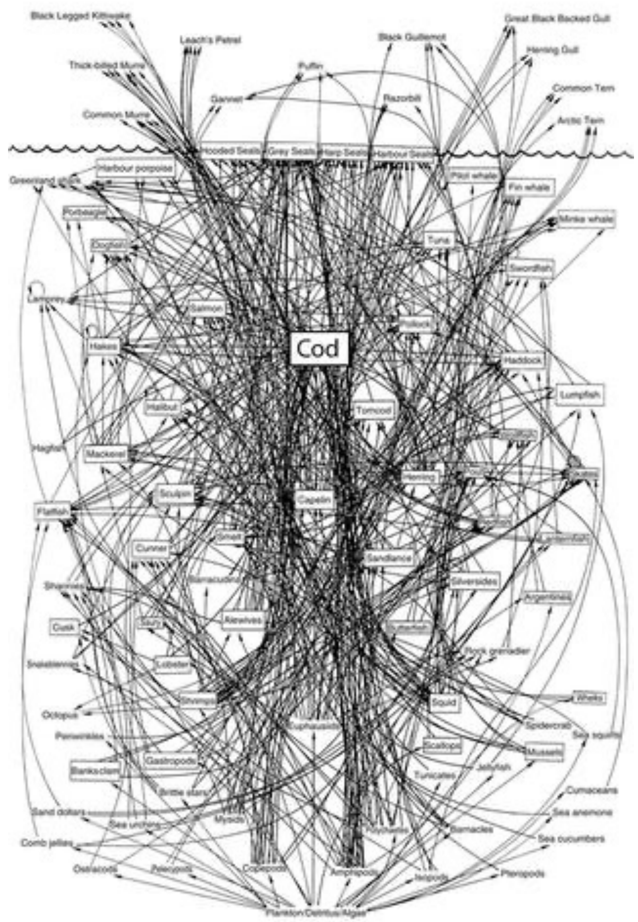
# Complexity and stability of empirical food webs

# Food webs

Complex systems




A simplified food web for the Northwest Atlantic. © IMMA

Will the ecosystem buffer or amplify a perturbation ?

# The complexity stability debate

Until the 70's:
Diversity stabilizes ecosystems (Odum 1953, MacArthur 1955)

*Guyane, tropical forest.*

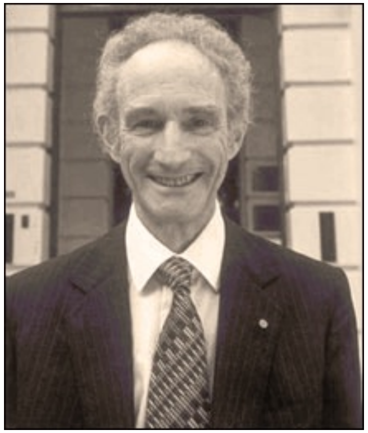
*Alaska, boreal forest.*

# The complexity stability debate

Complexity decreases ecosystem stability (May 1972)

**Complexity:**

- Species richness $S$
- Connectance $C$
- Variance of non-diagonal elements of the Jacobian matrix $\sigma^2$



*Professor Lord Robert May*

**Stability criterion** $\sigma\sqrt{SC} < 1$

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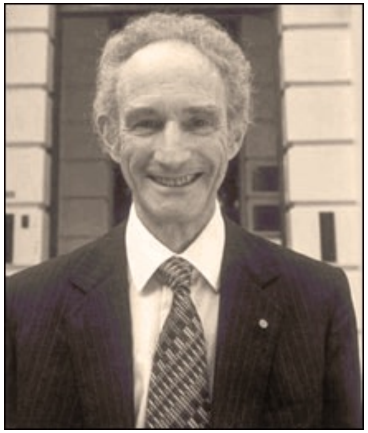

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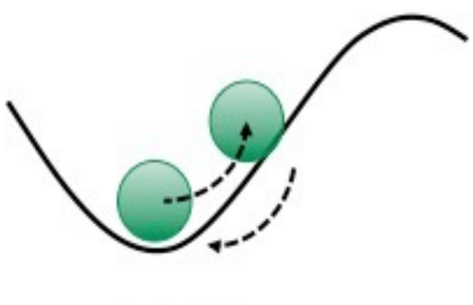
**Stability criterion** $\sigma\sqrt{SC} < 1$

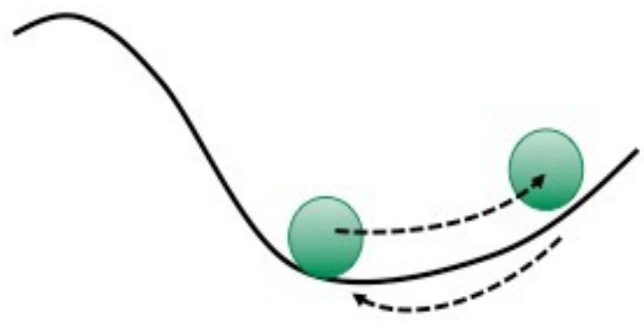
Where does this result come from?

# Local stability analysis

Asymptotic stability: rate at which species populations go back to their initial densities after a small perturbation



High stability



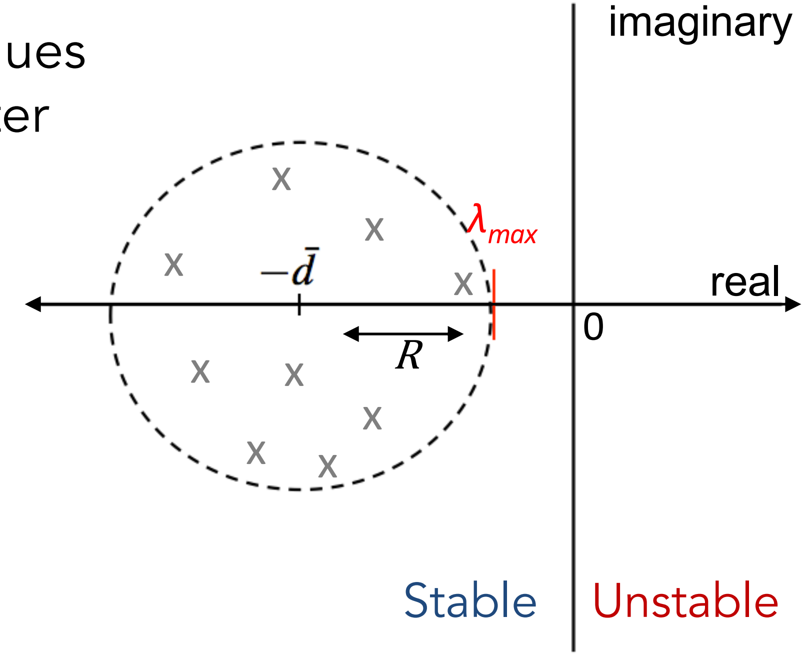
Low stability

Largest eigenvalue of the Jacobian matrix (its real part)

# The circular law

On a complex plan: all the eigenvalues are contained in a circle of center *(-d, 0)* and radius *R*.

The system is stable if $Re(\boldsymbol{\lambda}_{max}) < 0$.



# The circular law

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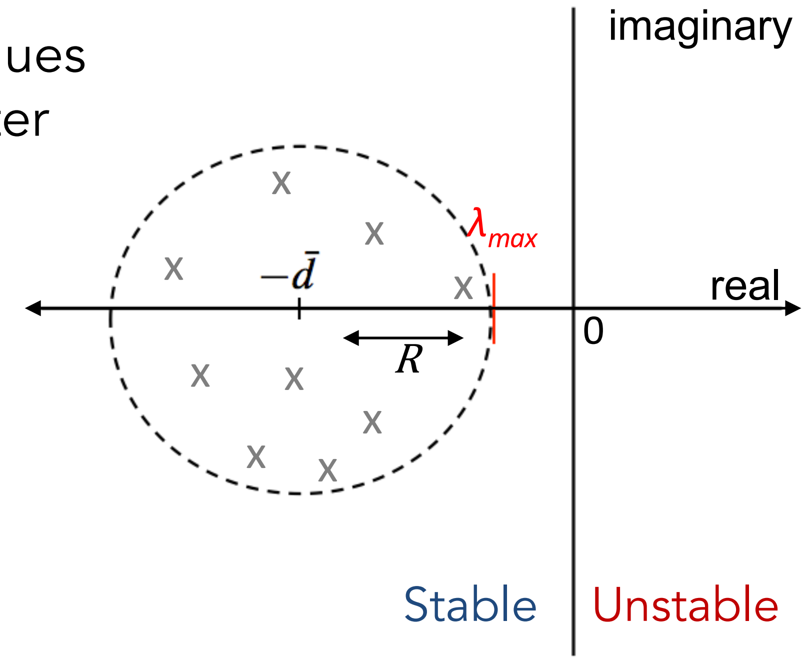
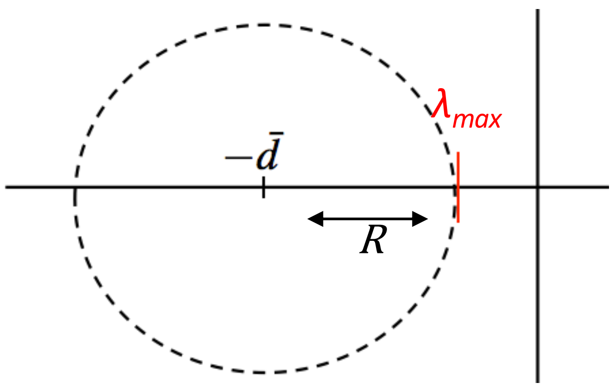
Stability criterion: R < d



# The circular law

Link the stability of a matrix to its properties




$$C = \begin{pmatrix} -d_1 & +c_{2,1} & +c_{3,1} & 0 \\ -c_{1,2} & -d_2 & 0 & +c_{4,2} \\ -c_{1,3} & 0 & -d_3 & +c_{4,3} \\ 0 & -c_{2,4} & -c_{3,4} & -d_4 \end{pmatrix}$$

$\bar{d}$ : mean of diagonal terms of C

In random matrices: $R = \sigma\sqrt{SC}$

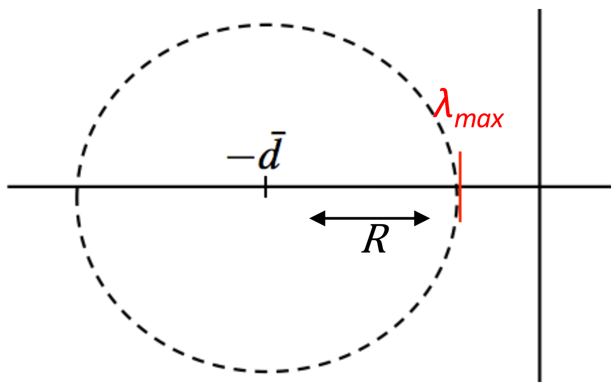
$\sigma^2$ : variance of non-diagonal elements $c_{ij}$

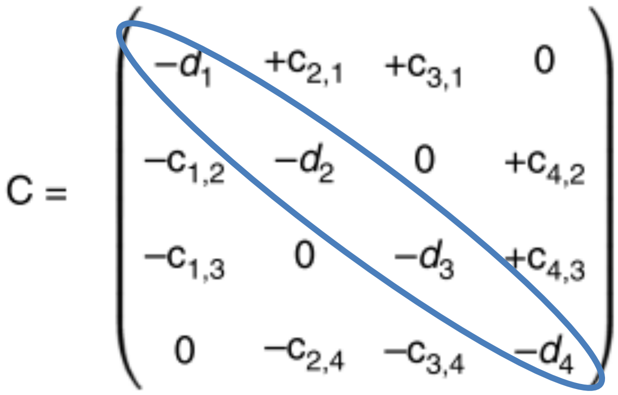
S : size of the matrix

C : proportion of non-zero elements

# The circular law

Link the stability of a matrix to its properties




$\bar{\boldsymbol{d}}$ : mean of diagonal terms of C (magnitude of density dependence)

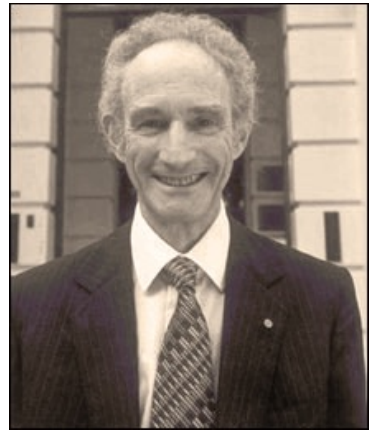
In ecological communities : $\boldsymbol{R = \sigma\sqrt{SC}}$

$\boldsymbol{\sigma^2}$**:** variance of non-diagonal elements $c_{ij} = \alpha_{ij}.N_i^*$

S: species richness

C: connectance

Let's check this result in R



*« In short, there is no confortable theorem assuring that increasing diversity and complexity beget community stability; rather, as a mathematical generality the opposite is true.*

*The task, therefore, is to elucidate the devious strategies which make for stability in enduring natural systems. »* (May 2001).

1. What is the actual complexity-stability relationship in empirical communities?

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2. What are the « *devious strategies* » of real communities that allow them to persist despite their complexity?

# Food-web dataset

116 quantitative food webs from Ecopath models (Christensen 1992)

For each species *i*:

- biomass $B_i$ (tons/km$^2$)
- *production* $(P/B)_i$ (year$^{-1}$)
- consumption $(Q/B)_i$ (year$^{-1}$)
- diet composition $DC_{ji}$

**Assumption: food webs are at equilibrium:** $B_i^* = B_i$

# Derivation of interaction strengths from data

**What we want:**

$\alpha_{rc}$ : per unit effect of consumer *c* on growth rate of resource *r*

$\alpha_{cr}$: per unit effect of resource *r* on growth rate of consumer *c*

Arditi et *al.* (2021) *The Dimensions and Units of the Population Interaction Coefficients. Front. Ecol. Evol.*

# Derivation of interaction strengths from data

## What we want:

$\alpha_{rc}$ : per unit effect of consumer $c$ on growth rate of resource $r$

$\alpha_{cr}$: per unit effect of resource $r$ on growth rate of consumer $c$

## What is measured:

- biomass $B_i$ (tons/km$^2$)
- production $(P/B)_i$ (year$^{-1}$)
- consumption $(Q/B)_i$ (year$^{-1}$)
- diet composition $DC_{ji}$

## From De Ruiter *et al.* (1995):

$$\alpha_{rc} = -\,(DC_{cr} \times (Q/B)_c)\ /\ \mathrm{B_r}$$

$$\alpha_{cr} = (DC_{cr} \times (P/B)_c)\ /\ \mathrm{B_r}$$

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$$\alpha_{cr} = \left(DC_{cr} \times (P/B)_c\right) / B_r$$

$$\alpha_{cr} = \alpha_{rc} \times e_{rc}\text{, with } e_{rc} = (P/B)_c \,/\, (Q/B)_c$$

$\rightarrow \alpha_{cr} \leq \alpha_{rc}$ (km$^2$/tons/year)

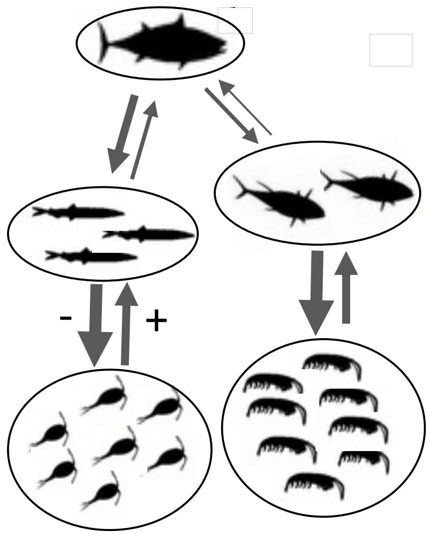
# Practice in R

1. computing food-web complexity and stability

2. analysing the relationship between complexity and stability in empirical food webs

3. comparing the complexity-stability relationship of empirical and « randomized » food webs

# What are the non-random properties of food webs?




$$M = \begin{pmatrix} -d_1 & +\mathbf{c}_{2,1} & +\mathbf{c}_{3,1} & 0 \\ -\mathbf{c}_{1,2} & -d_2 & 0 & +\mathbf{c}_{4,2} \\ -\mathbf{c}_{1,3} & 0 & -d_3 & +\mathbf{c}_{4,3} \\ 0 & -\mathbf{c}_{2,4} & -\mathbf{c}_{3,4} & -d_4 \end{pmatrix}$$

- $H_1$: food web topology (who eat whom)
- $H_2$: correlation between $+c_{ji}$ and $-c_{ij}$
- $H_{3:}$ distribution of non-diagonal elements