrete time and discrete space: coupled map lattices (CML)

(coupled map if the space is finite)

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(variable u is allowed to take continuous real-values)

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Structured Mathematical Model

Events to be modeled (chemical): birth-death, chemical reaction

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Structured Mathematical Model

- Events to be modeled (chemical): birth-death, chemical reaction
- Events to be modeled (physical): dispersal, transport, movement, (mutation)

N-D ODE

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General Form of the Model: $u_t = f(t, x, u, u_x, u_{xx})$

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Long distance dispersal: movement not necessarily to nearest neighbors

General Form of the Model:
$$u_t = f(t, x, u, u_x, u_{xx})$$

discrete case: $u_t = u(n, x) - u(n - 1, x)$,
 $u_x = u(n, x) - u(n, x - 1)$ (advection),
 $u_{xx} = u(n + 1, x) - 2u(n, x) + u(n, x - 1)$ (diffusion)

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Structured Mathematical Model

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continuous case:
$$u_t = \frac{du}{dt}$$
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local case: f is a function $f(t, x, u(x), u_x(x), u_{xx}(x))$ <u>nonlocal case</u>: f is an operator $f : u \mapsto f(t, x, u)$

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Structured Mathematical Model: Examples

<u>Two-Patch model</u>: $u_t = f(u) + d(v - u)$, $v_t = f(v) + d(u - v)$

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Structured Mathematical Model: Examples

<u>Two-Patch model</u>: $u_t = f(u) + d(v - u)$, $v_t = f(v) + d(u - v)$ <u>Lattice stepping stone model</u>: $(u_i)_t = (1 - 2d)u_i + du_{i-1} + du_{i+1} + f(u_i)$, $\overline{i = 0, \pm 1, \pm 2, \cdots}$

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Partial differential equations: Diffusion: $u_t = Du_{xx}$ (x is 1-D location) Advection: $u_t + u_a = f(t)$ (a is age, age-structured model) Reaction-Diffusion model: $u_t = Du_{xx} + u(1 - u)$
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Integral-differential equation (non-local equation): $u_t = \int_{\Omega} k(x, y) u(y, t) dy$

Structured Mathematical Model: Examples

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Integral-differential equation (non-local equation): $u_t = \int_{\Omega} k(x, y) u(y, t) dy$

 $\frac{\text{Delay equation:}}{u_t = f(u(t), u(t - \tau))}$

and combination of all above

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
ODE in	\mathbb{R}^1				

Consider a scalar ODE

$$\frac{du}{dt} = f(\lambda, u), \quad \lambda \in \mathbb{R}, u \in \mathbb{R}.$$

If f is smooth, and u(t) is a bounded solution, then $\lim_{t\to\infty} u(t)$ is an equilibrium. (there is no limit cycle, no chaos)

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So the bifurcation of equilibria determines the entire dynamics.

Suppose that $y = y_0$ is an equilibrium. 1. If $f_u(\lambda_0, y_0) < 0$, then y_0 is stable (sink); 2. If $f_u(\lambda_0, y_0) > 0$, then y_0 is unstable (source).

Solving the bifurcation point:

$$f(\lambda, u) = 0, \quad \frac{\partial f}{\partial u}(\lambda, u) = 0.$$

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Basic Bi	furcation in	ו \mathbb{R}^1			

Consider

 $f(\lambda, u) = 0, \quad \lambda \in \mathbb{R}, u \in \mathbb{R}.$

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Basic Bifurcation in \mathbb{R}^1

Consider

$$f(\lambda, u) = 0, \quad \lambda \in \mathbb{R}, u \in \mathbb{R}.$$

Condition for bifurcation: $f(\lambda_0, u_0) = 0$, $f_u(\lambda_0, u_0) = 0$.

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Basic Bifurcation in \mathbb{R}^1

Consider

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Condition for bifurcation: $f(\lambda_0, u_0) = 0$, $f_u(\lambda_0, u_0) = 0$. Saddle-node bifurcation:

$$f_{uu}(\lambda_0, u_0) \neq 0, \ f_{\lambda}(\lambda_0, u_0) \neq 0.$$

Basic Bifurcation in \mathbb{R}^1

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$$f_{uu}(\lambda_0, u_0) \neq 0, \ f_{\lambda}(\lambda_0, u_0) \neq 0.$$

Assume $f(\lambda, u_0) = 0$ for $\lambda \in \mathbb{R}$. Transcritical bifurcation:

 $f_{uu}(\lambda_0, u_0) \neq 0, \ f_{\lambda u}(\lambda_0, u_0) \neq 0.$

Basic Bifurcation in \mathbb{R}^1

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Condition for bifurcation: $f(\lambda_0, u_0) = 0$, $f_u(\lambda_0, u_0) = 0$. Saddle-node bifurcation:

$$f_{uu}(\lambda_0, u_0) \neq 0, \ f_{\lambda}(\lambda_0, u_0) \neq 0.$$

Assume $f(\lambda, u_0) = 0$ for $\lambda \in \mathbb{R}$. Transcritical bifurcation:

$$f_{uu}(\lambda_0, u_0) \neq 0, \ f_{\lambda u}(\lambda_0, u_0) \neq 0.$$

Pitchfork bifurcation:

$$f_{uu}(\lambda_0, u_0) = 0, \ f_{\lambda u}(\lambda_0, u_0) \neq 0, \ \text{ and } f_{uuu}(\lambda_0, u_0) \neq 0.$$

Basic Bifurcation in \mathbb{R}^1

Consider

$$f(\lambda, u) = 0, \quad \lambda \in \mathbb{R}, u \in \mathbb{R}.$$

Condition for bifurcation: $f(\lambda_0, u_0) = 0$, $f_u(\lambda_0, u_0) = 0$. Saddle-node bifurcation:

$$f_{uu}(\lambda_0, u_0) \neq 0, \ f_{\lambda}(\lambda_0, u_0) \neq 0.$$

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$$f_{uu}(\lambda_0, u_0) = 0, \ f_{\lambda u}(\lambda_0, u_0) \neq 0, \ \text{ and } f_{uuu}(\lambda_0, u_0) \neq 0.$$



Figure: Left: saddle-node; Middle: transcritical; Right: pitchfork

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Names o	f bifurcatio	ons			

Saddle-node bifurcation (fold bifurcation, blue sky bifurcation) a curve $(\lambda(s), u(s))$ near (λ_0, u_0) : $\lambda(s) > \lambda_0$: supercritical (forward) $\lambda(s) < \lambda_0$: subcritical (backward)

transcritical bifurcation/pitchfork bifurcation near (λ_0, u_0) : trivial solutions (λ, u_0) and nontrivial solutions on a curve $(\lambda(s), u(s))$ $\lambda(s) > \lambda_0$: supercritical (forward) pitchfork $\lambda(s) < \lambda_0$: subcritical (backward) pitchfork

If only "half" of the nontrivial solution curve is of physical importance $\lambda(s) > \lambda_0$: supercritical (forward) transcritical $\lambda(s) < \lambda_0$: subcritical (backward) transcritical

In the transcritical bifurcation/pitchfork bifurcation, sometimes people only use forward/backward as above, but use supercritical (subcritical) if the bifurcating solutions are stable (unstable)

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 $y' = f(\varepsilon, \lambda, y).$

Left: $\varepsilon < 0$ (monotone), middle: $\varepsilon = 0$, right: $\varepsilon > 0$ (with two saddle-node bifurcation points)

$$\frac{\partial f}{\partial \lambda}(\varepsilon,\lambda_0,y_0)\neq 0, \ \frac{\partial^2 f}{\partial y^2}(\varepsilon,\lambda_0,y_0)=0, \ \frac{\partial^3 f}{\partial y^3}(\varepsilon,\lambda_0,y_0)\neq 0$$

http://www.scholarpedia.org/article/Cusp_bifurcation

Imperfect bifurcation (two parameter bifurcation)

$$y' = f(\varepsilon, \lambda, y).$$

For $\varepsilon = \varepsilon_0$, there is a transcritical bifurcation or pitchfork bifurcation. What happens when ε is near ε_0 ?

Typical symmetry breaking of transcritical/pitchfork bifurcation [Shi, JFA, 1999], [Liu-Shi-Wang, JFA, 2007; JFA, 2013 to appear]



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Background

Scalar ODEs

ODEs in Biology

Planar systems

N-D ODE

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Conclusion

Saddle-node Bifurcation in \mathbb{R}^1



Annual catch of the Peruvian Anchovy Fishery from 1960-1990



Saddle-node Bifurcation in \mathbb{R}^1



Annual catch of the Peruvian Anchovy Fishery from 1960-1990

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$$\frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right) - H, \quad \text{steady state: } kP\left(1 - \frac{P}{N}\right) - H = 0$$
When $H > H_0 \equiv \frac{kN}{4}$, the fishery collapses.

 H_0 is the maximum sustainable yield (MSY)

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Hysteresi	s Bifurcat	tion in \mathbb{R}^1			



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A grazing system of herbivore-plant interaction $\frac{dV}{dt} = V(1-V) - \frac{rV^{p}}{h^{p} + V^{p}}, \quad h, r > 0, \quad p \ge 1.$ [Noy-Meir, J. Ecology 1975] Stability of Grazing Systems: An Application of Predator-Prey Graphs. [May, Nature 1975] Thresholds and breakpoints in ecosystems with a multiplicity of stable states.

Catastrophe theory: Thom, Arnold, Zeeman in 1960-70s

Potential catastrophes: Arctic sea, Greenland ice, Amazon rainforest, etc.

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Populatio	on models				

 $y' = yf(y), \quad f(y)$ is the growth rate per capita



Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Populatio	on models				

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y' = yf(y), f(y) is the growth rate per capita y' = ky [Malthus, 1798] (f(y) = k)

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Populati	on models				

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$$\begin{aligned} y' &= yf(y), \quad f(y) \text{ is the growth rate per capita} \\ y' &= ky \text{ [Malthus, 1798] } (f(y) = k) \\ y' &= ky(1 - \frac{y}{N}) \text{ [Verhulst, 1838] } (f(y) = (1 - \frac{y}{N}) \end{aligned}$$

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Populati	on models				

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The bifurcation diagram is shown by the graph $h = ky(1 - \frac{y}{N})$

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Populati	on models				

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Generalizing the model: y' = g(y) - rc(y) (g(y) growth function; c(y) predator functional response; r number of predator (bifurcation parameter).

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Populati	on models				

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Generalizing the model: y' = g(y) - rc(y) (g(y) growth function; c(y) predator functional response; r number of predator (bifurcation parameter).)

Growth function:

Logistic: g(y) = yh(y): h(0) > 0, h(N) = 0 and h(y) is decreasing in (0, N). Allee effect: g(y) = yh(y), max h(y) > 0, h(N) = 0, h(y) is increasing in (0, M), and h(y) is decreasing in (M, N).

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Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Function	al Respon	ses			

[Holling, 1959]

(Type I)

$$c(y) = \begin{cases} Ey, & 0 < y \le y_*, \\ Ey_*, & y \ge y_*, \end{cases}$$
(1)

$$c(y) = \frac{Ay}{B+y}, \qquad y > 0,$$
 (2)

(Type III)

$$c(y) = \frac{Ay^{\rho}}{B^{\rho} + y^{\rho}}, \quad y > 0, \rho > 1,$$
(3)

Their common characters:

(C1) c(0) = 0; c(y) in increasing; (C2) $\lim_{y \to \infty} c(y) = c_{\infty} > 0.$

Another type II: (Ivlev) $c(y) = A - Be^{-ry}$.

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Functiona	al Respor	ises			

Generalized Type II: c(y) satisfies (C1), (C2) and (C3) c'(0) > 0, and $c''(y) \le 0$ for almost every $y \ge 0$; Generalized Type III: c(y) satisfies (C1), (C2) and (C4) c'(0) = 0 and there exists $y_* > 0$ such that $c''(y)(y - y_*) \le 0$ for almost every $y \ge 0$.



Figure: (a) constant; (b) linear; (c) Type I; (d) Type II; (e) Type III.

Background

Bifurcation diagram for ecological model

Bifurcation diagram of y' = g(y) - rc(y) can be drawn using the graph of r = g(y)/c(y). But it does not work for systems or PDEs!



g(y) is Logistic, c(y) is Holling type II. Here $r_* = g'(0)/c'(0)$ is a transcritical bifurcation point on y = 0 (trivial solution). (r(y) = g(y)/c(y) is concave)



g(y) is Logistic, c(y) is Holling type III. (r(y) = g(y)/c(y) is convex-concave) g(y) = g(y)/c(y)

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Linear sy	ystems				

For a planar linear system

$$\begin{cases} x' = ax + by \\ y' = cx + dy \end{cases}$$

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Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Linear s	vstems				

For a planar linear system

$$\begin{cases} x' = ax + by \\ y' = cx + dy \end{cases}$$

An eigenvalue λ satisfies $\lambda^2 - (a + d)\lambda + ad - bc = 0$, or let T = a + d be the trace and let D = ad - bc be the determinant of the matrix, then

$$\lambda^2 - T\lambda + D = 0.$$

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Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Linear s	ystems				

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$$\lambda^2 - T\lambda + D = 0.$$

Since $\lambda_1 + \lambda_2 = T$, and $\lambda_1 \lambda_2 = D$, then generic cases are (A) T > 0, D > 0, $T^2 - 4D > 0$, and $\lambda_1 > \lambda_2 > 0$; (B) T < 0, D > 0, $T^2 - 4D > 0$, and $\lambda_1 < \lambda_2 < 0$; (C) D < 0, and $\lambda_1 < 0 < \lambda_2$; (D) T > 0, D > 0, $T^2 - 4D < 0$, and $\lambda_1, \lambda_2 = \alpha \pm i\beta$, $\alpha > 0$; (E) T < 0, D > 0, $T^2 - 4D < 0$, and $\lambda_1, \lambda_2 = \alpha \pm i\beta$, $\alpha < 0$. T-D plane (Trace-Determinant plane)



Background Scalar ODEs ODEs in Biology Planar systems N-D ODE

Phase portraits for linear systems



Figure: Phase portraits: (A) $\lambda_1 > \lambda_2 > 0$, (source or unstable node), (B) $\lambda_1 < \lambda_2 < 0$ (sink or stable node), (C) $\lambda_1 < 0 < \lambda_2$ (saddle); (D) $\lambda_1, \lambda_2 = \alpha \pm i\beta, \ \alpha < 0$ (spiral sink or stable spiral), (E) $\lambda_1, \lambda_2 = \alpha \pm i\beta, \ \alpha > 0$ (spiral source or unstable spiral)

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Nonlinea	r planar sv	vstems			

$$\begin{cases} x' = f(x, y) \\ y' = g(x, y). \end{cases}$$

If $(x_0, y_0) \in \mathbb{R}^2$ satisfies $f(x_0, y_0) = 0$ and $g(x_0, y_0) = 0$, then (x_0, y_0) is an equilibrium point. The Jacobian matrix J at (x_0, y_0) is

$$J = \begin{pmatrix} \frac{\partial f}{\partial x}(x_0, y_0) & \frac{\partial f}{\partial y}(x_0, y_0) \\ \frac{\partial g}{\partial x}(x_0, y_0) & \frac{\partial g}{\partial y}(x_0, y_0) \end{pmatrix}.$$

Then the stability of (x_0, y_0) is determined by the linear system $Y' = J \cdot Y$.

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Nonlinea	r planar sv	vstems			

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Then the stability of (x_0, y_0) is determined by the linear system $Y' = J \cdot Y$.

Stability Criterion:

- (a) If T < 0 and D > 0, then (x_0, y_0) is stable;
- (b) If T < 0, D > 0 or D < 0, then (x_0, y_0) is unstable;
- (c) If T = 0 or D = 0, then the stability cannot be determined by J.

Background

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Conclusion

Equilibrium Bifurcation Theorem

D = 0 and $T \neq 0$.

Consider ODE $x' = f(\lambda, x), \lambda \in \mathbb{R}, x \in \mathbb{R}^n$, and f is smooth. (i) Suppose that for λ near λ_0 the system has a family of equilibria $x^0(\lambda)$. (ii) Assume that its Jacobian matrix $A(\lambda) = f_x(\lambda, x^0(\lambda))$ has an eigenvalue $\mu(\lambda)$, $\mu(\lambda_0) = 0$, and all other eigenvalues of $A(\lambda)$ have non-zero real parts for all λ near λ_0 .

If $\mu'(\lambda_0) \neq 0$, then the system has another family of equilibria $(\lambda(s), x(s))$ for $s \in (-\delta, \delta)$, such that $\lambda(0) = \lambda_0$ and $x(0) = x^0(\lambda_0)$.

This corresponds to the transcritical bifurcation and pitchfork bifurcation. One can also define saddle-node bifurcation (in which there is given family of equilibria).

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Hopf Bif	urcation 7	Theorem			

D > 0 and T = 0.

Consider ODE $x' = f(\lambda, x)$, $\lambda \in \mathbb{R}$, $x \in \mathbb{R}^n$, and f is smooth. (i) Suppose that for λ near λ_0 the system has a family of equilibria $x^0(\lambda)$. (ii) Assume that its Jacobian matrix $A(\lambda) = f_x(\lambda, x^0(\lambda))$ has one pair of complex eigenvalues $\mu(\lambda) \pm i\omega(\lambda)$, $\mu(\lambda_0) = 0$, $\omega(\lambda_0) > 0$, and all other eigenvalues of $A(\lambda)$ have non-zero real parts for all λ near λ_0 .

If $\mu'(\lambda_0) \neq 0$, then the system has a family of periodic orbits $(\lambda(s), x(s))$ for $s \in (0, \delta)$ with period T(s), such that $\lambda(s) \to \lambda_0$, $T(s) \to 2\pi/\omega(\lambda_0)$, and $||x(s) - x^0(\lambda_0)|| \to 0$ as $s \to 0^+$.

http://www.scholarpedia.org/article/Andronov-Hopf_bifurcation



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Example: Brusselator model

$$u' = a - (b+1)u + u^2 v, v' = bu - u^2 v.$$

Unique equilibrium (a, b/a). Jacobian matrix

$$L(b) = \begin{pmatrix} b-1 & a^2 \\ -b & -a^2 \end{pmatrix}$$

So $T = b - 1 - a^2 = b - (1 + a^2)$, $D = a^2$. So D > 0 always holds and T = 0 if $b = 1 + a^2$. Suppose the eigenvalues are $\lambda = \alpha(b) \pm \beta(b)$, then $\lambda_1 + \lambda_2 = 2\alpha(b) = T(b)$. Then $\alpha'(b) = T'(b)/2 = 1/2 > 0$. So a Hopf bifurcation occurs at $b = a^2 + 1$.



- 1. Jacobian for local stability of equilibria (last page);
- 2. Lyapunov functional method (LaSalle Invariance Principle) for global stability of equilibrium;
- 3. Poincaré-Bendixson Theorem for existence of periodic orbits;
- 4. Hopf Bifurcation Theorem for existence of periodic orbits;
- 5. Dulac Criterion for nonexistence of periodic orbits (and global stability of equilibrium;

6. Zhang (Zhifen)'s Uniqueness Theorem for periodic orbit of Lienard system (good for many predator-prey systems).

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- 1. Jacobian for local stability of equilibria (last page);
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Goal: to apply these tools to achieve global bifurcation of phase portraits when a parameter varies.

Important: The Poincaré-Bendixson theory shows that the ω -limit set for planar system can only be either (i) an equilibrium; or (ii) a periodic orbit; or (iii) a heteroclinic/homoclinic loop.

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Background Scalar ODEs ODEs in Biology Planar systems N-D ODE Conclusion
Rosenzwing-MacArthur Model

[Rosenzwing-MacArthur, Amer. Naturalist, 1963], [Rosenzweig, Science, 1971]

$$\begin{cases} x' = x(1 - \frac{x}{K}) - \frac{mxy}{1 + x}, \\ y' = -\theta y + \frac{mxy}{1 + x}. \end{cases}$$
(4)

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Equilibria: (0,0), (K,0), (λ , V_{λ}), where

$$\lambda = \frac{\theta}{m - \theta}, \ V_{\lambda} = \frac{(K - \lambda)(1 + \lambda)}{Km},$$

We use λ (the horizontal coordinate of coexistence equilibrium) as bifurcation parameter.

Background Scalar ODEs ODEs in Biology Planar systems N-D ODE Conclusion
Rosenzwing-MacArthur Model

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We use λ (the horizontal coordinate of coexistence equilibrium) as bifurcation parameter.

Case 1: $\lambda \ge K$ No coexistence equilibrium, and (K, 0) is globally stable. Use Lyapunov function: $V(x, y) = \int_{K}^{x} \frac{g(s) - g(K)}{g(s)} ds + y$, where $g(x) = \frac{mx}{1 + x}$

Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Coexiste	nce: globa	al stability			

$$J(\lambda, V_{\lambda}) = \begin{pmatrix} \frac{\lambda(K - 1 - 2\lambda)}{K(1 + \lambda)} & -\theta \\ \frac{K - \lambda}{K(1 + \lambda)} & 0 \end{pmatrix}$$

For $0 < \lambda < K$, $\text{Det}(J) = \frac{\theta(K - \lambda)}{K(1 + \lambda)} > 0$, and $\text{Tr}(J) = \frac{\lambda(K - 1 - 2\lambda)}{K(1 + \lambda)}$. Hence (λ, V_{λ})

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is stable for $0 < \lambda < \frac{\kappa - 1}{2}$ and is unstable for $\frac{\kappa - 1}{2} < \lambda < K$.

 Background
 Scalar ODEs
 ODEs in Biology
 Planar systems
 N-D ODE
 Conclusion

 Coexistence:
 global
 stability

$$J(\lambda, V_{\lambda}) = egin{pmatrix} rac{\lambda(K-1-2\lambda)}{K(1+\lambda)} & - heta\ rac{K-\lambda}{K(1+\lambda)} & 0 \end{pmatrix}$$

For $0 < \lambda < K$, $Det(J) = \frac{\theta(K - \lambda)}{K(1 + \lambda)} > 0$, and $Tr(J) = \frac{\lambda(K - 1 - 2\lambda)}{K(1 + \lambda)}$. Hence (λ, V_{λ}) is stable for $0 < \lambda < \frac{K - 1}{2}$ and is unstable for $\frac{K - 1}{2} < \lambda < K$.

Case 2: $(K - 1)/2 < \lambda < K(\lambda, V_{\lambda})$ is locally stable. The global stability can be implied by using Dulac's criterion and the function $h(x, y) = \left(\frac{mx}{1+x}\right)^{\alpha} y^{\delta}$ for some appropriate α, δ [Hsu-Hubble-Waltman, 1978].

Coexistence: global stability

$$J(\lambda, V_{\lambda}) = \begin{pmatrix} \frac{\lambda(K - 1 - 2\lambda)}{K(1 + \lambda)} & -\theta \\ \frac{K - \lambda}{K(1 + \lambda)} & 0 \end{pmatrix}$$

For $0 < \lambda < K$, $Det(J) = \frac{\theta(K - \lambda)}{K(1 + \lambda)} > 0$, and $Tr(J) = \frac{\lambda(K - 1 - 2\lambda)}{K(1 + \lambda)}$. Hence (λ, V_{λ}) is stable for $0 < \lambda < \frac{K-1}{2}$ and is unstable for $\frac{K-1}{2} < \lambda < K$.

Case 2: $(K-1)/2 < \lambda < K$ (λ, V_{λ}) is locally stable. The global stability can be implied by using Dulac's criterion and the function $h(x, y) = \left(\frac{mx}{1+y}\right)^{\alpha} y^{\delta}$ for some appropriate α, δ [Hsu-Hubble-Waltman, 1978].

Lyapunov functions can also be used to prove the global stability. For $K - 1 \le \lambda < K$, $V(x,y) = \int^{\lambda} \frac{g(s) - g(\lambda)}{\sigma(s)} ds + \int^{V_{\lambda}} \frac{t - V_{\lambda}}{t} dt \text{ where } g(x) = \frac{mx}{1 + x}. \text{ [Hsu, 1978]};$ and for $(K - 1)/2 < \lambda < K - 1$. $V(x,y) = y^{\alpha} \int_{x}^{\lambda} \frac{g(s) - g(\lambda)}{g(s)} ds + \int_{y}^{V_{\lambda}} t^{\alpha-1} (t - V_{\lambda}) dt \text{ for some } \alpha > 0$ [Ardito-Ricciardi, 1995].

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Background	Scalar ODEs	ODEs in Biology	Planar systems	N-D ODE	Conclusion
Unique I	imit cycle				

Case 3: $0 < \lambda < (K - 1)/2$ (λ , V_{λ}) is unstable, hence there exists a periodic orbit from Poincaré-Bendixson Theorem. The system can be converted to a Lienard system so Zhang's uniqueness theorem implies the uniqueness (and also stability) of periodic orbit. [Cheng, 1981], [Kuang-Freedman, 1988], [Zhang, 1986]

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Bifurcation diagram and phase portraits



Figure: (Top) Bifurcation Diagram; (Lower Left)Phase portrait $(K-1)/2 < \lambda < K$; (Lower Right) Phase portrait $0 < \lambda < (K-1)/2$.

Background

Summary of Rosenzwing-MacArthur Model

 $\begin{array}{l} \displaystyle \frac{du}{dt} = u\left(1 - \frac{u}{K}\right) - \frac{muv}{1+u}, \quad \displaystyle \frac{dv}{dt} = -\theta v + \frac{muv}{1+u} \\ \displaystyle \text{Nullcline:} \quad u = 0, \; v = \frac{(K-u)(1+u)}{mK}; \; v = 0, \; d = \frac{mu}{1+u}. \\ \displaystyle \text{Solving} \; \theta = \frac{mu}{1+u}, \; \text{one have} \; u = \lambda \equiv \frac{\theta}{m-\theta}. \\ \displaystyle \text{Equilibria:} \; (0,0), \; (K,0), \; (\lambda, V_{\lambda}) \; \text{where} \; v_{\lambda} = \frac{(K-\lambda)(1+\lambda)}{mK} \\ \displaystyle \text{We take} \; \lambda \; \text{as a bifurcation parameter} \end{array}$

 $\begin{array}{l} \underline{\text{Case 1}: \ \lambda \geq K: \ (K,0) \text{ is globally asymptotically stable}} \\ \underline{\text{Case 2}: \ (K-1)/2 < \lambda < K: \ (\lambda, V_{\lambda}) \text{ is globally} \text{ asymptotically stable}} \\ \underline{\text{Case 3}: \ 0 < \lambda < (K-1)/2: \text{ unique limit cycle is globally}} \text{ asymptotically stable} \\ (\lambda = (K-1)/2: \text{ Hopf bifurcation point}) \end{array}$



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Generalized Rosenzwing-MacArthur Model

$$\begin{cases} u' = g(u) (f(u) - v), \\ v' = v (g(u) - d). \end{cases}$$
(5)

where f, g satisfy:

- (a1) $f \in C^1(\overline{\mathbb{R}}^+)$, f(0) > 0, there exists K > 0, such that for any u > 0, $u \neq K$, f(u)(u-K) < 0 and f(K) = 0; there exists $\overline{\lambda} \in (0, K)$ such that f'(u) > 0 on $[0, \overline{\lambda}), f'(u) < 0$ on $(\overline{\lambda}, K];$
- (a2) $g \in C^1(\overline{\mathbb{R}}^+)$, g(0) = 0; g(u) > 0 for u > 0 and g'(u) > 0 for $u \ge 0$; there exists a unique $\lambda \in (0, K)$ such that $g(\lambda) = d$.

Unique positive equilibrium (λ, v_{λ}) , where $d = g(\lambda)$, and $v_{\lambda} = f(\lambda)$.



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Background

Generalized Rosenzwing-MacArthur Model

Complete classification of dynamics:

- (1) when $\lambda \geq K$, (K, 0) is globally asymptotically stable;
- (2) when $\lambda^0 \leq \lambda < K$, (λ, v_{λ}) is globally asymptotically stable, where $\lambda^0 \in (\bar{\lambda}, K)$ is the unique one satisfied $f(0) = f(\lambda^0)$;
- (a) when $\lambda^0 < \lambda < K$, if one of the followings holds: (i) $(uf'(u))'' \leq 0$, $(u/g(u))'' \geq 0$ for $u \in [0, K]$, and $(uf'(u))' \leq 0$ for $u \in (\bar{\lambda}, K)$; or (ii) $f'''(u) \leq 0$ and $g''(u) \leq 0$ for $u \in [0, K]$, and $f''(u) \leq 0$ for $u \in (\bar{\lambda}, K)$, then (λ, v_{λ}) is globally asymptotically stable.

Is the unique bifurcation point where a backward Hopf bifurcation occurs;

So when $0 < \lambda < \overline{\lambda}$, there is a globally asymptotically stable periodic orbit if $h_{\lambda}(u) = f'(u)g(u)/[g(u) - g(\lambda)]$ is nonincreasing in $(0, \lambda) \cup (\lambda, K)$. [Kuang-Freedman, 1988]



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A Rosenzwing-MacArthur model with Allee effect

[Wang-Shi-Wei, 2011, JMB]

$$\begin{cases}
\frac{du}{dt} = g(u)(f(u) - v), \\
\frac{dv}{dt} = v(g(u) - d),
\end{cases}$$
(6)

where f,g satisfy: (here $\mathbb{R}=(0,\infty))$

- (a1) $f \in C^1(\mathbb{R}^+)$, f(b) = f(1) = 0, where 0 < b < 1; f(u) is positive for b < u < 1, and f(u) is negative otherwise; there exists $\overline{\lambda} \in (b, 1)$ such that f'(u) > 0 on $[b, \overline{\lambda})$, f'(u) < 0 on $(\overline{\lambda}, 1]$;
- (a2) $g \in C^1(\mathbb{R}^+)$, g(0) = 0; g(u) > 0 for u > 0 and g'(u) > 0 for u > 0, and there exists $\lambda > 0$ such that $g(\lambda) = d$.
- g(u): predator functional response
- g(u)f(u): the net growth rate of the prey
- f(u): the prey nullcline on the phase portrait

 $\lambda:$ a measure of how well the predator is adapted to the prey (main bifurcation parameter)

Complete classification: conditions

Theorem: Suppose that f(u) satisfies

(a1') $f \in C^3(\overline{\mathbb{R}^+})$, f(b) = f(1) = 0, where 0 < b < 1; f(u) is positive for b < u < 1, and f(u) is negative otherwise; there exists $\overline{\lambda} \in (b, 1)$ such that f'(u) > 0 on $[b, \overline{\lambda})$, f'(u) < 0 on $(\overline{\lambda}, 1]$;

(a3)
$$f''(\bar{\lambda}) < 0;$$

(a6)
$$uf'''(u) + 2f''(u) \le 0$$
 for all $u \in (b, 1)$;

and one of the following:

(a8)
$$(uf'(u))'' \le 0$$
 for $u \in [b, 1]$, and $(uf'(u))' \le 0$ for $u \in (\bar{\lambda}, 1)$; or
(a9) $f'''(u) \le 0$ for $u \in [b, 1]$, and $f''(u) \le 0$ for $u \in (\bar{\lambda}, 1)$,

and g(u) is one of the following:

$$g(u) = u$$
, or $g(u) = \frac{mu}{a+u}$, $a, m > 0$.

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 Complete classification:
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Theorem (cont.): Then with a bifurcation parameter λ defined by

$$\lambda = d$$
 if $g(u) = u$, or $\lambda = \frac{ad}{m-d}$ if $g(u) = \frac{mu}{a+u}$,

there exist two bifurcation points λ^{\sharp} and $\bar{\lambda}$ such that the dynamics of the predator-prey system can be classified as follows:

- If $0 < \lambda < \lambda^{\sharp}$, then the equilibrium (0,0) is globally asymptotically stable;
- If λ = λ[#], then there exists a unique heteroclinic loop, and the system is globally bistable with respect to the heteroclinic loop and (0,0);
- If λ[♯] < λ < λ
 , then there exists a unique limit cycle, and the system is globally bistable with respect to the limit cycle and (0,0);</p>
- If λ̄ < λ < 1, then there is no periodic orbit, and the system is globally bistable with respect to the coexistence equilibrium (λ, ν_λ) and (0,0);
- If \u03c6 > 1, then the system is globally bistable with respect to (1,0) and (0,0).





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Ordinary Differential Equations

ODE model:
$$\frac{dy}{dt} = f(\lambda, y), \quad y \in \mathbb{R}^n, f : \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$$

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 Ordinary Differential Equations

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ODE model:
$$\frac{dy}{dt} = f(\lambda, y), \quad y \in \mathbb{R}^n, f : \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$$

Equilibrium: $y = y_0$ so that $f(\lambda_0, y_0) = 0$

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ODE model:
$$\frac{dy}{dt} = f(\lambda, y), \quad y \in \mathbb{R}^n, f : \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$$

Equilibrium: $y = y_0$ so that $f(\lambda_0, y_0) = 0$

Jacobian Matrix: $J = f_y(\lambda_0, y_0)$ is an $n \times n$ matrix

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Characteristic equation: $P(\lambda) = Det(\lambda I - J) = \lambda^{n} + a_1 \lambda^{n-1} + a_2 \lambda^{n-2} + \dots + a_{n-1} \lambda + a_n$

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$$\mathsf{ODE model:} \ \frac{dy}{dt} = f(\lambda, y), \quad y \in \mathbb{R}^n, \ f : \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$$

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Routh-Hurwitz criterion: complicated for general n

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Routh-Hurwitz criterion: complicated for general n

 $n = 1: \ \lambda + a_1 = 0, \ \underline{a_1 > 0}$

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ODE model:
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Routh-Hurwitz criterion: complicated for general n

$$n = 1: \ \lambda + a_1 = 0, \ \underline{a_1 > 0} \\ n = 2: \ \lambda^2 + a_1 \lambda + a_2 = 0, \ \underline{a_1 > 0, \ a_2 > 0}$$

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Routh-Hurwitz criterion: complicated for general n

$$n = 1: \ \lambda + a_1 = 0, \ \underline{a_1 > 0} \\ n = 2: \ \lambda^2 + a_1 \lambda + a_2 = 0, \ \underline{a_1 > 0, \ a_2 > 0} \\ n = 3: \ \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3}{a_1}, \ a_3 > 0}$$

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$$n = 1: \ \lambda + a_1 = 0, \ \underline{a_1 > 0} \\ n = 2: \ \lambda^2 + a_1 \lambda + a_2 = 0, \ \underline{a_1 > 0, \ a_2 > 0} \\ n = 3: \ \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3}{a_1}, \ a_3 > 0} \\ n = 4: \ \lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1} + a_1^2 a_4} \\ a_1 a_3, \ a_3 > 0, \ a_4 > 0$$

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$$n = 1: \ \lambda + a_1 = 0, \ \underline{a_1 > 0} \\ n = 2: \ \lambda^2 + a_1 \lambda + a_2 = 0, \ \underline{a_1 > 0, \ a_2 > 0} \\ n = 3: \ \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3}{a_1}, \ a_3 > 0} \\ n = 4: \ \lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1} + a_1^2 a_4} \\ n = 5: \ a_1 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1} + a_1^2 a_4} \\ n \ge 5: \ a_1 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1} + a_1^2 a_4} \\ n \ge 5: \ a_1 + a_2 a_1 a_3 + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1} + a_1^2 a_4} \\ n \ge 5: \ a_1 + a_1 a_1 a_3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 = 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 + 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_3 + a_4 + 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_4 + a_4 + 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_4 + a_4 + 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_4 + a_4 + 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_4 + a_4 + 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_4 + a_4 + 0, \ \underline{a_1 > 0, \ a_2 > \frac{a_3^2}{a_1 a_3} + a_4 + a_4 + 0, \ \underline{$$

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- 1-D continuous ODE model can be analyzed by calculus. The asymptotical state must be an equilibrium.
- 2-D continuous ODE model can be analyzed by phase plane analysis and techniques mentioned above. The asymptotical state must be an equilibrium or a periodic orbit or a heteroclinic/homoclinic loop.
- N-D (N ≥ 3) continuous ODE models (or N-D (N ≥ 1) discrete models) can sometimes be analyzed, but it is known that chaos can occur for such models. Also more types of bifurcations can occur in these systems. We only consider the bifurcations of equilibria and periodic orbits.

• PDE or other structured models are different as the phase space is infinite dimensional.

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