Ecosystem competition and predation modelling and model analysis

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Outline

- Introduction
- Formulation of competition in two and three level food webs
  - Stoichiometry, Mass conservation
- Model analysis
  - Existence and stability analysis of system of ODE's
  - Bifurcation analysis for long-term dynamics dependence on model parameters

Ulrike Feudel: Biodiversity of Plankton Non-Equilibrium coexistence of competing species

Relevant Ecological principles:

- One resource – Two species
  - Competitive exclusion
- Two resources – Two species
  - Outcomes of competition: competitive exclusion where one of the species wins, stable coexistence of both the species or bistability where each of the species may win depending on the initial conditions
- Two resources – Two prey species – One predator
  - Paradox of enrichment: Oscillations for high resource input
- Three resources – four prey species
  - Supersaturation: Oscillatory systems required

- Competition of multiple species for multiple resources in a chemostat environment
  - Substitutable resources, *SUB-model*, Co-limitation
  - Perfect-essential resources *PER-model*, Sequential co-limitation, Tilman (1982)
  - Interactively-essential (or complementary) resources, *COM-model*, Simultaneous co-limitation, Kooijman (2010)
- Model analyses
  - MacArthur's simple graphic visualization and Tilman's representation of resource quarter plane analysis
  - Bifurcation analysis

Relevant Bifurcations and ecological interpretation:

- Transcritical bifurcation
  - Invasion of system by another species
- Hopf bifurcation
  - Stable equilibrium becomes unstable and a limit cycle emerges

One resource – One prey

N: resource density: P: prey density

When a prey meets a resource particle the prey ingests it:

- It takes time to handle and digest that resource particle
- The prey searches for another resource particle

h: handling time, v: catch rate,

$F(N)$: functional response is number of resource particles ingested per unit of time by one prey individual

Heuristic derivation (Diekmann and Metz 1986)

In 1 time unit following 1 prey individual:
Total handling time of $F(N)$ particles is $hF(N)$ hence in the remaining time $1-hF(N)$ the number of $(1-hF(N))vN$ particles are cached, and this is just $F(N)$:

$$F(N) = (1 - hF(N))vN \quad \Rightarrow \quad F(N) = v\frac{N}{1 + vhN}$$

Ecology: Holling type II	Biochemistry: Michaelis-Menten
$h = 1/I$: handling time	$K = 1/(vh)$: saturation constant
$v = I/K$: catch rate	$I = 1/h$: maximum ingestion rate

Ingestion rate per unit of time by one prey individual reads

$$F(N) = I\frac{N/K}{1 + N/K} = I\frac{N}{K + N} = If(N)$$

where $f(N)$ is the scaled functional response

Note: on the individual level

Derivation of Holling type II functional response with time-scale difference

pseudo-reaction scheme

$$\mathsf{P^s} + \mathsf{N} \xrightarrow{v} \mathsf{P^h} \stackrel{1/h}{\rightarrow} \mathsf{P^s} \quad \text{or} \quad \mathsf{P^s} + \mathsf{N} \xrightarrow{I/K} \mathsf{P^h} \stackrel{I}{\rightarrow} \mathsf{P^s}$$

Now three state variables: resource N, searching prey P_s and handling prey P_h, Law of mass action gives

$$\frac{dN}{dt} = -vP_s\, N + \cdots \text{(slow time scale)}$$
$$\frac{dP_s}{dt} = -vN\, P_s + P_h/h + \cdots \text{(slow time scale)}$$
$$\frac{dP_h}{dt} = vN\, P_s - P_h/h + \cdots \text{(slow time scale)}$$

where $P = P_s + P_h$

Note: P, P_s is small and N is large therefore vN and $1/h$ are large and no distinction between numbers and biomass

We assume equilibrium of the fast variables P_s^*, P_h^* (often called Quasi Steady State Assumption QSSA)

$$0 = -vP_s^*N + P_h^*/h$$

Hence:

$$P_s^* = \frac{P}{1 + vhN}$$

Proportion of searchers in the prey population varies at the slow time-scale

That is:

$$F(N)P = vP_s^*N = v\frac{NP}{1 + vhN} = I\frac{N/K}{1 + N/K}P = If(N)P$$

Note: on the population level

Later maximum growth rate per unit of time μ is introduced and the quotient called the efficiency or yield $Y = \mu/I$ is to be constant

Two resources – One prey Complementary
O'Neill et al. (1989) and Kooijman (2010)

pseudo-reaction scheme

$$\mathsf{P}^{\mathsf{s}} + \mathsf{N} \xrightarrow{I_N/K_N} \mathsf{P}^{\mathsf{hN}} \quad , \quad \mathsf{P}^{\mathsf{hN}} + \mathsf{S} \xrightarrow{I_S/K_S} \mathsf{P}^{\mathsf{hNS}}$$

$$\mathsf{P}^{\mathsf{s}} + \mathsf{S} \xrightarrow{I_S/K_S} \mathsf{P}^{\mathsf{hS}} \quad , \quad \mathsf{P}^{\mathsf{hS}} + \mathsf{N} \xrightarrow{I_N/K_N} \mathsf{P}^{\mathsf{hNS}}$$

$$\mathsf{P}^{\mathsf{hNS}} \xrightarrow{I_{NS}} \mathsf{P}^{\mathsf{s}}$$

Assuming $I = I_N = I_S$ and I_{NS} finite, we obtain for the scaled functional response

$$I_{NP} f(N,S) = I \frac{N/K_N \; S/K_S}{1 + N/K_N + S/K_S - \frac{N/K_N \; S/K_S}{N/K_N + S/K_S}}$$

and when furthermore I_{NS} infinite

$$I_{SP} f(N,S) = I \frac{N/K_N \; S/K_S}{N/K_N + S/K_S - \frac{N/K_N \; S/K_S}{N/K_N + S/K_S}}$$

Stoichiometry and mass balance

There are now two efficiencies namely:
$Y_{NP} = \mu_{NP}/I_{NP}$ and $Y_{SP} = \mu_{SP}/I_{SP}$

This freedom is used in the growth rate formulation. It is the sum to obey mass conservation as well as stoichiometric constraints. Then the growth rate $\mu_{NSP}(N, S)$ becomes

$$\mu_{NSP}(N, S) = Y_{NP} I_{NP} f(N, S) + Y_{SP} I_{SP} f(N, S)$$

Stoichiometry and mass balance

Growth rate $\mu_{NSP}(N,S)$ is

$$\mu_{NSP}(N,S) = Y_{NP}I_{NP}f(N,S) + Y_{SP}I_{SP}f(N,S)$$

with constant ingestion ratio

$$\frac{Y_{NP}I_{NP}}{Y_{SP}I_{SP}}$$

For phytoplankton: Carbon, Nitrogen and Phosphorus ratio is for instance the Redfield C/N/P- 105/15/1 ratio

This ratio has to be the same as prey composition ratio

Two resources – One prey *SUB-model*

pseudo-reaction scheme

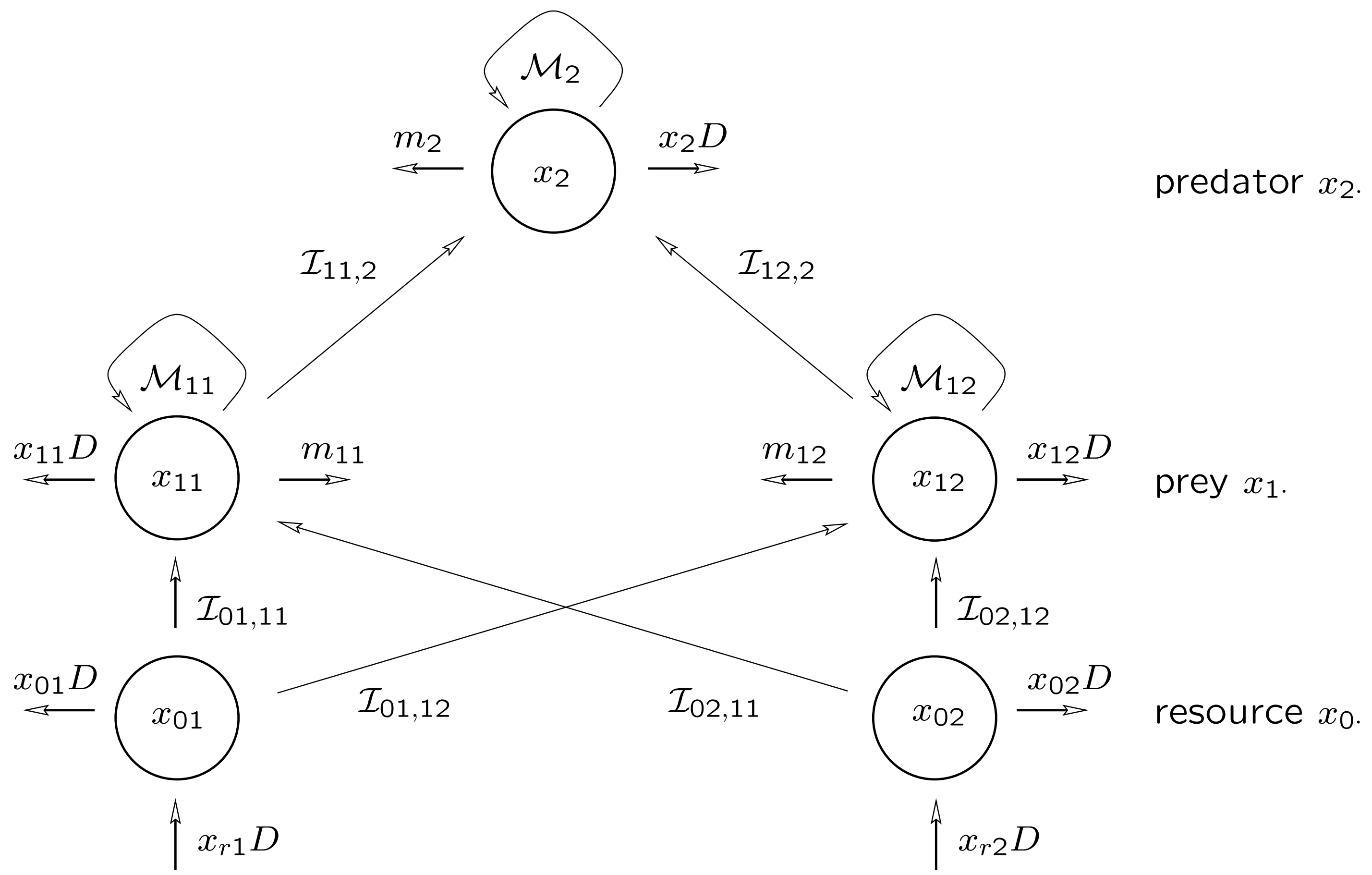
$$\mathrm{P^s} + \mathrm{N} \xrightarrow{I_N/K_N} \mathrm{P^{hN}} \xrightarrow{K_N} \mathrm{P^s}$$

$$\mathrm{P^s} + \mathrm{S} \xrightarrow{I_S/K_S} \mathrm{P^{hS}} \xrightarrow{K_S} \mathrm{P^s}$$

Using similar technique we obtain for the scaled functional response

$$If(N,S) = I\frac{N/K_N + S/K_S}{1 + N/K_N + S/K_S}$$

Three level food web



First subindex: Resource $_{0\cdot}$, Prey $_{1\cdot}$, Predator $_2$.

Functional responses: 2-resources x_{uv} and x_{uw}, prey x_{iv}

SUB-model Substitutable formulation

$$f^{sub}_{uv,iv}(x_{uv},x_{uw}) = \frac{x_{uv}/k_{uv,iv}}{1 + x_{uv}/k_{uv,iv} + x_{uw}/k_{uw,iv}}$$

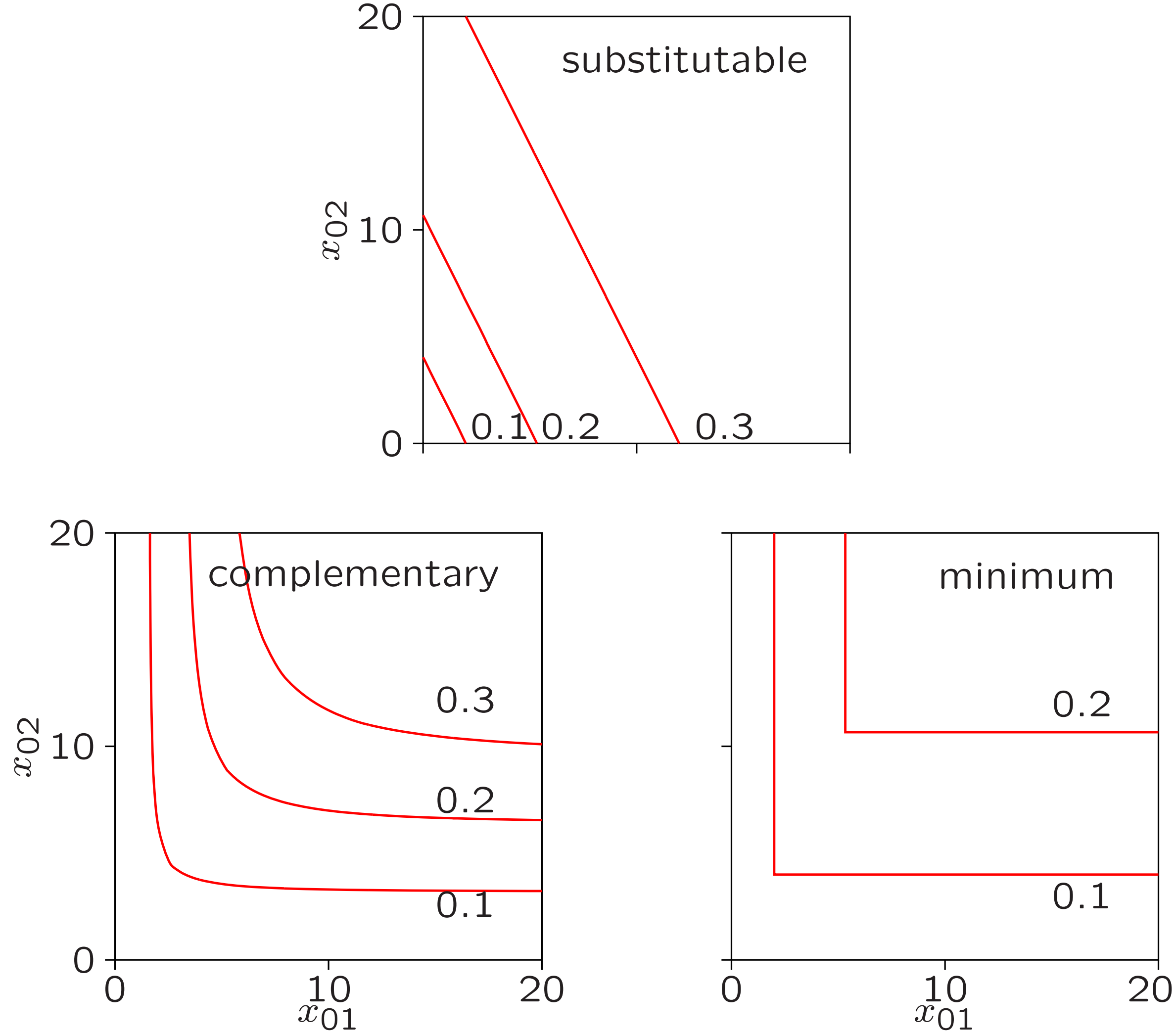
$$f^{sub}_{uw,iv}(x_{uv},x_{uw}) = \frac{x_{uw}/k_{uw,iv}}{1 + x_{uv}/k_{uv,iv} + x_{uw}/k_{uw,iv}}$$

PER-model Liebig's minimum formulation

$$f^{min}_{uv,iv}(x_{uv},x_{uw}) = f^{min}_{uw,iv}(x_{uv},x_{uw}) =$$
$$= \min\left(\frac{x_{uv}}{k_{uv,iv} + x_{uv}}, \frac{x_{uw}}{k_{uw,iv} + x_{uw}}\right)$$

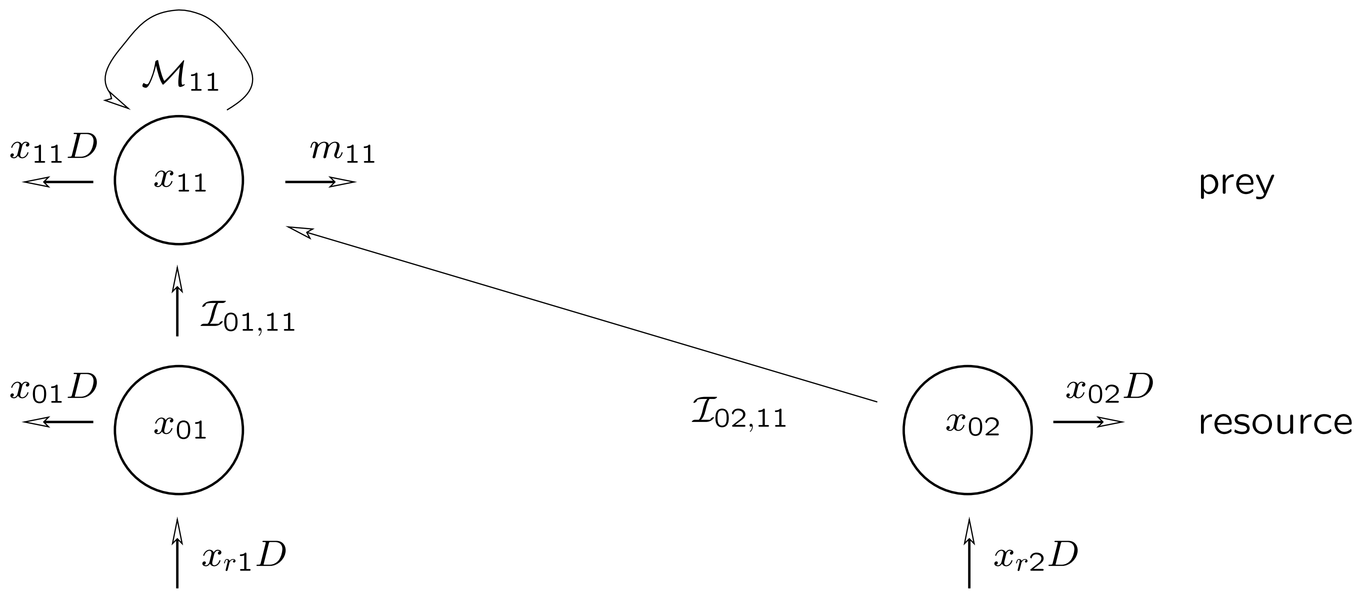
COM-model Complementary formulation

$$f^{com}_{uv,iv}(x_{uv},x_{uw}) = f^{com}_{uw,iv}(x_{uv},x_{uw}) =$$
$$= \frac{x_{uv}/k_{uv,iv}\; x_{uw}/k_{uw,iv}}{x_{uv}/k_{uv,iv} + x_{uw}/k_{uw,iv} - \frac{x_{uv}/k_{uv,iv}\; x_{uw}/k_{uw,iv}}{x_{uv}/k_{uv,iv} + x_{uw}/k_{uw,iv}}}$$

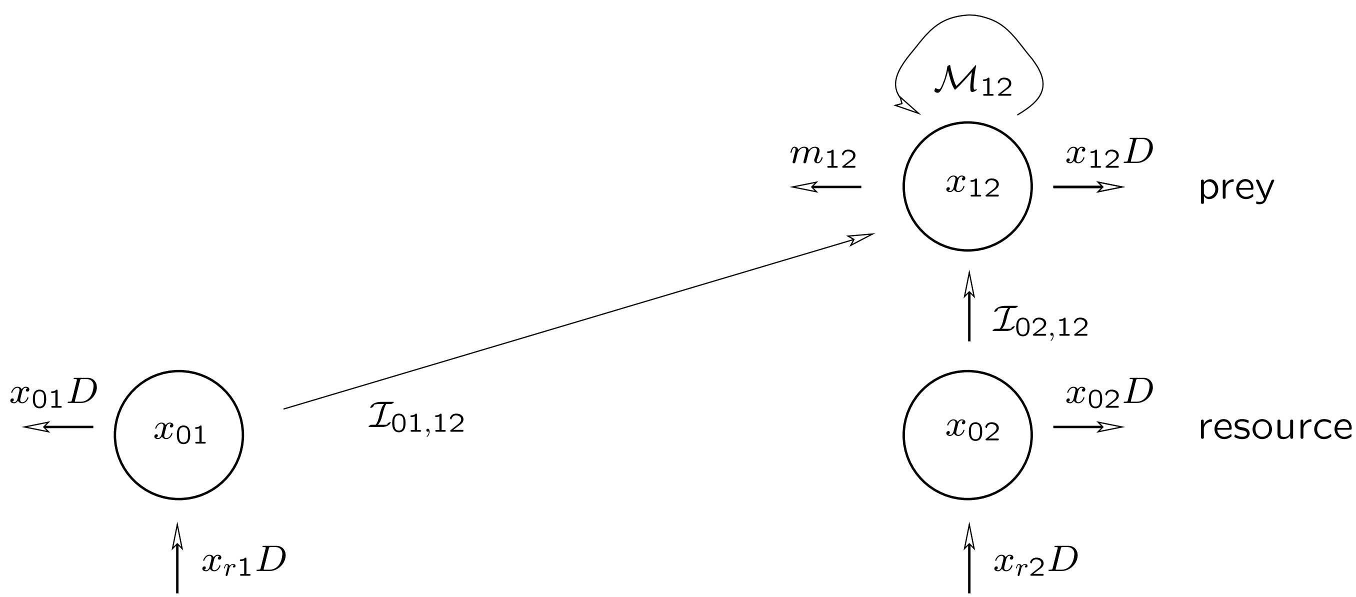


Iso-growth rate $\mathcal{M}_{01,11} = \mu_{01,11} f_{01,11}(x_{01}, x_{02})$
curves on two resources: x_{01}, x_{02} with $\mu_{01,11} = 0.5$

Two resources x_{01}, x_{02} – One prey x_{11}



Two resources x_{01}, x_{02} – One prey x_{12}



Two level food web chemostat mass balance equations

Parameters

Parameter	Interpretation
x_{0i}	Resource density $i = 1, \cdots, k$
x_{1j}	Prey density $j = 1, \cdots, n$
D	Dilution rate
x_{ri}	Resource density in inflow
$I_{0i,1j}$	Maximum ingestion rate
$\mu_{0i,1j}$	Maximum growth rate
$k_{0i,1j}$	Half-saturation constant
$y_{0i,1j}$	Yield coefficient
m_{1j}	Loss rate (mortality, maintenance)

Two resources x_{01}, x_{02} – One prey x_{11}

$$\frac{dx_{01}}{dt} = (x_{r1} - x_{01})D - \mathcal{I}_{01,11}x_{11}$$
$$\frac{dx_{02}}{dt} = (x_{r2} - x_{02})D - \mathcal{I}_{02,11}x_{11}$$
$$\frac{dx_{11}}{dt} = \Big(\mathcal{M}_{01,11} + \mathcal{M}_{02,11} - D - m_{11}\Big)x_{11}$$

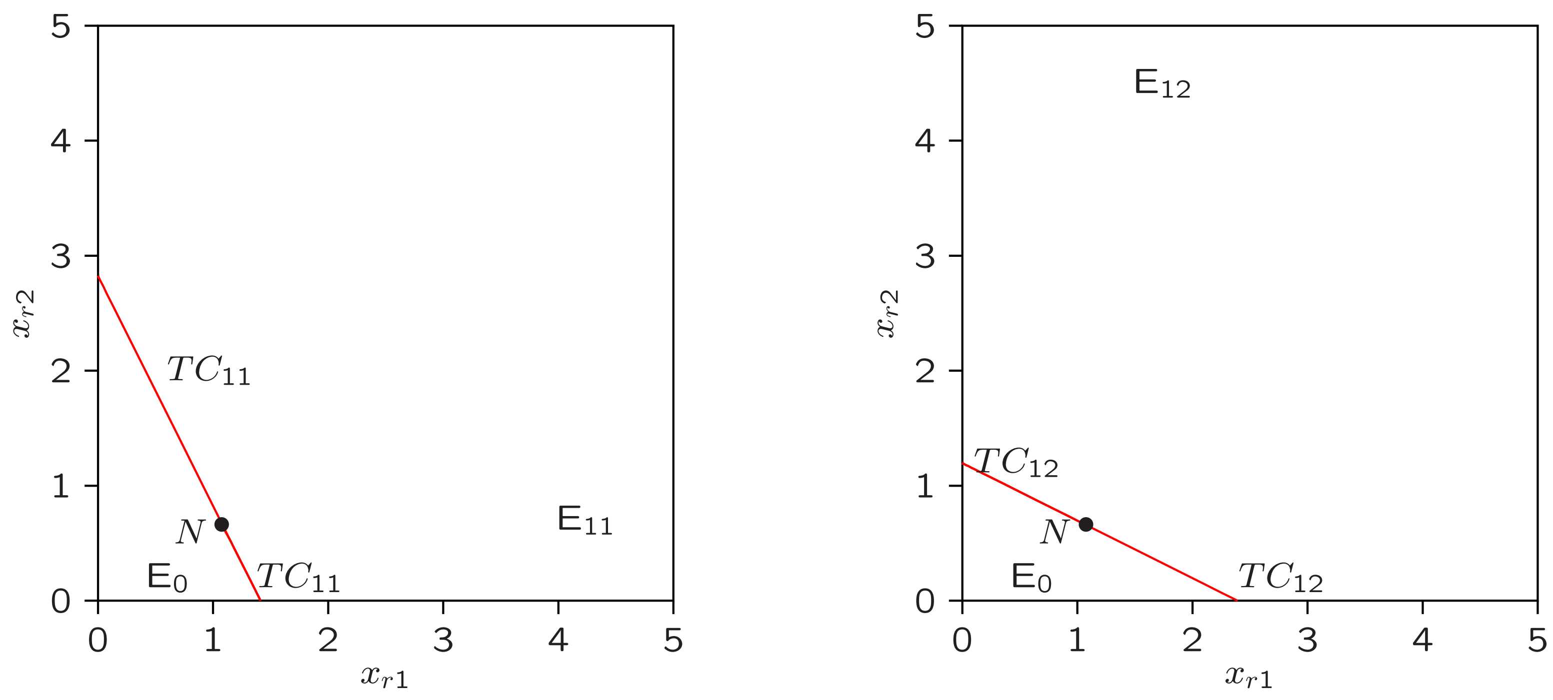
Ingestion and growth

$$\mathcal{I}_{uv,iv} = I_{uv,iv}f_{uv,iv}(x_{uv}, x_{uw})$$
$$\mathcal{M}_{uv,iv} = \mu_{uv,iv}f_{uv,iv}(x_{uv}, x_{uw}) = y_{uv,iv}I_{uv,iv}f_{uv,iv}(x_{uv}, x_{uw})$$
$$\mathcal{I}_{uw,iv} = I_{uw,iv}f_{uw,iv}(x_{uv}, x_{uw})$$
$$\mathcal{M}_{uw,iv} = \mu_{uw,iv}f_{uw,iv}(x_{uv}, x_{uw}) = y_{uw,iv}I_{uw,iv}f_{uw,iv}(x_{uv}, x_{uw})$$

SUB-model

Two resources – One prey population

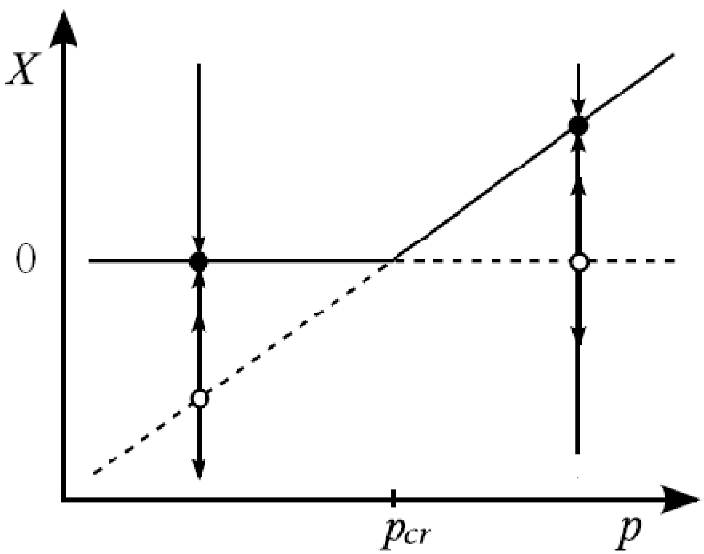
$$x_{11} \text{ — } x_{12}$$

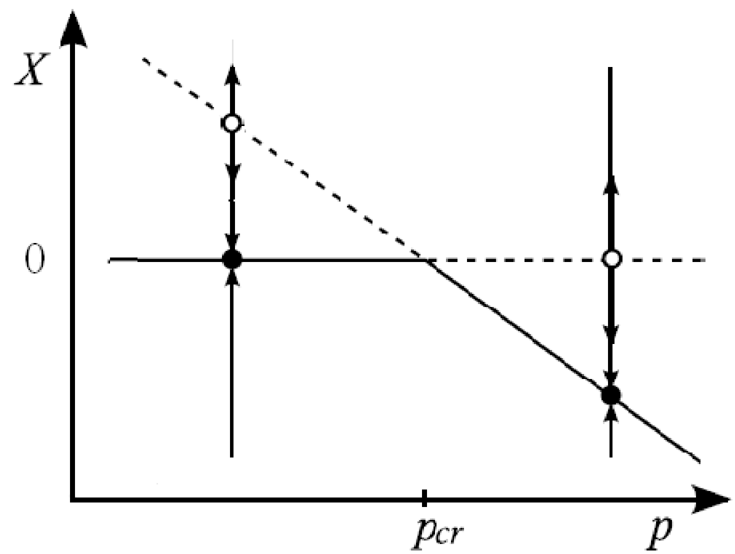


Transcritical bifurcation TC: Normalform

super: $\frac{dX}{dt} = pX - X^2$

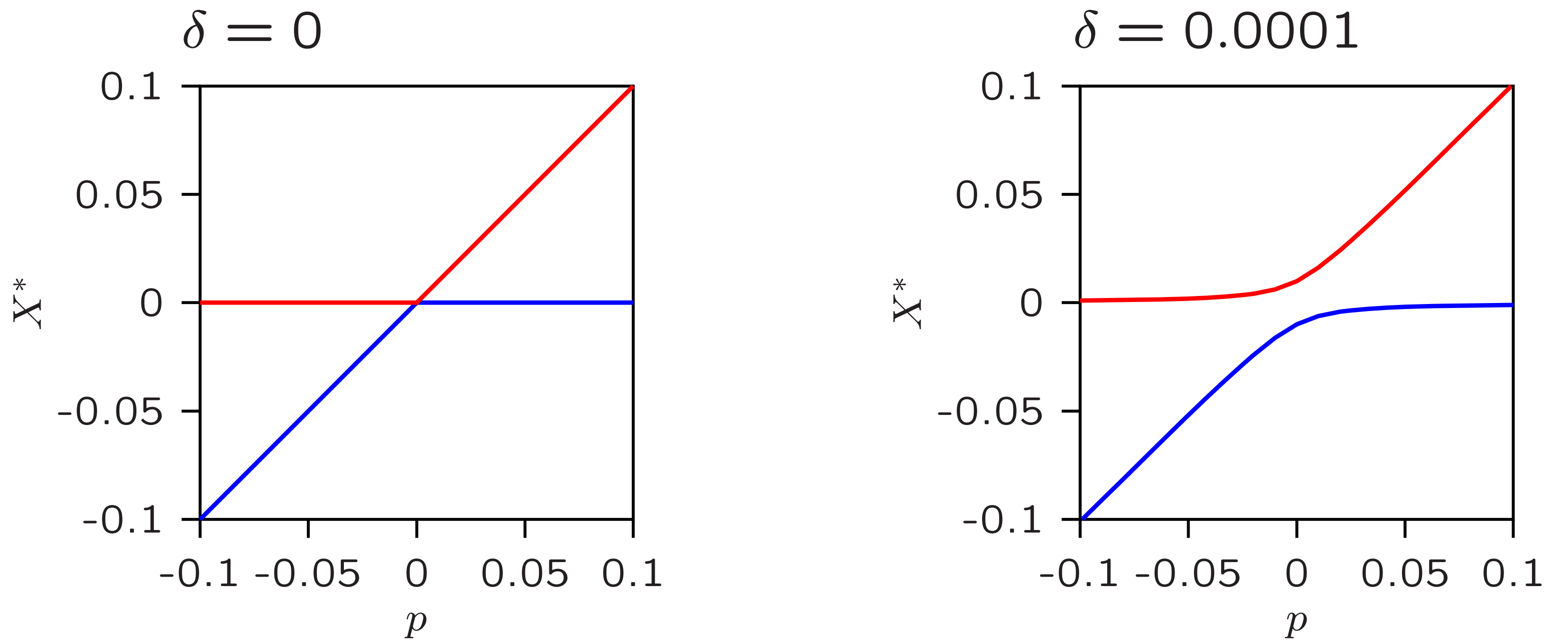
sub: $\frac{dX}{dt} = pX + X^2$





Unperturbed and Perturbed TC

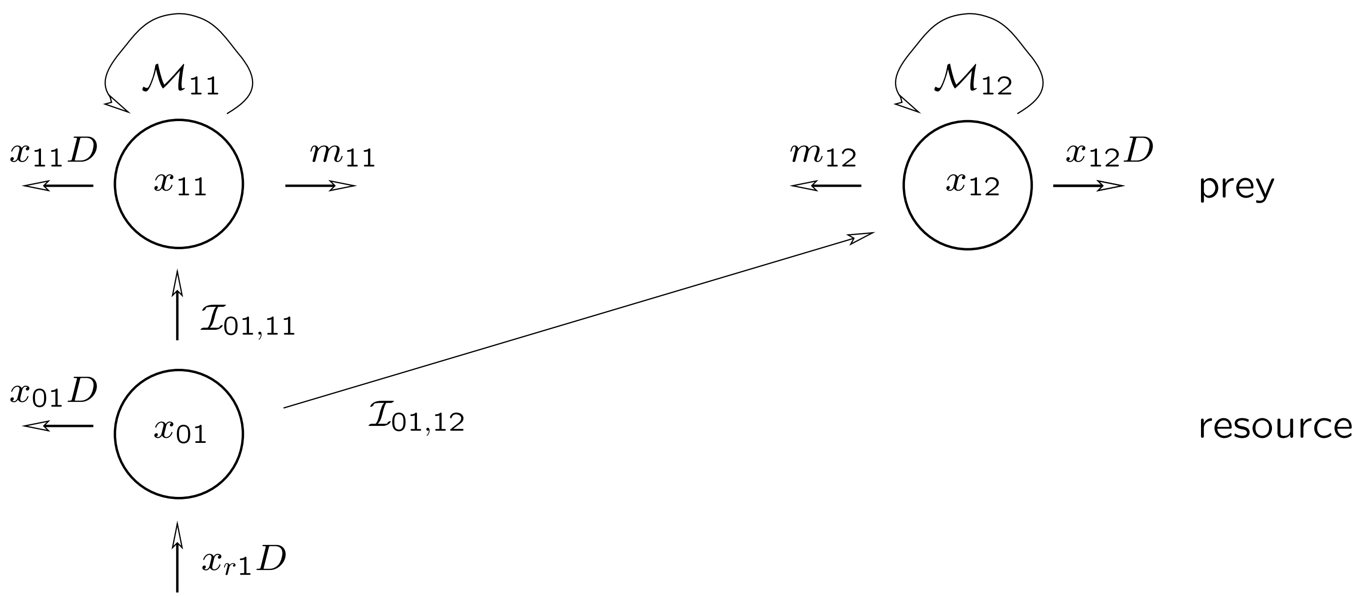
supercritical: $\frac{dX}{dt} = pX - X^2 + \delta$



Stable Unstable

Competition for one resource

One resource x_{01} – Two prey x_{11}, x_{12}



Competition for one resource

One resource x_{01} – Two prey x_{11}, x_{12}

$$\frac{dx_{01}}{dt} = (x_{r1} - x_{01})D - \frac{I_{01,11}x_{01}}{k_{01,11} + x_{01}}x_{11} - \frac{I_{01,12}x_{01}}{k_{01,12} + x_{01}}x_{12}$$

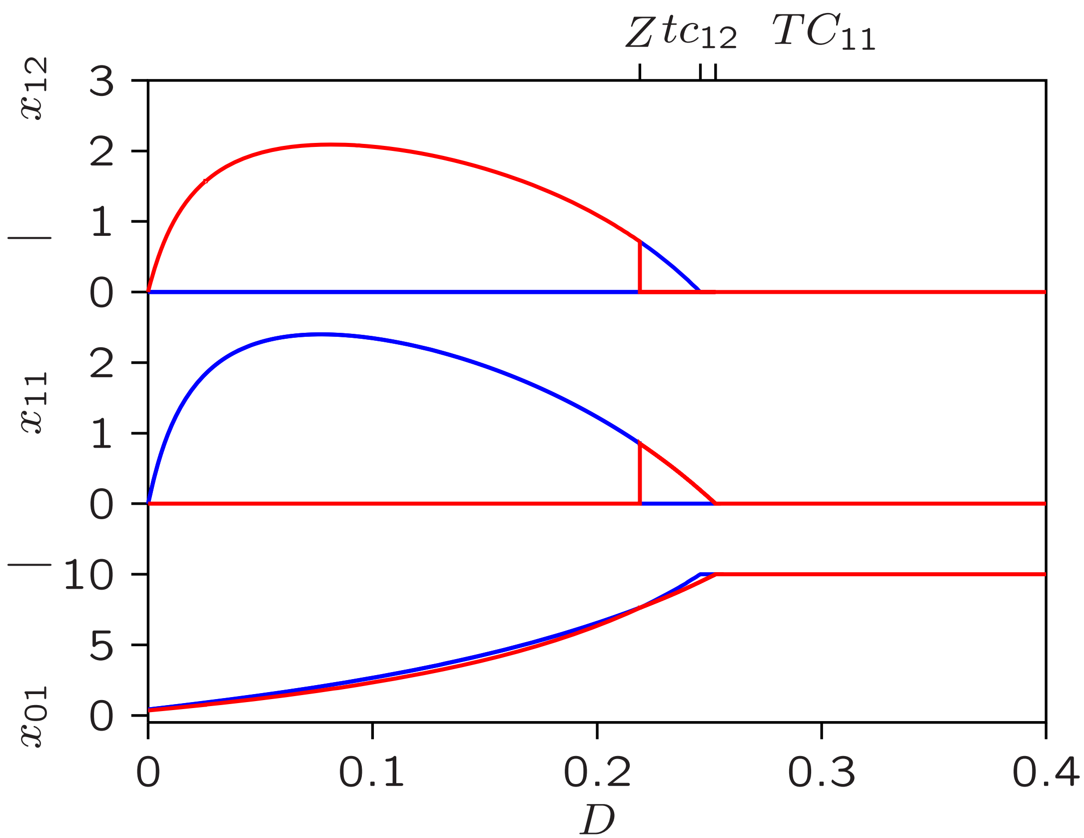
$$\frac{dx_{11}}{dt} = (\frac{\mu_{01,11}x_{01}}{k_{01,11} + x_{01}} - D - m_{11})x_{11}$$

$$\frac{dx_{12}}{dt} = (\frac{\mu_{01,12}x_{01}}{k_{01,12} + x_{01}} - D - m_{12})x_{12}$$

Competition for one resource

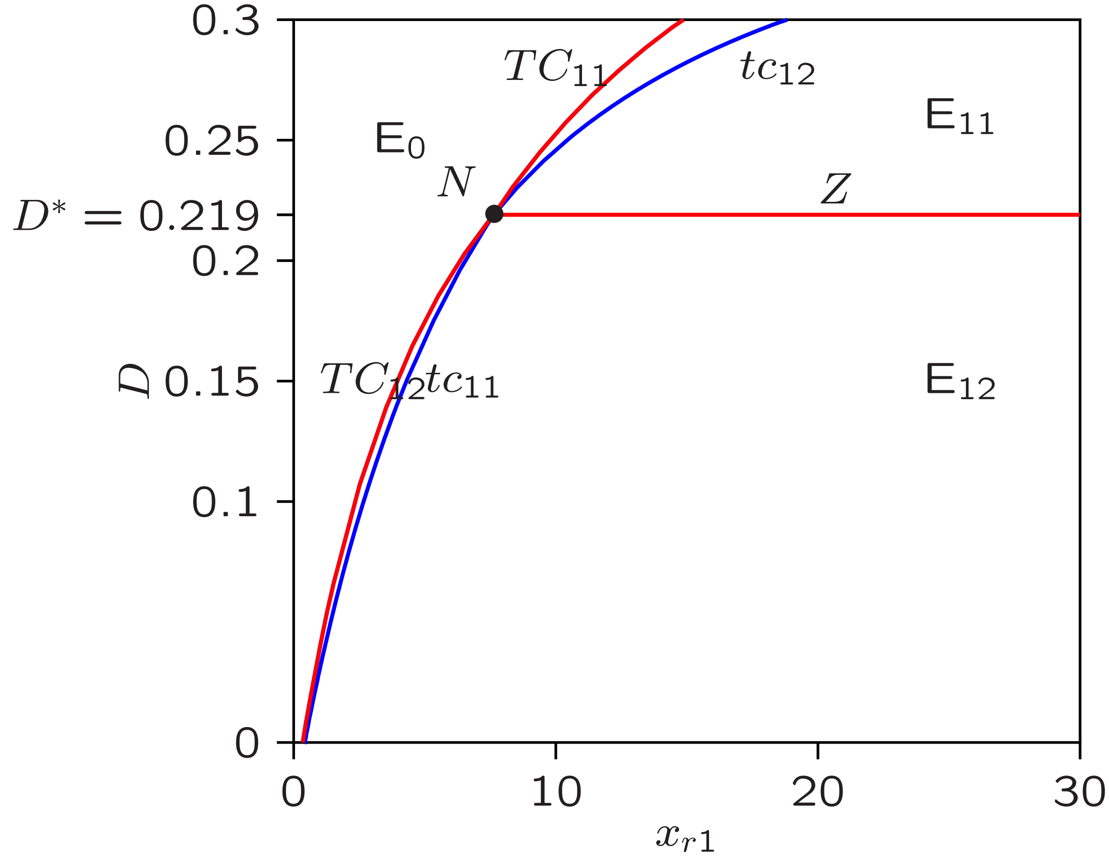
One resource x_{01} – Two prey x_{11}, x_{12}

One-parameter diagram: $x_{r1} = 10$

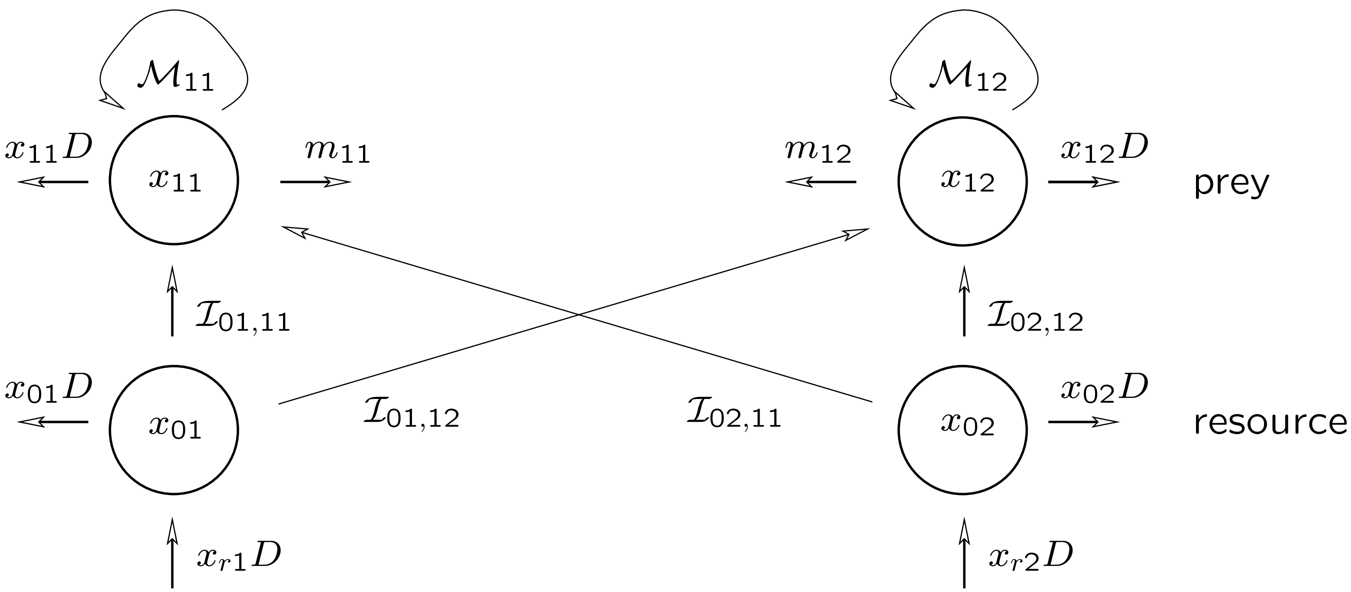


One resource x_{01} – Two prey x_{11}, x_{12}

Two-parameter diagram: x_r, D



Two resource x_{01}, x_{02} – Two prey x_{11}, x_{12}



Chemostat model

Two resources x_{01}, x_{02} – Two prey x_{11}, x_{12}

$$\frac{dx_{01}}{dt} = (x_{r1} - x_{01})D - \mathcal{I}_{01,11}x_{11} - \mathcal{I}_{01,12}x_{12}$$

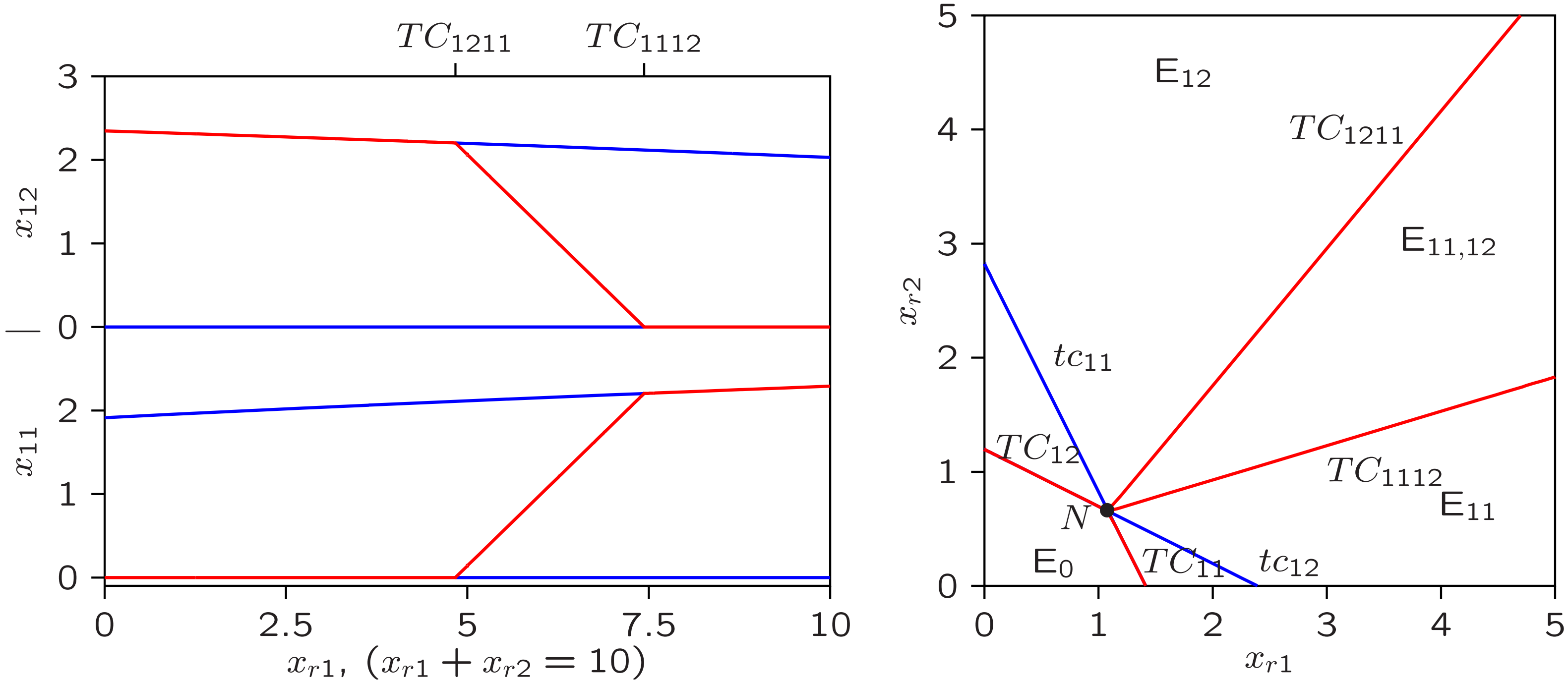
$$\frac{dx_{02}}{dt} = (x_{r2} - x_{02})D - \mathcal{I}_{02,11}x_{11} - \mathcal{I}_{02,12}x_{12}$$

$$\frac{dx_{11}}{dt} = \Big(y_{01,11}\mathcal{I}_{01,11} + y_{02,11}\mathcal{I}_{02,11} - D - m_{11}\Big)x_{11}$$

$$\frac{dx_{12}}{dt} = \Big(y_{01,12}\mathcal{I}_{01,12} + y_{02,12}\mathcal{I}_{02,12} - D - m_{12}\Big)x_{12}$$

SUB-model competition

One-parameter $x_{r1} + x_{r2} = 10$ — Two parameter diagram



Monod/Liebig model *PER-model*

k Resources

$$\frac{dx_{0i}}{dt} = (x_{ri} - x_{0i})D - \sum_{j=1}^{n} \frac{r_{1j}x_{1j}}{y_{0i,1j}} \min_i\left(\frac{x_{0i}}{k_{0i,1j} + x_{0i}}\right), \quad i = 1, \cdots, k$$

n Species

$$\frac{dx_{1j}}{dt} = r_{1j}x_{1j}\Big(\min_i\left(\frac{x_{0i}}{k_{0i,1j} + x_{0i}}\right) - D - m_{1j}\Big), \quad j = 1, \cdots, n$$

Huisman & Weissing

Biodiversity of plankton by species oscillations and chaos

Nature 402: 407–410, (1999)

Mass-balance model *COM-model*

Resources

$$\frac{dx_{0i}}{dt} = (x_{ri} - x_{0i})D - \sum_{j=1}^{n} I_{0i,1j} f_{0i,1j} x_{1j} \ , \quad i = 1, \cdots, k$$

Species

$$\frac{dx_{1j}}{dt} = x_{1j} \Big(\sum_{i=1}^{k} y_{0i,1j} I_{0i,1j} f_{0i,1j} - D - m_{1j} \Big) \ , \quad j = 1, \cdots, n$$

Yield coefficient: $y_{0i,1j} = \mu_{0i,1j}/I_{0i,1j}$

perfect-essential Liebig (1840)

PER-model: $i = 1, 2,\ j = 1, 2$

$$f^{min}_{0i,1j}(x_{01}, x_{02}) = \min\Big(\frac{x_{01}}{k_{01,1j} + x_{01}}, \frac{x_{02}}{k_{02,1j} + x_{02}}\Big)$$

interactively-essential or complementary Kooijman (2010)

COM-model: $i = 1, 2,\ j = 1, 2$

$$f^{com}_{0i,1j}(x_{01}, x_{02}) = \frac{x_{01}/k_{01,1j}\ x_{02}/k_{02,1j}}{x_{01}/k_{01,1j} + x_{02}/k_{02,1j} - \frac{x_{01}/k_{01,1j}\ x_{02}/k_{02,1j}}{x_{01}/k_{01,1j}+x_{02}/k_{02,1j}}}$$

Parameter values

Par's	Units		Values			
		Resources	$i=1$	$i=1$	$i=2$	$i=2$
		Species	$j=1$	$j=2$	$j=1$	$j=2$
$\mu_{0i,1j}$	h^{-1}		0.5	0.42	$0.5+0.4\epsilon$	0.42
$I_{0i,1j}$	h^{-1}		1.25	1.05	$1.25+\epsilon$	1.05
$y_{0i,1j}$	–		0.4	0.4	0.4	0.4
$k_{0i,1j}$	$\mathrm{mg\,dm}^{-3}$		8	11	16	5.5
m_{1j}	h^{-1}			0.025		

ϵ is a measure for the difference in the maximum growth and ingestion rate, respectively, for the two resources used by species 1. For species 2 the ingestion rates for both resources are entirely equivalent.

In equilibrium:

$$Y(I_{11}+I_{21})f_1^* = D + m_1$$
$$Y(I_{12}+I_{22})f_2^* = D + m_2$$

or

$$f_1^* = \text{min}(\frac{x_{01}^*}{k_{11}+x_{01}^*}, \frac{x_{02}^*}{k_{21}+x_{02}^*}) = \frac{D+m_1}{Y(I_{11}+I_{21})}$$
$$f_2^* = \text{min}(\frac{x_{01}^*}{k_{12}+x_{01}^*}, \frac{x_{02}^*}{k_{22}+x_{02}^*}) = \frac{D+m_2}{Y(I_{12}+I_{22})}$$

$$\begin{pmatrix}(x_{r1}-x_{01}^*)D \\ (x_{r2}-x_{02}^*)D\end{pmatrix} = \begin{pmatrix}I_{11} & I_{12} \\ I_{21} & I_{22}\end{pmatrix} \begin{pmatrix}f_1^* x_{11}^* \\ f_2^* x_{12}^*\end{pmatrix}$$

or

$$\begin{pmatrix}f_1^* x_{11}^* \\ f_2^* x_{12}^*\end{pmatrix} = \begin{pmatrix}I_{11} & I_{12} \\ I_{21} & I_{22}\end{pmatrix}^{-1} \begin{pmatrix}(x_{r1}-x_{01}^*)D \\ (x_{r2}-x_{02}^*)D\end{pmatrix}$$

Linear Algebra says that:

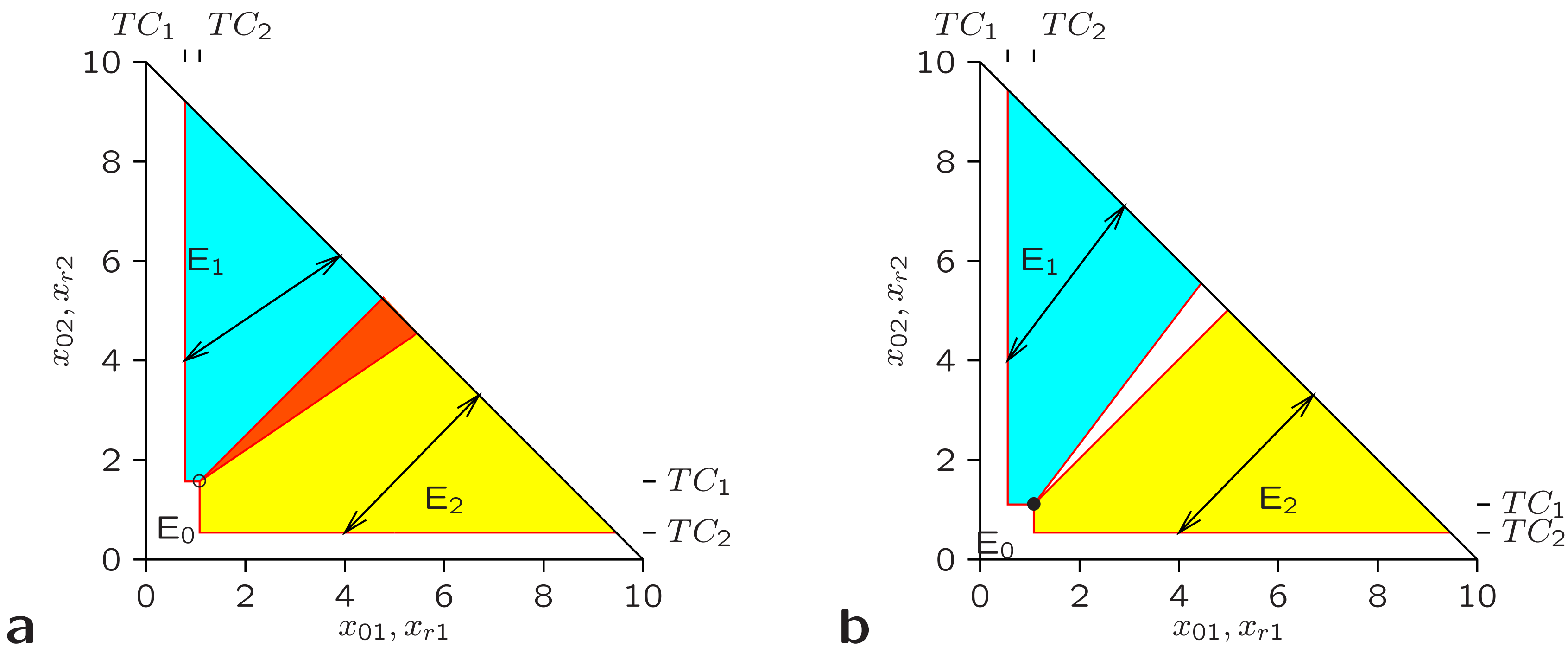
if the corresponding homogeneous system has only the zero solution, then there is a unique solution. Then the matrix with the ingestion rates I_{ij} is nonsingular and this occurs for instance when $\epsilon \neq 0$

if the corresponding homogeneous system has a non-zero solution, it is not unique, since only the sum of P_1^* and P_2^* is fixed, but not the two state variables separately. In this case the matrix with the ingestion rates I_{ij} is singular and this occurs for instance when $\epsilon = 0$

Bifurcation diagram *PER-model*

Two species – Two resources

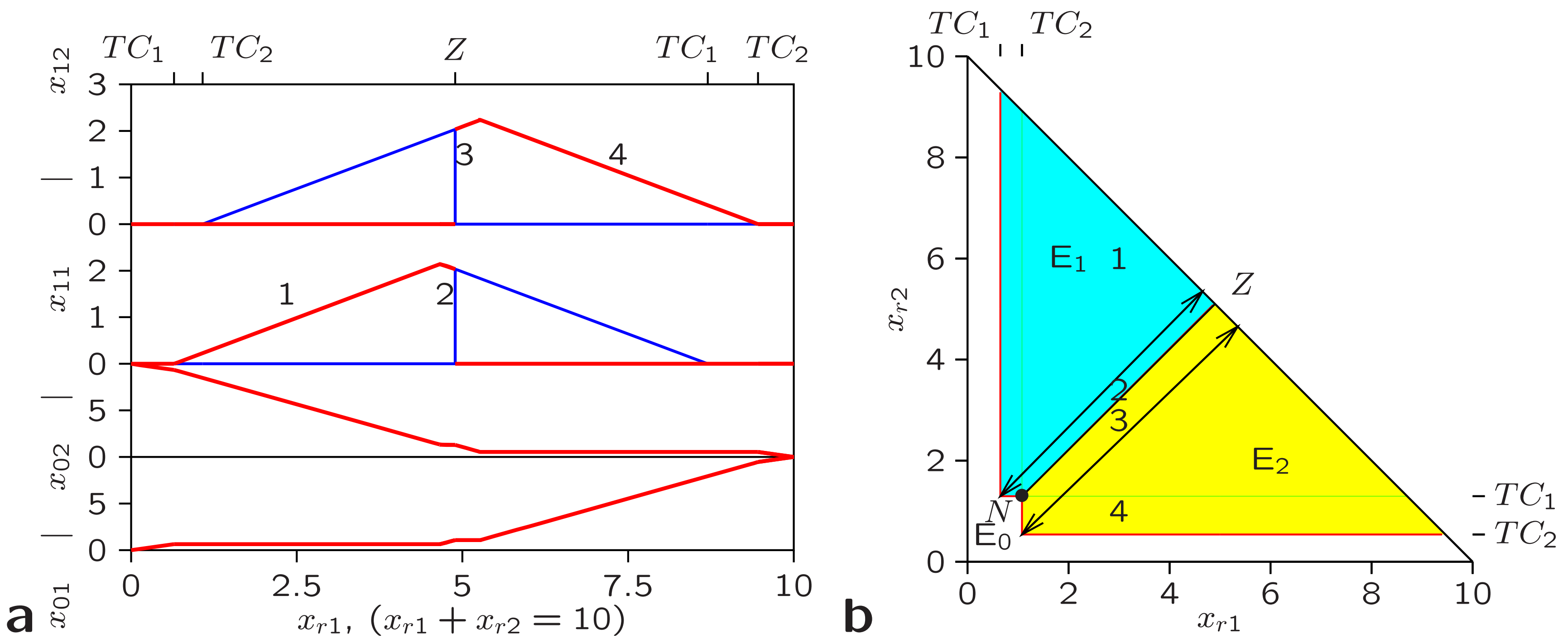
a) $\epsilon = 0.4$ b) $\epsilon = -0.4$



● Coexistence ○ Bistability

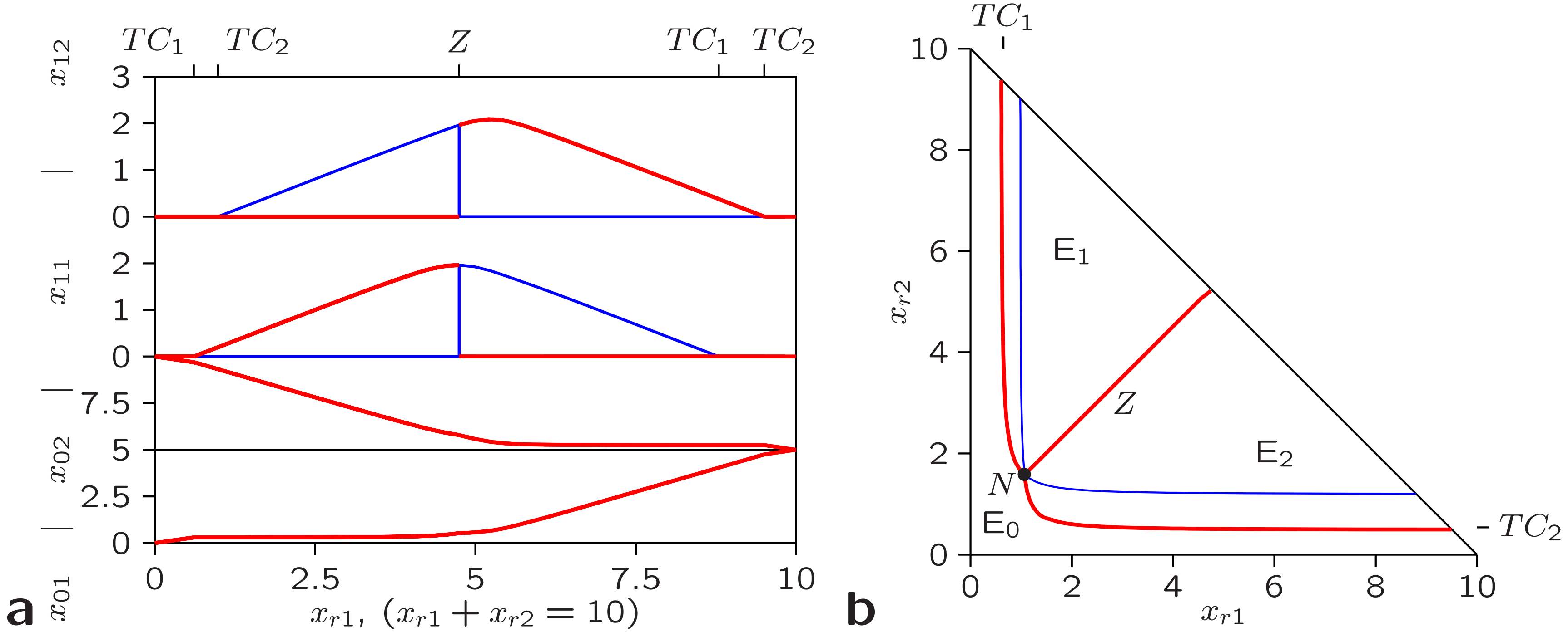
Bifurcation analysis *PER-model*

a) $x_{r1} + x_{r2} = 10$ b) $\epsilon = 0$



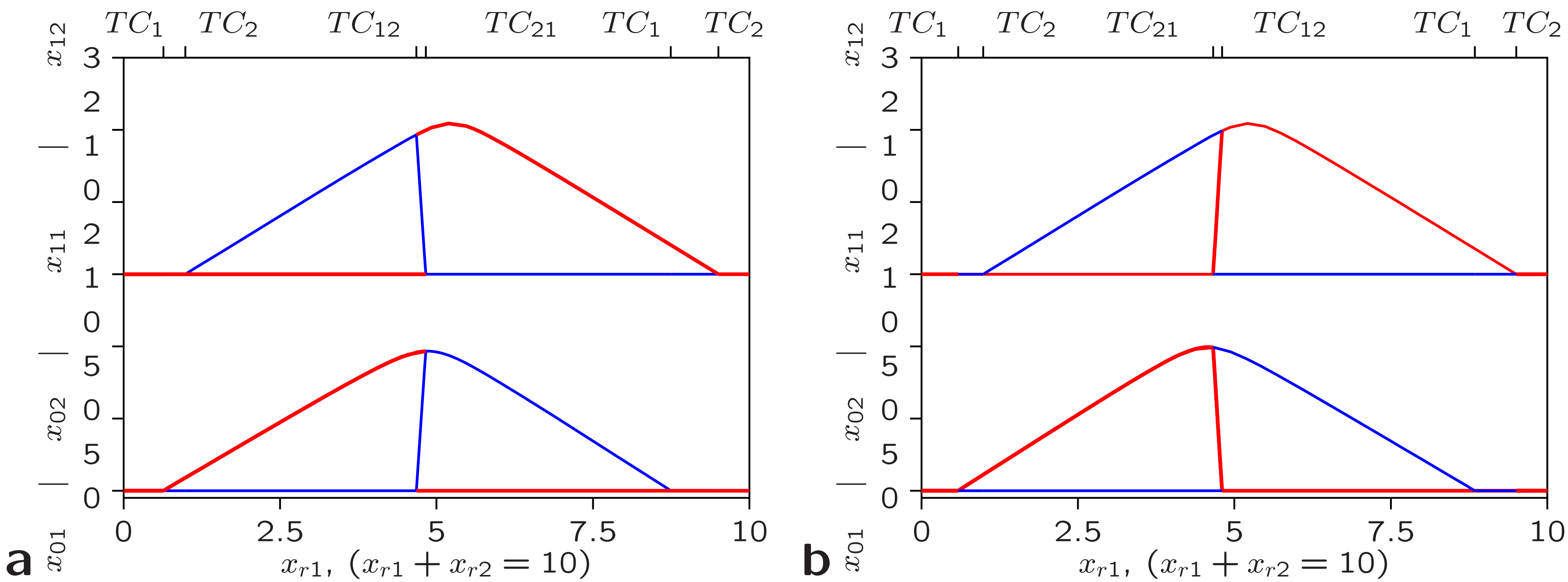
Bifurcation analysis *COM-model*

a) $x_{r1} + x_{r2} = 10$ b) $\epsilon = 0$

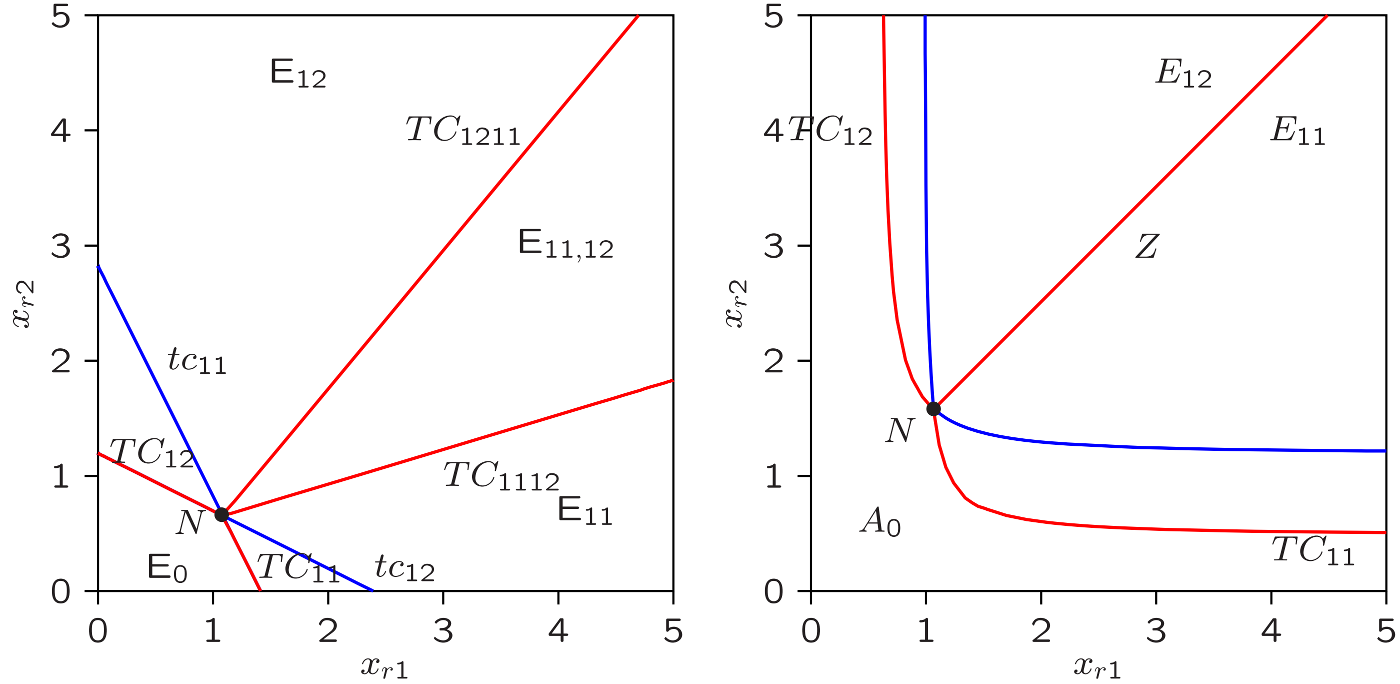


Bifurcation analysis *COM-model*

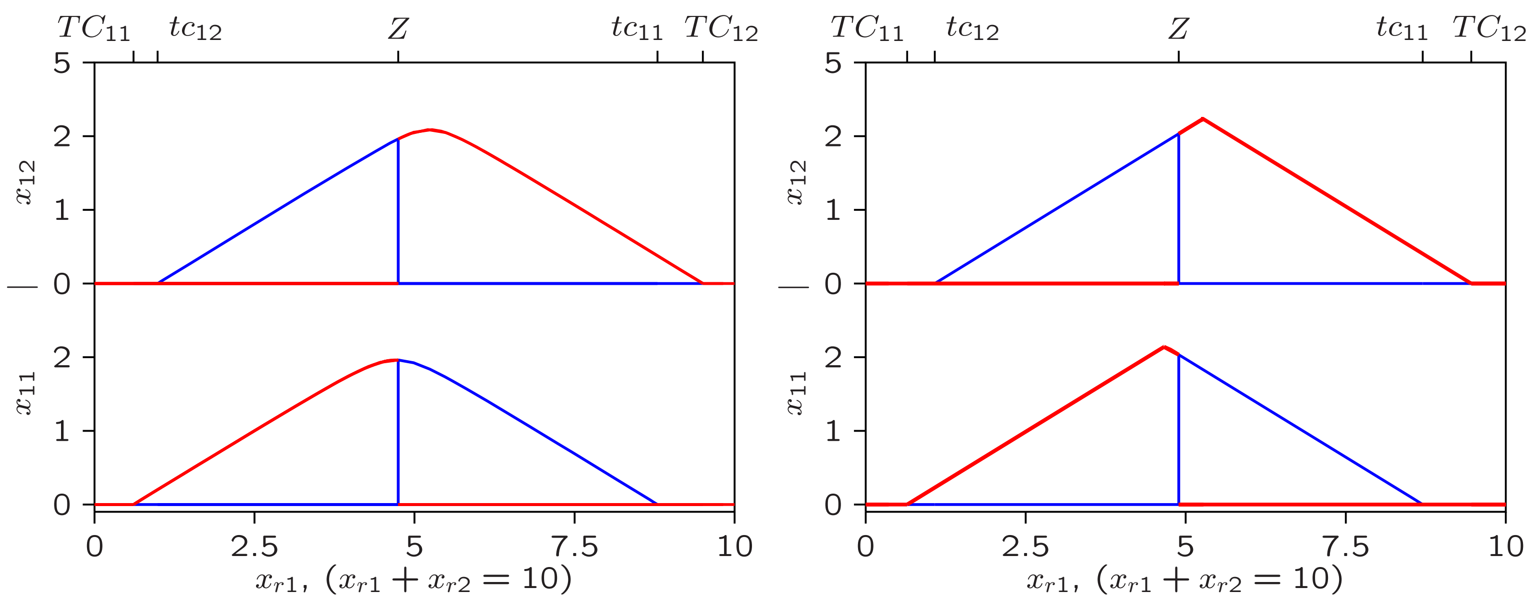
a) $\epsilon = 0.4$ b) $\epsilon = -0.4$



SUB-model versus *COM-model*



COM-model versus *PER-model*

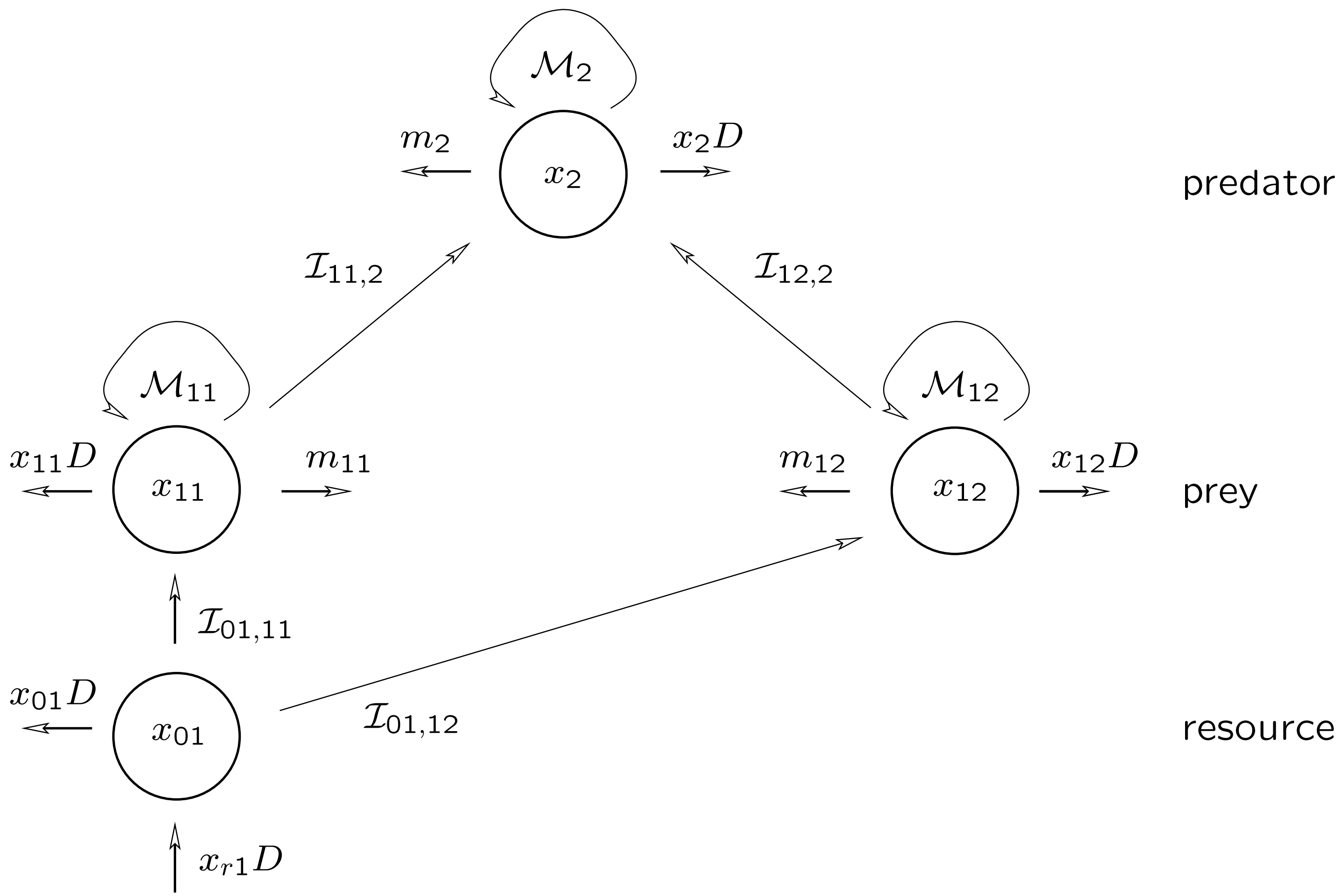


Conclusion

- Comparing these results with two resourse with those for one resourse we conclude that the presence of a second resource can reverse the outcome of the existing prey population.

- One resource: Competitive exclusion
  Two resources: One prey wins or other prey wins or Stable Coexistence or Bistability

Three level food web: one resource



Three level food web model: one resource

$$\frac{dx_{01}}{dt} = (x_{r1} - x_{01})D - \mathcal{I}_{01,11}x_{11} - \mathcal{I}_{01,12}x_{12}$$

$$\frac{dx_{11}}{dt} = \Big(\mathcal{M}_{01,11} - m_{11} - D\Big)x_{11}$$

$$\frac{dx_{12}}{dt} = \Big(\mathcal{M}_{01,12} - m_{12} - D\Big)x_{12}$$

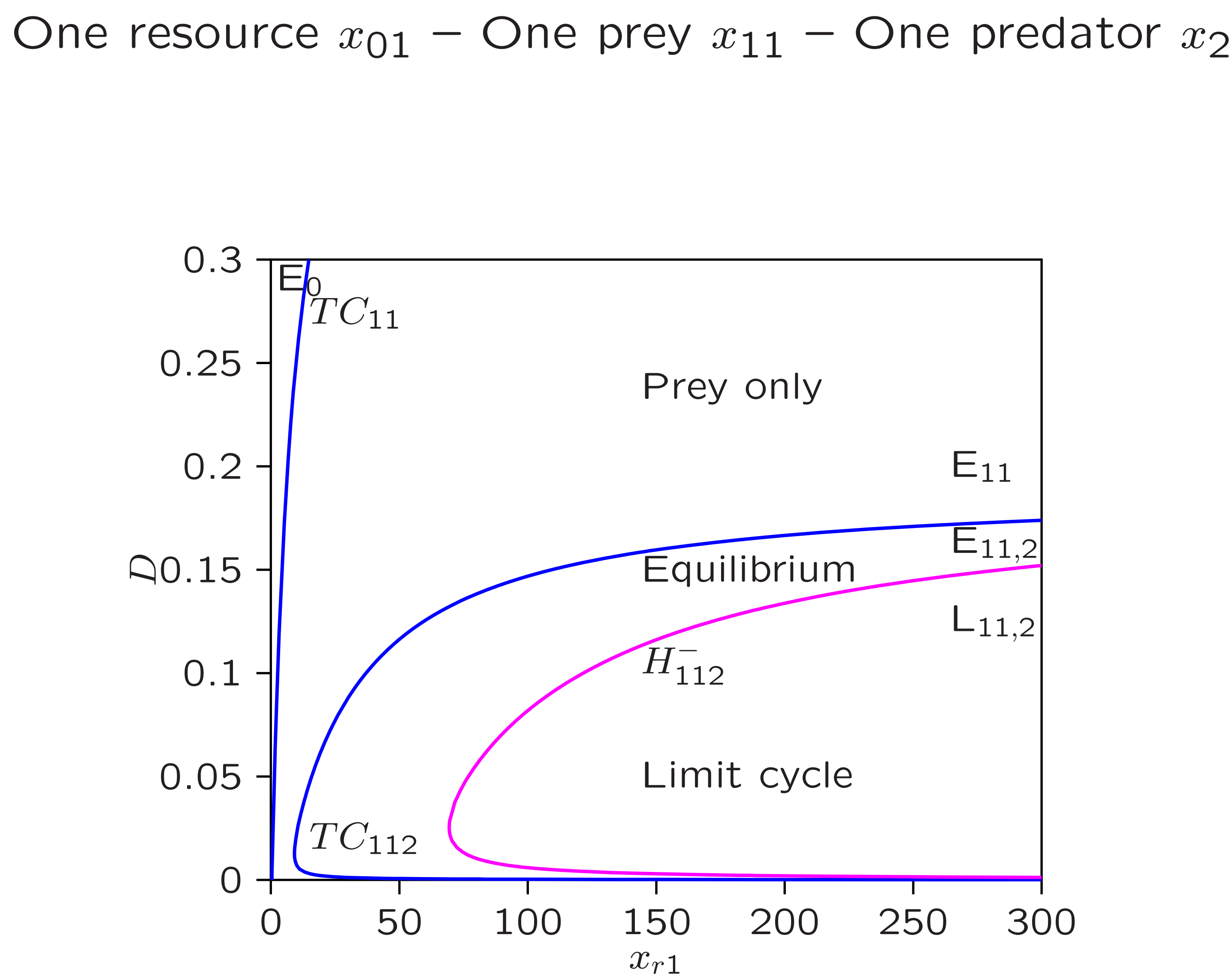
$$\frac{dx_{2}}{dt} = \Big(\mathcal{M}_{11,2} + \mathcal{M}_{12,2} - m_{2} - D\Big)x_{2}$$

$$\mathcal{I}_{uv,iv} = I_{uv,iv}f_{uv,iv}(x_{uv}, x_{uw})$$

$$\mathcal{I}_{uw,iv} = I_{uw,iv}f_{uw,iv}(x_{uv}, x_{uw})$$

$$\mathcal{M}_{uv,iv} = \mu_{uv,iv}f_{uv,iv}(x_{uv}, x_{uw})$$

$$\mathcal{M}_{uw,iv} = \mu_{uw,iv}f_{uw,iv}(x_{uv}, x_{uw})$$

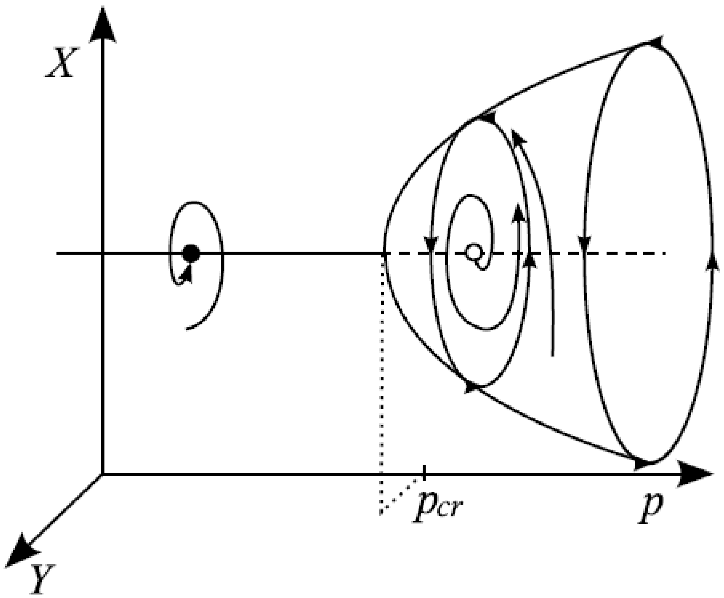


One resource x_{01} – One prey x_{11} – One predator x_2
0.3
0.25
0.2
0.15
0.1
0.05
0
D
0
50
100
150
200
250
300
x_{r1}
E_0
TC_{11}
Prey only
E_{11}
$E_{11,2}$
Equilibrium
$L_{11,2}$
H^{-}_{112}
Limit cycle
TC_{112}

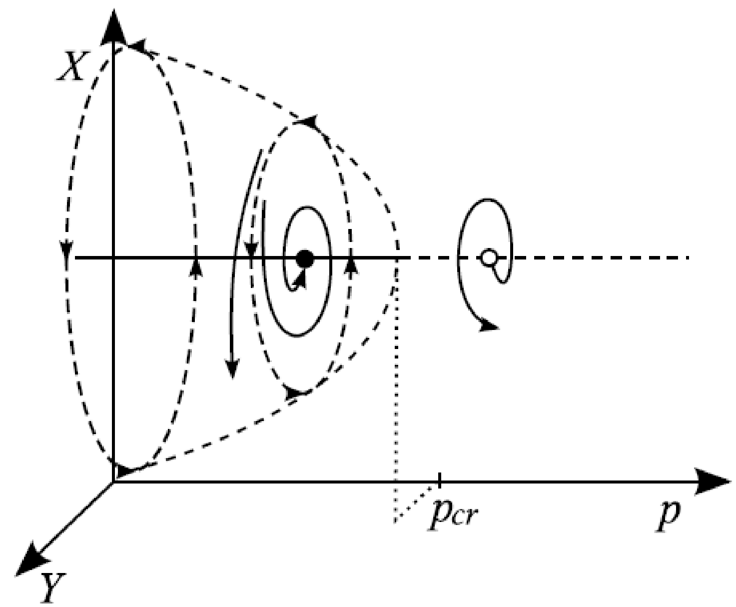
Hopf bifurcation H: Normalform:

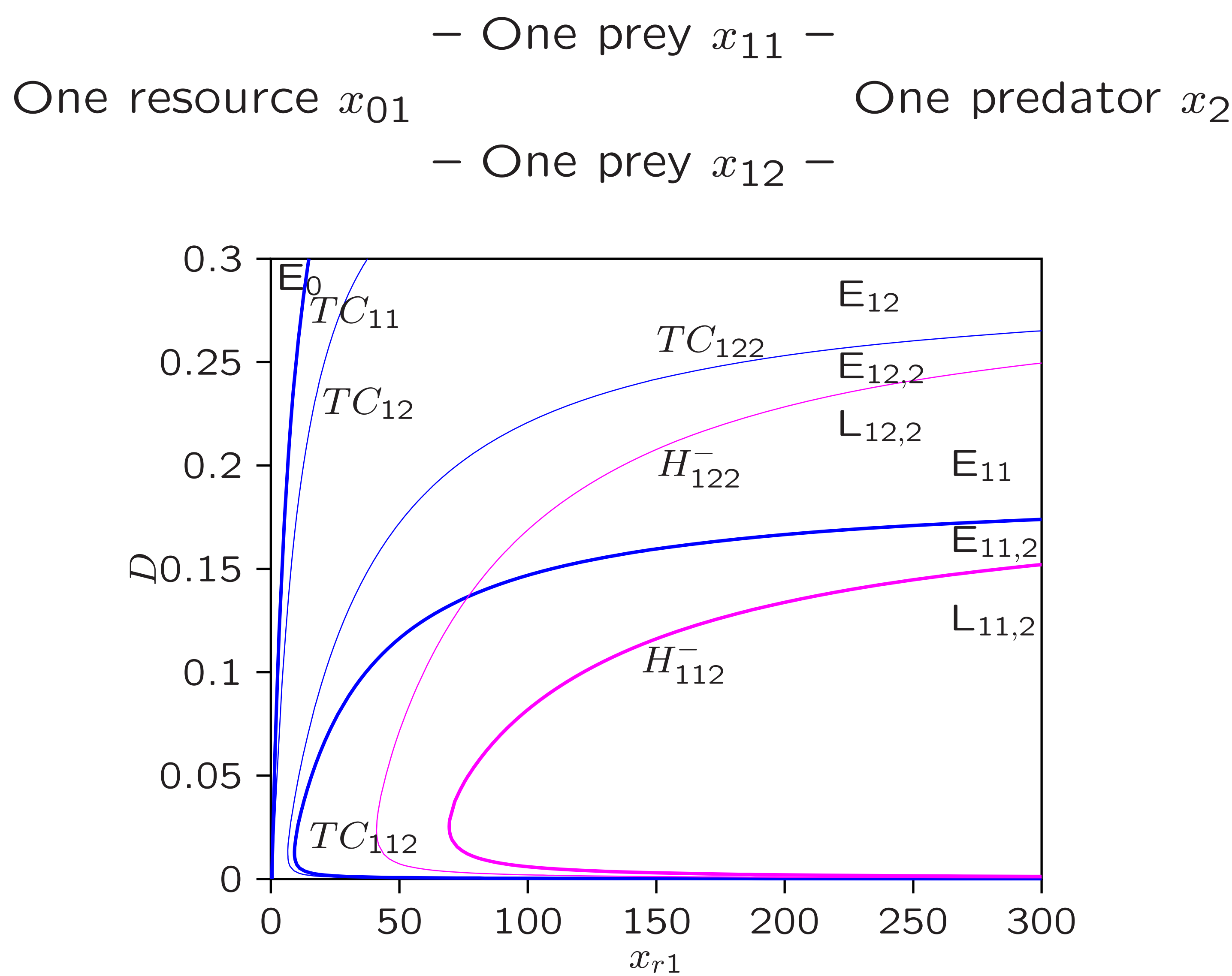
$$\frac{dX}{dt} = pX - Y \pm X(X^2 + Y^2)$$
$$\frac{dY}{dt} = X + pY \pm Y(X^2 + Y^2)$$

$p = p_{cr} = 0$: super: $\pm = -$

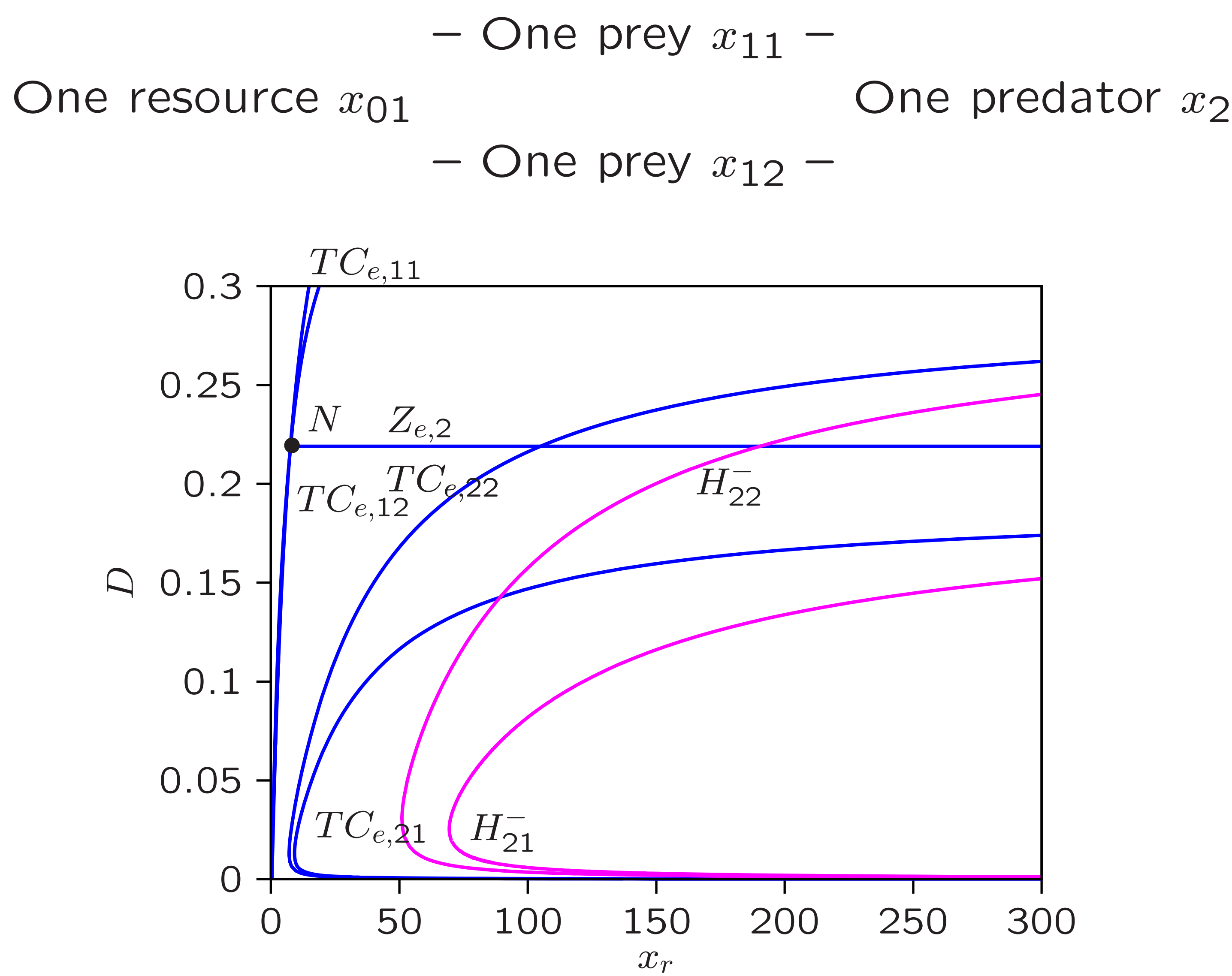


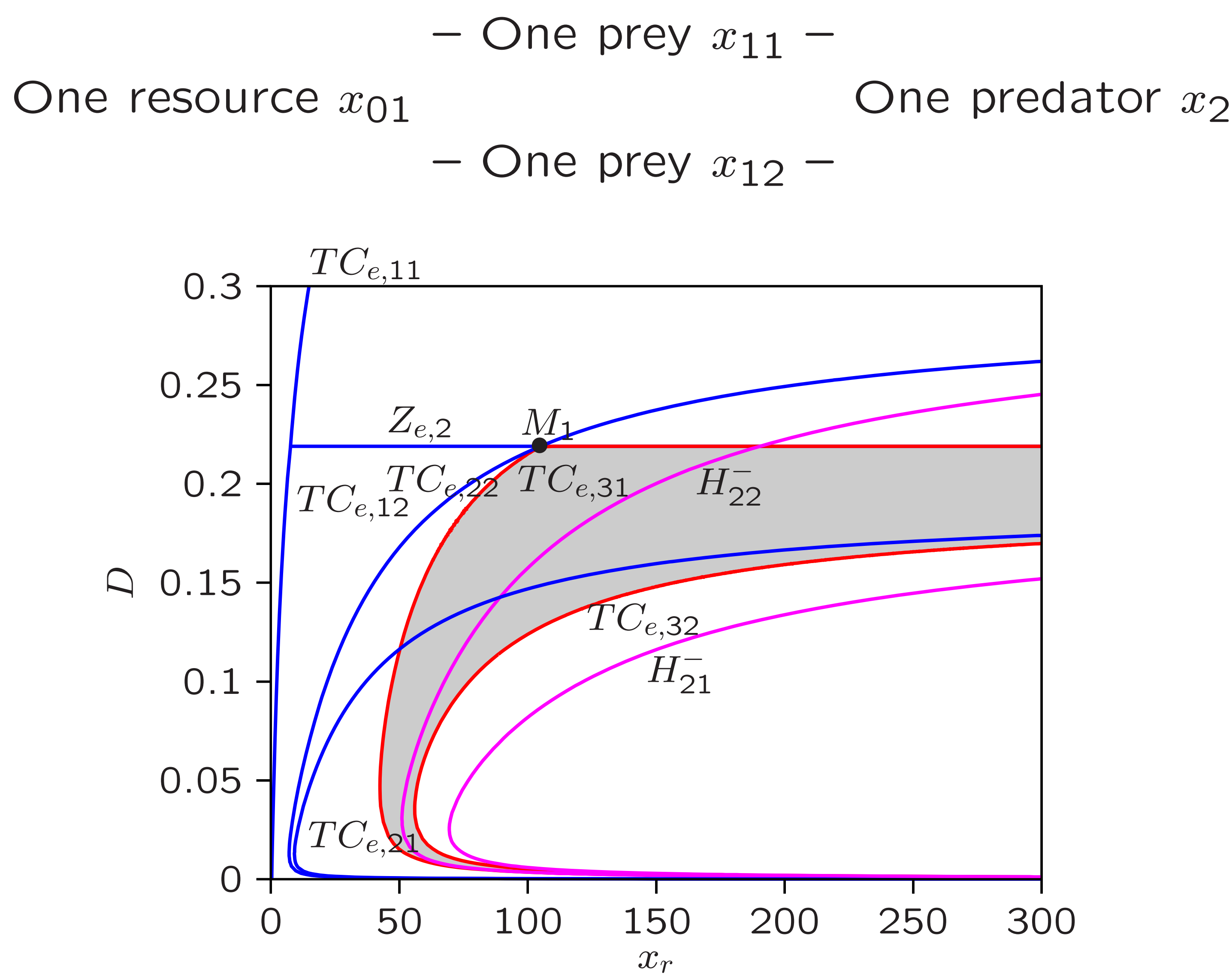
sub: $\pm = +$





– One prey x_{11} –
One resource x_{01}
One predator x_2
– One prey x_{12} –
E$_0$
TC_{11}
TC_{12}
TC_{122}
TC_{112}
E$_{12}$
E$_{12,2}$
L$_{12,2}$
H^-_{122}
E$_{11}$
E$_{11,2}$
L$_{11,2}$
H^-_{112}
D
x_{r1}
0.3
0.25
0.2
0.15
0.1
0.05
0
0
50
100
150
200
250
300


– One prey x_{11} –
One resource x_{01}
One predator x_2
– One prey x_{12} –
$TC_{e,11}$
N
$Z_{e,2}$
$TC_{e,22}$
$TC_{e,12}$
H_{22}^{-}
$TC_{e,21}$
H_{21}^{-}
D
x_r
0.3
0.25
0.2
0.15
0.1
0.05
0
0
50
100
150
200
250
300

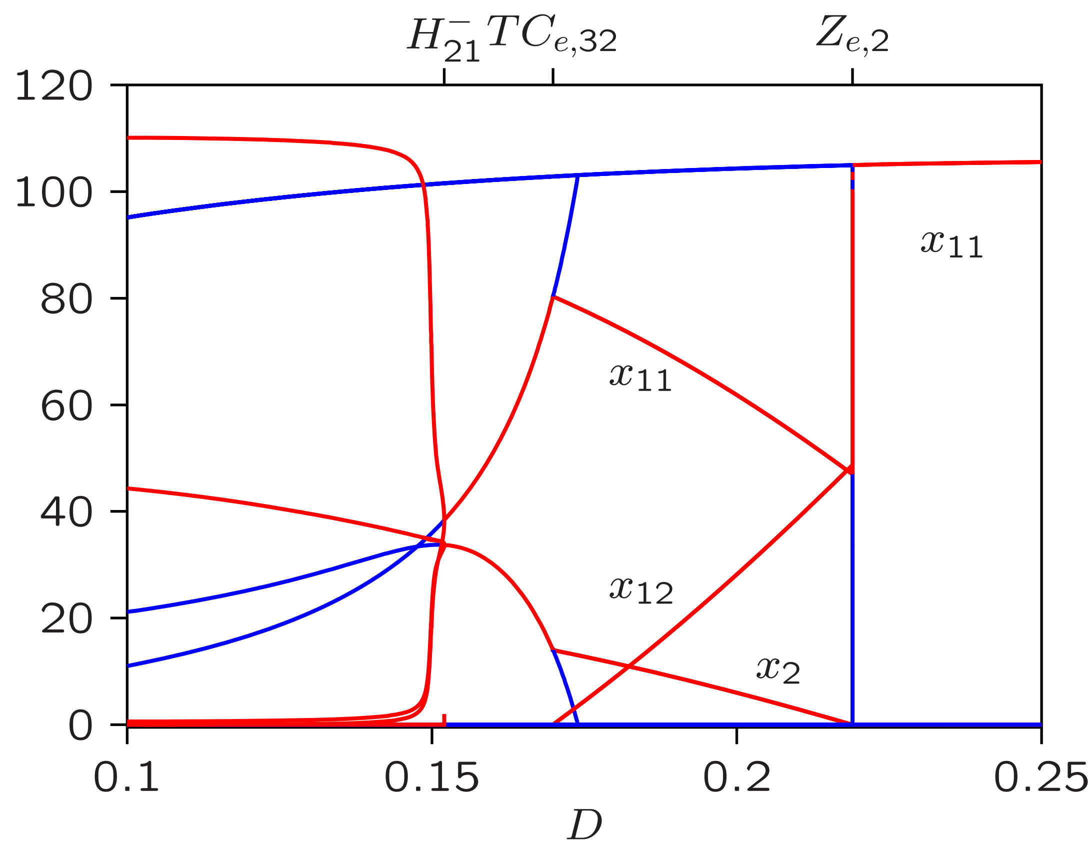


– One prey x_{11} –
One resource x_{01}
One predator x_2
– One prey x_{12} –
$TC_{e,11}$
0.3
0.25
0.2
0.15
0.1
0.05
0
D
$Z_{e,2}$
M_1
$TC_{e,22}$
$TC_{e,12}$
$TC_{e,31}$
H^-_{22}
$TC_{e,32}$
H^-_{21}
$TC_{e,21}$
0
50
100
150
200
250
300
x_r

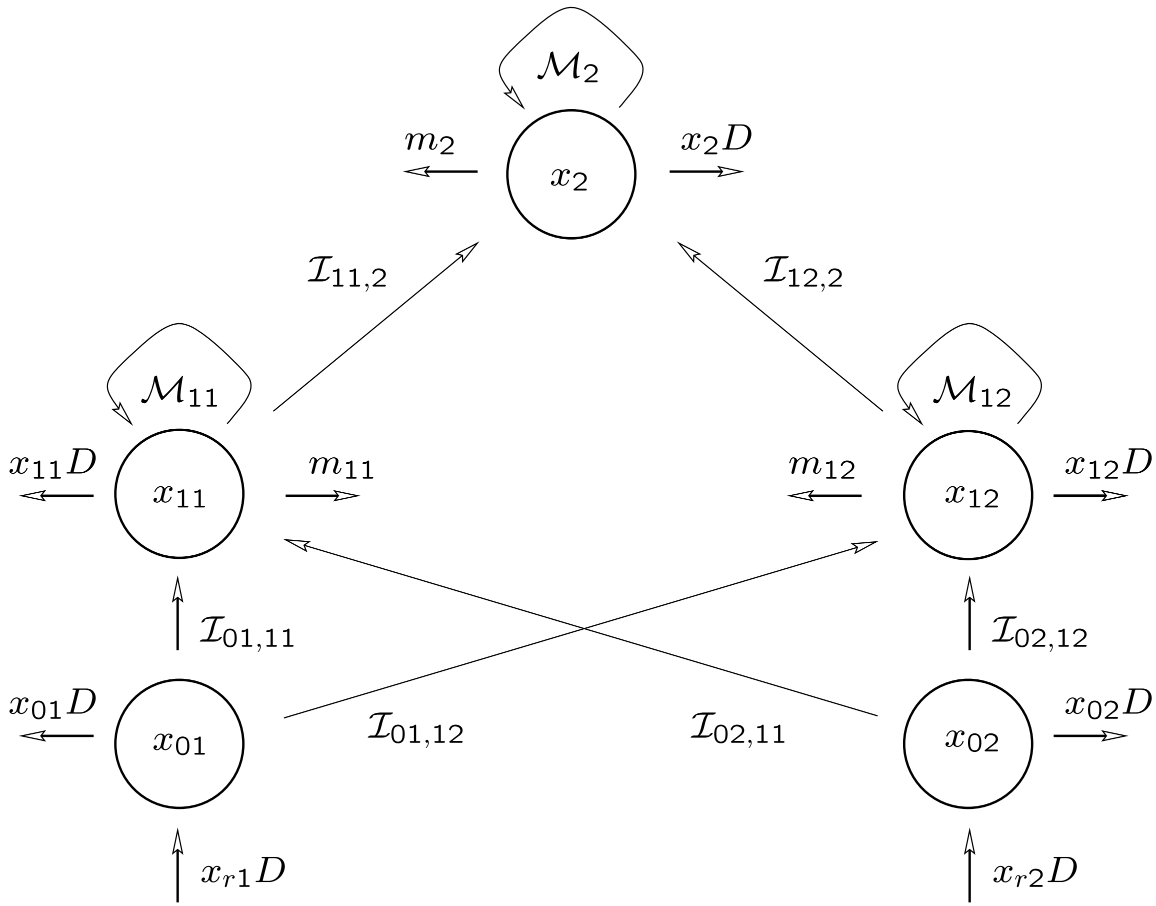
$-$ One prey x_{11} $-$

One resource x_{01} One predator x_2

$-$ One prey x_{12} $-$



Three level food web



predator $x_{2\cdot}$

prey $x_{1\cdot}$

resource $x_{0\cdot}$

Three trophic food web model

$$\frac{dx_{01}}{dt} = (x_{r1} - x_{01})D - \mathcal{I}_{01,11}x_{11} - \mathcal{I}_{01,12}x_{12}$$

$$\frac{dx_{02}}{dt} = (x_{r2} - x_{02})D - \mathcal{I}_{02,11}x_{11} - \mathcal{I}_{02,12}x_{12}$$

$$\frac{dx_{11}}{dt} = \Big(\mathcal{M}_{01,11} + \mathcal{M}_{02,11} - m_{11} - D\Big)x_{11} - \mathcal{I}_{11,2}x_2$$

$$\frac{dx_{12}}{dt} = \Big(\mathcal{M}_{01,12} + \mathcal{M}_{02,12} - m_{12} - D\Big)x_{12} - \mathcal{I}_{12,2}x_2$$

$$\frac{dx_2}{dt} = \Big(\mathcal{M}_{11,2} + \mathcal{M}_{12,2} - m_2 - D\Big)x_2$$

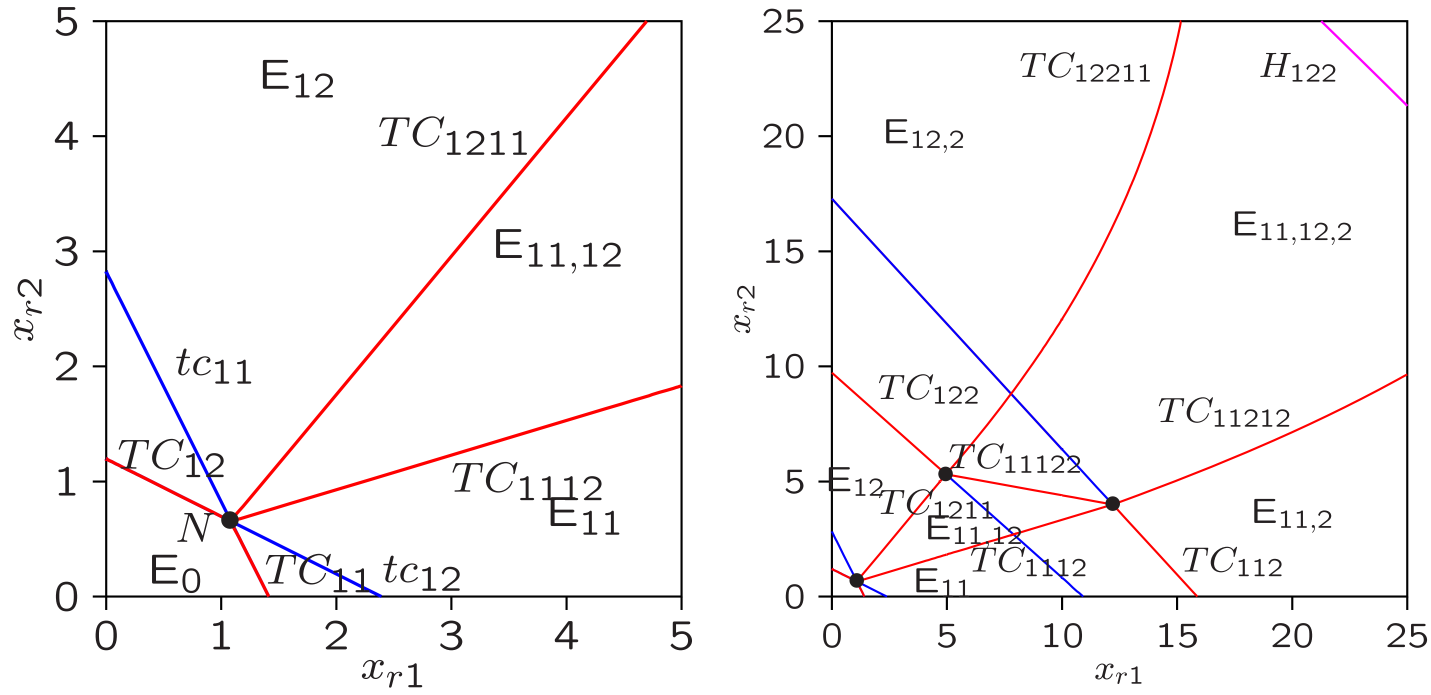
$$\mathcal{I}_{uv,iv} = I_{uv,iv}f_{uv,iv}(x_{uv}, x_{uw}), \mathcal{I}_{uw,iv} = I_{uw,iv}f_{uw,iv}(x_{uv}, x_{uw})$$

$$\mathcal{M}_{uv,iv} = \mu_{uv,iv}f_{uv,iv}(x_{uv}, x_{uw}), \mathcal{M}_{uw,iv} = \mu_{uw,iv}f_{uw,iv}(x_{uv}, x_{uw})$$

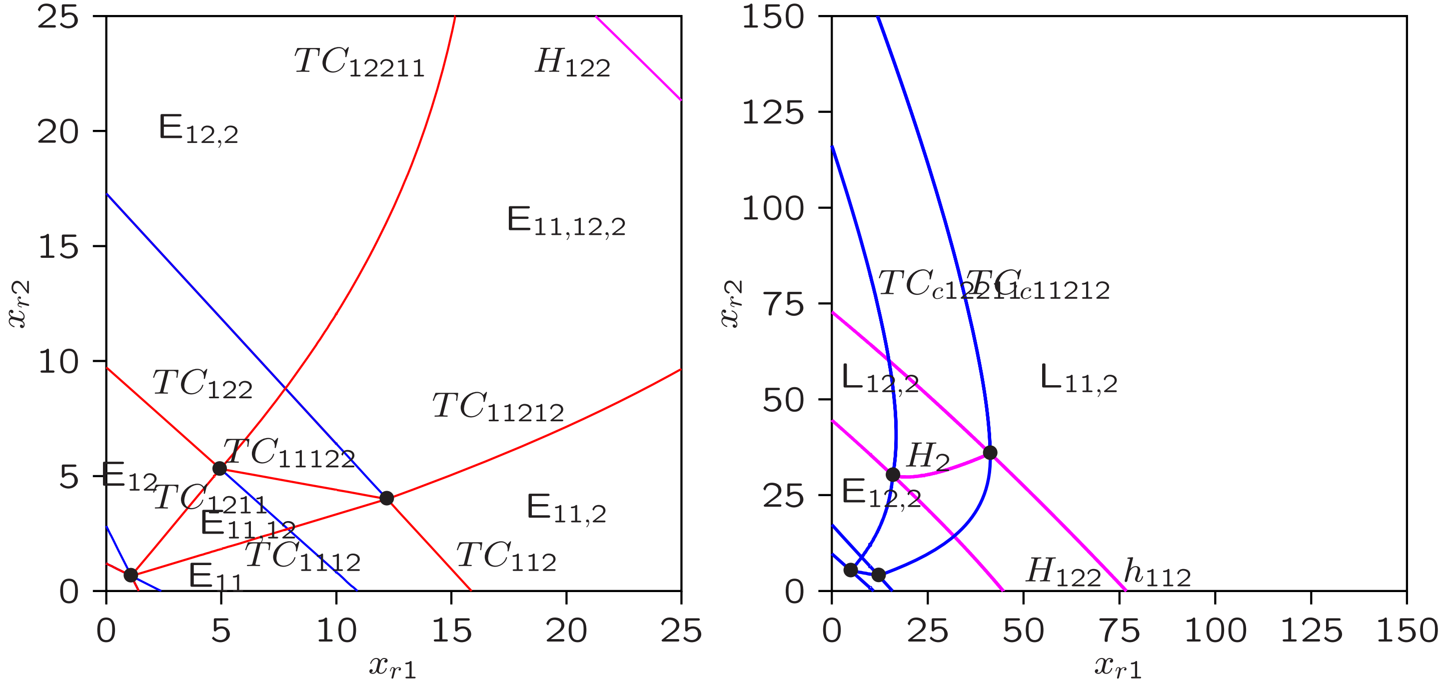
Two prey – One predator: *SUB-model*

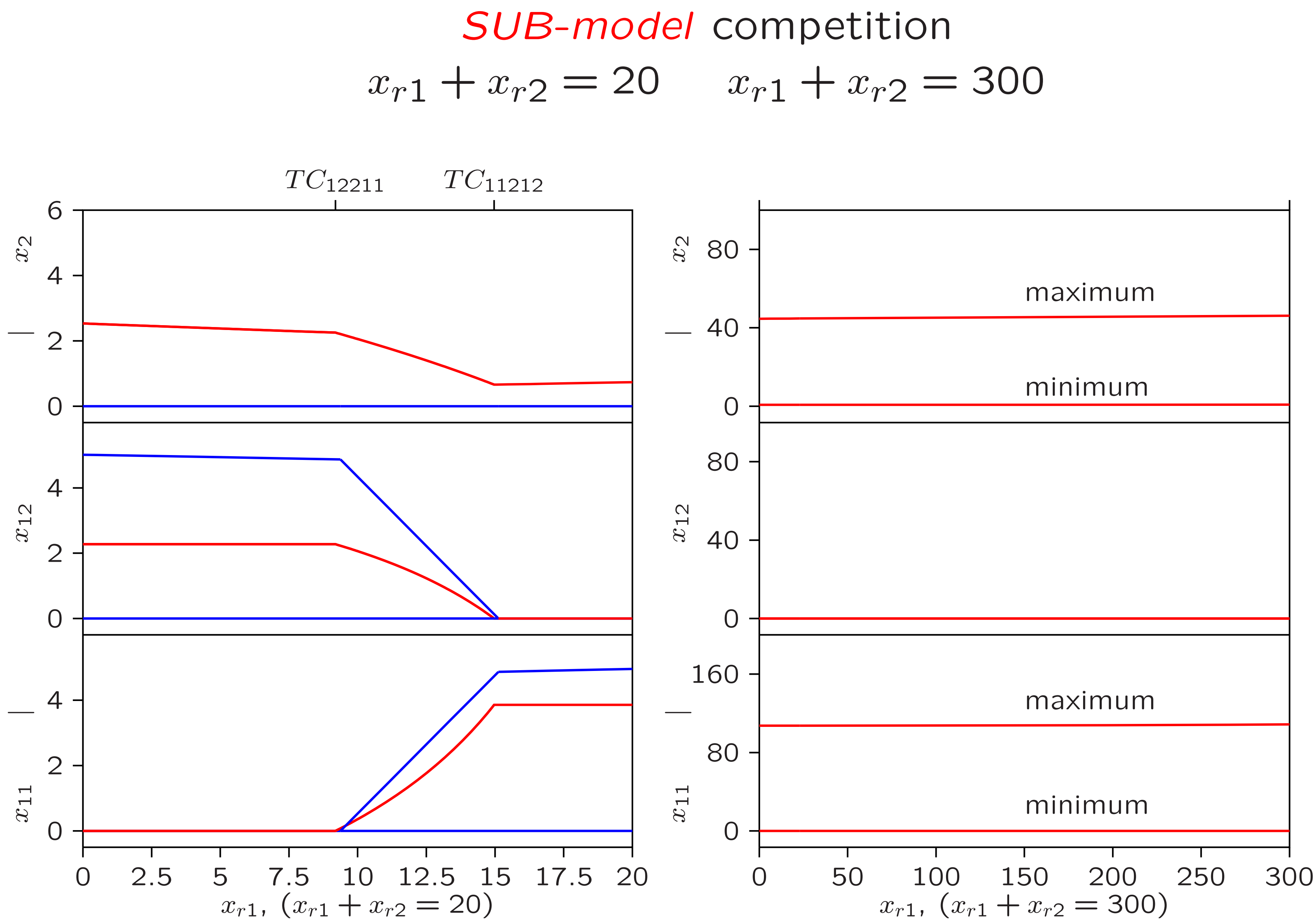
SUB-model competition

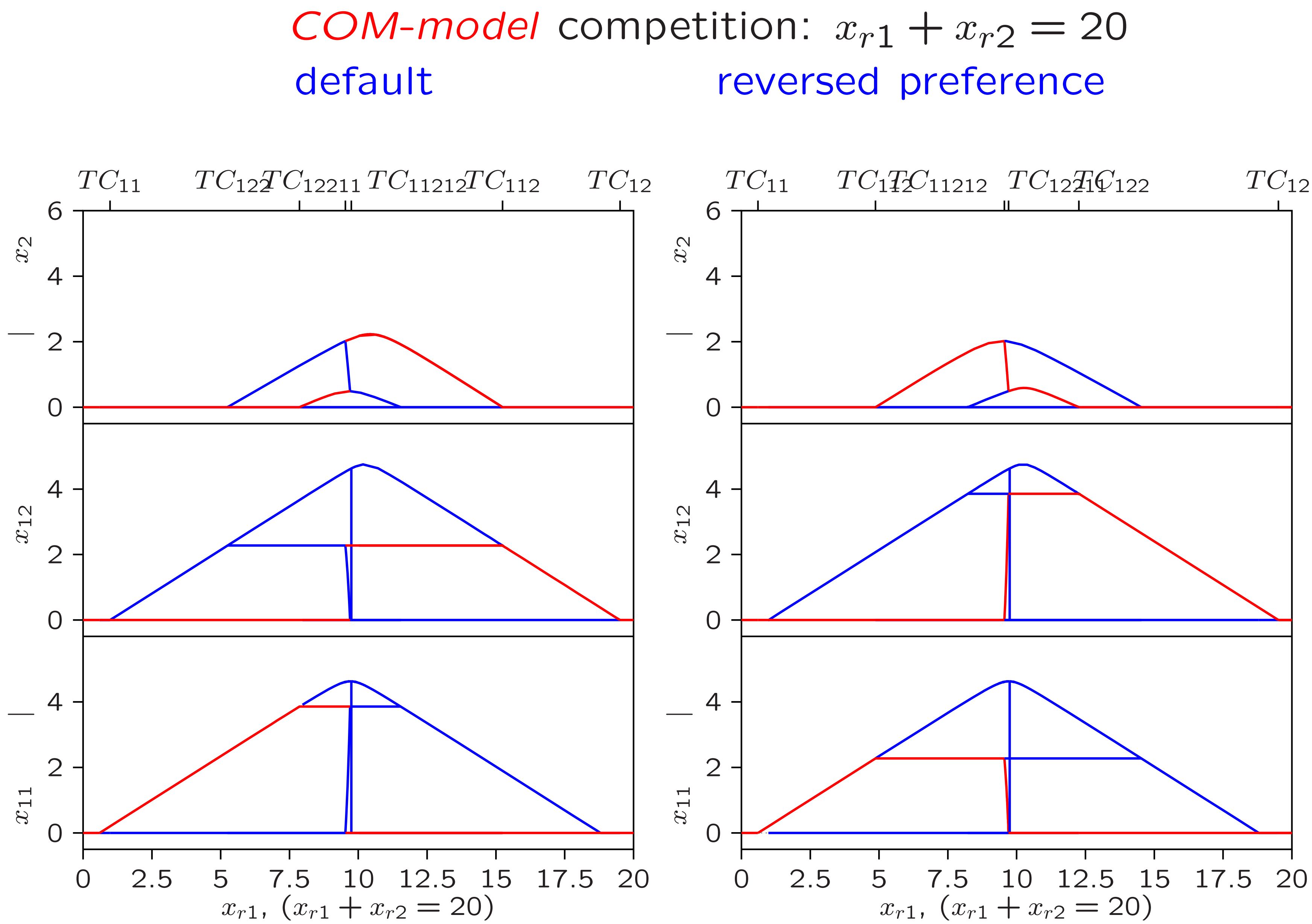
2 level − 3 level

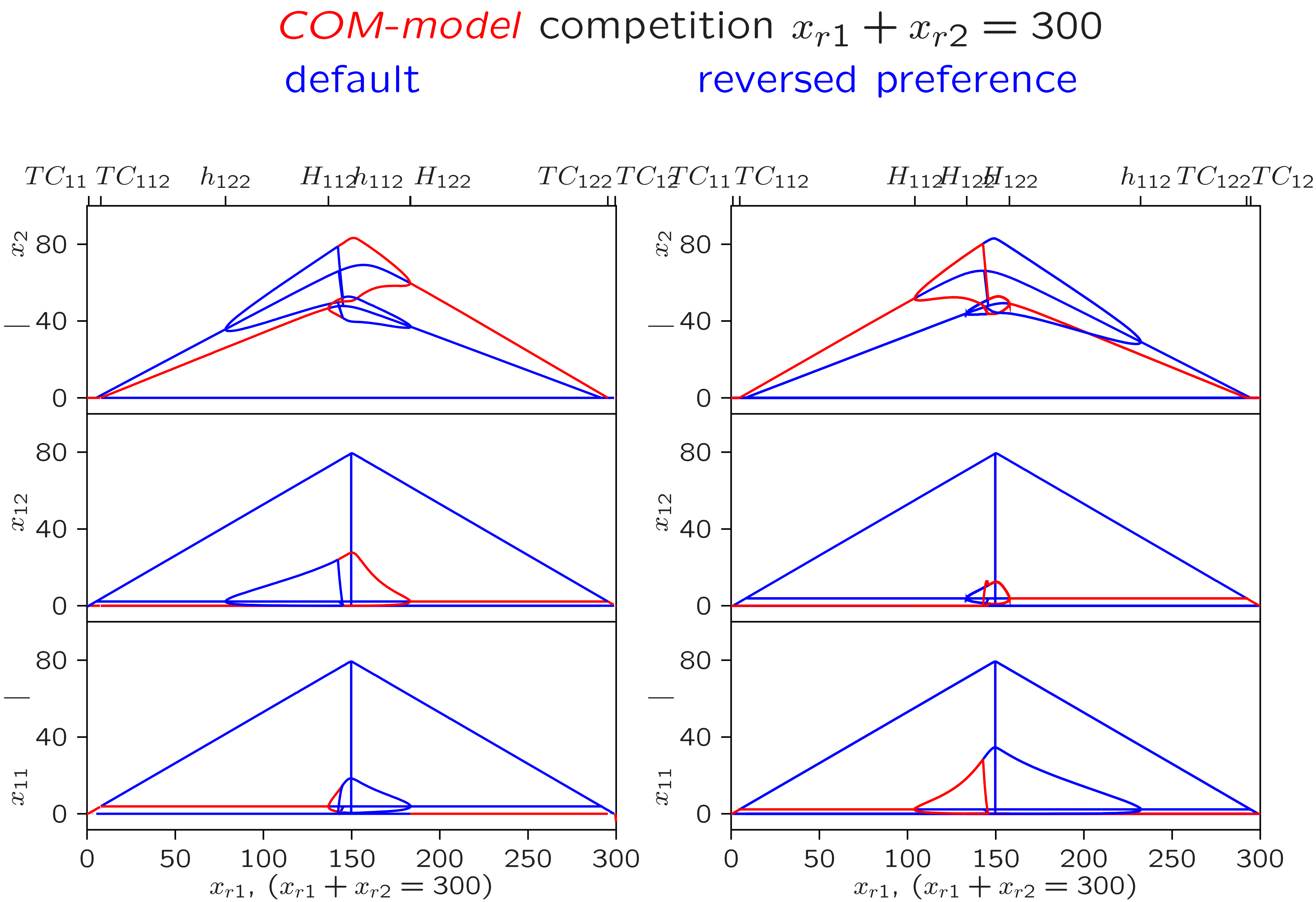


SUB-model competition




SUB-model competition
$x_{r1} + x_{r2} = 20$
$x_{r1} + x_{r2} = 300$
TC_{12211}
TC_{11212}
x_2
x_{12}
x_{11}
maximum
minimum
maximum
minimum
0
2
4
6
2.5
5
7.5
10
12.5
15
17.5
20
40
80
160
50
100
150
200
250
300
x_{r1}, $(x_{r1} + x_{r2} = 20)$
x_{r1}, $(x_{r1} + x_{r2} = 300)$

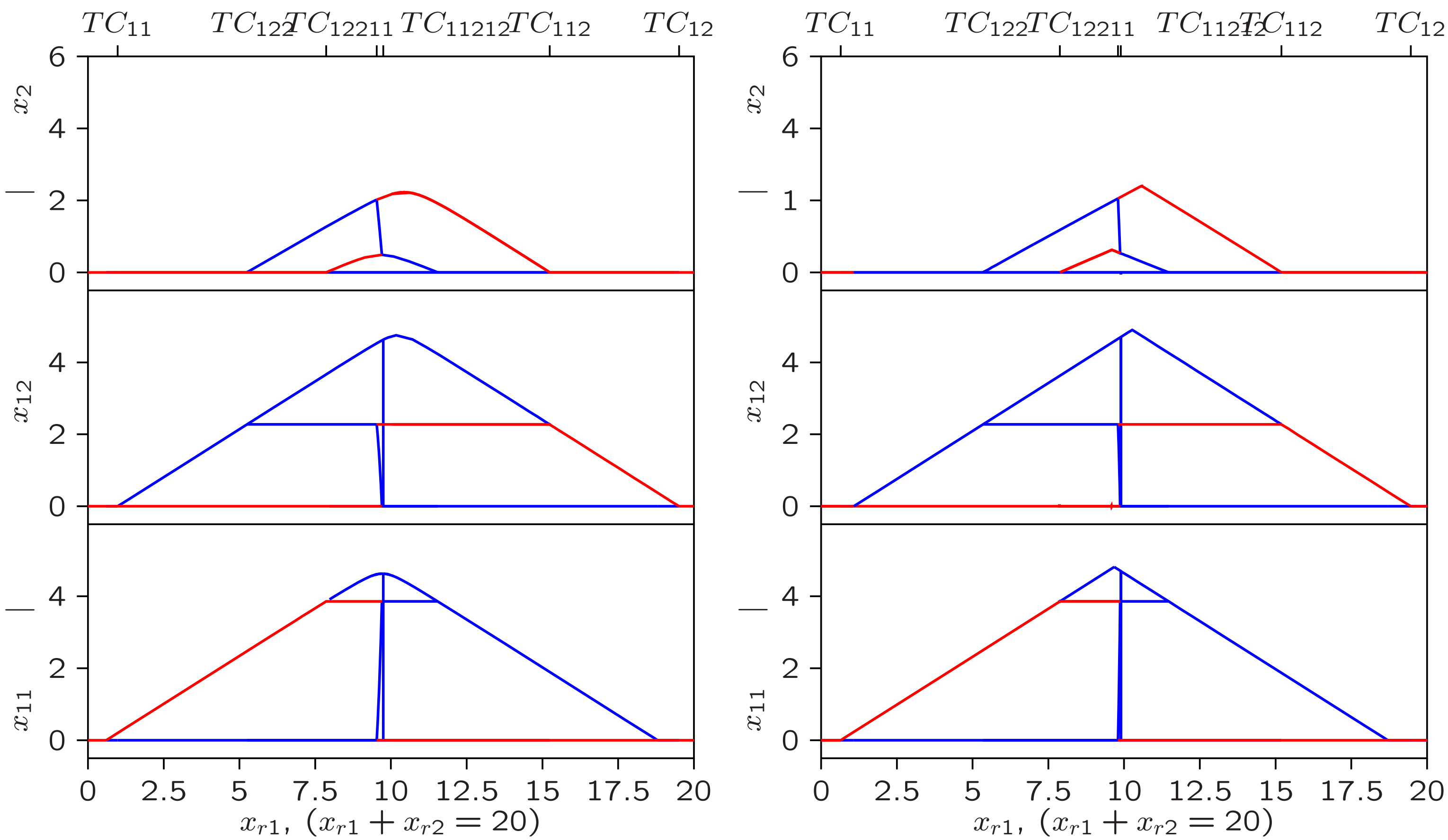

COM-model competition: $x_{r1} + x_{r2} = 20$
default
reversed preference
TC_{11} TC_{122} TC_{12211} TC_{11212} TC_{112} TC_{12}
TC_{11} TC_{112} TC_{11212} TC_{12211} TC_{122} TC_{12}
x_2
x_{12}
x_{11}
x_{r1}, $(x_{r1} + x_{r2} = 20)$
x_{r1}, $(x_{r1} + x_{r2} = 20)$



COM-model competition $x_{r1}+x_{r2}=300$
default
reversed preference
TC_{11} TC_{112} h_{122} H_{112} h_{112} H_{122} TC_{122} TC_{12}
TC_{11} TC_{112} H_{112} H_{122} H_{122} h_{112} TC_{122} TC_{12}
x_2
x_{12}
x_{11}
0 40 80
0 50 100 150 200 250 300
x_{r1}, $(x_{r1}+x_{r2}=300)$

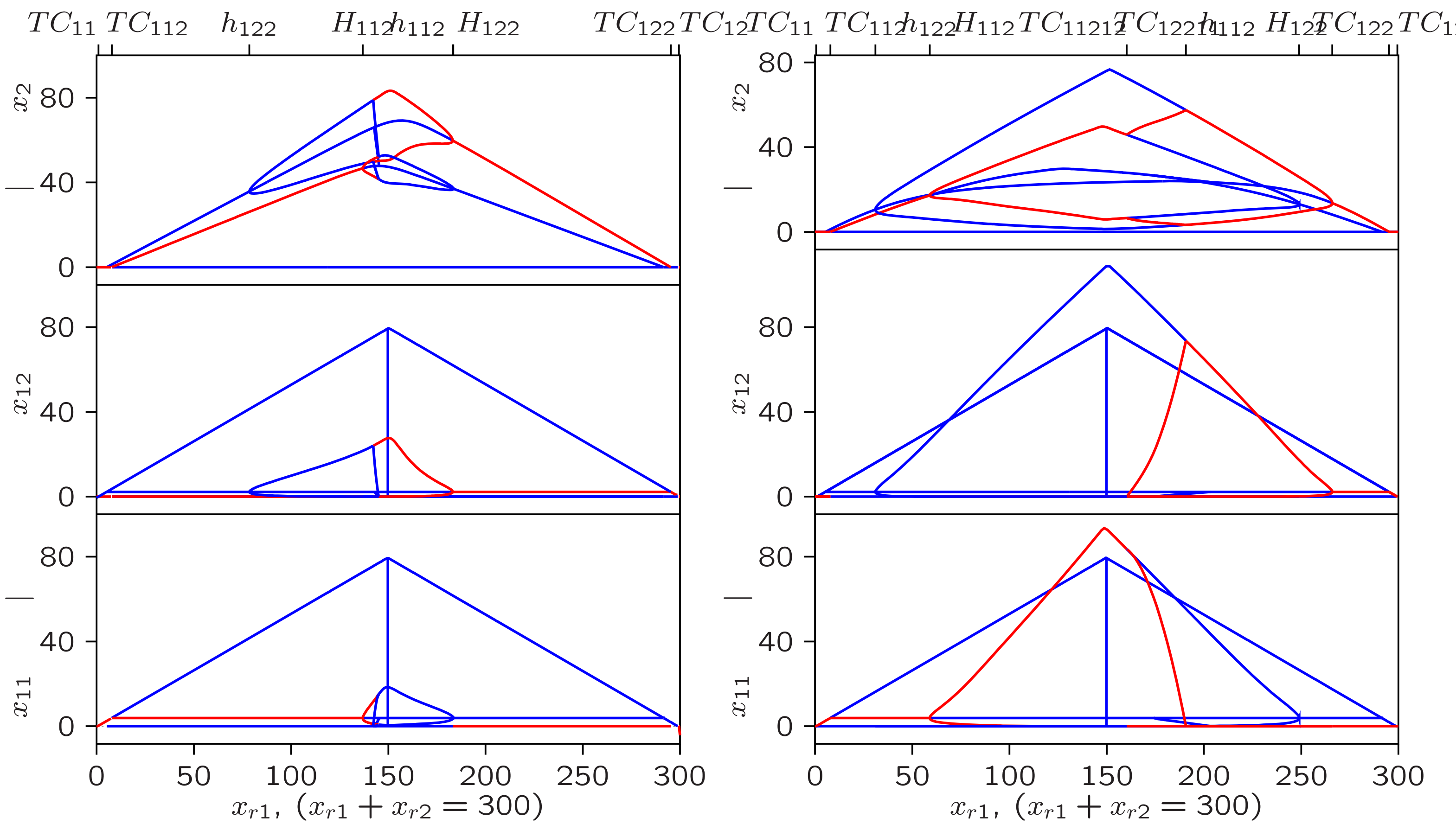
Food web: *COM-model* versus *PER-model*:

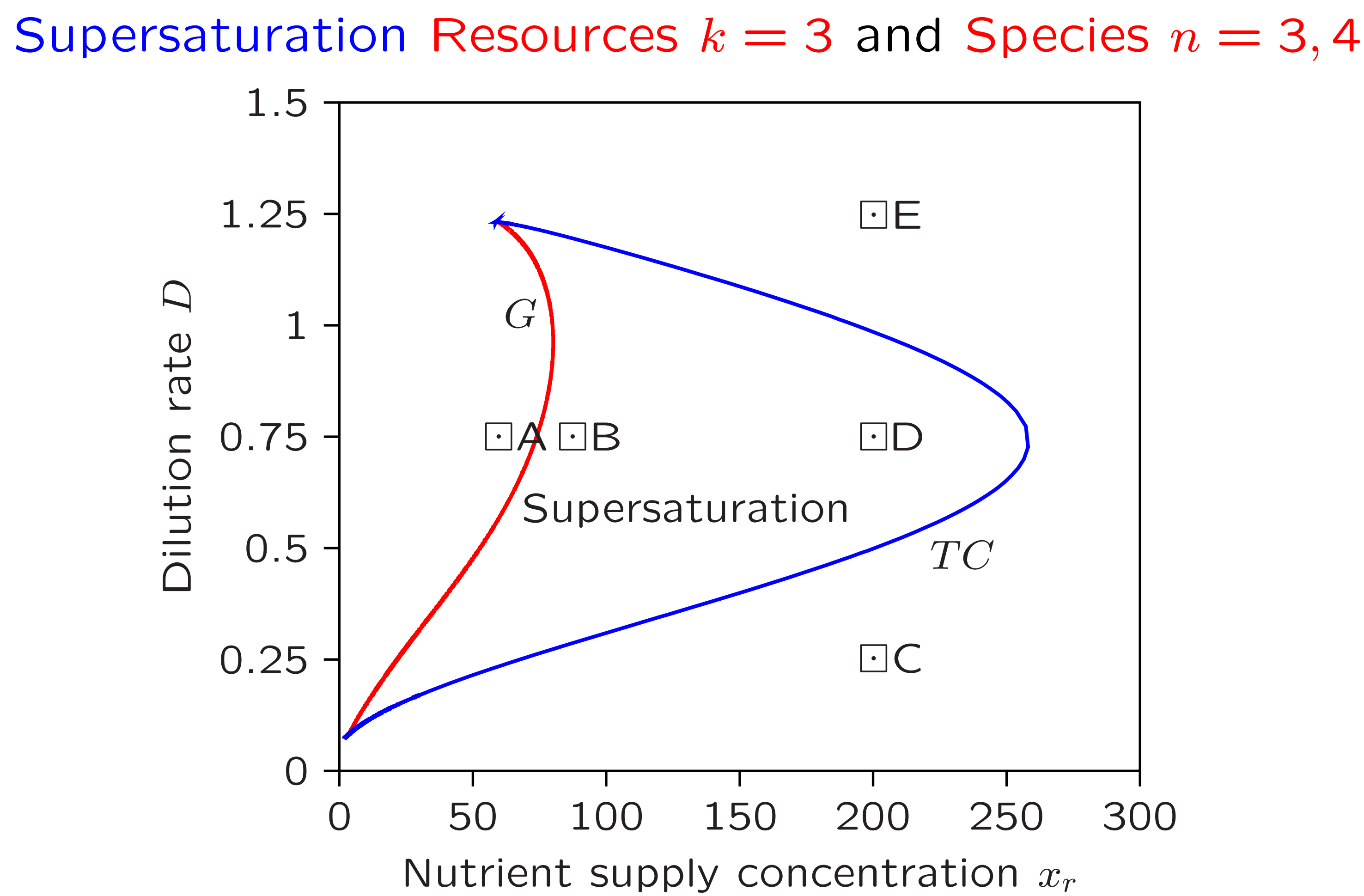
$x_{r1} + x_{r2} = 20$

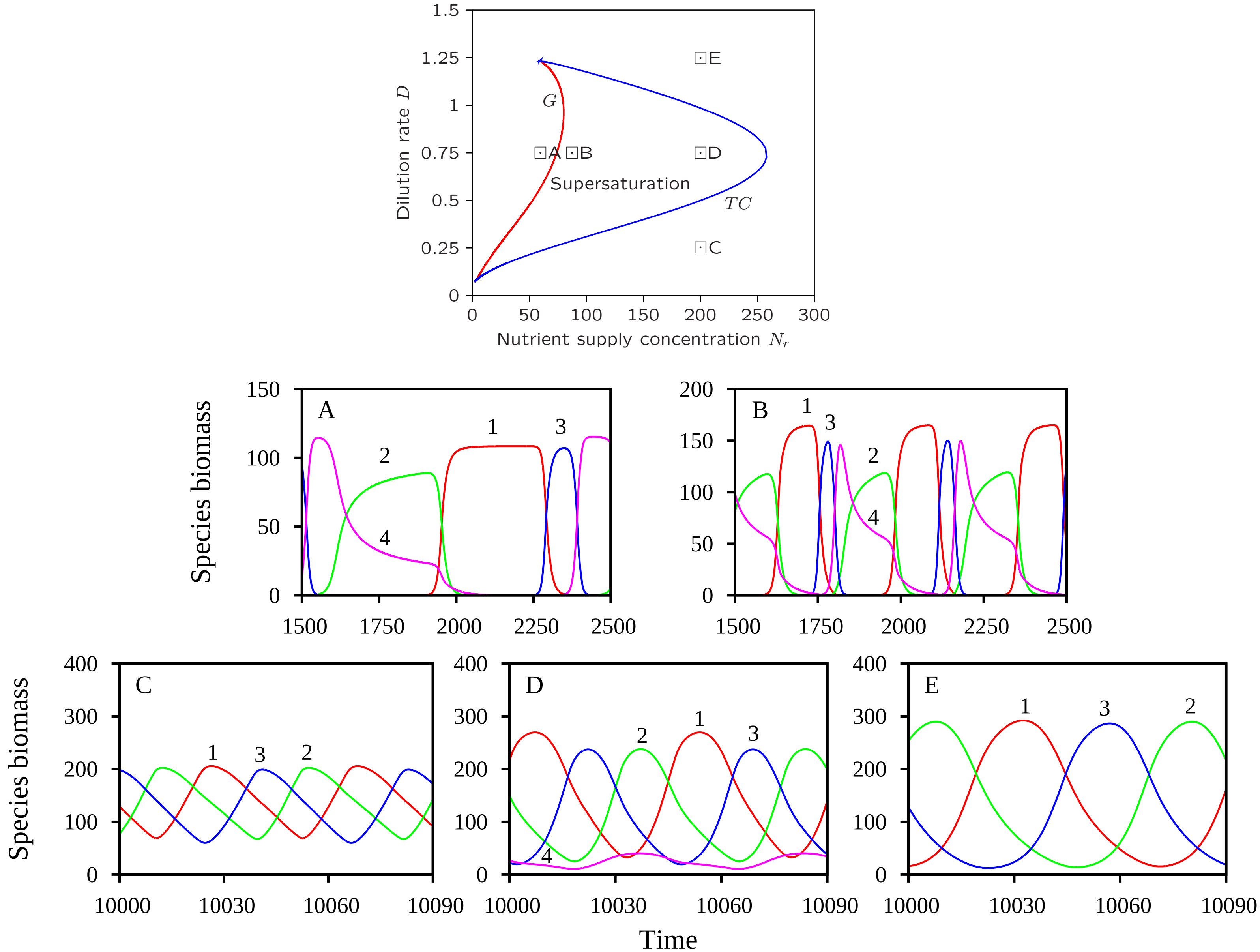


Food web: *COM-model* versus *PER-model*:

$x_{r1} + x_{r2} = 300$




Supersaturation Resources $k = 3$ and Species $n = 3, 4$
Dilution rate D
Nutrient supply concentration x_r
1.5
1.25
1
0.75
0.5
0.25
0
0
50
100
150
200
250
300
G
TC
Supersaturation
⊡A
⊡B
⊡C
⊡D
⊡E



Dilution rate D
Nutrient supply concentration N_r
G
TC
Supersaturation
A
B
C
D
E
Species biomass
Time
1
2
3
4

Conclusions (*Modelling, Analysis*)

- The most prominent approach to analyse the model resources is the graphical method by Tilman which was represented in resource quarter plane plots

- We developed a framework for analysing resource competition models based on bifurcation theory
  Same techniques from modelling and analysis techniques based on bifurcation theory can be used
  Computer packages: auto and MatCont running under Matlab

- We reanalyzed the problem of competition of two species for two resources in a chemostat and thereafter with a top-predator

Conclusions (*Ecology*)

- One resource: Competitive exclusion
  Two resources: One prey wins or other prey wins or Stable Coexistence or Bistability

- Introduction of a second substitutable resource allows for the coexistence of the two prey populations

- Introduction of second substitutable resource can reverse the outcome of the completion between the prey under same environmental conditions (Bottom up)

Conclusions (*Ecology*)

- Introduction of predator gives oscillatory dynamics and "Paradox of Enrichment"

- Emergence of predator-prey cycles gives strong deviations between predictions of competition based on Liebig's minimum law and on complementary resources

- The versatile effects emphasize how strong the predator affects the outcome of competition between prey populations beyond simple predator-mediated coexistence (Top down)

- Confirmed of Paine's postulate (1966) : "Local species diversity is directly related to the efficiency with which predators prevent monopolisation of the major environmental requisities by one species"

Literature

Kooi BW, Kooijman SALM, 2000. Invading species can stabilize simple trophic systems *Ecological Modelling*, **(133)**, 57–72.

Dutta PS, Kooi BW, Feudel U (2014) Multiple resource limitation: non-equilibrium coexistence of species in a competition model using a synthesizing unit, *Theoretical Ecology*, **(7)**, 407–421.

Kooi BW, PS Dutta, Feudel U (2013) Resource competition: A bifurcation theory approach, *Math Model Nat Pheno*, **(8)**, 165–185.

Dutta PS, Kooi BW, Feudel U (2017) The impact of a predator on the outcome of competition in the three-trophic food web, *Journal of Theoretical Biology*, **(417)**, 28–42.