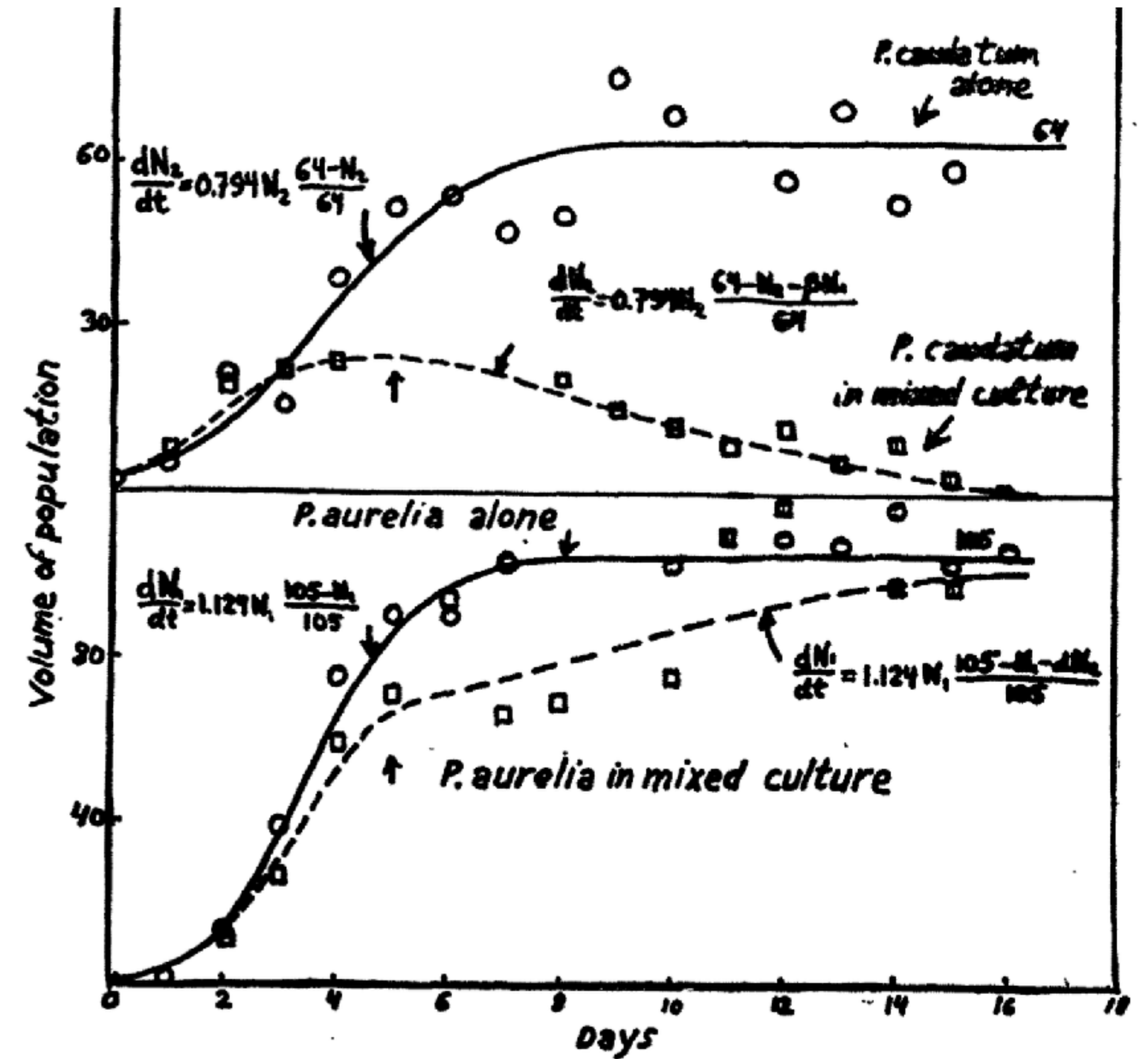
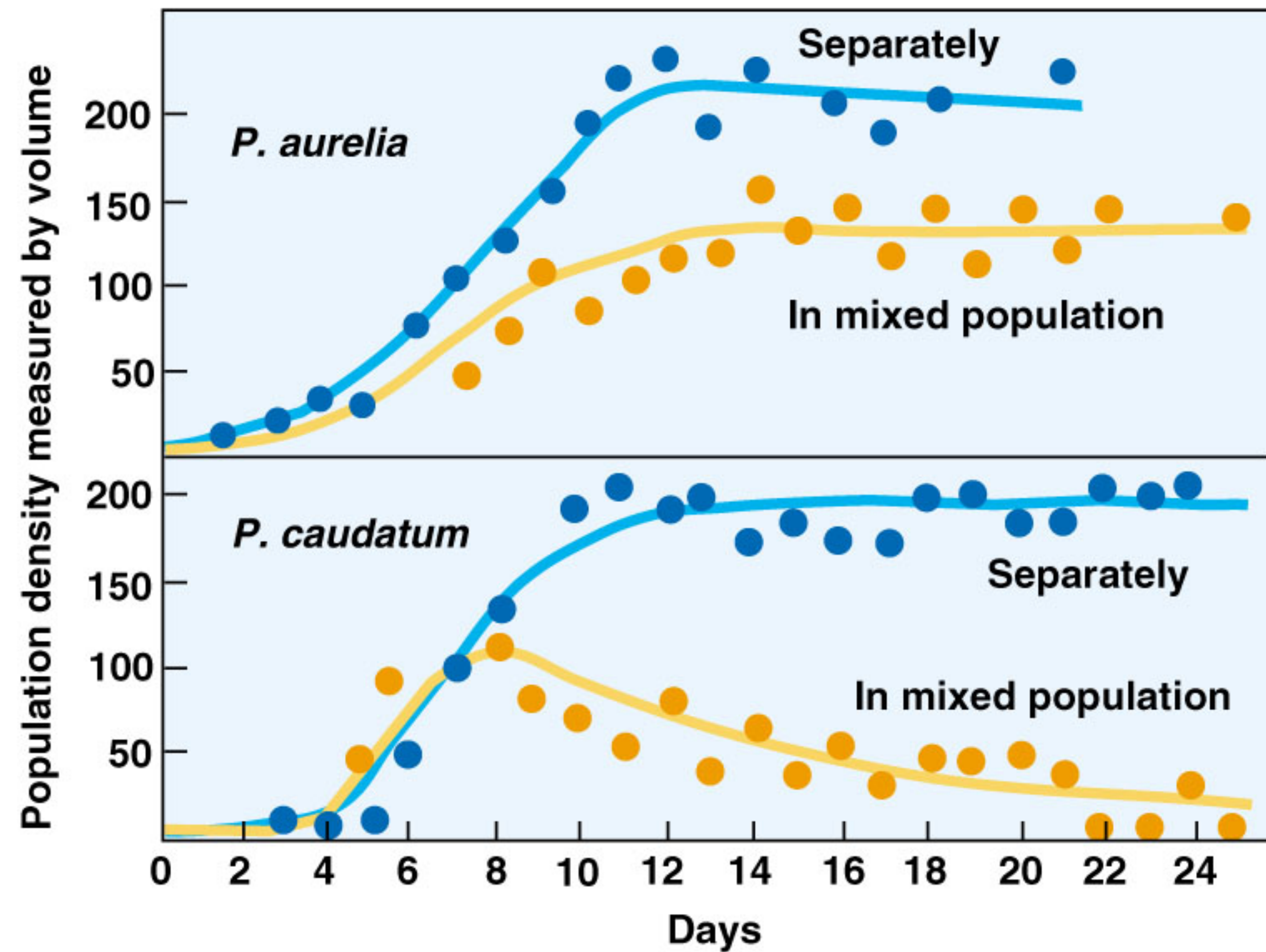


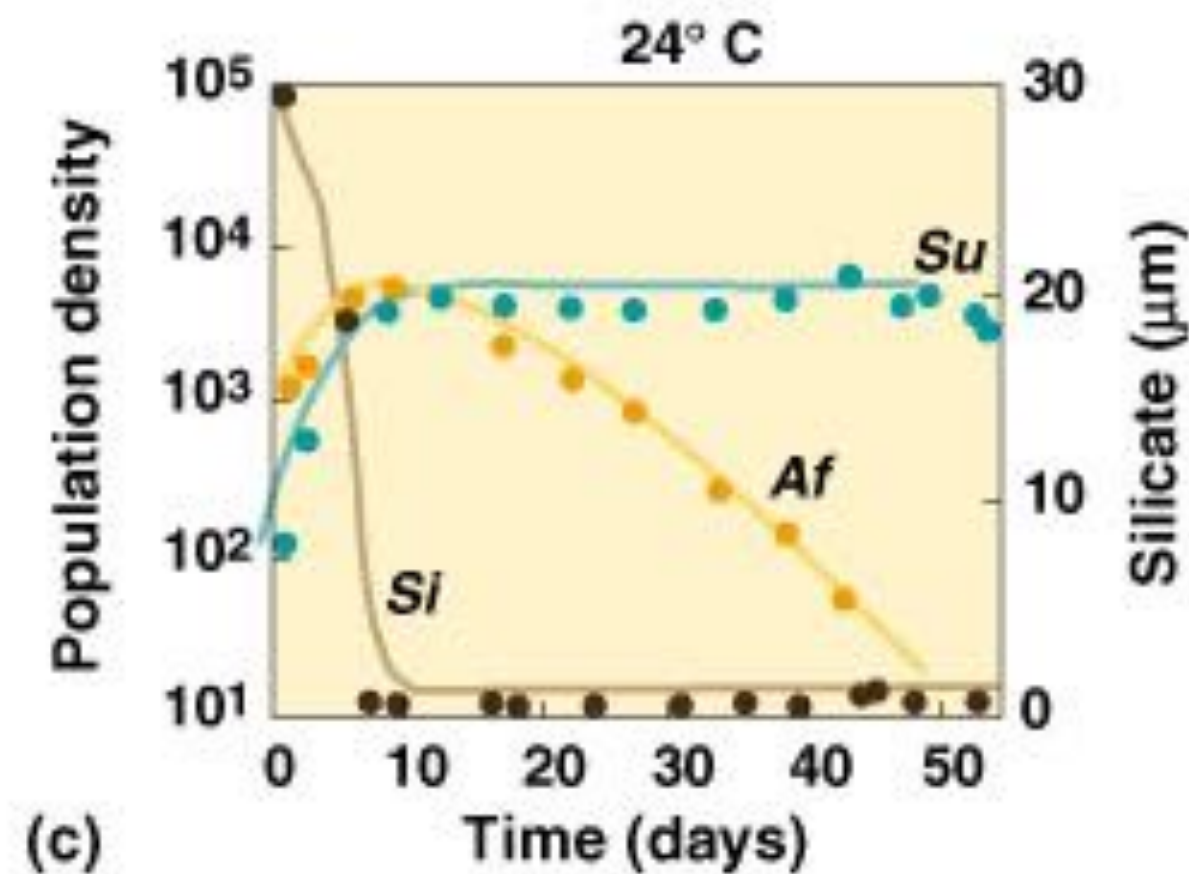
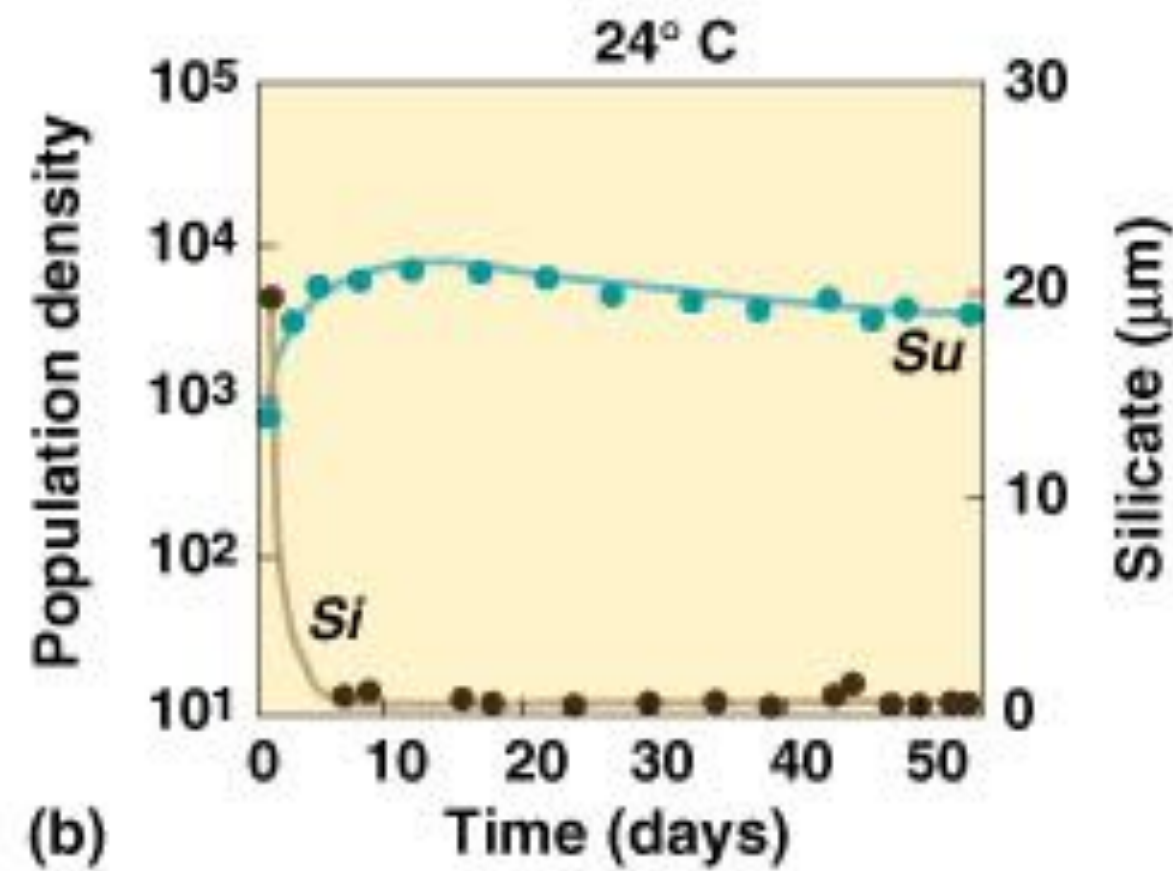
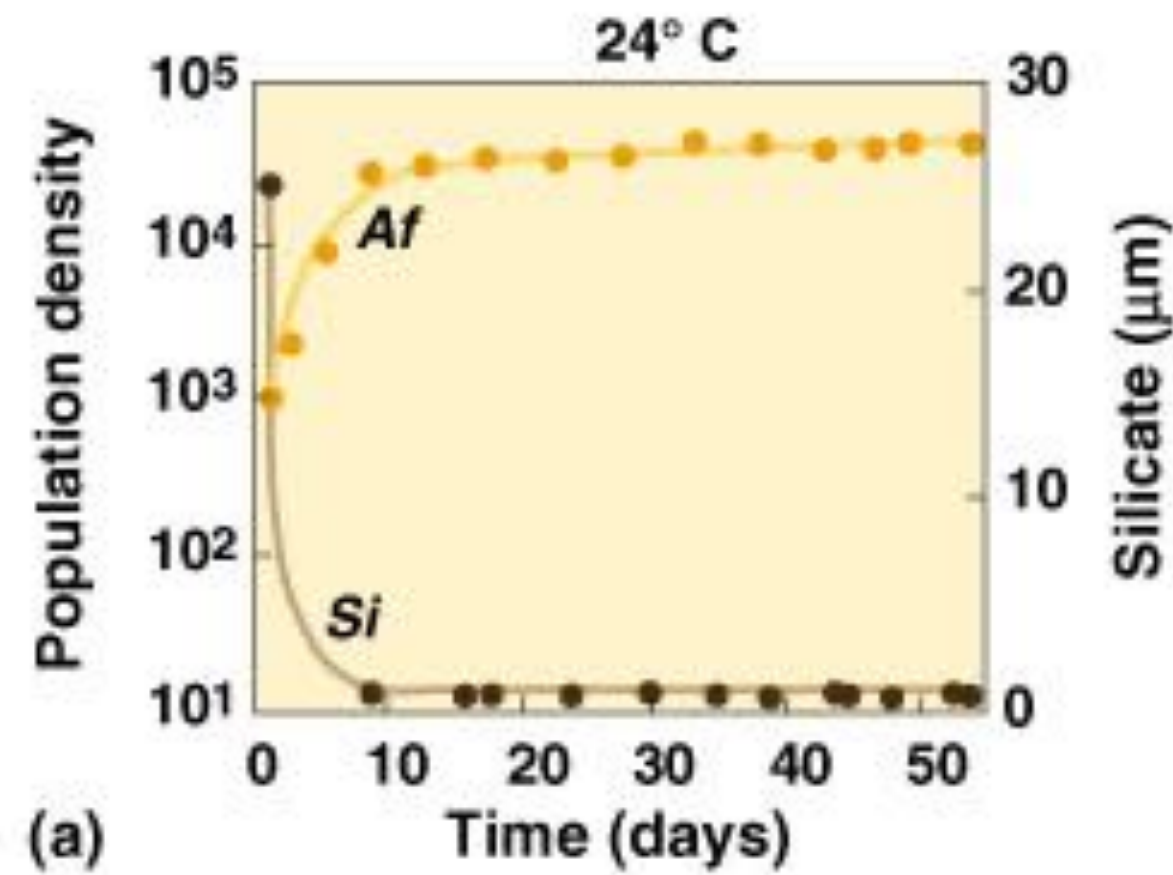
Chapter 9: Competition



From: Gause 1934

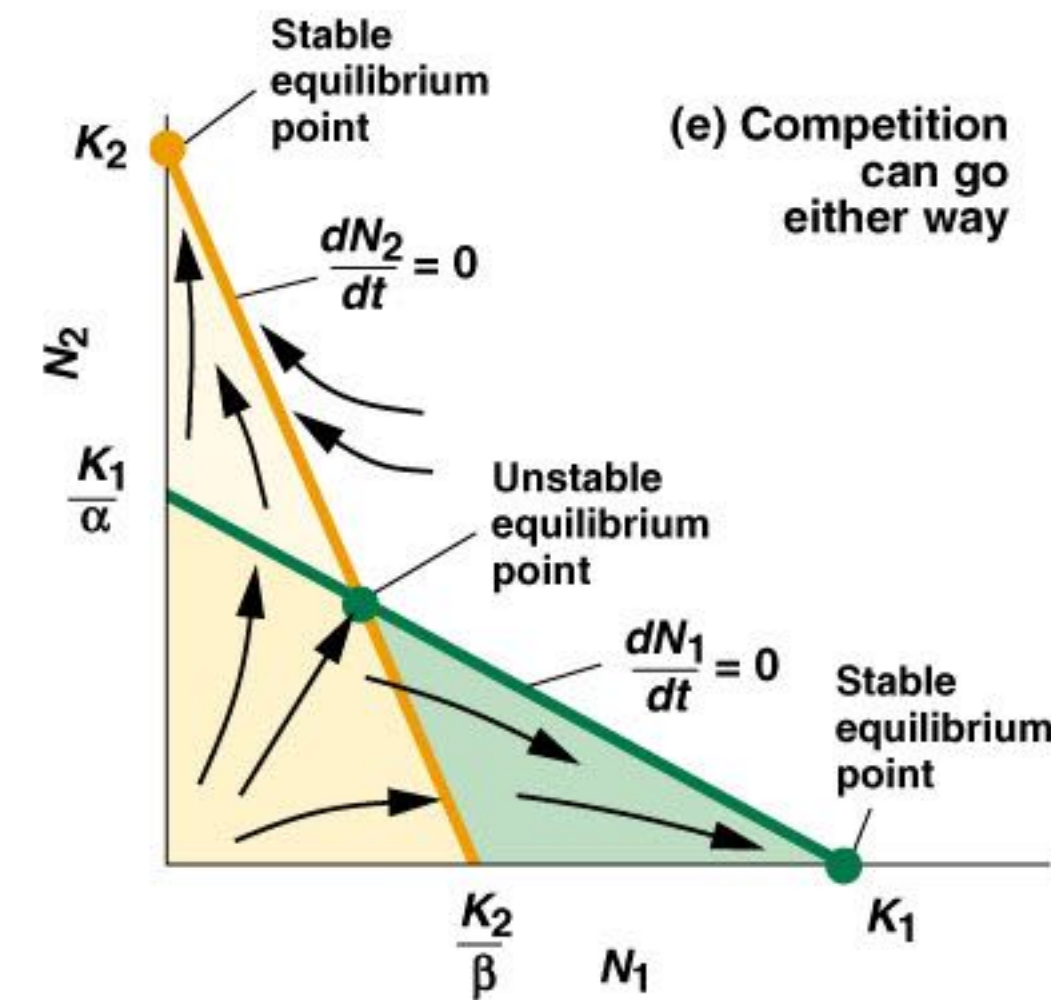
Competitive exclusion and co-existence

Asterionella formosa

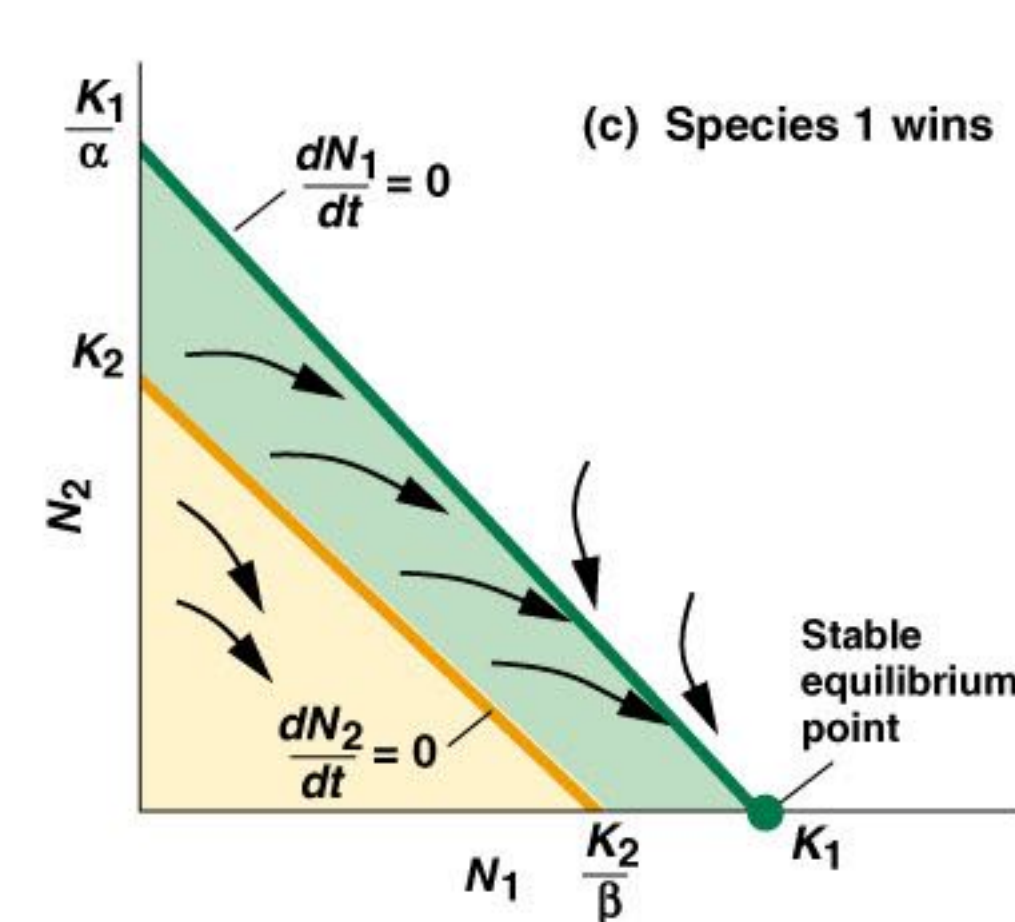
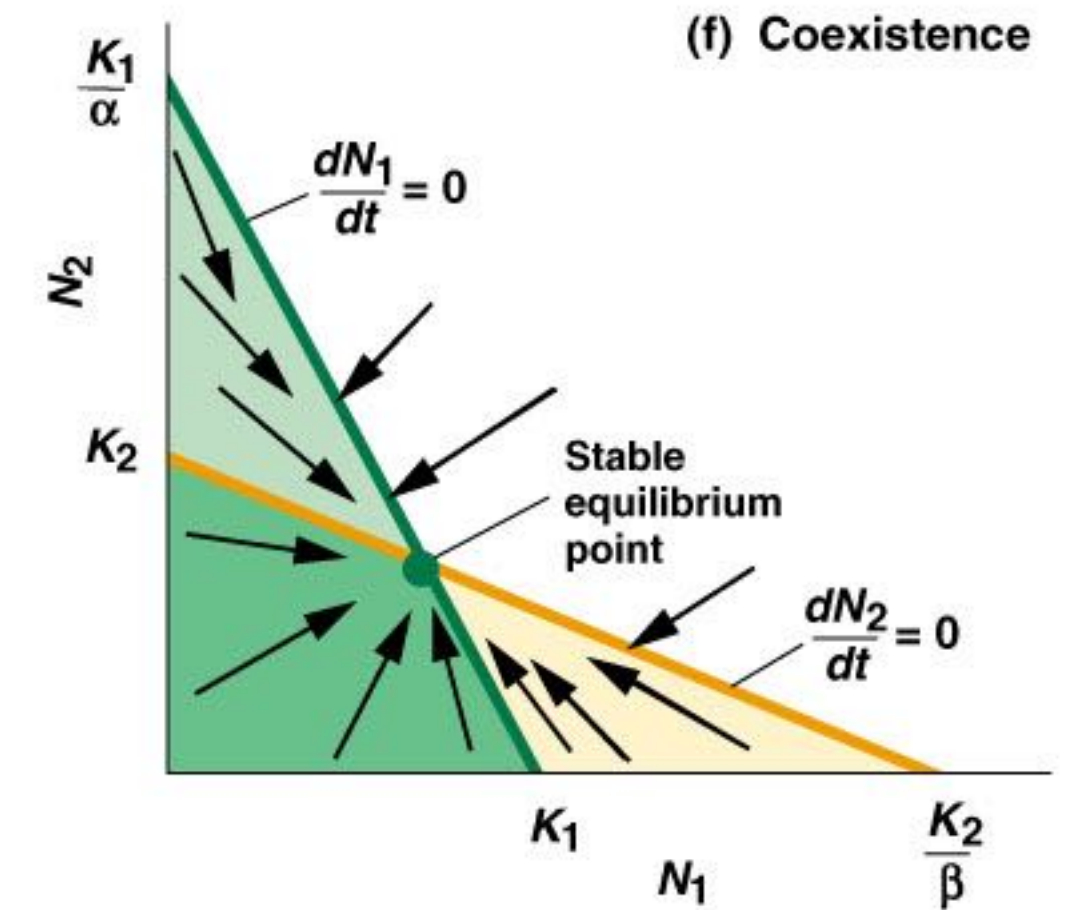


Synedra ulna

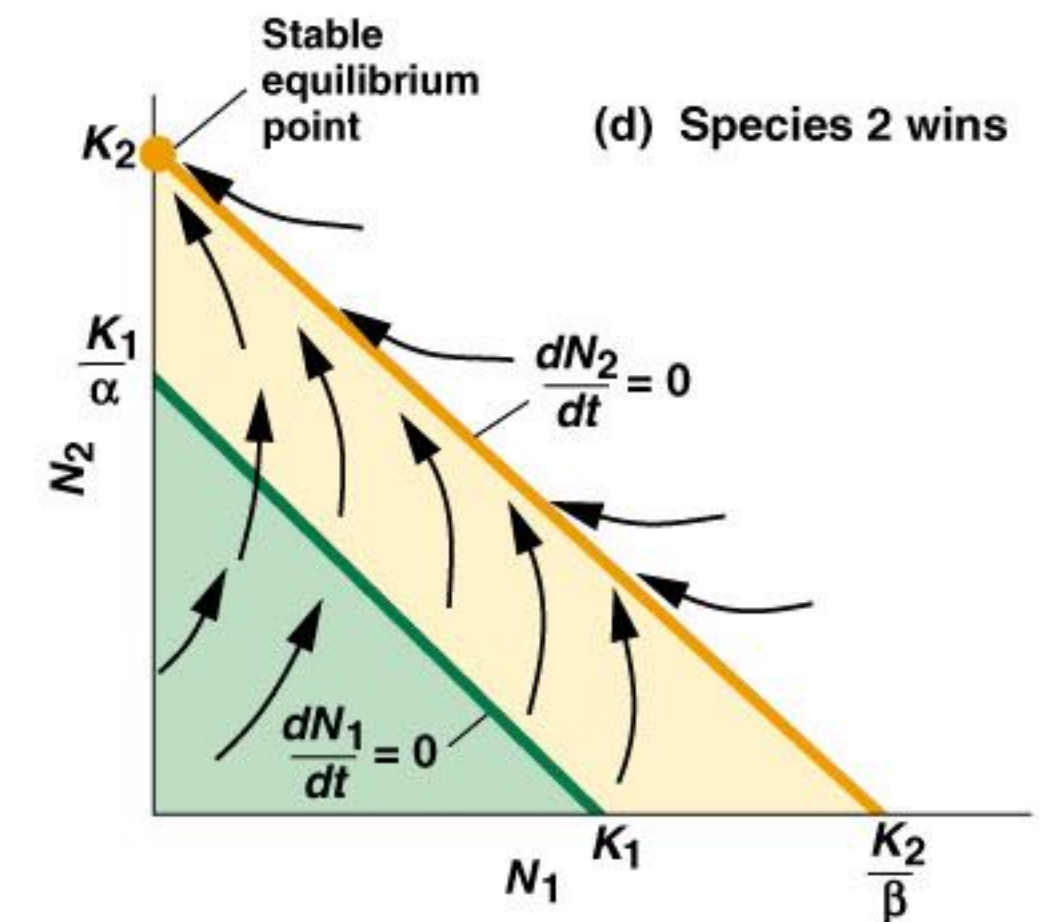
Together



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Competitive exclusion: several consumers using 1 resource

Closed system with fixed amount of resource K :

$$F = K - \sum_i^n e_i N_i, \quad \frac{dN_i}{dt} = N_i(b_i F - d_i), \quad \text{for } i = 1, 2, \dots, n, \quad R_{0_i} = \frac{b_i K}{d_i}$$

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

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

Nullclines for 2-D closed system

$$F = K - \sum_i^n e_i N_i , \quad \frac{dN_i}{dt} = N_i(b_i F - d_i) , \quad \text{for } i = 1, 2, \dots, n , \quad (9.1)$$

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

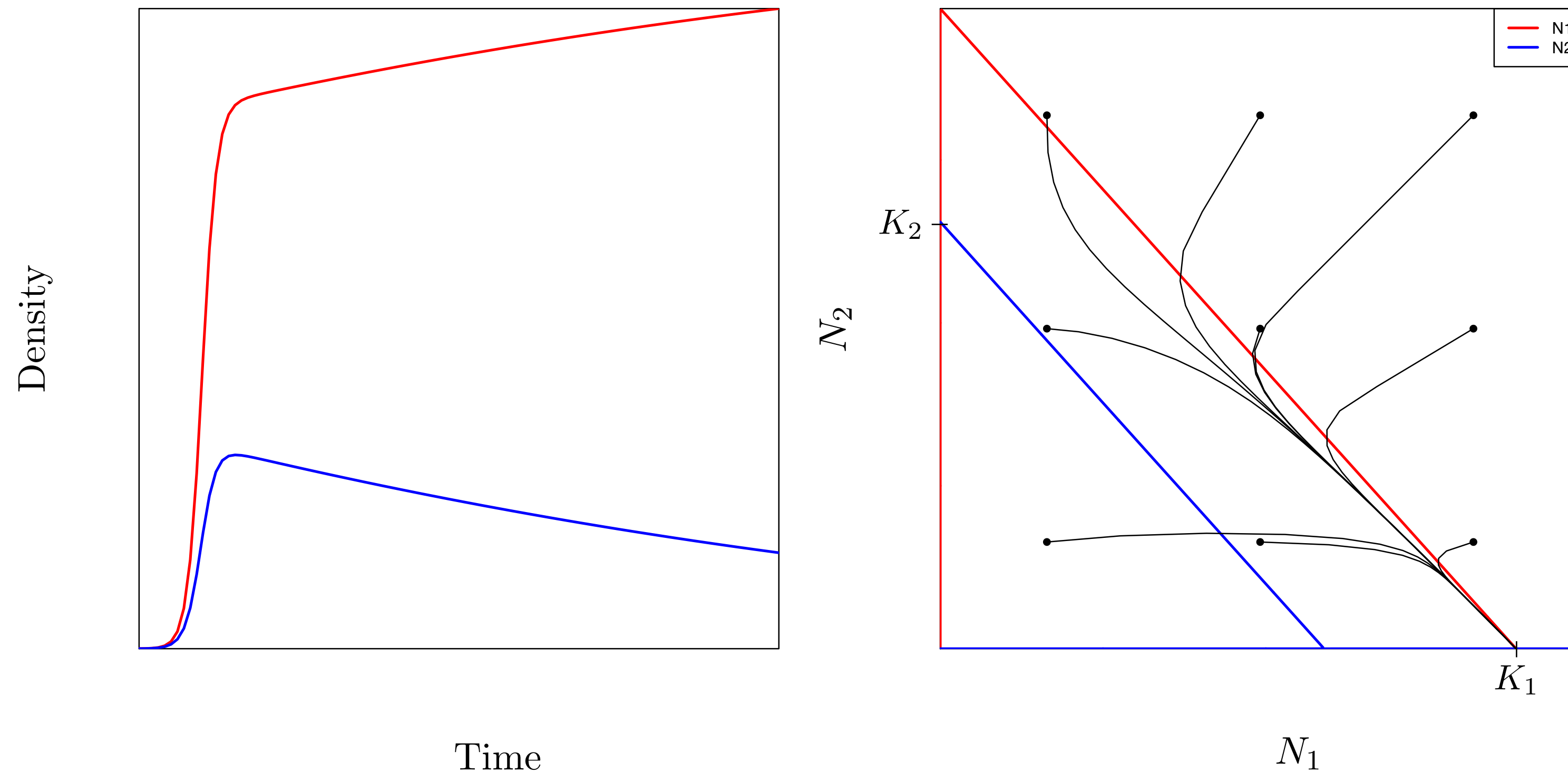
$$N_2 = \frac{K - d_1/b_1}{e_2} - \frac{e_1}{e_2} N_1 = \frac{K(1 - 1/R_{0_1})}{e_2} - \frac{e_1}{e_2} N_1 \quad \text{and} \quad N_2 = \frac{K(1 - 1/R_{0_2})}{e_2} - \frac{e_1}{e_2} N_1 , \quad (9.4)$$

Nullclines for 2-D closed system

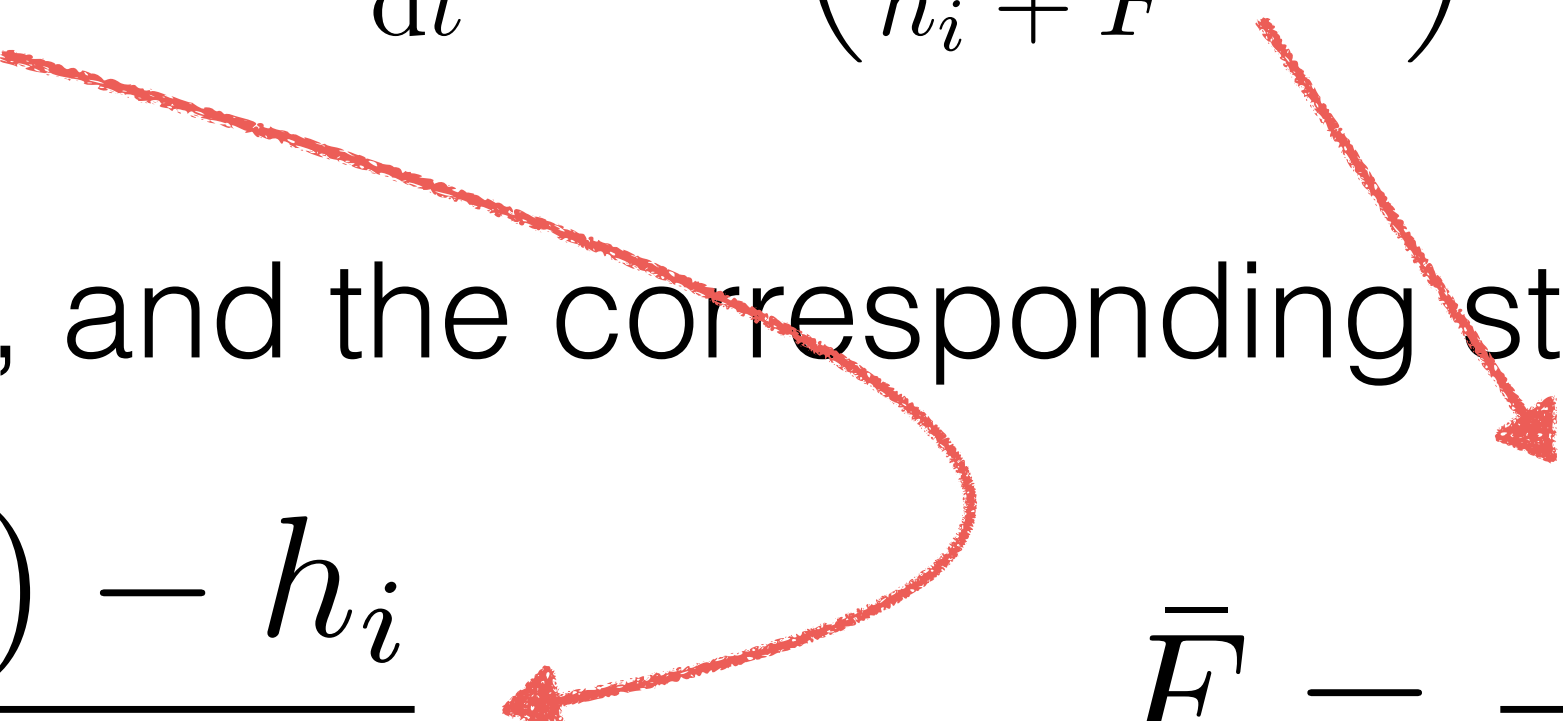
$$F = K - \sum_i^n e_i N_i, \quad \frac{dN_i}{dt} = N_i(b_i F - d_i), \quad \text{for } i = 1, 2, \dots, n, \quad (9.1)$$

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

$$N_2 = \frac{K - d_1/b_1}{e_2} - \frac{e_1}{e_2} N_1 = \frac{K(1 - 1/R_{01})}{e_2} - \frac{e_1}{e_2} N_1 \quad \text{and} \quad N_2 = \frac{K(1 - 1/R_{02})}{e_2} - \frac{e_1}{e_2} N_1, \quad (9.4)$$



Competitive exclusion when birth rate is saturated (**closed**)

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


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)

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

Exclusion because

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

Quasi steady state to reveal interactions: resource with source

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

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

$$\frac{dN_i}{dt} = N_i \left(\frac{b_i s}{s + (h_i/c_i)(d + \sum c_j N_j)} - d_i \right) = N_i \left(\frac{\beta_i}{1 + \sum N_j/k_j} - d_i \right)$$

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

Quasi steady state to reveal interactions: logistic resource

- $\frac{dR}{dt} = rR(1 - R/K) - R \sum_{i=1}^n c_i N_i$ with $\frac{dN_i}{dt} = N_i \left(\frac{b_i c_i R}{h_i + c_i R} - d_i \right)$

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

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

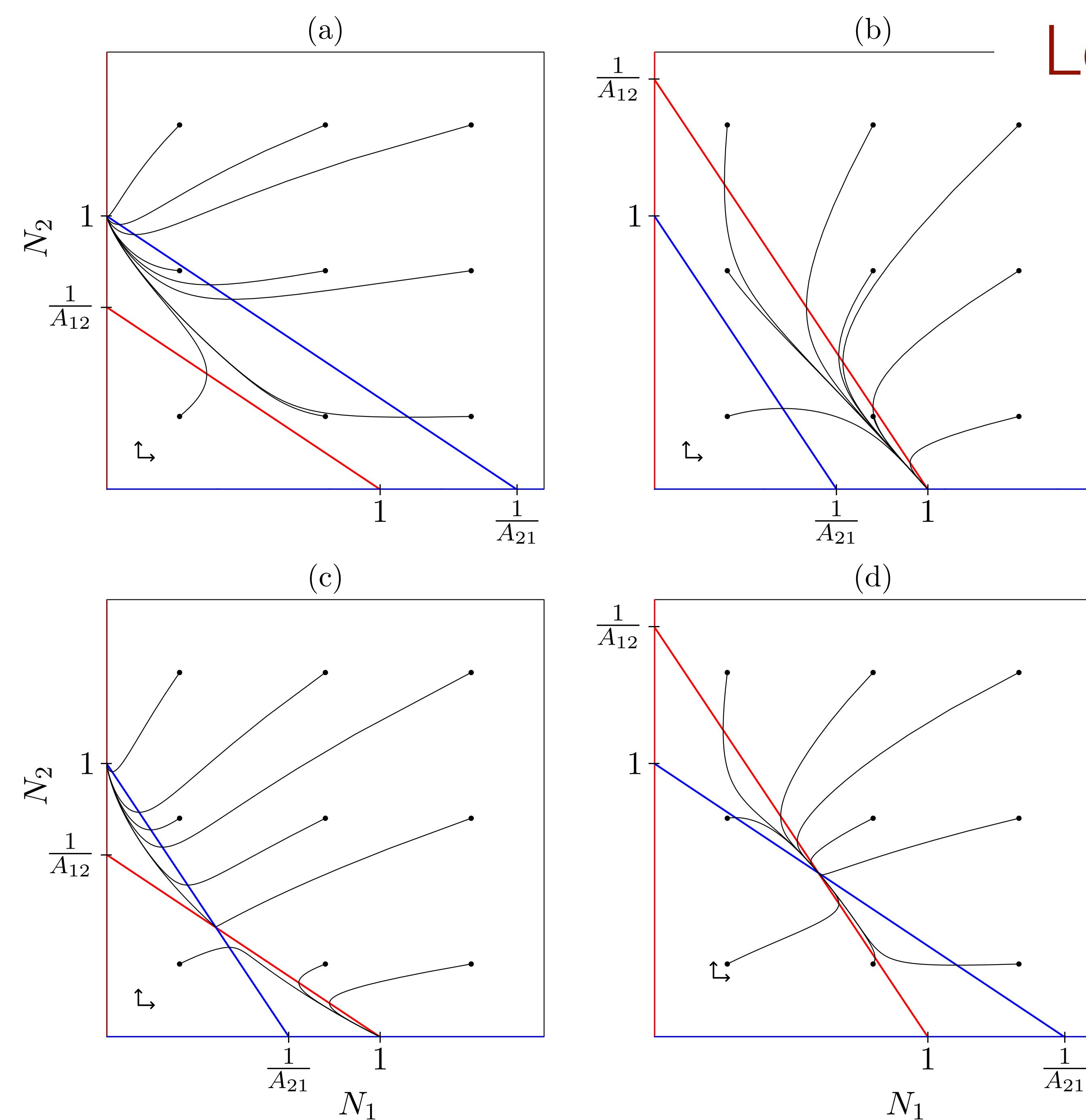
$$\bar{N}_i = \frac{r}{c_i} \left(1 - \frac{R_i^*}{K} \right)$$

Lotka-Volterra competition model

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^n A_{ij} N_j \right)$$

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

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



Several consumers on two substitutable resources

$$\frac{dN_i}{dt} = \left(\beta_i \frac{\sum_j c_{ij} R_j}{h_i + \sum_j c_{ij} R_j} - \delta_i \right) N_i, \quad \frac{dR_j}{dt} = s_j - d_j R_j - \sum_i c_{ij} N_i R_j$$

Consumer nullcline depends on resources only:

$$R_2 = \frac{h_i}{c_{i2}(R_{0i} - 1)} - \frac{c_{i1}}{c_{i2}} R_1 \quad \text{Straight line with slope } -c_{i1}/c_{i2}$$

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

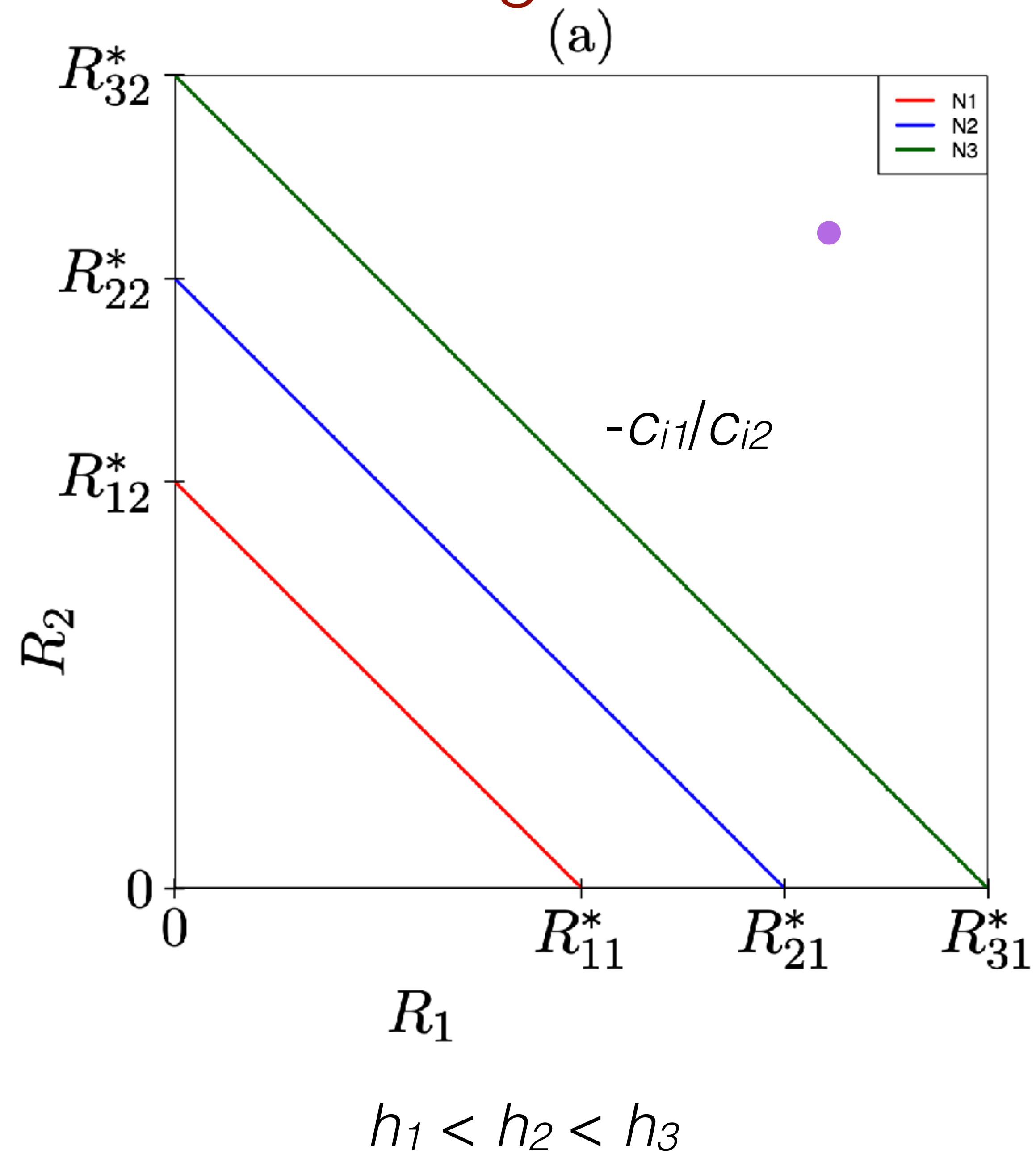
Starting and ending at critical resource density: $R_{ij}^* = \frac{h_i}{c_{ij}(R_{0i} - 1)}$

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

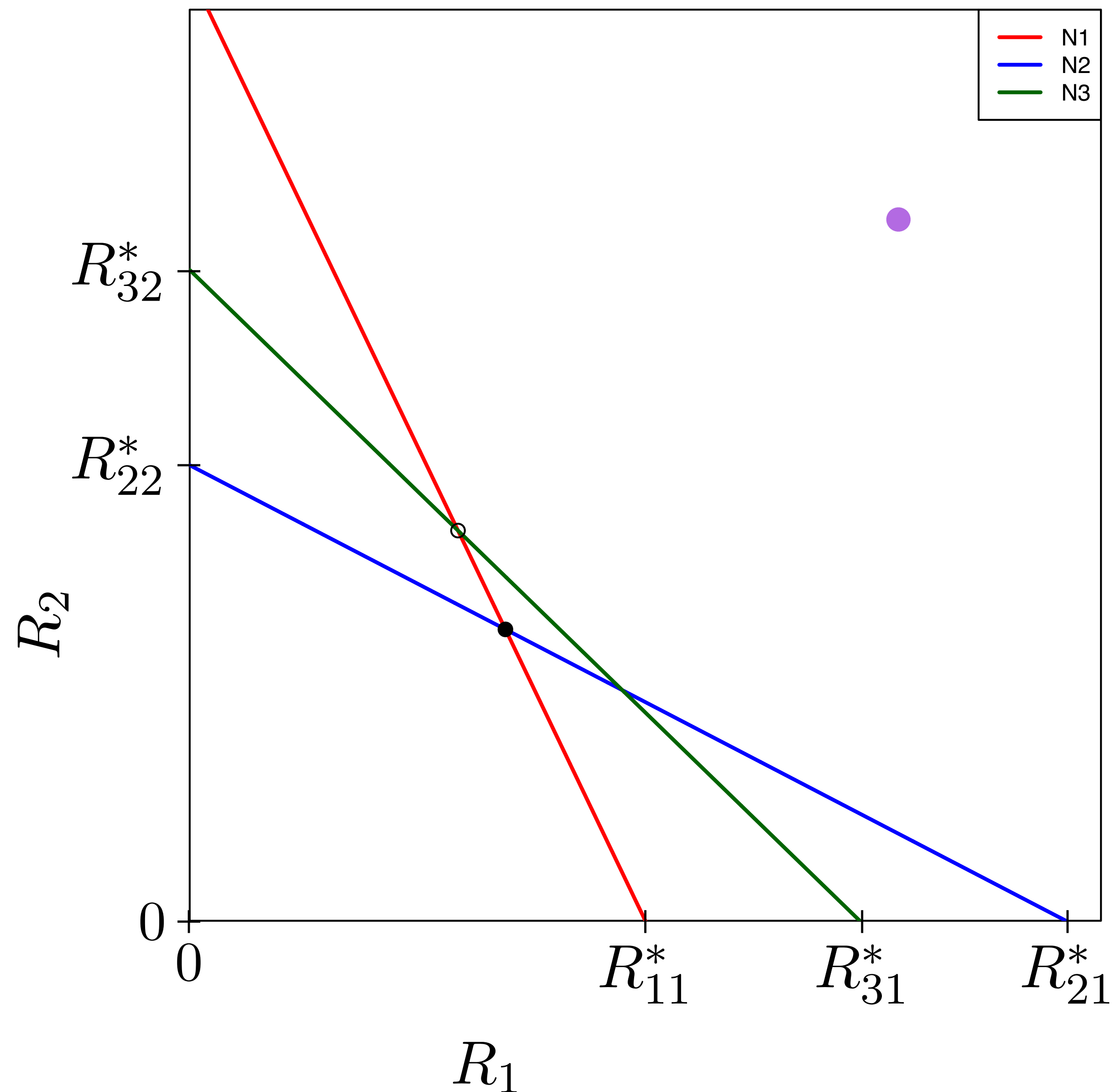
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Several consumers having the same diet c_{i1} and c_{i2} .



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:

$$\frac{dN_i}{dt} = \left(\beta_i \prod_j \frac{c_{ij} R_j}{h_{ij} + c_{ij} R_j} - \delta_i \right) N_i, \quad \frac{dR_j}{dt} = s_j - d_j R_j - \sum_i c_{ij} N_i R_j$$

Two consumers using two resources:

$$\begin{aligned} \frac{dN_1}{dt} &= \left(\beta_1 \frac{c_{11} R_1}{h_{11} + c_{11} R_1} \frac{c_{12} R_2}{h_{12} + c_{12} R_2} - \delta_1 \right) N_1 \\ \frac{dN_2}{dt} &= \left(\beta_2 \frac{c_{21} R_1}{h_{21} + c_{21} R_1} \frac{c_{22} R_2}{h_{22} + c_{22} R_2} - \delta_2 \right) N_2 \end{aligned}$$

David Tilman



Essential resources

$$\begin{aligned}\frac{dN_1}{dt} &= \left(\beta_1 \frac{c_{11}R_1}{h_{11} + c_{11}R_1} \frac{c_{12}R_2}{h_{12} + c_{12}R_2} - \delta_1 \right) N_1 \\ \frac{dN_2}{dt} &= \left(\beta_2 \frac{c_{21}R_1}{h_{21} + c_{21}R_1} \frac{c_{22}R_2}{h_{22} + c_{22}R_2} - \delta_2 \right) N_2\end{aligned}$$

Asymptotes defined by letting
 $R_1 \rightarrow \infty$ or $R_2 \rightarrow \infty$

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

Local steepness defines stability

