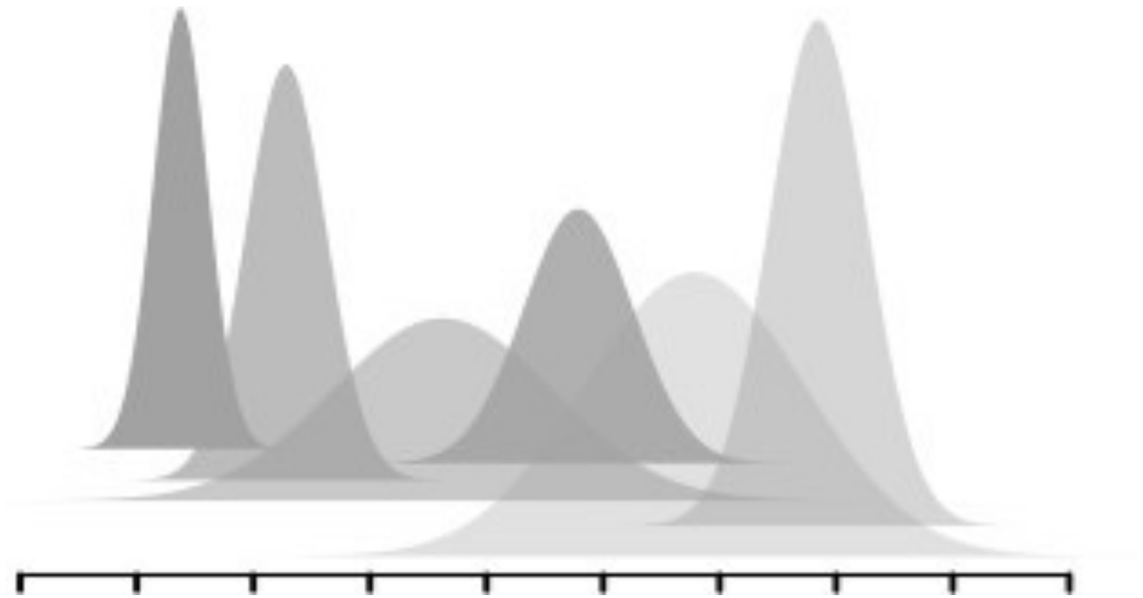
5.1 Equilibrium and stability analysis



Jelena H. Pantel

Faculty of Biology

University of Duisburg-Essen

jelena.pantel@uni-due.de

What is equilibrium?

A system at equilibrium does not change over time (plural: equilibria). A particular value of a variable is called an equilibrium value if, when the variable is started at this value, the variable never changes.

Why is this useful? It informs us where the system might end up (species going extinct, or coexisting? Etc)

What is stability?

- An equilibrium is *locally stable* if a system near the equilibrium approaches it (locally attracting).
- An equilibrium is *globally stable* if a system approaches the equilibrium regardless of its initial position.
- An equilibrium is *unstable* if a system near the equilibrium moves away from it (repelling).

How can I find an equilibrium?

- In a continuous-time model: replace n with n* and set dn/dt = 0
- Then solve for n*

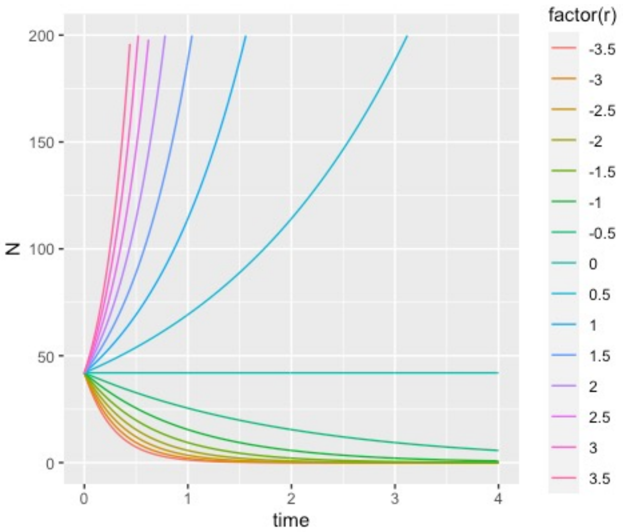
Exponential growth

$$\frac{dn}{dt} = rn$$

Graphical techniques: develop a feeling for your model
Equilibria and stability analyses

Equilibrium

$$\frac{dn}{dt} = 0 \longrightarrow 0 = rn^* \longrightarrow \frac{0}{r} = n^* \longrightarrow n^* = 0$$



Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

$$0 = rn^*\left(1 - \frac{n^*}{K}\right) \longrightarrow n^* = 0$$

$$\left(1 - \frac{n^*}{K}\right) = 0 \longrightarrow 1 = \frac{n^*}{K} \longrightarrow K = n^*$$

How can I determine if an equilibria is stable?

- An equilibrium is *locally stable* if a system near the equilibrium approaches it (locally attracting).
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$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

$$n^* = 0$$
$$n^* = K$$

General solution

$$n(t) = \frac{e^{rt}n_0}{1 - \frac{n_o}{K} + \frac{e^{rt}n_0}{K}}$$

If we plug an equilibrium value into the original equation :

$$n(t) = \frac{e^{rt}0}{1 - \frac{0}{K} + \frac{e^{rt}0}{K}} = 0$$

$$n(t) = \frac{e^{rt}K}{1 - \frac{K}{K} + \frac{e^{rt}K}{K}} = K$$

$$\frac{dn}{dt} = rn$$

$$n^* = 0$$

General solution

$$n(t) = n_0 e^{rt}$$

$$n(t) = 0e^{rt} = 0$$

The system will remain at that equilibrium (that is the definition of equilibrium)

```
> r <- 1.7
> K <- 100
> t <- 90
> (exp(r*t)*K) / (1-(K/K) + ((exp(r*t)*K))/K)
[1] 100
```

But what if we start the population *near* (not exactly at) an equilibrium? Will it approach that equilibrium, or move away? That is *stability analysis*

How can I determine if an equilibria is stable?

- Continuous equation: rename the differential equation dn/dt as f(n)
- Evaluate *local stability* (response to a small perturbation from the equilibria) of any equilibrium n* by:
- 1. Differentiate f(n) with respect to n to obtain df/dn
- 2. Replace every instance of n in this derivative with the equilibrium value n* to obtain $(df/dn)|_{n=n^*}$
- 3. Define $r = (df/dn)|_{n=n^*}$
- 4. Determine the sign of r
- 5. Evaluate the stability of the equilibrium n* according to the following:

Case C:	$r < 0$	$r > 0$
	$\hat{n}$ is stable	$\hat{n}$ is unstable

How can I determine if an equilibria is stable?

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) \longrightarrow$$

$$f(n) = rn\left(1 - \frac{n}{K}\right)$$

$$\frac{df}{dn} = \frac{d}{dn}\left[rn\left(1 - \frac{n}{K}\right)\right] = \frac{d}{dn}\left[rn - \frac{rn^2}{K}\right] \longrightarrow r - \frac{2rn}{K}$$

$\longrightarrow$ $n^* = 0$

$\longrightarrow$ $\frac{df}{dn}\Big|_{n=0} = r - \frac{2r0}{K} = r$

UNSTABLE !

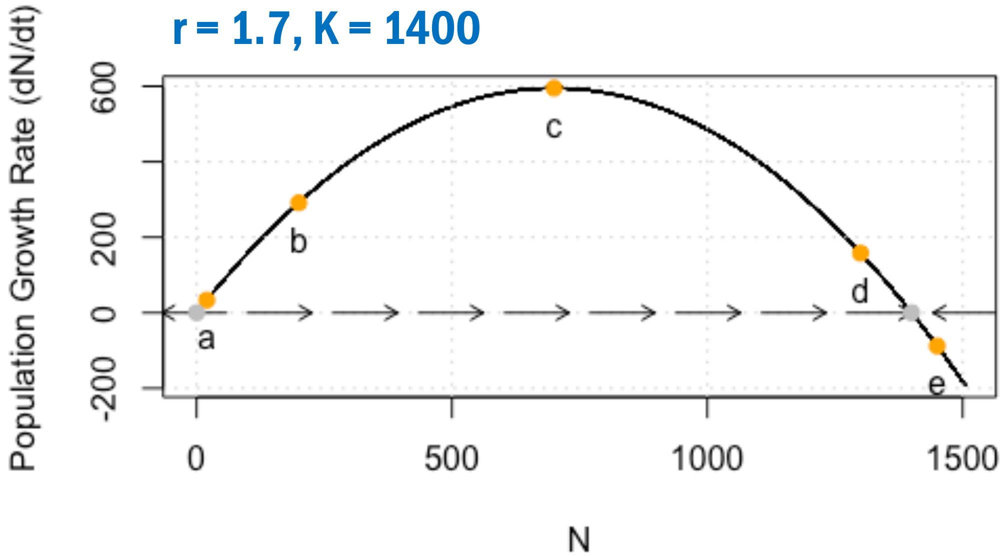
Case C:	$r < 0$	$r > 0$
	$\hat{n}$ is stable	$\hat{n}$ is unstable

$\longrightarrow$ $n^* = K$

$\longrightarrow$ $\frac{df}{dn}\Big|_{n=K} = r - \frac{2rK}{K} = r - 2r = -r$

STABLE !

- **Note the direction of the arrows along the axis of N (the state variable) – equilibrium analysis asks – what equilibria does the system move towards when N is moved *away* from one of these**
  - **This is *perturbation analysis***
  - **If N > 0, N=K is the stable equilibrium**



How can I analyze equilibria and stability in non-linear models with multiple variables (dn_1/dt and dn_2/dt etc)?

Lotka Volterra competition model

$$\frac{dn_1}{dt} = rn_1\left(1 - \frac{n_1 + \alpha_{12}n_2}{K_1}\right)$$

$$\frac{dn_2}{dt} = rn_2\left(1 - \frac{n_2 + \alpha_{21}n_1}{K_2}\right)$$

Multiple equilibria

$$n_1^* = \frac{K_1 - \alpha_{12}K_2}{1 - \alpha_{12}\alpha_{21}}$$

$$n_2^* = \frac{K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}}$$

7.3 Dynamics at the Equilibria

Here we use eigenanalysis to analyze the properties of the equilibrium, whether they are attractors, repellers, or both, and whether the system oscillates around these equilibria.

For logistic growth, we assessed stability with the partial derivative of the growth rate, with respect to population size. If it was negative the population was stable, and the more negative the value, the shorter the return time. Here we build on this, and present a general recipe for stability analysis (Morin 1999):

1. Determine the equilibrium abundances of each species by setting its growth equation to zero, and solving for N.
2. Create the Jacobian matrix. This matrix represents the response of each species to changes in its own population and to changes in each other's populations. The matrix elements are the partial derivatives of each species' growth rate with respect to each population.
3. Solve the Jacobian. Substitute the equilibrium abundances into the partial derivatives of the Jacobian matrix to put a real number into each element of the Jacobian matrix.
4. Use the Jacobian matrix to find the behavior of the system near the equilibria. The trace, determinant, and eigenvalues of the Jacobian can tell us how stable or unstable the system is, and whether and how it cycles.

How can I analyze equilibria and stability in Lotka Volterra competition model?

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(Roughgarden 1998). For instance, the $\boxed{\textit{Routh-Hurwitz criterion}}$ for stability tells us that a two-species equilibrium will be locally stable, only if $\mathbf{J}_{11} + \mathbf{J}_{22} < 0$ and if $\mathbf{J}_{11}\mathbf{J}_{22} - \mathbf{J}_{12}\mathbf{J}_{21} > 0$. The biological

7.3.3 Solve the Jacobian at an equilibrium

To solve the Jacobian at an equilibrium, we substitute N_1^* (7.8) and N_2^* (7.9) into the Jacobian matrix (7.13). Refer to those equations now. What is the value of N_1 in terms of α_{ii} and α_{ij}? Take that value and stick it in each element of the Jacobian (7.14). Repeat for N_2. When we do this, and rearrange, we get,

$$\mathbf{J} = \begin{pmatrix} -r_1\alpha_{11}\left(\frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}\right) & -r_1\alpha_{12}\left(\frac{\alpha_{22}-\alpha_{12}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}\right) \\ -r_2\alpha_{21}\left(\frac{\alpha_{11}-\alpha_{21}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}\right) & -r_2\alpha_{22}\left(\frac{\alpha_{11}-\alpha_{21}}{\alpha_{11}\alpha_{22}-\alpha_{12}\alpha_{21}}\right) \end{pmatrix}. \tag{7.14}$$

This depends on the exact values of r, α

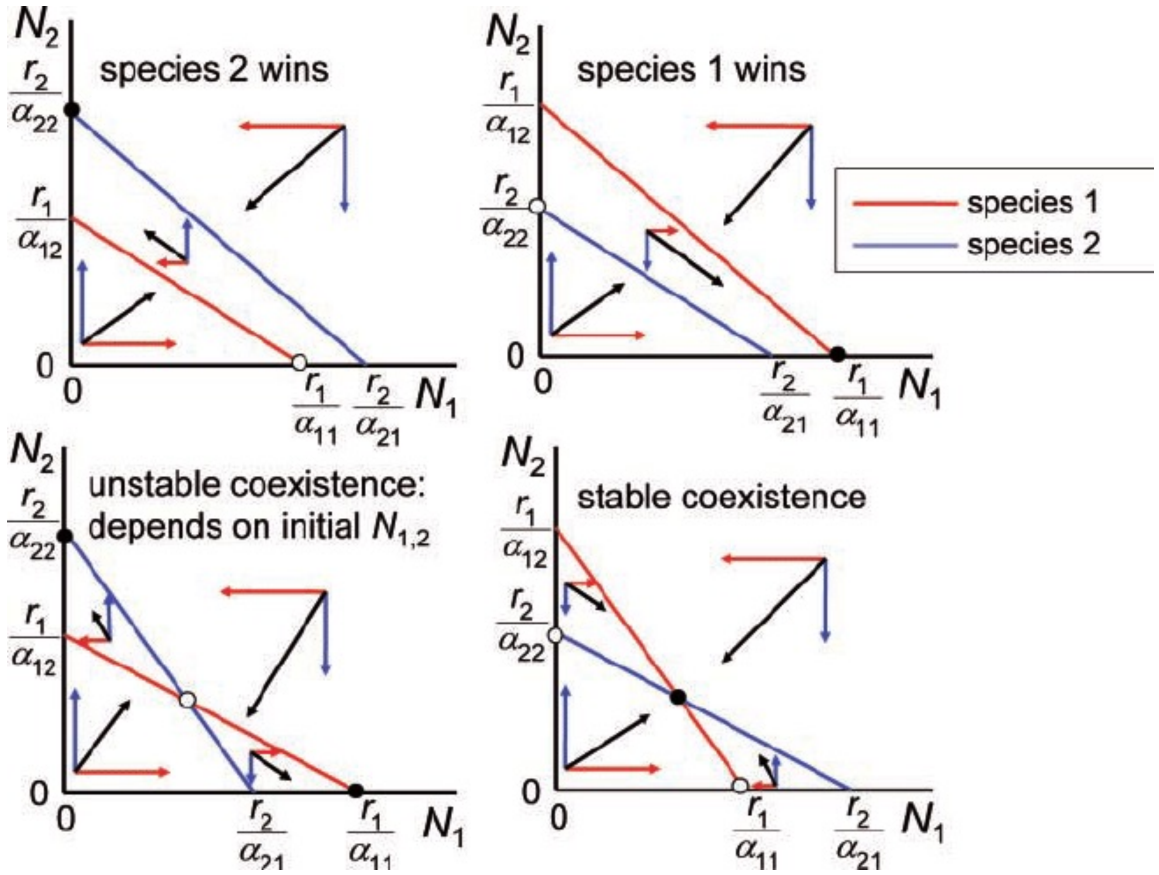
equilibrium. For $\alpha_{ii} = 0.01$ and $\alpha_{ij} = 0.001$ (see above) we find

```
r1 <- r2 <- 1
J1 <- eval(J)
J1
```

```
##             [,1]        [,2]
## [1,] -0.90909091 -0.09090909
## [2,] -0.09090909 -0.90909091
```

How can I analyze equilibria and stability in Lotka Volterra competition model?

Phase plane diagrams



How can I analyze equilibria and stability in other models??

- We are officially out of time ;)
- This class was presented to me as a ”just a seminar” class – I was told students in the Master program would be unlikely to have more interest in statistical / mathematical modelling courses (!!)
- I knew they would be wrong! – you present students with interesting new topics, try your best to teach at their level (not my level), and let them decide if they are interested!
- Math is biology is math.
- Let people in the Master know that you’re hungry for a theory course, an advanced statistical modelling course, some probability theory and linear algebra!
- Think, always, about the mathematical patterns that might help explain the biological dynamics you are observing. Consider a model to help being out these patterns and better understand your system.