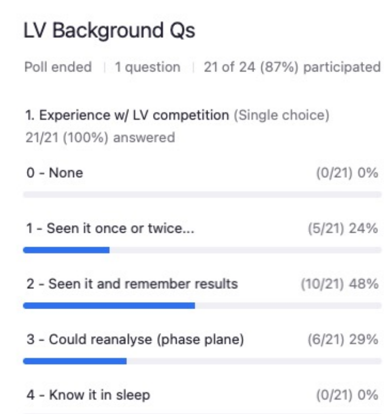
Two-Species Lotka-Volterra Competition

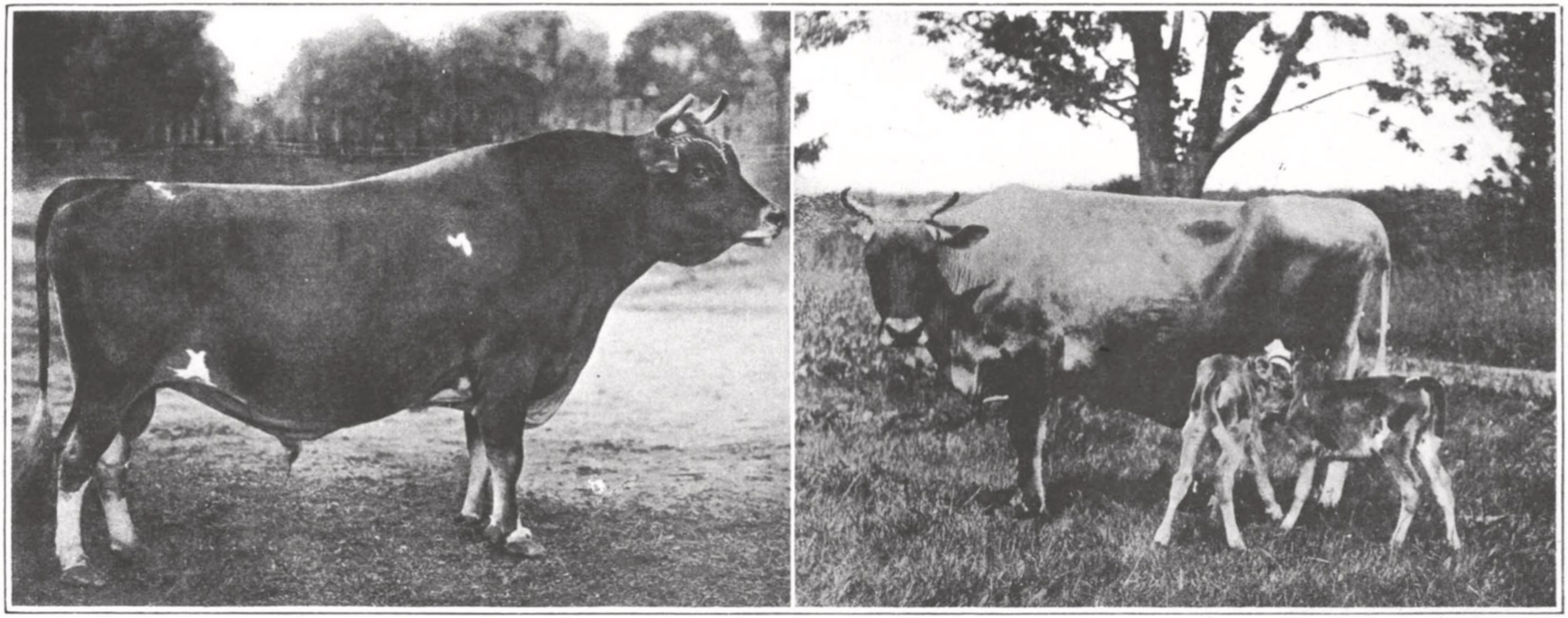


Lotka-Volterra Competition Model

Vito Volterra

Alfred Lotka

(Kingsland 1995)



AT THE LEFT: THE SIRE OF A LEADING DAIRY-FARM HERD. AT THE RIGHT: ONE OF THE COWS, WHO IN FIFTEEN MONTHS HAS HAD THREE CALVES AND PRODUCED IN A 365-DAY TEST 11,728 POUNDS OF MILK TESTING 6-32 PERCENT BUTTER FAT

THE HIGH PRICE OF MILK

SOME OF THE CAUSES, AND THE REMEDY

BY ALFRED J. LOTKA

Lotka-Volterra Competition Model (r-K form)

Start with two logistic equations (intraspecific competition)…

$$\frac{dN_1}{dt} = r_1\left(1 - \frac{N_1}{K_1} \qquad\qquad\qquad \right)N_1$$

$$\frac{dN_2}{dt} = r_2\left(1 - \frac{N_2}{K_2} \qquad\qquad\qquad \right)N_2$$

r_i — intrinsic growth rates
K_i — carrying capacities

Lotka-Volterra Competition Model (r-K form)

Add interspecific competition…

$$\frac{dN_1}{dt} = r_1\left(1 - \frac{N_1}{K_1} - \qquad \frac{N_2}{K_1}\right) N_1$$

$$\frac{dN_2}{dt} = r_2\left(1 - \frac{N_2}{K_2} - \qquad \frac{N_1}{K_2}\right) N_2$$

r_i — intrinsic growth rates
K_i — carrying capacities

Lotka-Volterra Competition Model (r-K form)

Include competition coefficients to scale strength of intra- vs interspecific competition…

$$\frac{dN_1}{dt} = r_1 \left(1 - \frac{N_1}{K_1} - \alpha_{12} \frac{N_2}{K_1}\right) N_1$$

$$\frac{dN_2}{dt} = r_2 \left(1 - \frac{N_2}{K_2} - \alpha_{21} \frac{N_1}{K_2}\right) N_2$$

r_i — intrinsic growth rates
K_i — carrying capacities
α_{ij} — competition coefficients

Lotka-Volterra Competition Model (r-α form)

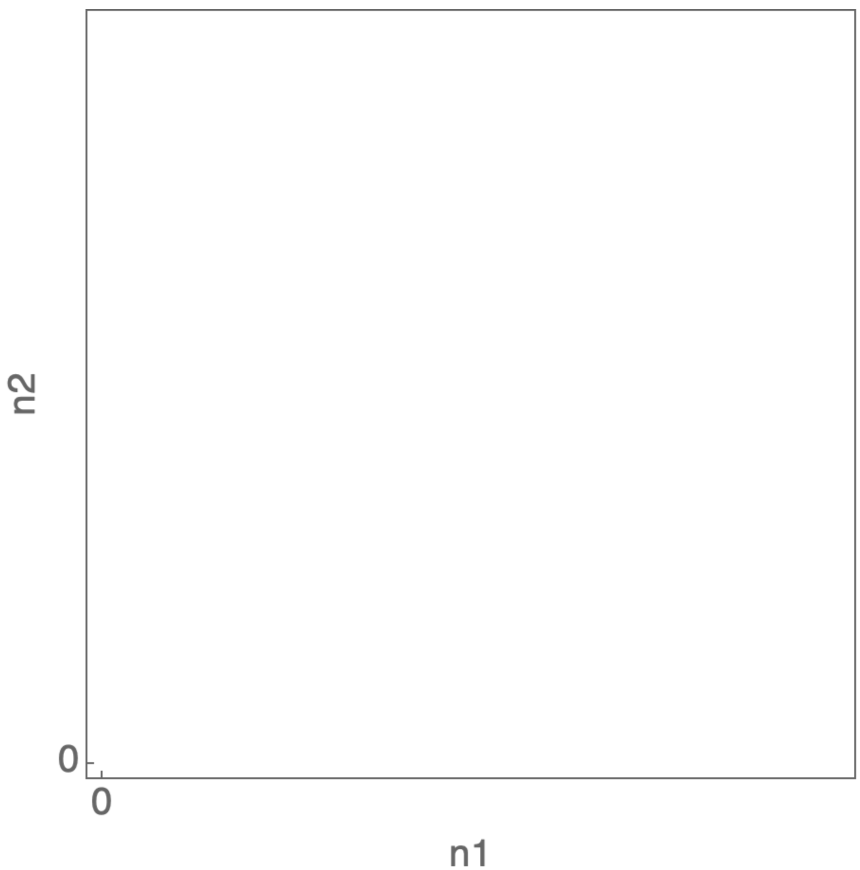
$$\frac{dN_1}{dt} = (r_1 - \alpha_{11}N_1 - \alpha_{12}N_2)N_1$$

$$\frac{dN_2}{dt} = (r_2 - \alpha_{21}N_1 - \alpha_{22}N_2)N_2$$

$$K_i = r_i/\alpha_{ii}$$

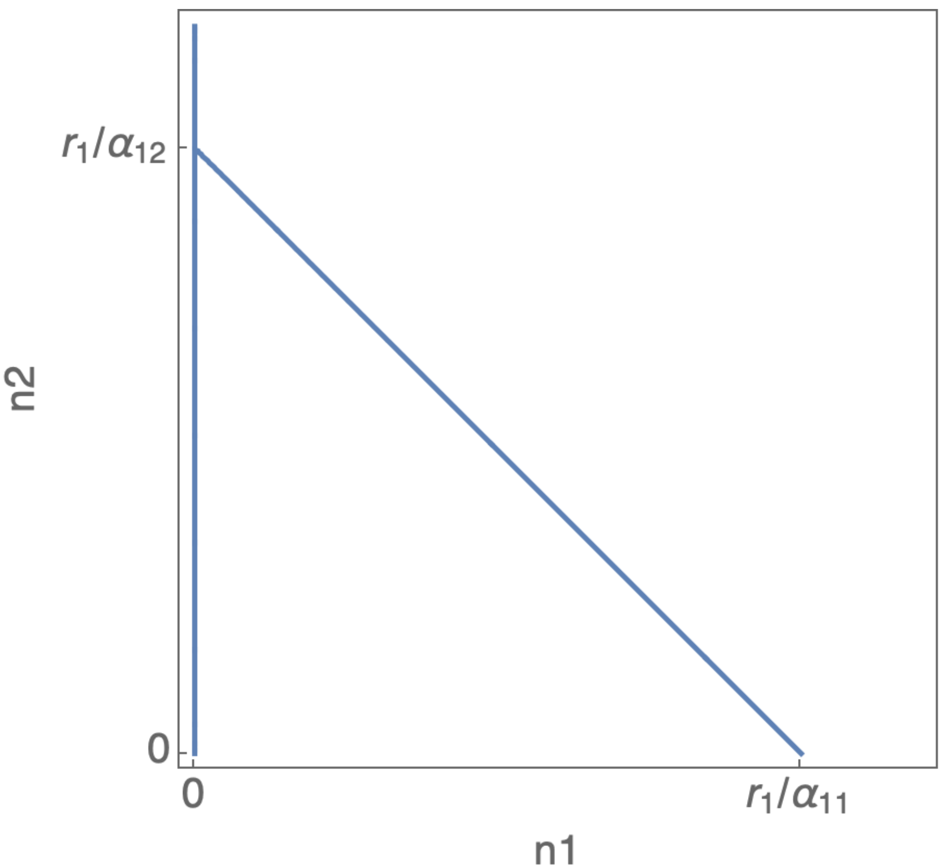
(Mallet 2012)

Phase-Plane Analysis



- Classic approach in theoretical ecology
- Each point is a state of the system
- Plot change in each species at each point

N_1 Isocline



$$\frac{dN_1}{dt} = 0$$

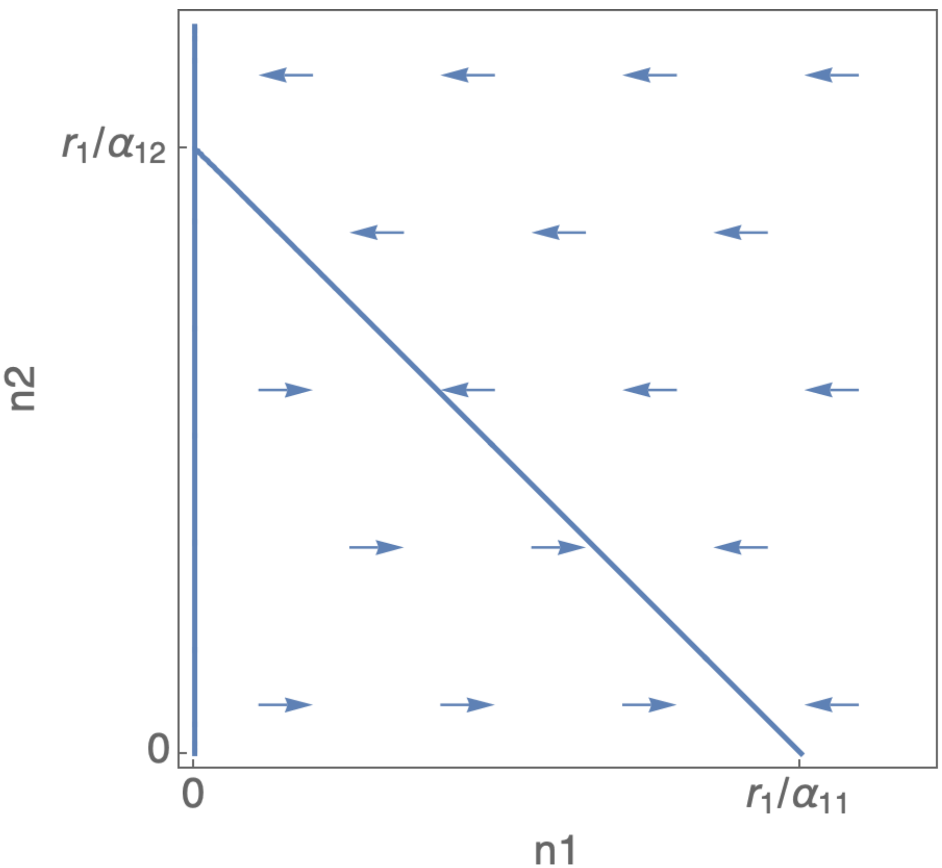
$$(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2)N_1 = 0$$

$$N_1 = 0$$

or

$$r_1 - \alpha_{11}N_1 - \alpha_{12}N_2 = 0$$

N_1 Isocline



$$\frac{dN_1}{dt} = 0$$

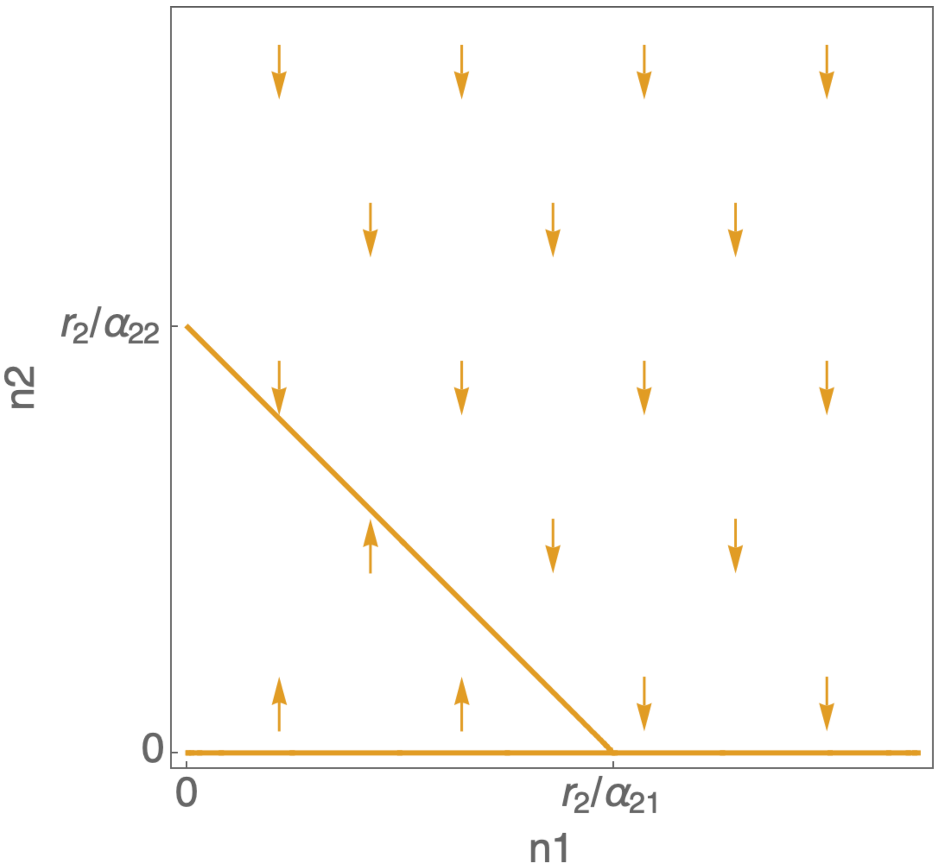
$$(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2)N_1 = 0$$

$$N_1 = 0$$

or

$$r_1 - \alpha_{11}N_1 - \alpha_{12}N_2 = 0$$

N_2 Isocline



$$\frac{dN_2}{dt} = 0$$

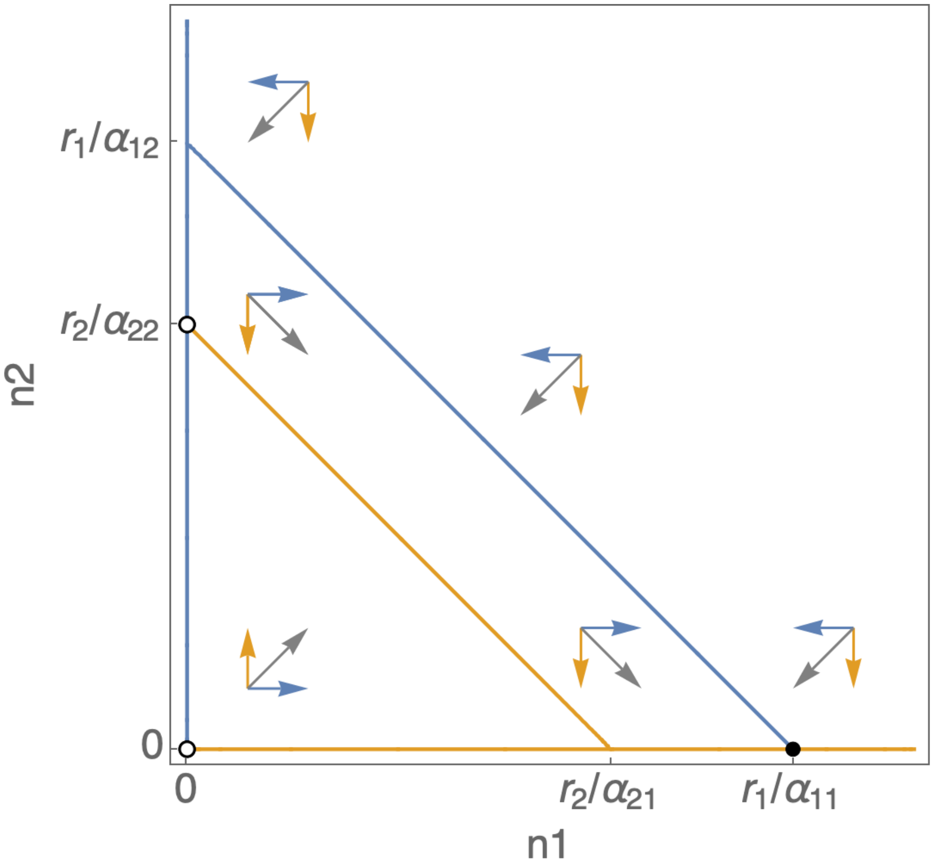
$$(r_2 - \alpha_{21}N_1 - \alpha_{22}N_2)N_2 = 0$$

$$N_2 = 0$$

or

$$r_2 - \alpha_{21}N_1 - \alpha_{22}N_2 = 0$$

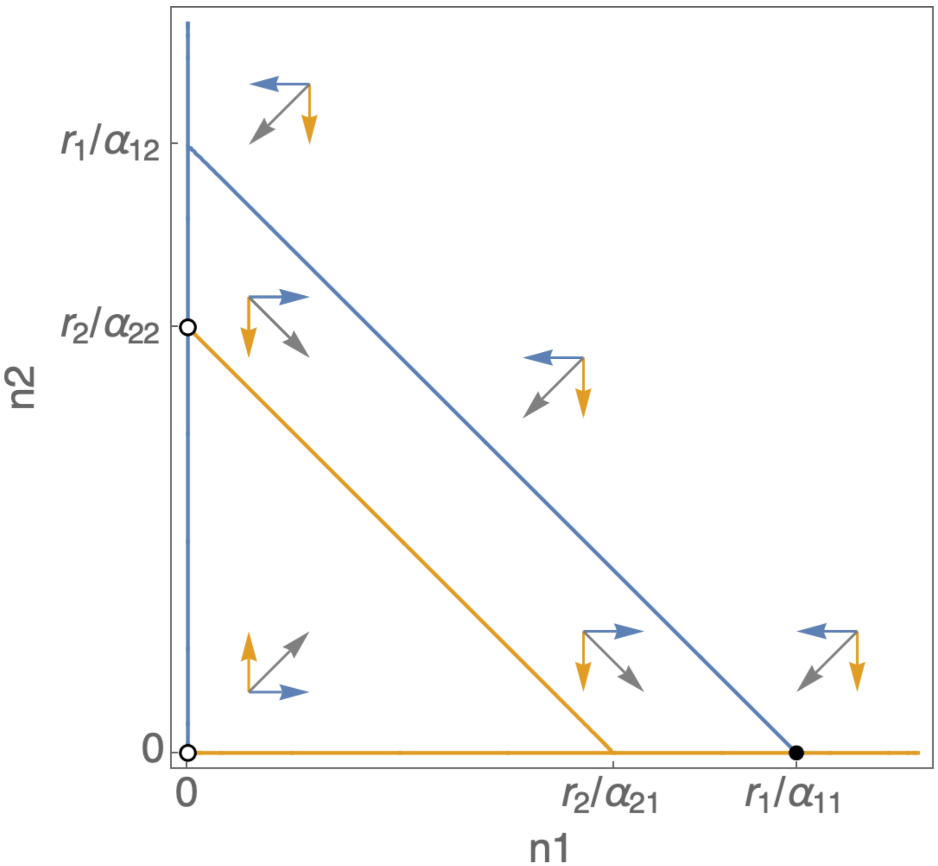
Put isoclines together



- Focus on long-term dynamics ($t \rightarrow \infty$)
- Isoclines are where ONE species doesn't change
- Equilibria are where BOTH species don't change

Five Cases of LV Competition

Case I – 1 outcompetes 2



$$r_1/\alpha_{11} > r_2/\alpha_{21}$$
$$r_1/\alpha_{12} > r_2/\alpha_{22}$$

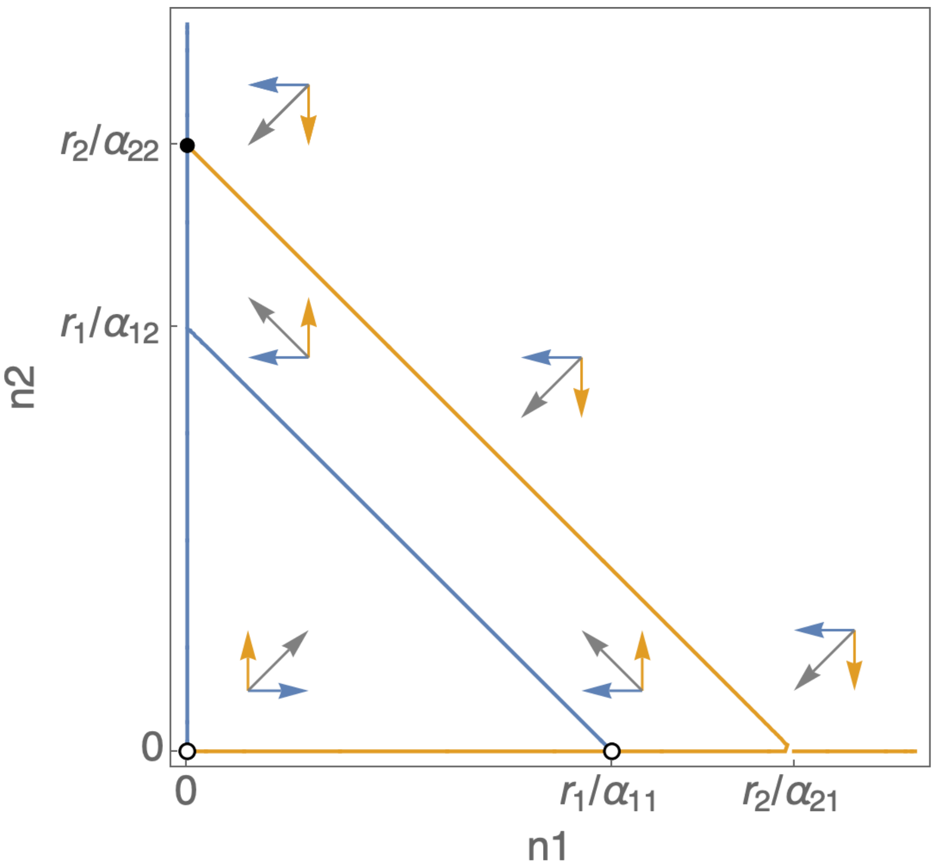
Equilibria $(\hat{N}_1, \hat{N}_2)$:

$(0, 0)$ — unstable

$(r_1/\alpha_{11}, 0)$ — stable

$(0, r_2/\alpha_{22})$ — unstable

Case II – 2 outcompetes 1



$$r_2/\alpha_{21} > r_1/\alpha_{11}$$
$$r_2/\alpha_{22} > r_1/\alpha_{12}$$

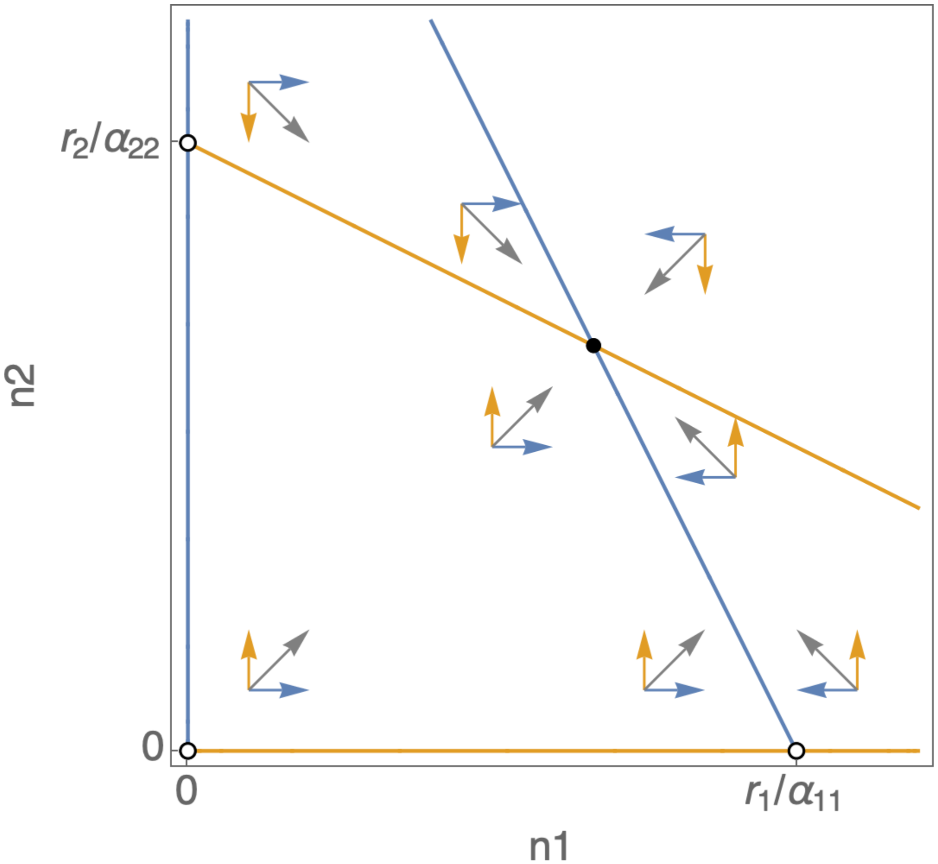
Equilibria $(\hat{N}_1, \hat{N}_2)$:

$(0, 0)$ — unstable

$(r_1/\alpha_{11}, 0)$ — unstable

$(0, r_2/\alpha_{22})$ — stable

Case III – 1 & 2 coexist



$$r_2/\alpha_{21} > r_1/\alpha_{11}$$
$$r_1/\alpha_{12} > r_2/\alpha_{22}$$

Equilibria $(\hat{N}_1, \hat{N}_2)$:

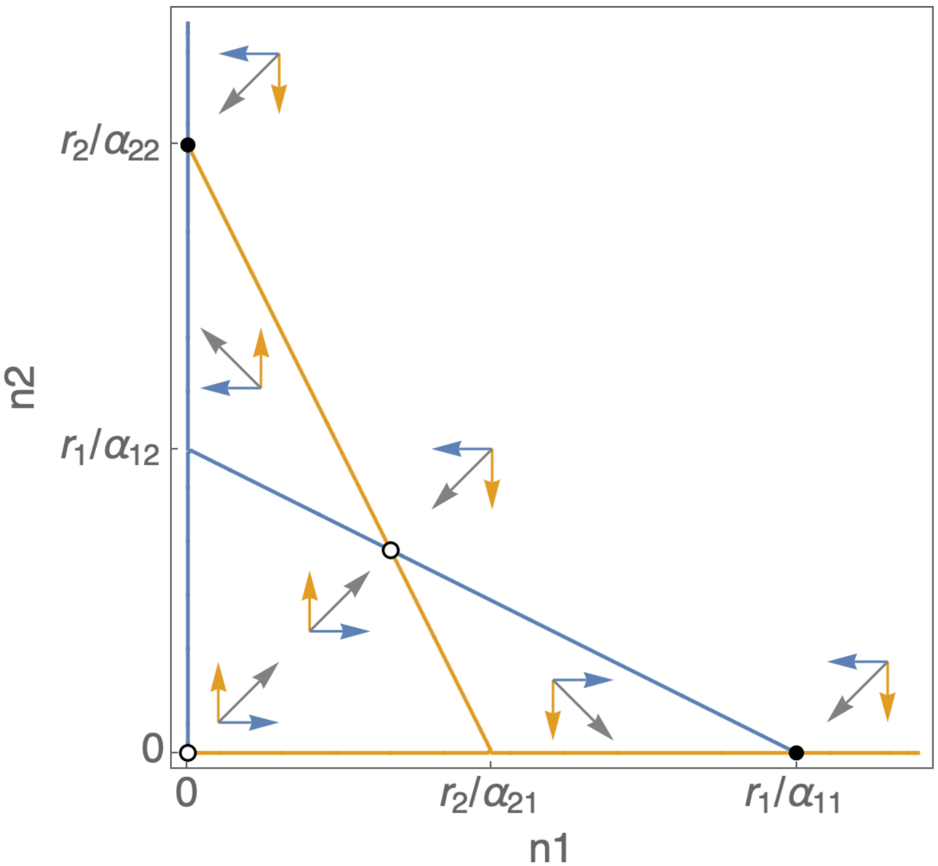
$(0, 0)$ — unstable

$(r_1/\alpha_{11}, 0)$ — unstable

$(0, r_2/\alpha_{22})$ — unstable

$\left(\frac{r_1\alpha_{22} - r_2\alpha_{12}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}, \frac{r_2\alpha_{11} - r_1\alpha_{21}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}\right)$ — stable

Case IV – 1 or 2 wins (founder control)



$$r_1/\alpha_{11} > r_2/\alpha_{21}$$
$$r_2/\alpha_{22} > r_1/\alpha_{12}$$

Equilibria $(\hat{N}_1, \hat{N}_2)$:

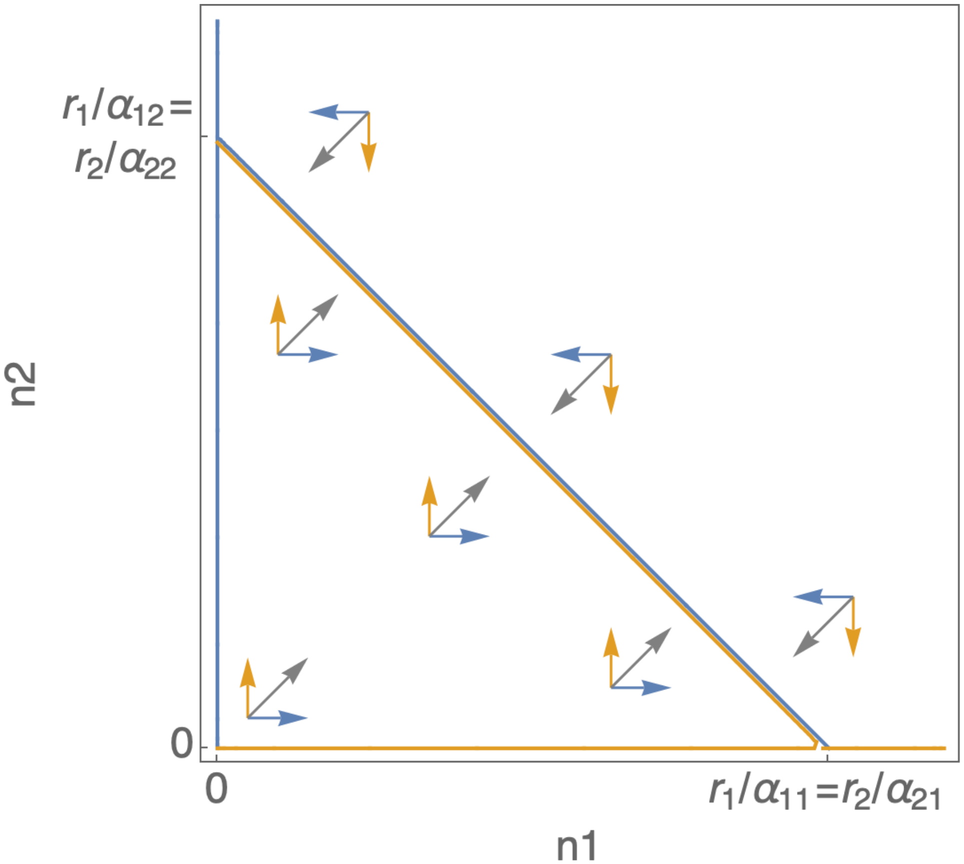
$(0,0)$ — unstable

$(r_1/\alpha_{11}, 0)$ — stable

$(0, r_2/\alpha_{22})$ — stable

$\left(\frac{r_1\alpha_{22}-r_2\alpha_{12}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}, \frac{r_2\alpha_{11}-r_1\alpha_{21}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}\right)$ — unstable

Case 0 –neutrality



$$r_1/\alpha_{11} = r_2/\alpha_{21}$$
$$r_2/\alpha_{22} = r_1/\alpha_{12}$$

Equilibria $(\hat{N}_1, \hat{N}_2)$:

$(0,0)$ — unstable

line of equilibria — neutrally stable

More analysis (general)…

Find Equilibria

Solve

$$\begin{cases} \dfrac{dN_1}{dt} = f_1(N_1, N_2) = 0 \\ \dfrac{dN_2}{dt} = f_2(N_1, N_2) = 0 \end{cases}$$

for $(\widehat{N}_1, \widehat{N}_2)$

Converts differential equations into algebraic equations.

Linear Stability Analysis

Consider a *small* perturbation from an equilibrium.

Calculate eigenvalues λ of Jacobian matrix J evaluated at an equilibrium $\widehat{N}$:

$$J = \begin{bmatrix} \dfrac{\partial f_1}{\partial N_1} & \dfrac{\partial f_1}{\partial N_2} \\ \dfrac{\partial f_2}{\partial N_1} & \dfrac{\partial f_2}{\partial N_2} \end{bmatrix}_{\widehat{N}}$$

Rules:

Equilibrium is stable if all eigenvalues have negative real part.

Equilibrium is unstable if any eigenvalue has positive real part.

If largest eigenvalue is 0, linear stability analysis fails (possibly neutral).

Invasion Analysis

Can each species i invade a monoculture of the other j?

Calculate its *per capita* growth rate when *rare:*

$$\lambda_{ij} = \frac{1}{N_i}\frac{dN_i}{dt}\bigg|_{(\hat{N}_j,\hat{N}_i)=(K_j,0)}$$

Rules:

If $\lambda_{12} > 0$ and $\lambda_{21} < 0$, 1 outcompetes 2

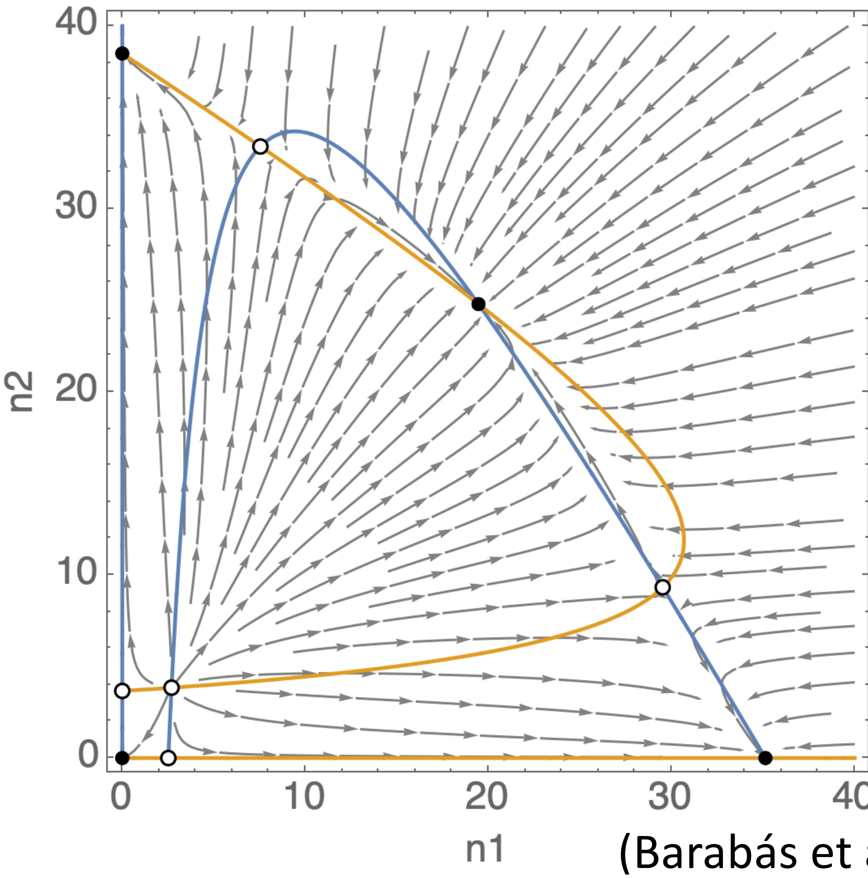
If $\lambda_{12} < 0$ and $\lambda_{21} > 0$, 2 outcompetes 1

If $\lambda_{12} > 0$ and $\lambda_{21} > 0$, 1 & 2 coexist (“mutual invasibility”)

If $\lambda_{12} < 0$ and $\lambda_{21} < 0$, founder control

(Metz et al. 1992, Grainger et al. 2019)

Invasion Analysis Limitations



(Barabás et al. 2018)

- Unprotected coexistence (Allee effects)
- Resident strikes back
- Demographic stochasticity
- Not clear how to apply to >2 species

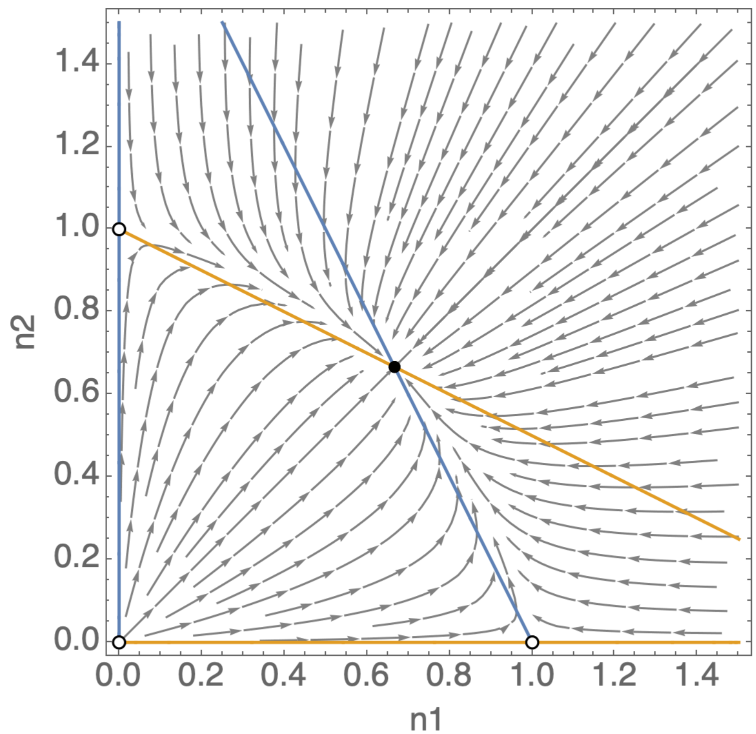
Mathematica examples…

see “2 – lv competition.nb”

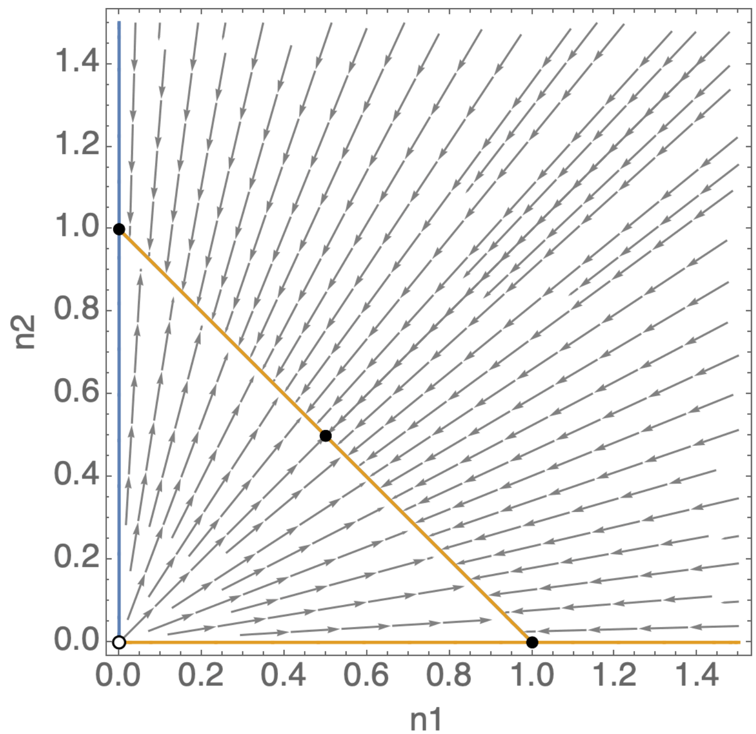
Varying strength of competition

$\alpha_{11} = \alpha_{22} = 1$

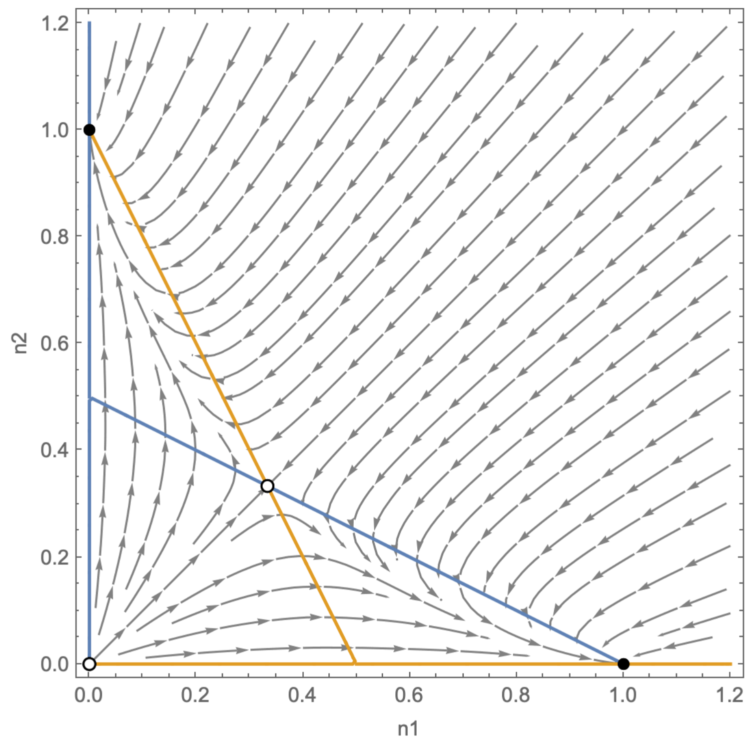
$\alpha_{12} = \alpha_{21} = 0.5$ stable coexistence



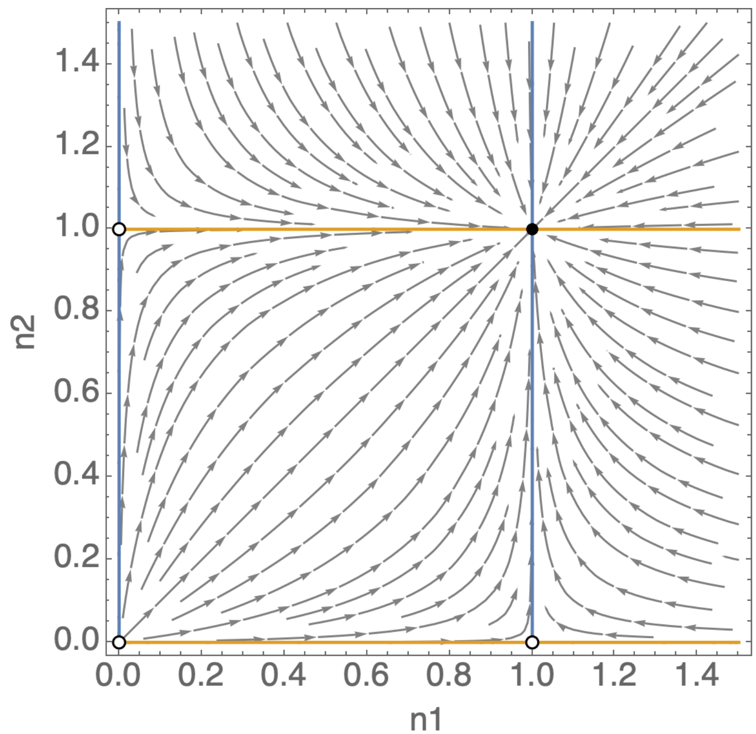
$\alpha_{12} = \alpha_{21} = 1$ neutral



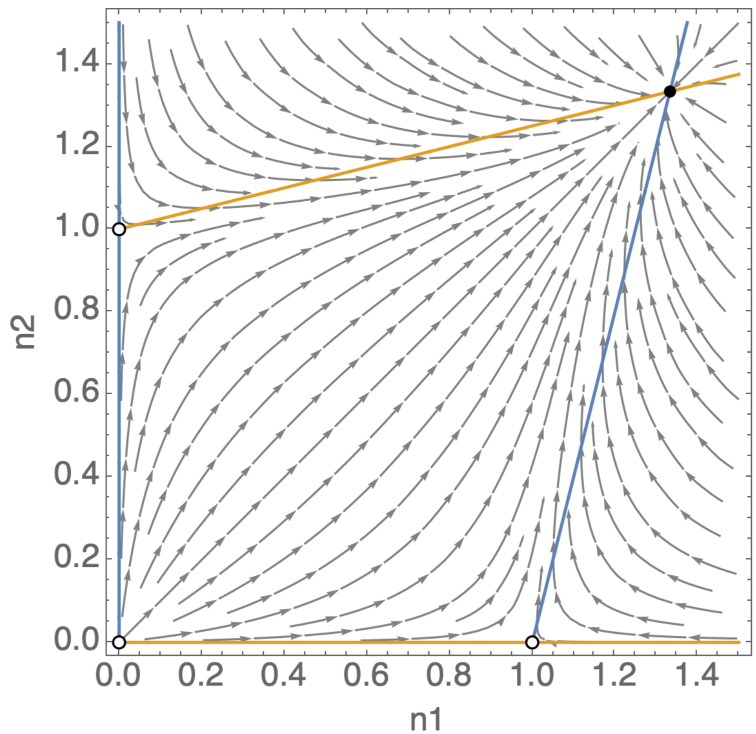
$\alpha_{12} = \alpha_{21} = 2$ founder control



$\alpha_{12} = \alpha_{21} = 0$ non-interacting

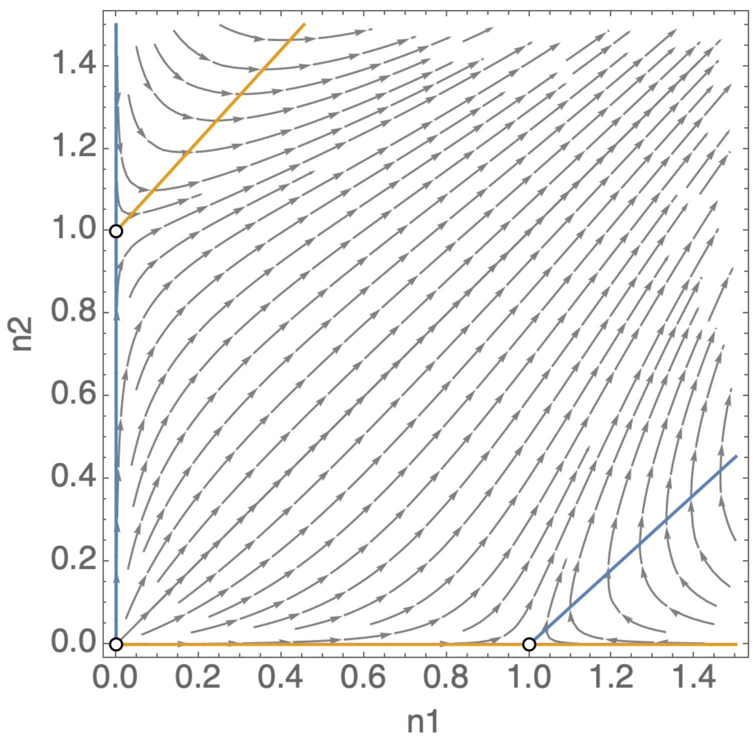


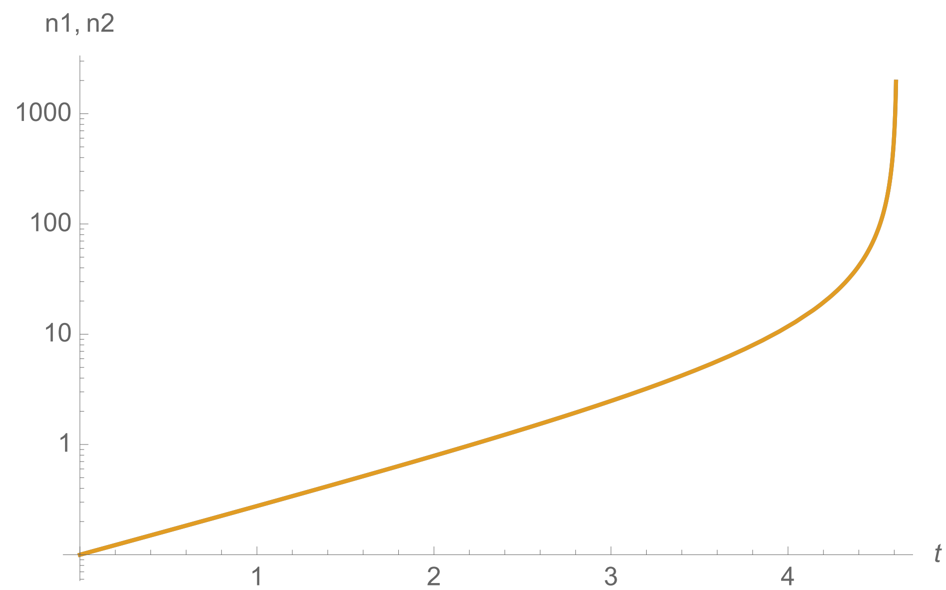
$\alpha_{12} = \alpha_{21} = -0.25$ weak mutualism



(Gause & Witt 1935)

$\alpha_{12} = \alpha_{21} = -1.1$ strong mutualism





n1 & n2 <u>reach</u> infinity in finite time! 🤯

Modern coexistence theory

Modern coexistence theory

- Based on work of Peter Chesson (*e.g.* 2000, 2020)
- Two strains
  - LV-based
  - Invasion-based
- Understand coexistence based on niche differences & fitness differences
- See also Barabás et al. 2018

Rearrange invasion criteria

1 & 2 coexist if $\lambda_{12} > 0, \lambda_{21} > 0$:

$$r_1 > \frac{r_2 \alpha_{12}}{\alpha_{22}}, r_2 > \frac{r_1 \alpha_{21}}{\alpha_{11}}$$

Combine with r_1/r_2 in the middle:

$$\frac{\alpha_{12}}{\alpha_{22}} < \frac{r_1}{r_2} < \frac{\alpha_{11}}{\alpha_{21}}$$

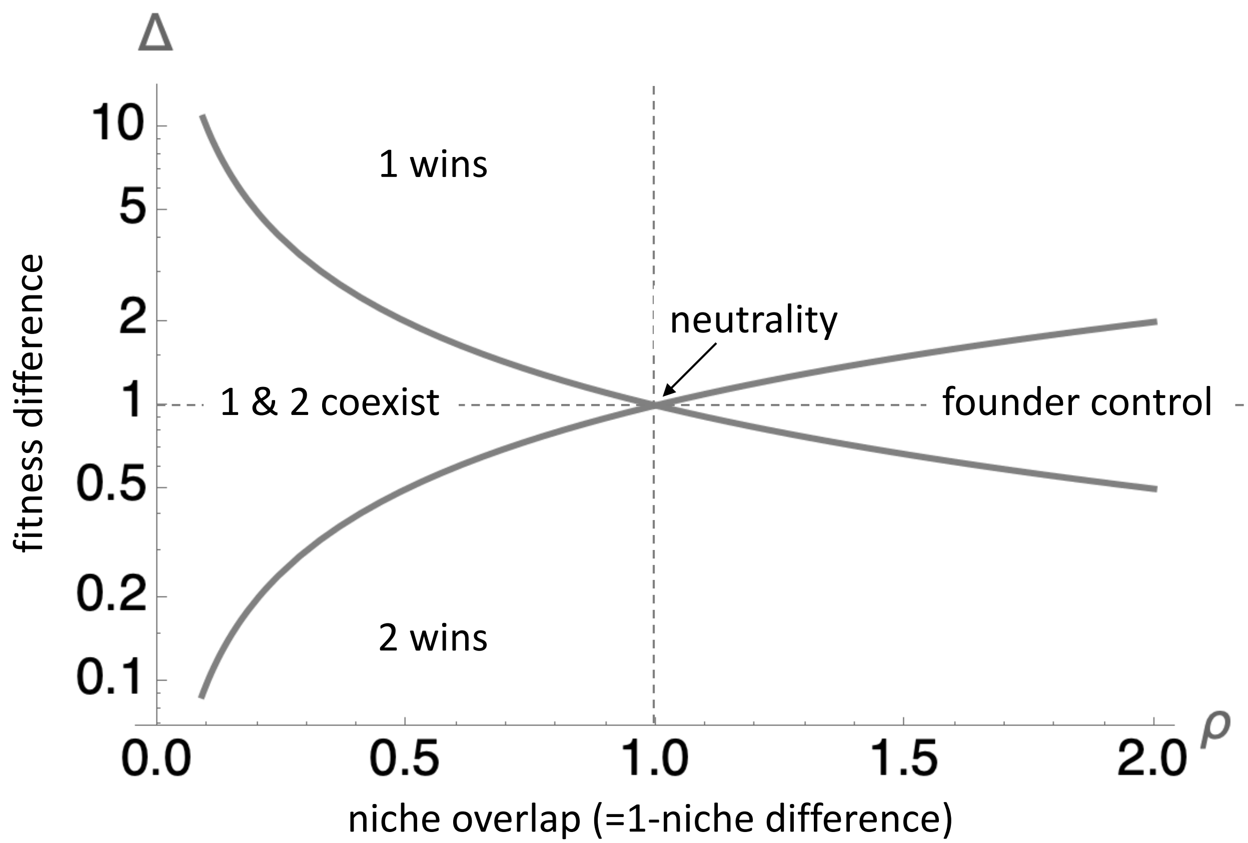
Symmetrize:

$$\sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} < \sqrt{\frac{\alpha_{22}\alpha_{12}}{\alpha_{11}\alpha_{21}}} \frac{r_1}{r_2} < \sqrt{\frac{\alpha_{11}\alpha_{22}}{\alpha_{12}\alpha_{21}}}$$

$$\frac{1}{\rho} < \Delta < \rho$$

Δ — fitness difference
ρ — niche overlap

Stabilizing & equalizing coexistence mechanisms



LV Competition: Pros & Cons

Pros

- Analytically tractable
- Graphical approach
- Shows 5 outcomes of competition
- Phenomenological

Cons

- Linear competitive effects
- No physical meaning to parameters
- How does competitive outcome depend on environmental gradients?
- Curse of dimensionality
- How are parameters related / constrained?

References

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