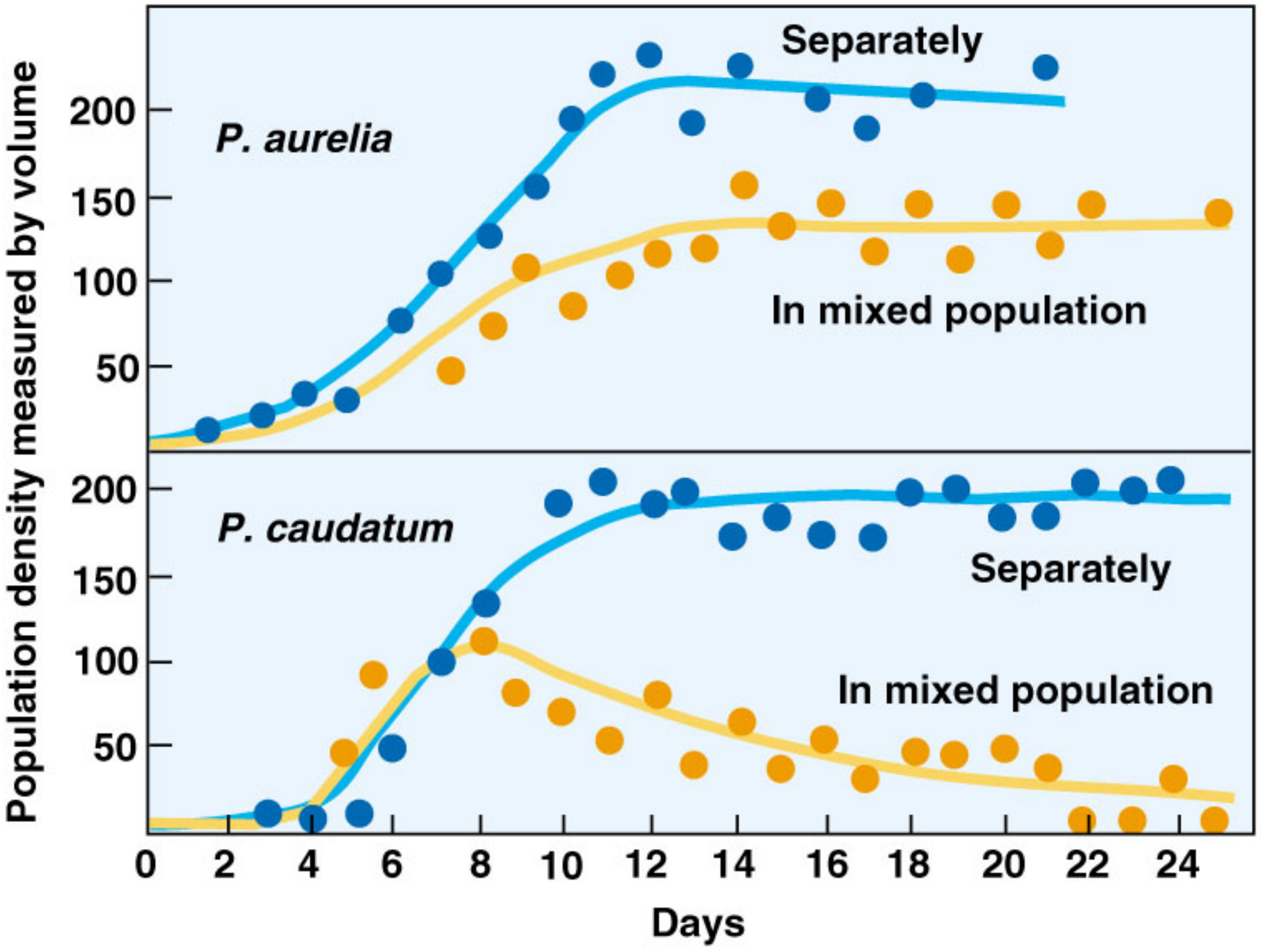
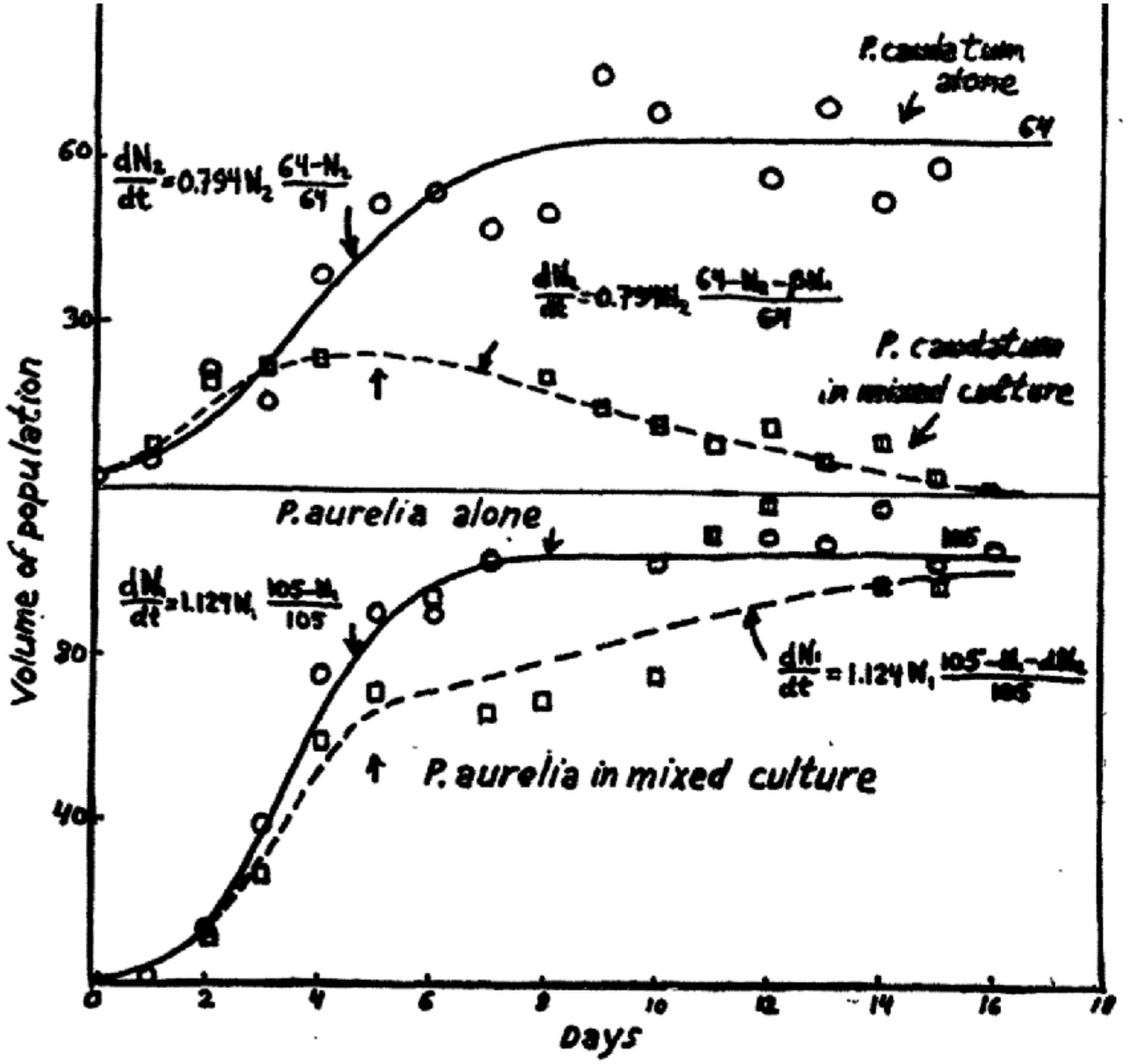
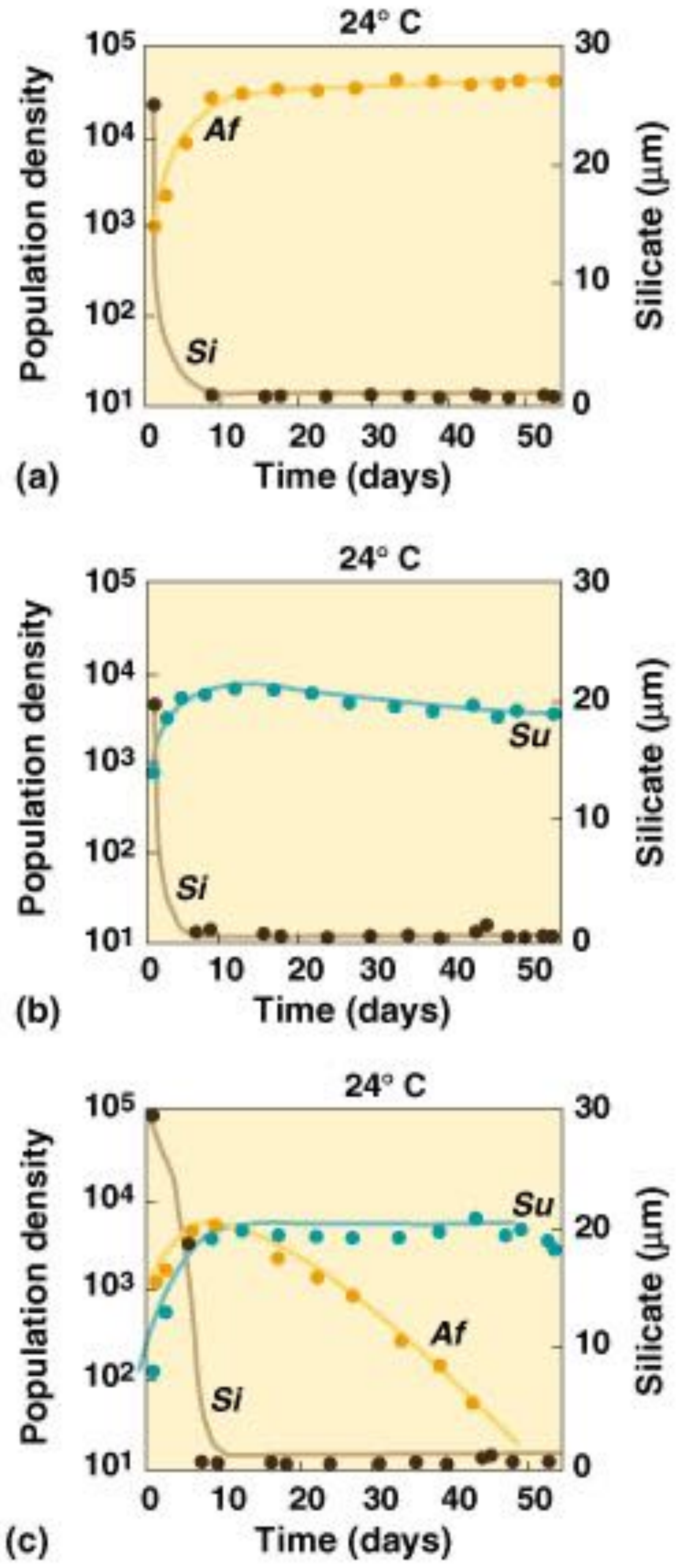
Chapter 9: Competition





From: Gause 1934

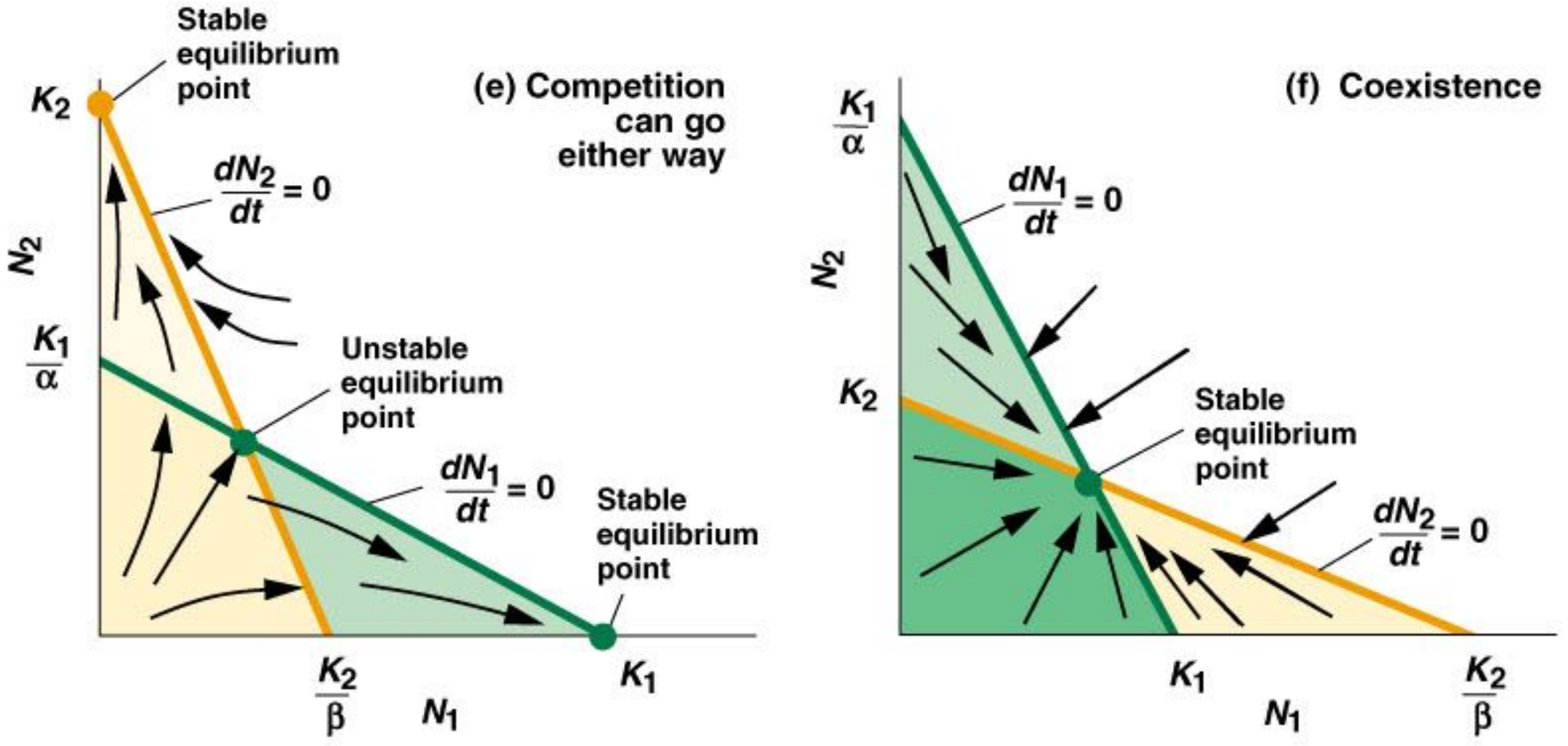
Competitive exclusion and co-existence

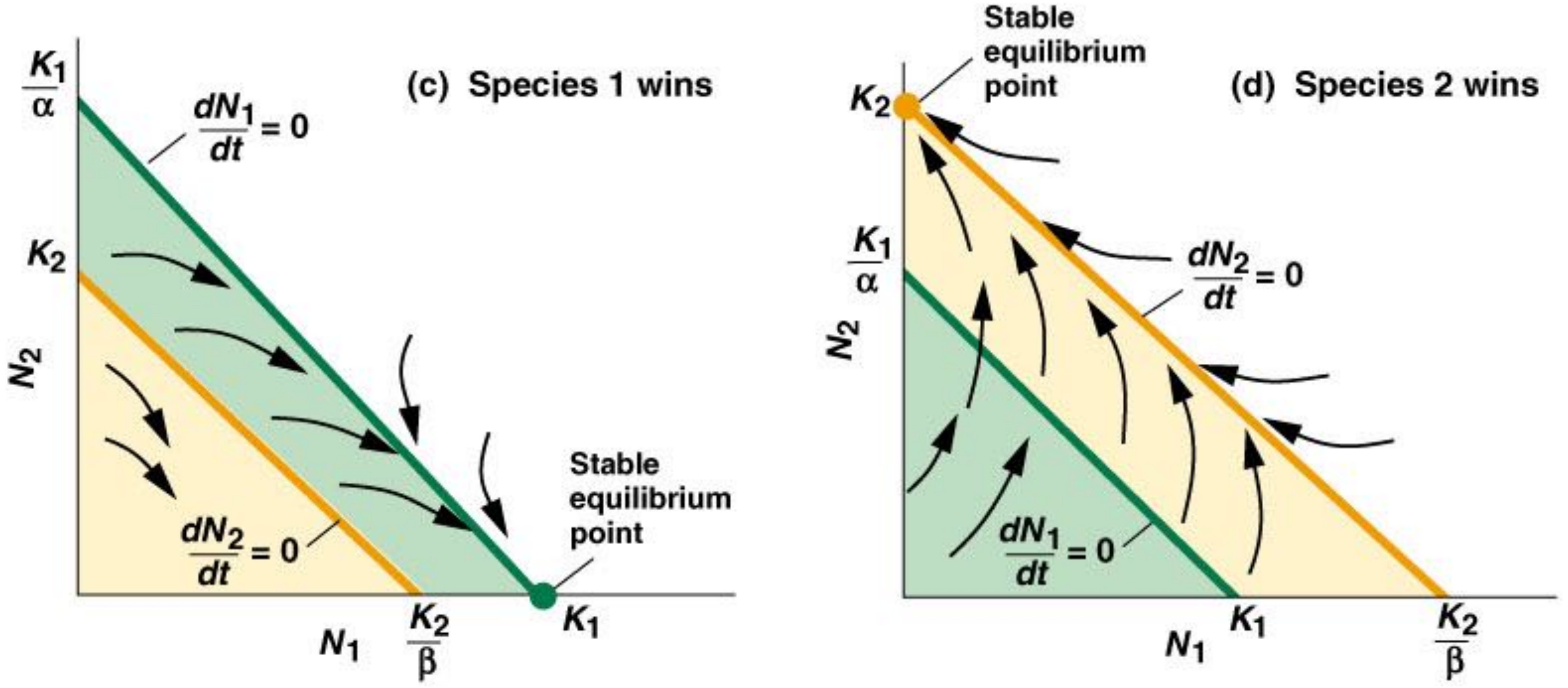


Asterionella formosa

Synedra ulna

Together





Competitive exclusion: several consumers using 1 resource

Closed system with fixed amount of resource *K*:

$$F = K - \sum_{i}^{n} e_i N_i \ , \qquad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(b_i F - d_i) \ , \quad \text{for } i = 1, 2, \ldots, n \ , \ R_{0_i} = \frac{b_i K}{d_i}$$

Since for each species $\bar{F} = d_i/b_i = K/R_{0_i}$ they have to exclude each other

$$b_i \bar{F} - d_i > 0 \quad \text{or} \quad b_i \frac{d_1}{b_1} - d_i > 0 \quad \text{or} \quad \frac{b_i}{d_i} \frac{d_1}{b_1} > 1 \quad \text{or} \quad \frac{b_i}{d_i} > \frac{b_1}{d_1} \ ,$$

Competitive exclusion: several consumers using 1 resource

Closed system with fixed amount of resource K:

$$F = K - \sum_{i}^{n} e_i N_i \ , \qquad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(b_i F - d_i) \ , \quad \text{for } i = 1, 2, \ldots, n \ ,$$

Carrying capacity of one species:

$$K_i = \bar{N}_i = \frac{K - d_i/b_i}{e_i} = \frac{K(1 - 1/R_{0_i})}{e_i}$$

Nullclines for 2-D closed system

$$F = K - \sum_{i}^{n} e_i N_i \ , \qquad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(b_i F - d_i) \ , \quad \text{for } i = 1, 2, \ldots, n \ , \qquad (9.1)$$

$$F = K - e_1N_1 - e_2N_2$$

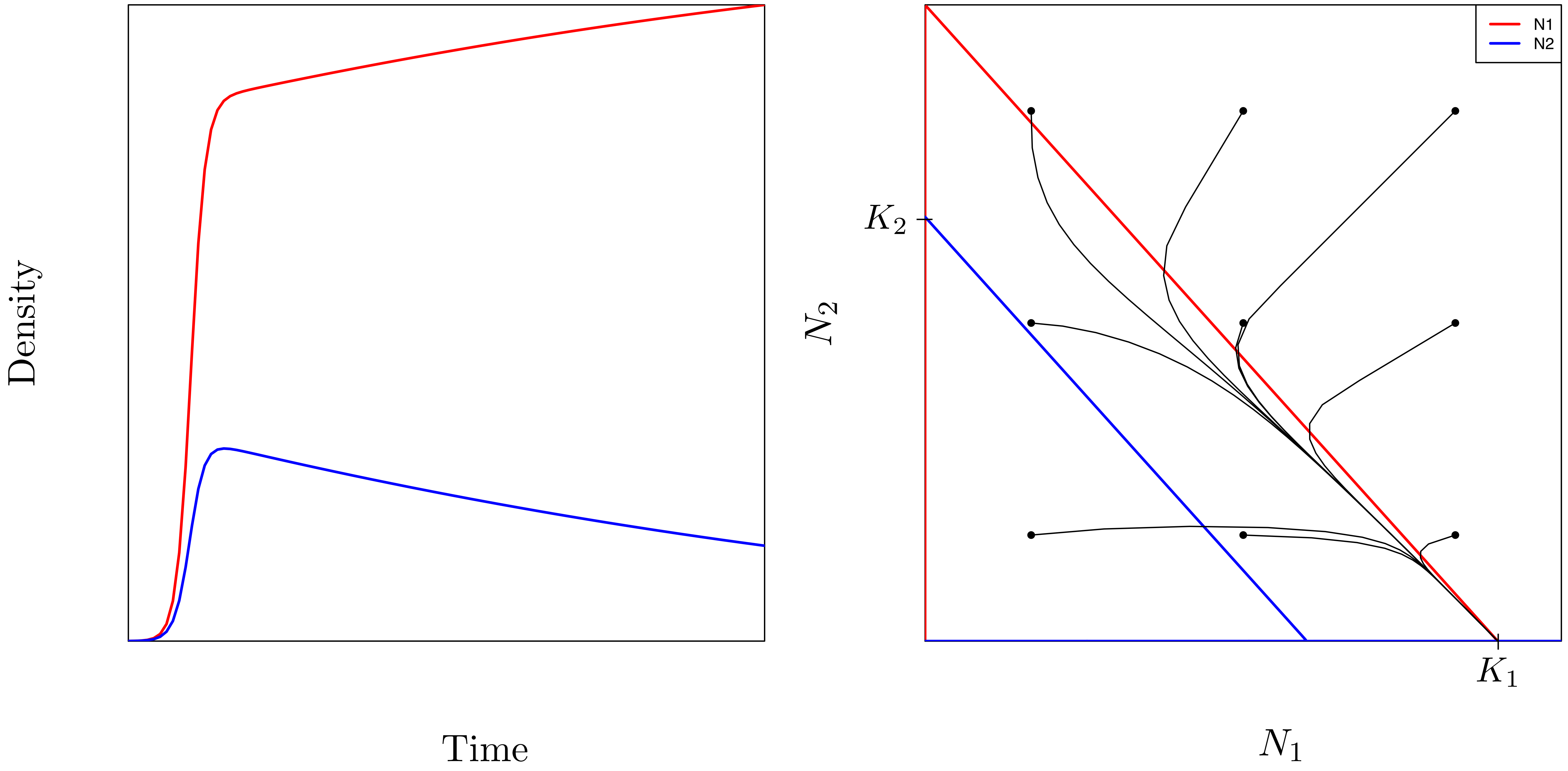
$$N_2 = \frac{K - d_1/b_1}{e_2} - \frac{e_1}{e_2} N_1 = \frac{K(1 - 1/R_{0_1})}{e_2} - \frac{e_1}{e_2} N_1 \quad \text{and} \quad N_2 = \frac{K(1 - 1/R_{0_2})}{e_2} - \frac{e_1}{e_2} N_1 \ , \ (9.4)$$

Nullclines for 2-D closed system

$$F = K - \sum_{i}^{n} e_i N_i \ , \qquad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(b_i F - d_i) \ , \quad \text{for } i = 1, 2, \ldots, n \ , \qquad (9.1)$$

$$F = K - e_1 N_1 - e_2 N_2$$

$$N_2 = \frac{K - d_1/b_1}{e_2} - \frac{e_1}{e_2} N_1 = \frac{K(1 - 1/R_{0_1})}{e_2} - \frac{e_1}{e_2} N_1 \quad \text{and} \quad N_2 = \frac{K(1 - 1/R_{0_2})}{e_2} - \frac{e_1}{e_2} N_1 \ , \ (9.4)$$



Competitive exclusion when birth rate is saturated (closed)

$$F = K - \sum_i^n e_i N_i \ , \quad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i \left(\frac{b_i F}{h_i + F} - d_i \right)$$

Carrying capacity of one species, and the corresponding steady state for *F*:

$$\bar{N}_i = \frac{K(R_{0_i} - 1) - h_i}{e_i(R_{0_i} - 1)} \qquad \bar{F} = \frac{h_i}{R_{0_i} - 1}$$

Thus the consumer with the lowest h_i over R_0-1 ratio depletes the resource most.

At the lowest $\bar{F}$ the other species cannot invade:

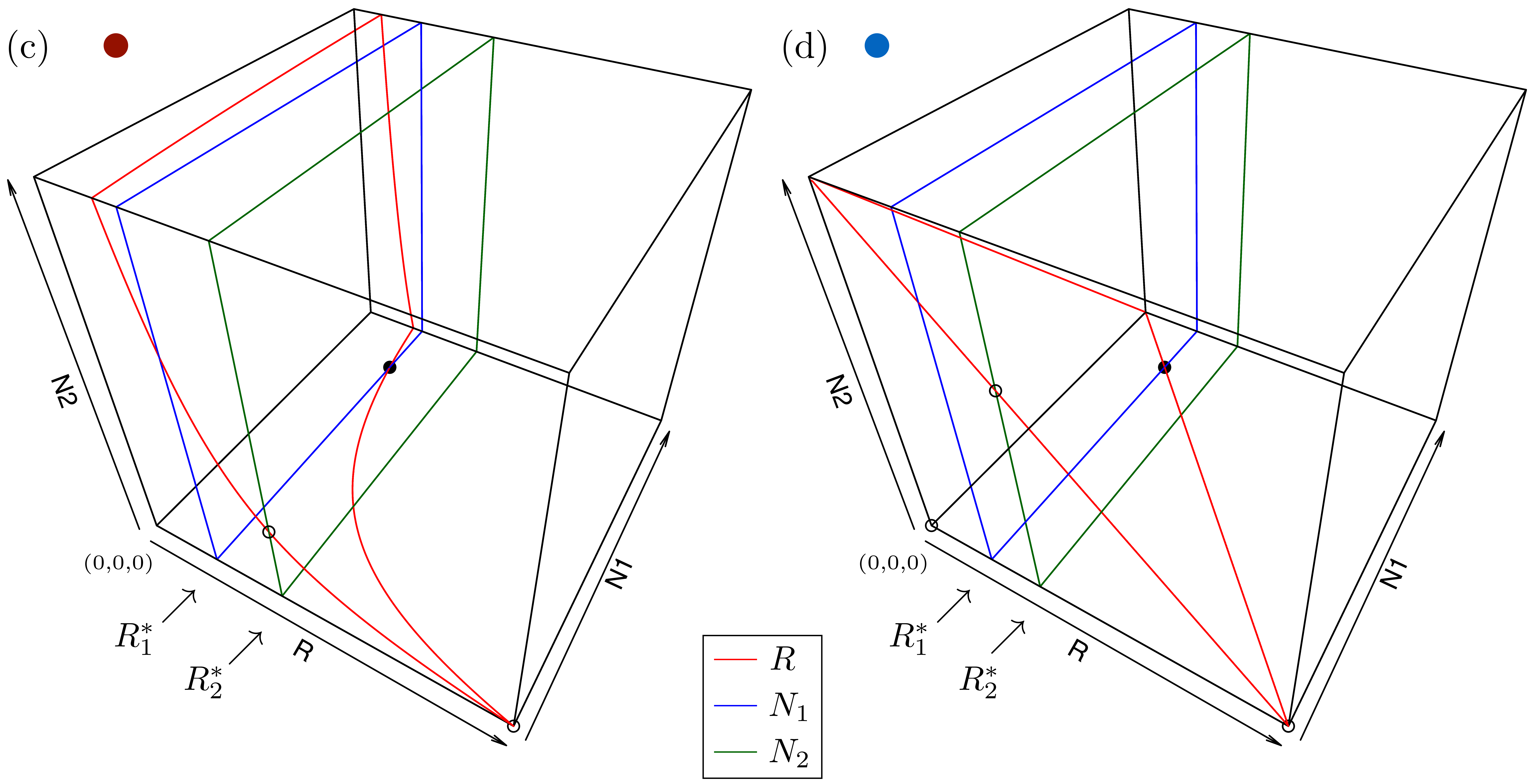
$$\frac{b_j \bar{F}}{h_j + \bar{F}} > d_j \quad \text{or} \quad \bar{F} > \frac{h_j}{R_{0_j} - 1}$$

Competition in open systems (one resource)

- $$\frac{\mathrm{d}R}{\mathrm{d}t} = s - dR - R\sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\frac{b_i c_i R}{h_i + c_i R} - d_i\right) \quad \text{or}$$
  $$\frac{\mathrm{d}R}{\mathrm{d}t} = s - dR - R\sum_{i=1}^{n} \frac{c_i N_i}{h_i + R} \quad \text{with} \quad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\frac{b_i R}{h_i + R} - d_i\right) \quad \text{or}$$
- $$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - R\sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\frac{b_i c_i R}{h_i + c_i R} - d_i\right) \quad \text{or}$$
  $$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - R\sum_{i=1}^{n} \frac{c_i N_i}{h_i + R} \quad \text{with} \quad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\frac{b_i R}{h_i + R} - d_i\right) \ ,$$

Exclusion because

$$R_i^* = \frac{h_i/c_i}{R_{0_i} - 1} \quad \text{or} \quad R_i^* = \frac{h_i}{R_{0_i} - 1}\ , \quad \text{where} \quad R_{0_i} = \frac{b_i}{d_i}\ ,$$



(c)
(d)
N2
N1
R
(0,0,0)
R_1^*
R_2^*
R
N_1
N_2

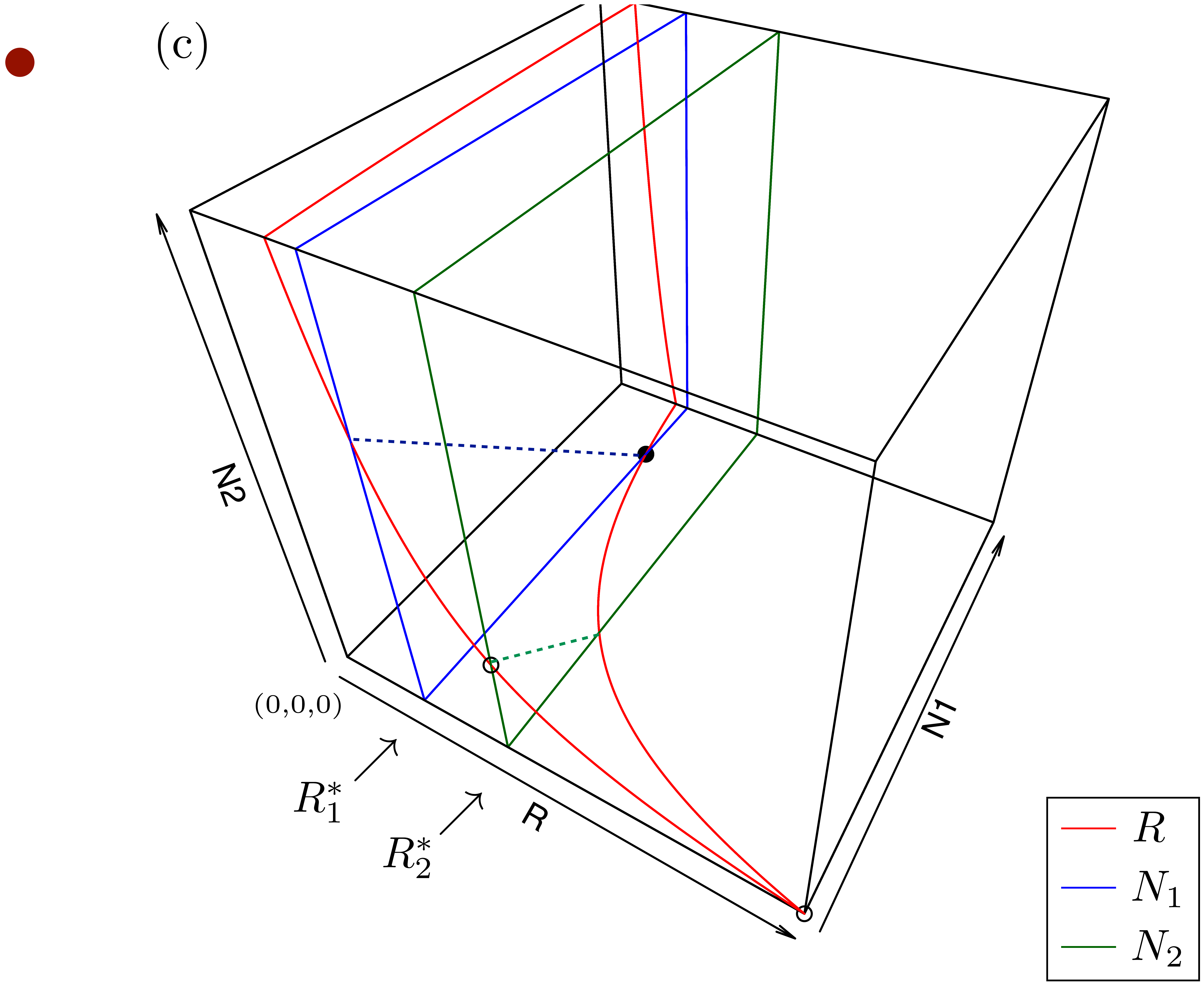
Quasi steady state to reveal interactions: resource with source

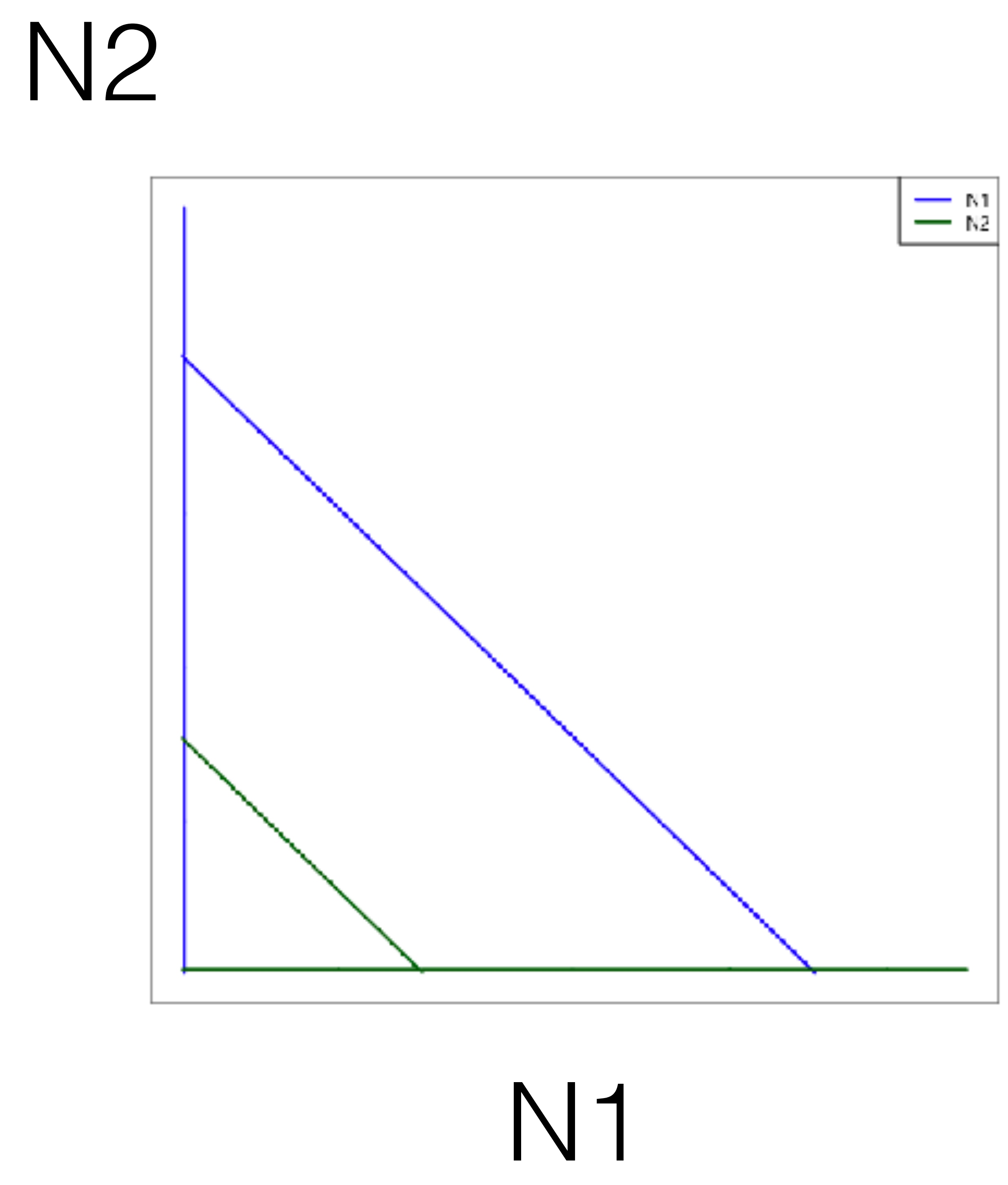
- $$\frac{\mathrm{d}R}{\mathrm{d}t} = s - dR - R\sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\frac{b_i c_i R}{h_i + c_i R} - d_i\right)$$

$$\hat{R} = \frac{s}{d + \sum c_i N_i}$$

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\Big(\frac{b_i s}{s + (h_i/c_i)(d + \sum c_j N_j)} - d_i\Big) = N_i\Big(\frac{\beta_i}{1 + \sum N_j/k_j} - d_i\Big)$$

$$K_i = \frac{s}{h_i}\Big(R_{0_i} - 1\Big) - \frac{d}{c_i} = \frac{s}{c_i R_i^*} - \frac{d}{c_i}$$


(c)
N2
(0,0,0)
R_1^*
R_2^*
R
N1
R
N_1
N_2


N2
N1

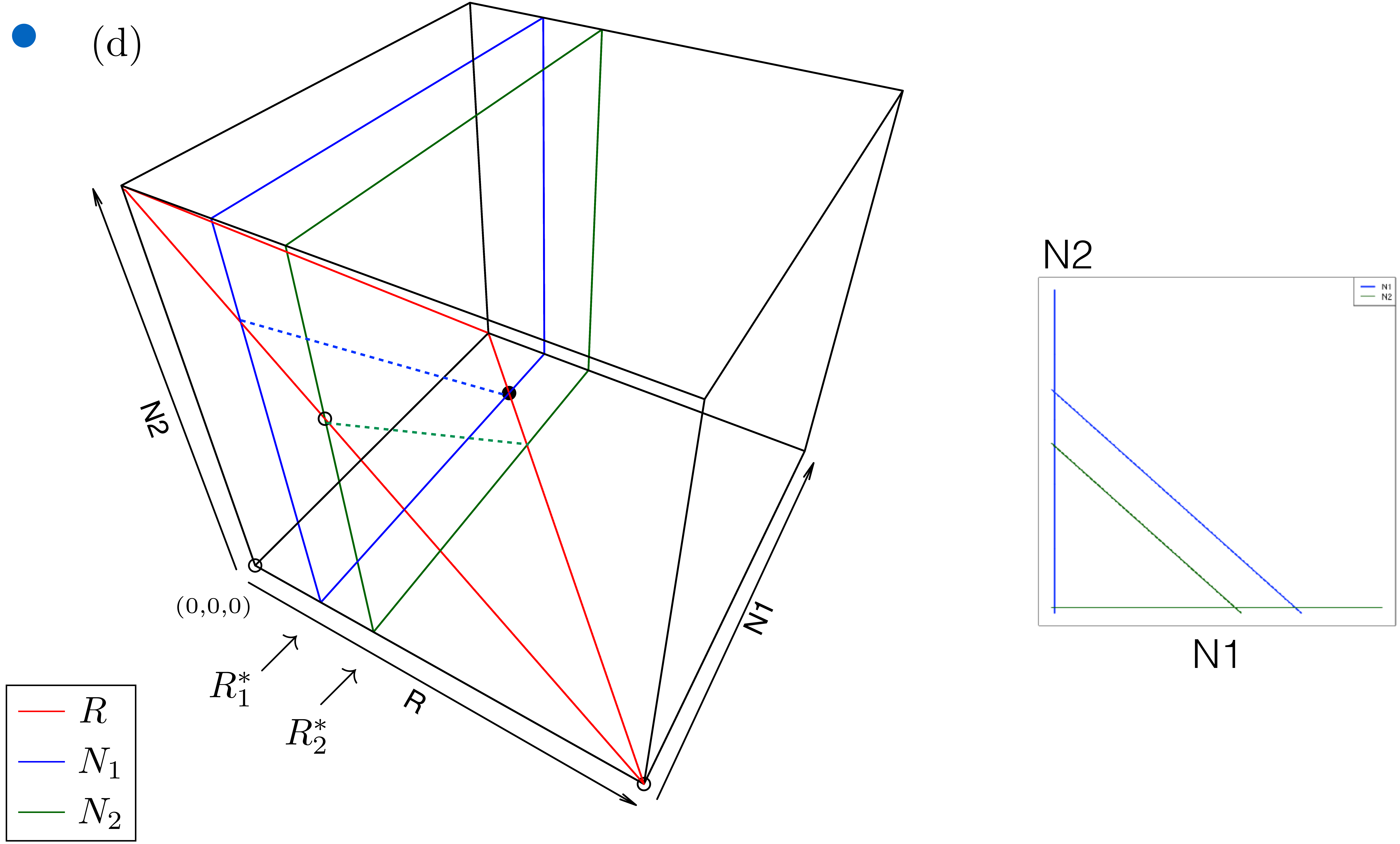
Quasi steady state to reveal interactions: logistic resource

- $$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - R\sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\frac{b_i c_i R}{h_i + c_i R} - d_i\right)$$

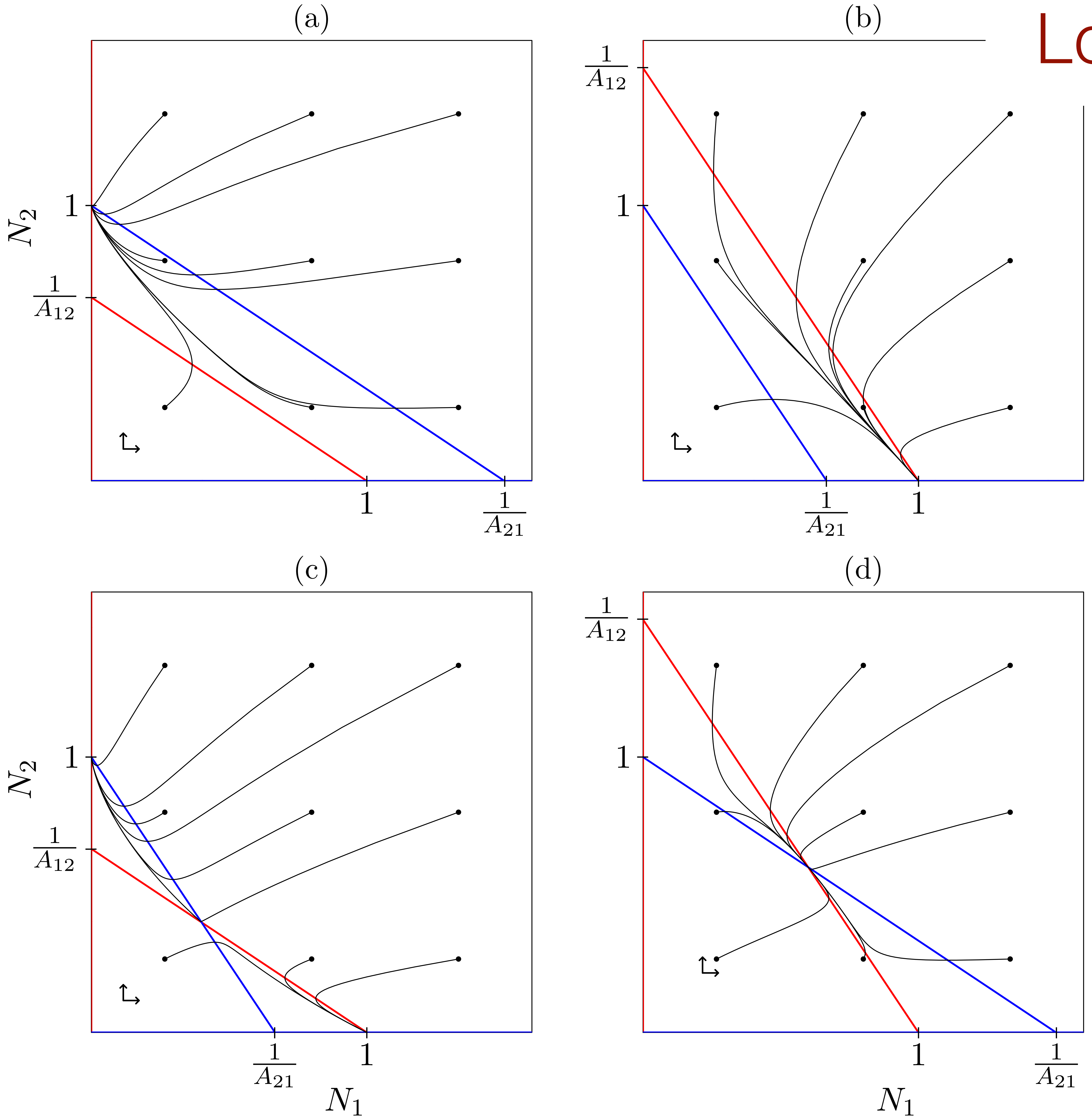
$$\hat{R} = K\left(1 - \frac{1}{r}\sum c_i N_i\right)$$

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\frac{b_i(r - \sum c_j N_j)}{(h_i/c_i)(r/K) + r - \sum c_j N_j} - d_i\right)$$

$$\bar{N}_i = \frac{r}{c_i}\left(1 - \frac{R_i^*}{K}\right)$$


(d)
N2
(0,0,0)
R_1^*
R_2^*
R
N1
R
N_1
N_2
N2
N1
N1
N2

Lotka-Volterra competition model



$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i N_i \Big(1 - \sum_{j=1}^{n} A_{ij} N_j\Big)$$

$$N_2 = \frac{1}{A_{12}} - \frac{A_{11}}{A_{12}}\ N_1 = \frac{1}{A_{12}}\ (1 - N_1)$$

$$N_2 = \frac{1}{A_{22}} - \frac{A_{21}}{A_{22}}\ N_1 = (1 - A_{21} N_1)$$

Several consumers on two substitutable resources

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \left(\beta_i \, \frac{\sum_j c_{ij} R_j}{h_i + \sum_j c_{ij} R_j} - \delta_i\right) N_i \ , \qquad \frac{\mathrm{d}R_j}{\mathrm{d}t} = s_j - d_j R_j - \sum_i c_{ij} N_i R_j$$

Consumer nullcline depends on resources only:

$$R_2 = \frac{h_i}{c_{i2}(R_{0_i} - 1)} - \frac{c_{i1}}{c_{i2}} \ R_1$$

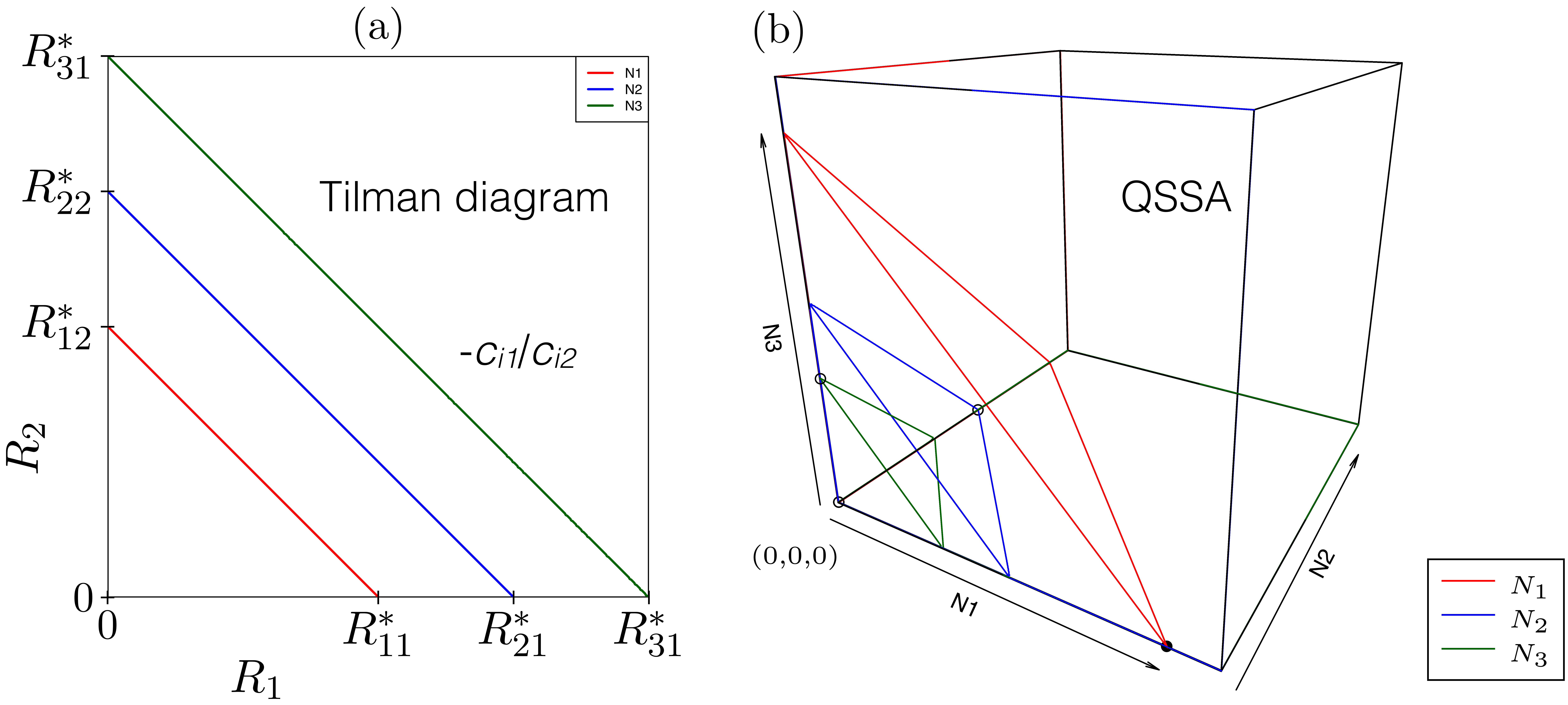
Straight line with slope $-c_{i1}/c_{i2}$

where $R_{0i} = \beta_i/\delta_i$

Starting and ending at critical resource density: $R^*_{ij} = \frac{h_i}{c_{ij}(R_{0_i} - 1)}$

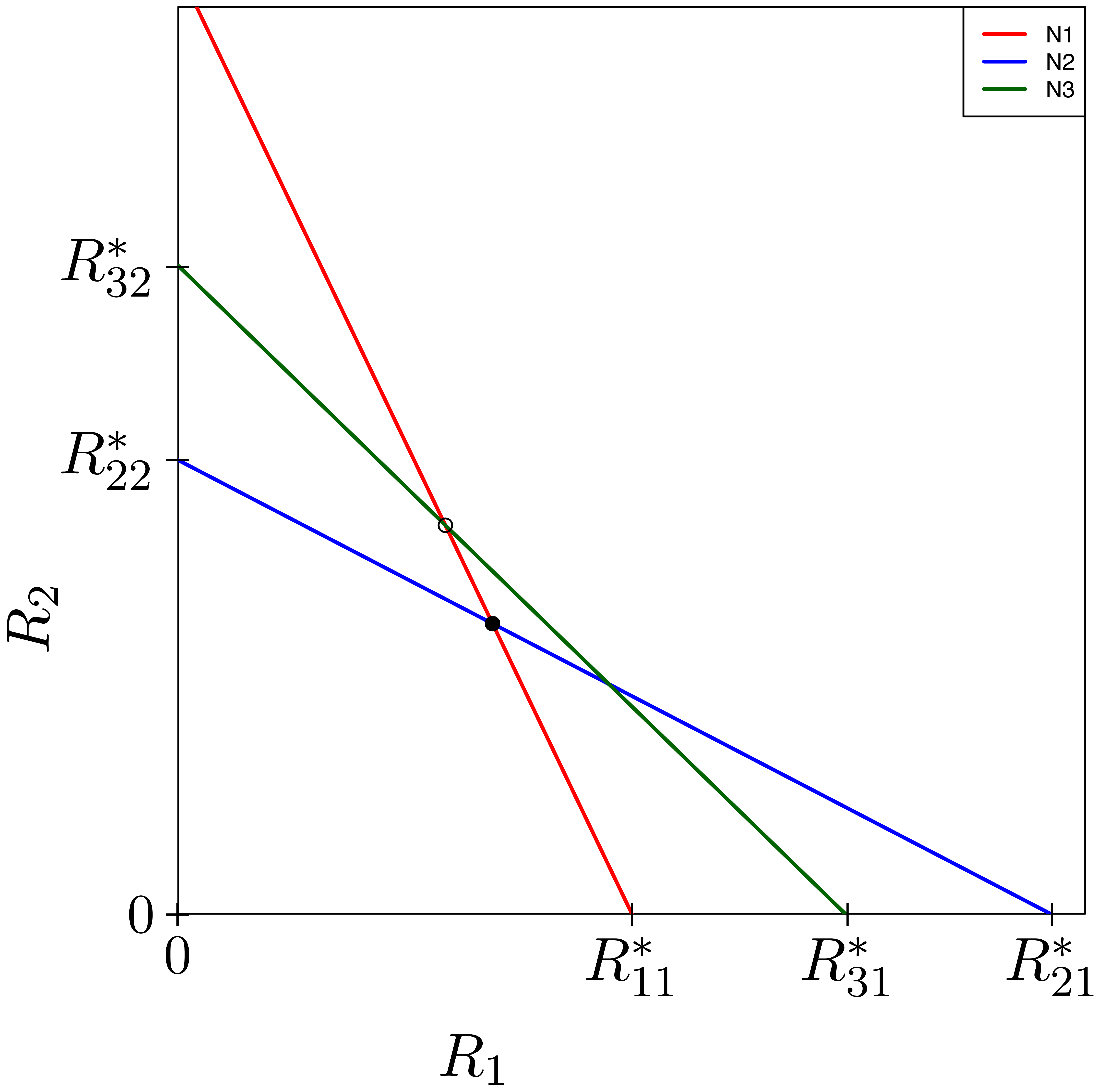
Simplified nullcline: $R_2 = R^*_{i2} - \frac{c_{i1}}{c_{i2}} \ R_1$

Several consumers with same diet c_{i1} and c_{i2}.



$h_1 < h_2 < h_3$

Several consumers having different diets c_{i1} and c_{i2}.



Generically only one intersection point between all nullclines:

maximally two co-existing species on two resources.

Lowest intersection not invadable by other consumers (but no guarantee that this is a steady state).

Essential resources

Several consumers:

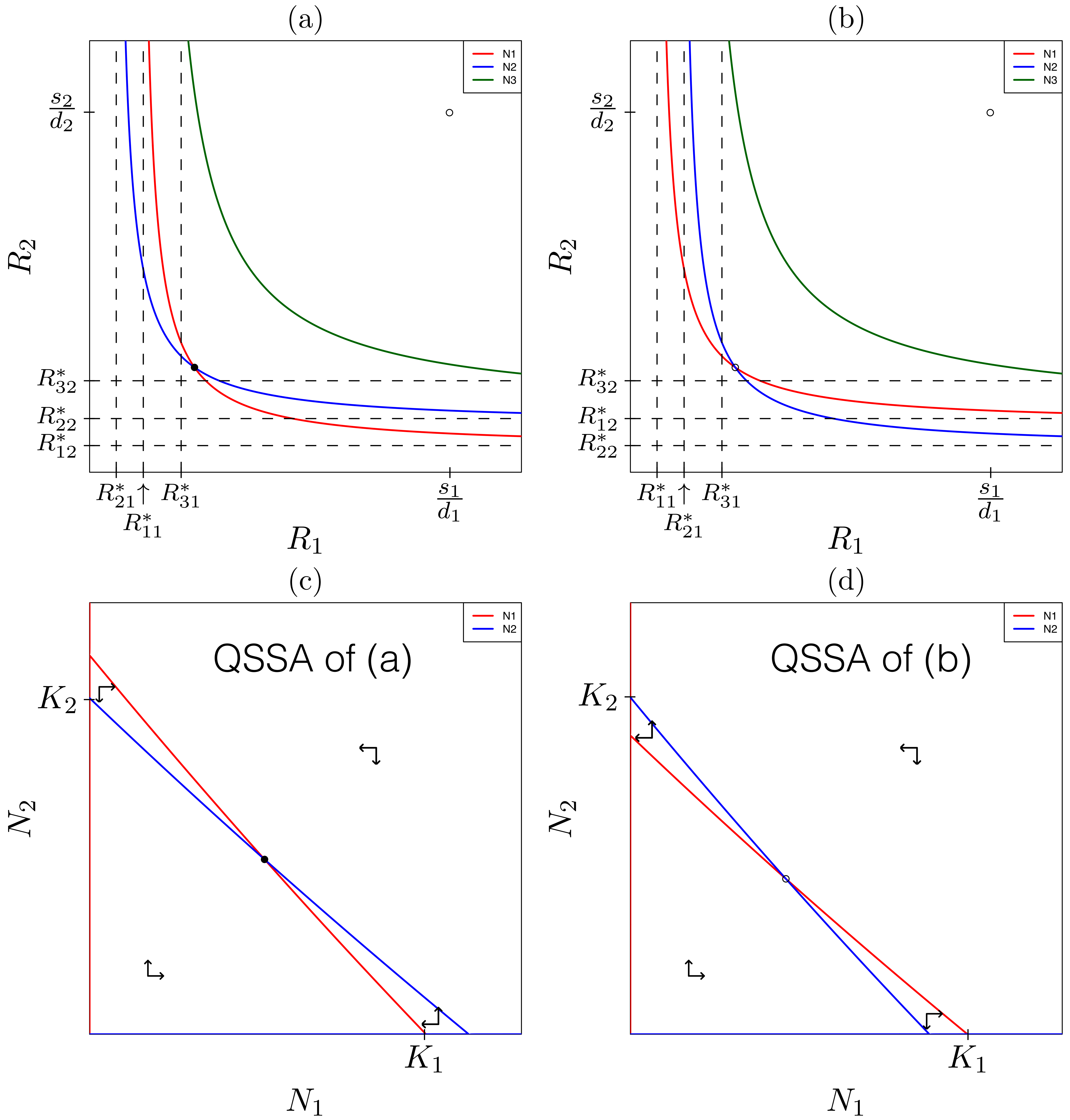
$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \left(\beta_i \prod_j \frac{c_{ij} R_j}{h_{ij} + c_{ij} R_j} - \delta_i\right) N_i \ , \qquad \frac{\mathrm{d}R_j}{\mathrm{d}t} = s_j - d_j R_j - \sum_i c_{ij} N_i R_j$$

Two consumers using two resources:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = \left(\beta_1 \frac{c_{11} R_1}{h_{11} + c_{11} R_1} \frac{c_{12} R_2}{h_{12} + c_{12} R_2} - \delta_1\right) N_1$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = \left(\beta_2 \frac{c_{21} R_1}{h_{21} + c_{21} R_1} \frac{c_{22} R_2}{h_{22} + c_{22} R_2} - \delta_2\right) N_2$$

Essential resources



$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = \left(\beta_1 \frac{c_{11}R_1}{h_{11}+c_{11}R_1} \frac{c_{12}R_2}{h_{12}+c_{12}R_2} - \delta_1\right) N_1$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = \left(\beta_2 \frac{c_{21}R_1}{h_{21}+c_{21}R_1} \frac{c_{22}R_2}{h_{22}+c_{22}R_2} - \delta_2\right) N_2$$

Asymptotes defined by letting

$$R_1 \to \infty \text{ or } R_2 \to \infty$$

$$c_{11} > c_{12},\ c_{22} > c_{21} \text{ and } c_{31} \simeq c_{32},$$

Local steepness defines stability