

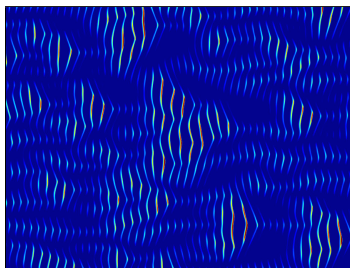
# Ecological Dynamics

## Competition (1 / 2)

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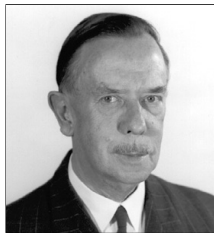
February 19, 2015



# Density-dependence vs. density-independence

## What controls the abundance and distribution of organisms?

Nicholson (1933) argued that natural populations were regulated by **density-dependent processes** such as competition and predation whereas Andrewartha and Birch (1954) argued that **density-independent processes** such as environmental fluctuations limited population size.



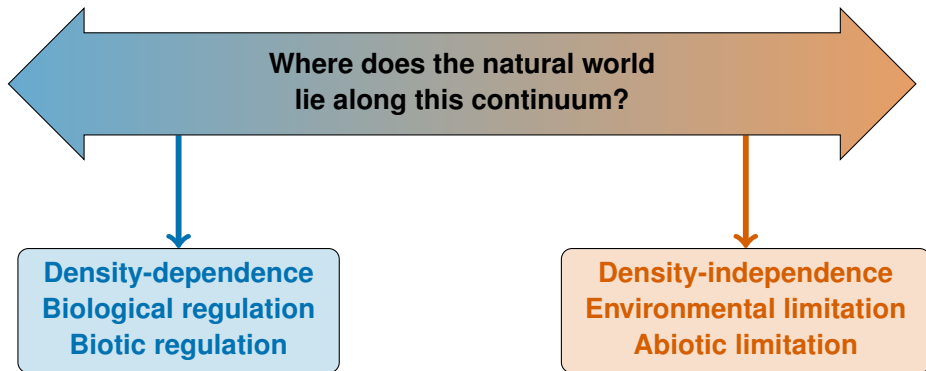
**Alexander Nicholson**



**Herbert Andrewartha**

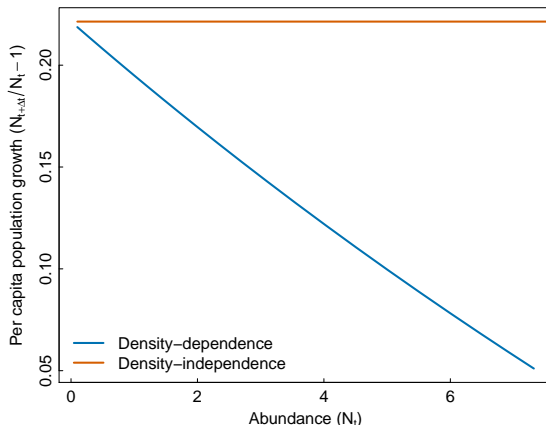
The debate gets resurrected every decade (Coulson et al., 2004) even though it represents a false dichotomy (Ziebarth et al., 2010).

# Density-dependence vs. density-independence



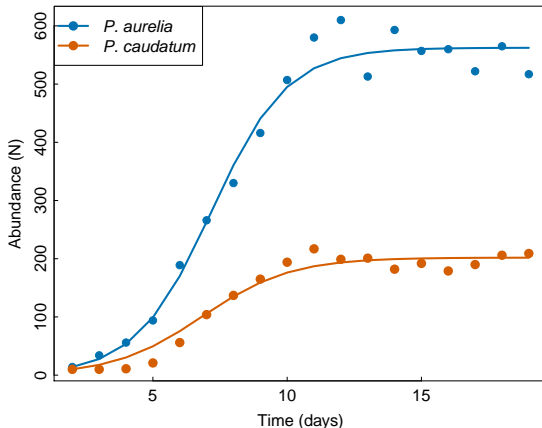
The rationale for the latest resurrection of the debate is predicting the ecosystem-level effects of climate change.

# The case for density-dependence



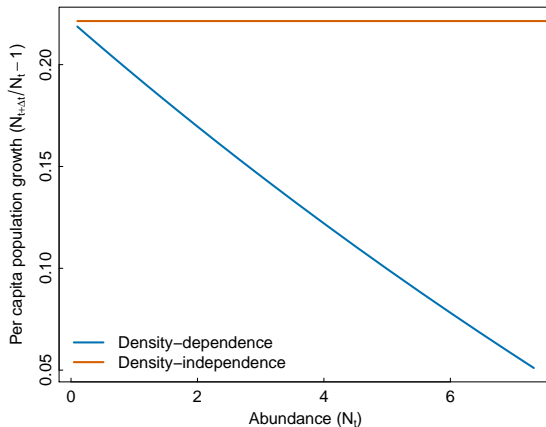
Natural populations exhibit incredible levels of stability and persistence: they neither explode nor go to extinction. Density-dependence provides a mechanism to explain how population growth gets buffered.

# Evidence of density-dependence in microbes



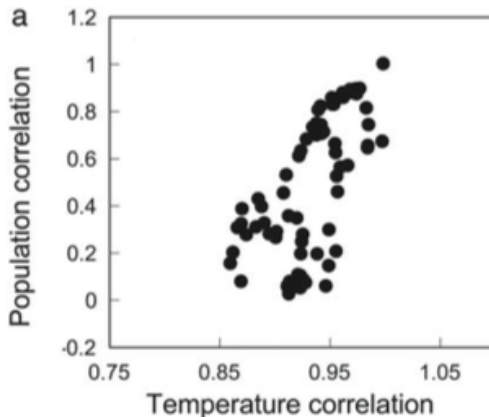
The experiments of Gause (1934) on *Paramecium* show that microbial populations tend to reach a carrying capacity over time.

# The case for density-independence



Year-to-year environmental fluctuations can strongly limit population growth and thus act as a form of environmental buffer.

# Evidence of density-independence



The pairwise correlation between different caribou populations is strongly related to the pairwise temperature correlation (Post and Forchhammer, 2004). This suggests that the geographical distribution of temperature fluctuations influences that of caribou abundance.

## A stale and largely resolved debate

This acrimonious debate lasted long because Andrewartha and Birch (1954) were arguing that **environmental limitation** controls the abundance of species over the short term whereas Nicholson (1933) was arguing that **biological regulation** controls the abundance of species over the long term.

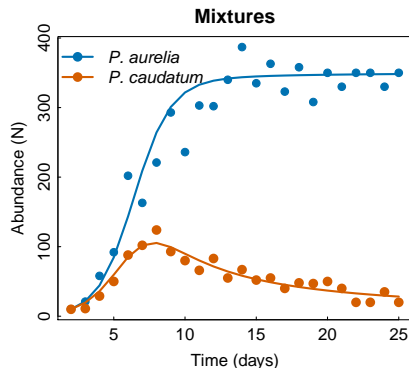
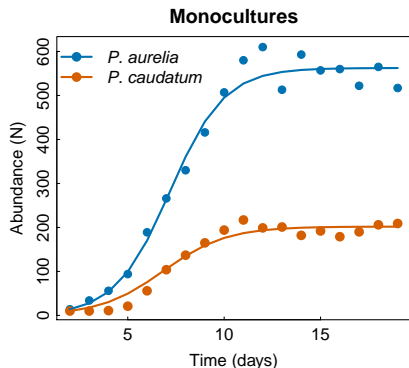
Recent work has shown that both processes can (and do) operate simultaneously in natural populations (Ziebarth et al., 2010).

One of the lasting legacies of the debate is the notion that populations tend to be stable because of the buffering effect of density-dependent mechanisms such as competition and predation (the so-called balance of nature) and that environment fluctuations tend to be destabilizing (Guichard and Gouhier, 2014).

This is at odds with the work of May (1974) who showed that linear density-dependent competition could lead to destabilization by generating limit cycles and chaotic fluctuations in population size.

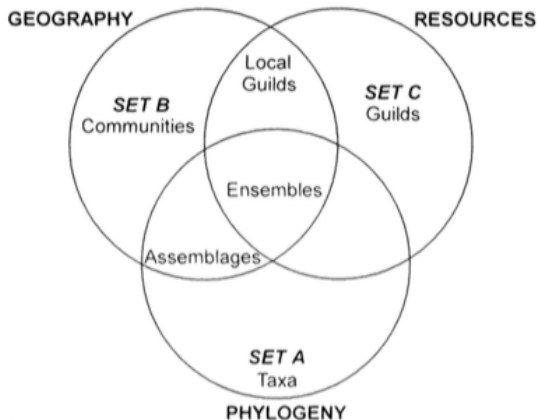


# Microbial competition set the research agenda in ecology



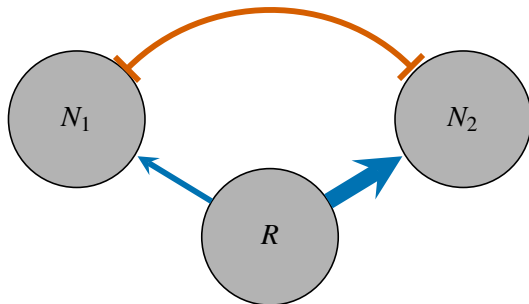
The pioneering work by Gause (1934) led to a shift from **autecology** (i.e., population biology) to **synecology** (community ecology).

# Defining an ecological community (Fauth et al., 1996)



Competition is a process that typically occurs within guilds (i.e., species occupying the same trophic level and competing for the same resources).

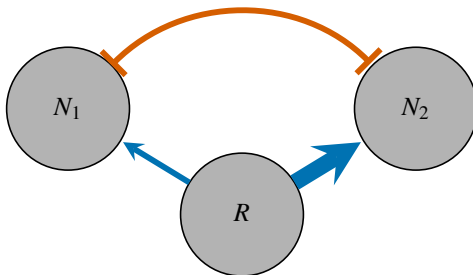
# Modeling competition: a conceptual overview



Competition essentially comes in two flavors:

- **Resource or exploitative competition:** organisms **indirectly** compete with one another by consuming resources (e.g., nutrient uptake by plants)
- **Interference competition:** organisms directly **interfere** with one another to maintain access to resources (e.g., antibiotic production by microbes)

# Phenomenological vs. mechanistic modeling



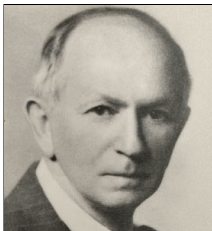
The depiction of competition above can be modeled in two ways:

- **Phenomenologically**: by modeling the indirect effects species have on one another through competition without explicit reference to the resource(s) or mechanism(s) at play
- **Mechanistically**: by modeling the uptake of resource(s) and letting the indirect effects species have on one another emerge indirectly

# Competition: a phenomenological modeling approach

## The Lotka-Volterra competition model

Lotka (1932) and Volterra (1931) independently developed a phenomenological approach for modeling the dynamics of multiple competing species.



**Alfred Lotka**



**Vito Volterra**

# Deriving the Lotka-Volterra model

We begin with the following stipulations:

- When grown in isolation, each species undergoes logistic growth at rate  $r_i$  and until it reaches its carrying capacity  $K_i$
- When grown in mixtures, there are four possible outcomes: extinction, a monoculture of each species, and coexistence
- Competition  $\alpha_{ij}$  is modeled phenomenologically as the reduction in the maximum population size of species  $i$  due to the population size of species  $j$

Given these rules (and no Googling), let's see if we can derive the simple 2-species Lotka-Volterra model.

# Deriving the Lotka-Volterra model

The continuous-time version of the Lotka-Volterra competition model reads as follows:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left( \frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left( \frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right)\end{aligned}$$

Where the interspecific competition coefficients  $\alpha_{ij} \geq 0$  and the intraspecific competition coefficients  $\alpha_{ii} = \alpha_{jj} = 1$ .

You can perform a dimensional analysis and set each species to zero to verify that this model satisfies the stipulations from the previous slide.

## Solving the model at equilibrium

This model has four possible equilibrium solutions: two monocultures such that  $\hat{N}_i = K_i$  and  $\hat{N}_j = 0$ , one extinction such that  $\hat{N}_i = \hat{N}_j = 0$ , and the **interior equilibrium** where  $\hat{N}_i > 0$  and  $\hat{N}_j > 0$ .

At the interior equilibrium, the growth rate of both species is zero so we have:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left( \frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right) = 0 \\ \frac{dN_2}{dt} &= r_2 N_2 \left( \frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right) = 0\end{aligned}$$



## Solving the model at equilibrium

This can happen if the initial abundances  $N_i(0) = 0$ , the growth rates  $r_i = 0$  or, more interestingly, if the term in the parentheses is zero:

$$K_1 - N_1 - \alpha_{12}N_2 = 0$$

$$K_2 - N_2 - \alpha_{21}N_1 = 0$$

We can isolate the  $N_i$  terms in both equations:

$$N_1 = K_1 - \alpha_{12}N_2$$

$$N_2 = K_2 - \alpha_{21}N_1$$

We now replace  $N_2$  in the first equation with its expression from the second equation:

$$N_1 = K_1 - \alpha_{12}(K_2 - \alpha_{21}N_1)$$

## Solving the model at equilibrium

We now isolate  $N_1$ :

$$\hat{N}_1 = \frac{K_1 - \alpha_{12}K_2}{1 - \alpha_{12}\alpha_{21}}$$

We proceed in the same way to get  $N_2$ :

$$\hat{N}_2 = \frac{K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}}$$

We now need to determine when this equilibrium solution is **biologically feasible** (i.e.,  $\frac{\hat{N}_i}{\hat{N}_j} > 0$ ). This means that we must have:

$$\frac{\hat{N}_i}{\hat{N}_j} = \frac{K_1 - \alpha_{12}K_2}{K_2 - \alpha_{21}K_1} > 0$$

## Solving the model at equilibrium

This leads to two separate conditions:

$$\frac{K_1}{K_2} > \alpha_{12}$$
$$\frac{K_2}{K_1} > \alpha_{21}$$

Combining these two conditions via multiplication yields:

$$1 > \alpha_{12}\alpha_{21}$$

The trick is to note that by definition,  $\alpha_{11} = \alpha_{22} = 1$ , so we can write:

$$\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}$$

This expression means that **intraspecific competition** must be greater than **interspecific competition** for coexistence to occur.

# Invasion analysis

Turelli (1978) introduced and Chesson (2000) popularized the use of the **invasibility criterion** for determining the stability of equilibria.

The idea is that an interior equilibrium is stable if a rare species  $i$  can invade a monoculture of the other species  $j$ .

In the context of the 2-species Lotka-Volterra model, this means that we set species 1 at its carrying capacity  $K_1$  and species 2 at zero and determine whether its population growth rate is greater than zero:

$$\frac{dN_2}{dt} = r_2 K_2 \left( \frac{K_2 - 0 - \alpha_{21} K_1}{K_2} \right) > 0$$

# Invasion analysis

The population growth rate of species 2 is greater than zero when:

$$\frac{K_2}{K_1} > \alpha_{21}$$

We now do the same for species 1; set  $N_2 = K_2$  and determine the population growth rate of species 1:

$$\frac{K_1}{K_2} > \alpha_{12}$$

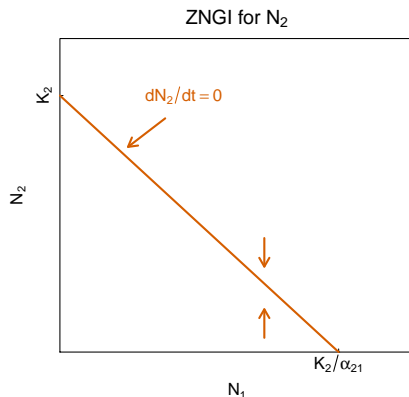
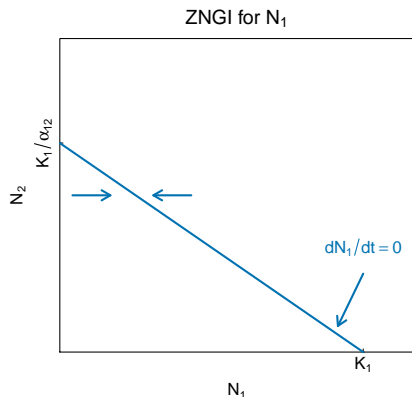
We now combine these inequalities via multiplication to yield the familiar coexistence condition:

$$1 > \alpha_{21}\alpha_{12}$$

Noting that  $\alpha_{11} = \alpha_{22} = 1$ , we can rewrite the last expression as:

$$\alpha_{11}\alpha_{22} > \alpha_{21}\alpha_{12}$$

# Graphical analysis: Zero Net Growth Isoclines (ZNGI)

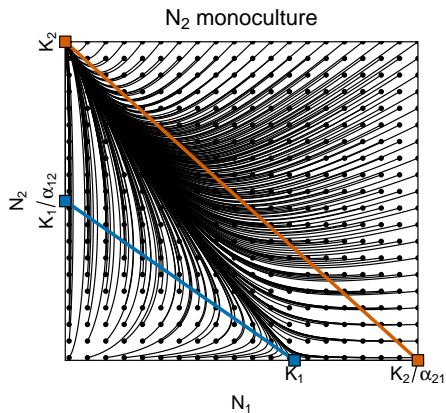
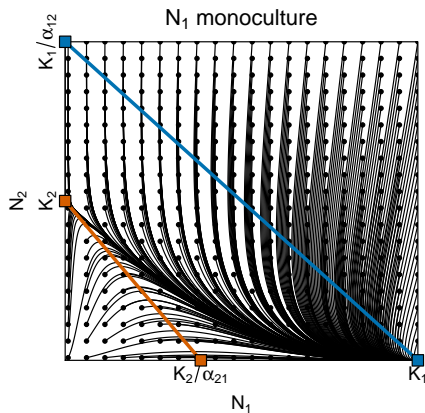


The ZNGI are found by computing the x- and y- intercepts of the following:

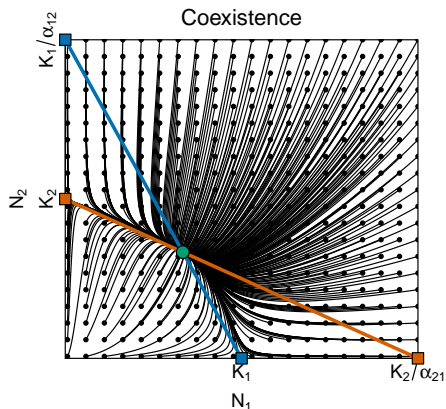
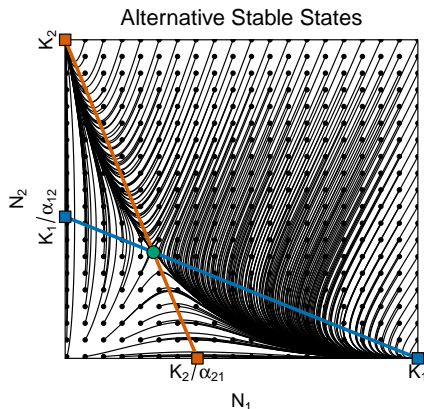
$$N_1 = K_1 - \alpha_{12}N_2$$

$$N_2 = K_2 - \alpha_{21}N_1$$

# Graphical presentation of the monoculture outcomes



# Graphical presentation of the other outcomes





# Stability analysis

We can use Taylor expansion to determine the stability of the equilibrium  $\{\hat{x}, \hat{y}\}$  of a 2-variable function  $F(x, y)$  by linearizing as follows:

$$f(x, y) \approx f(\hat{x}, \hat{y}) + \frac{1}{1!} \left[ (x - \hat{x}) \frac{\partial f(\hat{x}, \hat{y})}{\partial x} + (y - \hat{y}) \frac{\partial f(\hat{x}, \hat{y})}{\partial y} \right] + \dots$$

Doing this for each growth equation  $f_i = \dot{N}_i = \frac{dn_i}{dt}$  in the model yields the following equations describing how each perturbation  $n_1 = N_1 - \hat{N}_1$  and  $n_2 = N_2 - \hat{N}_2$  of the equilibrium behaves over time:

$$\begin{aligned}\dot{n}_1 &= \frac{\partial f_1(\hat{N}_1, \hat{N}_2)}{\partial N_1} n_1 + \frac{\partial f_1(\hat{N}_1, \hat{N}_2)}{\partial N_2} n_2 \\ \dot{n}_2 &= \frac{\partial f_2(\hat{N}_1, \hat{N}_2)}{\partial N_1} n_1 + \frac{\partial f_2(\hat{N}_1, \hat{N}_2)}{\partial N_2} n_2\end{aligned}$$

# Stability analysis

This system can more easily be represented by using matrix notation as the product of the **Jacobian matrix  $\mathbf{J}$**  and the vector of perturbations  **$\mathbf{n}$** :

$$\begin{bmatrix} \frac{dn_1}{dt} \\ \frac{dn_2}{dt} \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \end{bmatrix}$$

Setting  $\mathbf{J} = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{bmatrix}$  and  $\mathbf{n} = \begin{bmatrix} n_1 \\ n_2 \end{bmatrix}$  yields:

$$\frac{d\mathbf{n}}{dt} = \mathbf{J}\mathbf{n}$$

This equation is strikingly similar to the equation for exponential growth, whose solution was:

$$\mathbf{n}(t) = \mathbf{n}_0 e^{\mathbf{J}t}$$

# Stability analysis

We now need to find the eigenvalues  $\lambda$  and eigenvector  $\tilde{\mathbf{n}}$  such that  $\mathbf{J}\tilde{\mathbf{n}} = \lambda\tilde{\mathbf{n}}$  so we can write:

$$\mathbf{n}(t) = \mathbf{n}_0 e^{\mathbf{J}t} = e^{\lambda t} \tilde{\mathbf{n}}$$

The perturbations  $\tilde{\mathbf{n}}$  will grow exponentially if  $\lambda > 0$  but decay exponentially if  $\lambda < 0$ . **Hence, the equilibrium will be locally stable (unstable) if the real part of all eigenvalues is smaller (greater) than zero.**

# Eigenvalues and the stability of model equilibria

Eigenvalues  $\lambda = a + i \cdot b$  can have both a real ( $a$ ) and imaginary part ( $b$ ), each of which reveals important details about the behavior of the model around the equilibrium:

- The magnitude and the sign of the real part  $a$  determines the rate at which perturbations grow or decay over time
- The magnitude of the imaginary part  $b$  determines the frequency of the oscillations around the equilibrium

# Types of equilibria

To understand this link, write a general solution to the previous equation:

$$\mathbf{n}(t) = \tilde{\mathbf{n}}_1 e^{\lambda_1 t} + \tilde{\mathbf{n}}_2 e^{\lambda_2 t} + \dots + \tilde{\mathbf{n}}_k e^{\lambda_k t}$$

If the eigenvalues  $\lambda_j$  are complex, then each  $e$  term can be expressed as:

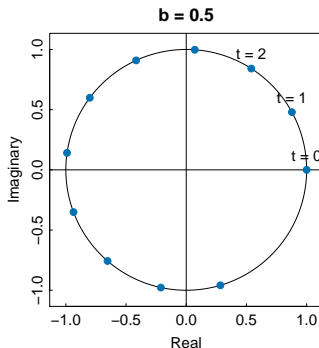
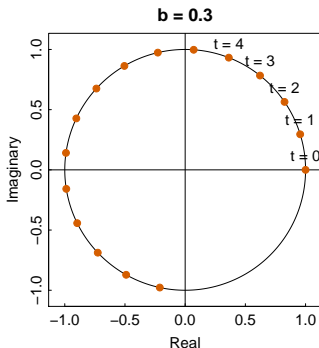
$$e^{(a+bi) \cdot t} = e^{a \cdot t} e^{bi \cdot t}$$

The last expression is the product of a real part ( $e^{a \cdot t}$ ) and an imaginary part ( $e^{bi \cdot t}$ ), where  $i = \sqrt{-1}$ . The imaginary part can also be expressed using Euler's formula:

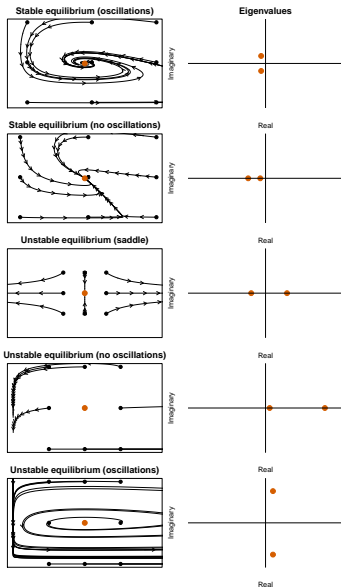
$$e^{bi \cdot t} = \cos(b \cdot t) + i \cdot \sin(b \cdot t)$$

# Types of equilibria

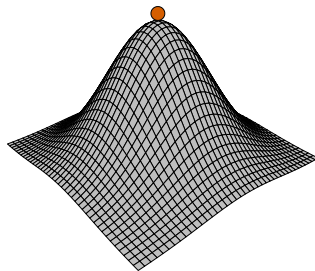
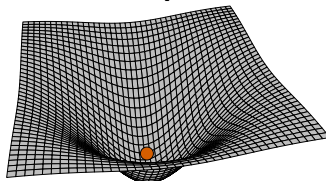
Euler's formula and the figure below show that the imaginary part  $b$  does not control the amplitude of the oscillations (i.e., whether they grow or decay), only their frequency:



# Types of equilibria



## Stable equilibrium



## Unstable equilibrium

# Stability analysis of the Lotka-Volterra model

To assess the stability of the equilibria, we must first write the Jacobian matrix  $\mathbf{J}$  by taking the partial derivatives of each population growth rate  $\dot{N}_i$  with respect to each variable  $N_i$ :

$$\mathbf{J} = \begin{bmatrix} \frac{r_1}{K_1} (K_1 - 2\hat{N}_1 - \alpha_{12}\hat{N}_2) & \frac{-r_1}{K_1} (\alpha_{12}\hat{N}_1) \\ \frac{-r_2}{K_2} (\alpha_{21}\hat{N}_2) & \frac{r_2}{K_2} (K_2 - 2\hat{N}_2 - \alpha_{21}\hat{N}_1) \end{bmatrix}$$

We now assess the stability of the boundary (i.e., non-interior) equilibria. We begin with the extinction equilibrium  $\{\hat{N}_1 = 0, \hat{N}_2 = 0\}$ :

$$\mathbf{J}(0,0) = \begin{bmatrix} r_1 & 0 \\ 0 & r_2 \end{bmatrix}$$



# Stability analysis of the Lotka-Volterra model

To determine the eigenvalues, we subtract  $\lambda \mathbf{I}$  from  $\mathbf{J}(0, 0)$  and find the characteristic polynomial by computing the determinant:

$$0 = (r_1 - \lambda_1)(r_2 - \lambda_2)$$

There are two solutions to this equation:  $\lambda_1 = r_1$  and  $\lambda_2 = r_2$ . This means that as long as the growth rates are greater than zero, both eigenvalues will be positive and the extinction equilibrium will be unstable.

We now determine the stability of the species 1 monoculture  $\{\hat{N}_1 = K_1, \hat{N}_2 = 0\}$ :

$$\mathbf{J}(K_1, 0) = \begin{bmatrix} -r_1 & -r_1\alpha_{12} \\ 0 & \frac{r_2}{K_2}(K_2 - K_1\alpha_{21}) \end{bmatrix}$$

# Stability analysis of the Lotka-Volterra model

The eigenvalues of  $\mathbf{J}(K_1, 0)$  are:

$$0 = (-r_1 - \lambda_1) \left( \frac{r_2}{K_2} (K_2 - K_1 \alpha_{21}) - \lambda_2 \right)$$

There are two solutions to this equation:  $\lambda_1 = -r_1$  and  $\lambda_2 = \frac{r_2}{K_2} (K_2 - K_1 \alpha_{21})$ . The second eigenvalue is negative only if  $\frac{K_2}{K_1} < \alpha_{21}$ .

Hence, this equilibrium is stable only if the growth rate of species 1 is positive and the ratio of the carrying capacity of species 2 relative to that of species 1 is smaller than the competitive effect of species 1 on species 2.

We now determine the stability of the species 2 monoculture  $\{\hat{N}_1 = 0, \hat{N}_2 = K_2\}$ :

$$\mathbf{J}(0, K_2) = \begin{bmatrix} \frac{r_1}{K_1} (K_1 - K_2 \alpha_{12}) & 0 \\ -r_2 \alpha_{21} & -r_2 \end{bmatrix}$$

# Stability analysis of the Lotka-Volterra model

The eigenvalues of  $\mathbf{J}(0, K_2)$  are:

$$0 = \left( \frac{r_1}{K_1} (K_1 - K_2 \alpha_{12}) - \lambda_1 \right) (-r_2 - \lambda_2)$$

There are two solutions to this equation:  $\lambda_1 = \frac{r_1}{K_1} (K_1 - K_2 \alpha_{12})$  and  $\lambda_2 = -r_2$ . The first eigenvalue is negative only if  $\frac{K_1}{K_2} < \alpha_{12}$ .

Hence, this equilibrium is stable only if the growth rate of species 2 is positive and the ratio of the carrying capacity of species 1 relative to that of species 2 is smaller than the competitive effect of species 2 on species 1.

# Stability analysis of the Lotka-Volterra model

We now determine the stability of the interior equilibrium  $\{\hat{N}_1 = \frac{K_1 - \alpha_{12}K_2}{1 - \alpha_{12}\alpha_{21}}, \hat{N}_2 = \frac{K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}}\}$ . To do so we'll use a trick:

$$\mathbf{J}(\hat{N}_1, \hat{N}_2) = \begin{bmatrix} -\frac{r_1\hat{N}_1}{K_1} & -\frac{r_1\hat{N}_1}{K_1}\alpha_{12} \\ -\frac{r_2\hat{N}_2}{K_2}\alpha_{21} & -\frac{r_2\hat{N}_2}{K_2} \end{bmatrix}$$

This matrix can be rewritten as the product of matrix **A** with zeros everywhere but on the diagonal and a matrix **B** containing the interaction coefficients on the diagonal and ones everywhere else:

$$\mathbf{J}(\hat{N}_1, \hat{N}_2) = \mathbf{AB} = \begin{bmatrix} -\frac{r_1\hat{N}_1}{K_1} & 0 \\ 0 & -\frac{r_2\hat{N}_2}{K_2} \end{bmatrix} \begin{bmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{bmatrix}$$

# Stability analysis of the Lotka-Volterra model

In this case, the eigenvalues of  $\mathbf{J}(\hat{N}_1, \hat{N}_2)$  will be negative if the eigenvalues of the second matrix  $\mathbf{B}$  are positive. This means that we can determine the stability of this equilibrium by evaluating the eigenvalues of  $\mathbf{B}$  only:

$$0 = (1 - \lambda)(1 - \lambda) - \alpha_{12}\alpha_{21}$$

This leads to the following characteristic polynomial:

$$0 = \lambda^2 - 2\lambda + (1 - \alpha_{12}\alpha_{21})$$

Using the quadratic formula with  $a = 1$ ,  $b = -2$ ,  $c = 1 - \alpha_{12}\alpha_{21}$  yields:

$$\lambda = \sqrt{1} \pm \sqrt{\alpha_{12}\alpha_{21}}$$

# Stability analysis of the Lotka-Volterra model

The two eigenvalues are:  $\lambda_1 = \sqrt{1} + \sqrt{\alpha_{12}\alpha_{21}}$  and  $\lambda_2 = \sqrt{1} - \sqrt{\alpha_{12}\alpha_{21}}$ . The first eigenvalue will always be positive, so the stability of the equilibrium depends on  $\lambda_2 > 0$ :

$$1 > \alpha_{12}\alpha_{21}$$

Using the fact that  $\alpha_{11} = \alpha_{22} = 1$ , we can write:

$$\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}$$

This is the same condition that we obtained when determining the feasibility of the interior equilibrium.

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