# A (not so) gentle introduction to networks in ecology

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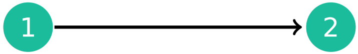
## Why should I care about networks?

- A good way to harness complexity (especially of emergent niche patterns)
- A solid mathematical foundation
- Elegant algorithms
- Visualisations look *awesome*
- I'm going to talk about them for, like, two hours...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## What is a network?

### A mathematical approach

A *graph* is a **representation** of a **set of objects** where some pairs of objects are **connected** by **links**.

Or more formally, $G = (V, E)$, a *graph* $G$ is an ordered pair of *vertices* $V$ linked together by *edges* $E$.

Each element of $E$ is a two-element subset of $V$.

The *order* of a graph is $|V|$, and its *size* is $|E|$.

# What is a network?

## An example

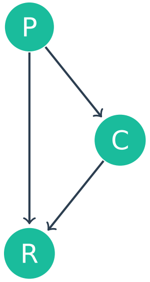
In an omnivory scenario, one top predator $P$ consumes both an intermediate consumer $C$ and a primary producer $R$. The intermediate consumer also consumes the producer.

This network is specified by

$$G = (\{P, C, R\}, \{\{P, C\}, \{P, R\}, \{C, R\}\})$$

Or for brevity

$$G = (\{P, C, R\}, \{PC, PR, CR\})$$



# What is a network?

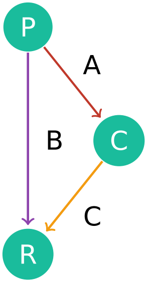
## The adjacency matrix

Networks are often represented by their **adjacency matrix**.

The adjacency matrix $\mathbf{A}$ of a graph $G = (V, E)$ has elements $A_{ij}$ with value 1 if there is an edge between the node $V_i$ and the node $V_j$, and 0 otherwise.

# What is a network?

## From the graph to the matrix




| | P | C | R |
|---|---|---|---|
| P | | A | B |
| C | | | C |
| R | | | |

Exercise: Re-draw this graph (and the matrix) if $C$ is carnivorous.

# What is a network?

## Edge direction

Edges can be *directed* (arcs, directed edges) or not. An edge between a vertex and itself (cannibalism) is a *self-loop*.

In an **undirected graph**, there are at most $|V|(|V|-1)/2$ edges if there are no *self-loops*.

In a **directed graph**, there are at most $|V|(|V|-1)$ edges if there are no *self-loops*.

Exercise: What is the maximal size of a graph of order $n$ if there are self-loops? What is the *minimal* size of the same graph?

# What is a network?

## Edge weight

Edges in a network can have a **weight** (for example, the number of contacts between individuals).

The elements of the adjacency matrix $\mathbf{A}$ can be given *continuous* values.

It's possible to work both on the *weighted* and *unweighted* properties of a graph. However, there are many methods that (as of now) can only be applied to **undirected, unweighted** networks.

# Number of partners

The number of vertices *receiving* a link from a focal vertex are called its **successors**

The number of vertices *establishing* a link towards a focal vertex are called its **predecessors**

The *total* number of edges connected to a focal vertex is this vertex **degree**

## Some remarks on degrees

In a graph with $n$ nodes, the degree $k$ of a node $i$ is $k_i = \sum_{j=1}^{n} A_{ij}$ (*iff* the graph is undirected).

If there are $m$ edges, there are $2m$ *ends* of edges, with $2m = \sum_{i=1}^{n} k_i$. In an undirected graph, this is equal to the sum of degrees.

Thus, $m = \frac{1}{2} \sum_{i=1}^{n} k_i = \frac{1}{2} \sum_i \sum_j A_{ij}$

As the mean degree of nodes is simply $c = \frac{1}{n} \sum k_i$, we can write $c = \frac{2m}{n}$.

## Some exercises on degrees

Exercise(s):

Using the same approach, find **the expression of the mean number of predecessors and successors** in a directed graph.

Discuss the relationship between these two values.

Is the mean degree different in a directed/undirected network?

# Unipartite and bipartite graphs

In a **bipartite** graph, vertices are divided into two distinct sets, with edges established between two vertices from *different* sets.

This do not happen in **unipartite** graphs.

Exercise: Discuss the application of bipartite and unipartite networks to ecological systems.

In a bipartite graph, the adjacency matrix is (formally) called the **incidence matrix**.

# Trees and cycles

# Paths

A **path** is a sequence of nodes, so that every consecutive pair of nodes are connected through an edge. You can “walk” along edges from the first to the last node along a path.

The **length** of a path is the number of *edges* in that path.

If nodes $i$ and $j$ are connected, then *there is a path of length 1 between them*. If they are connected through $k$, there is *a path of length 2*.

## Cycles

A **cycle** is a path from node $i$ to itself, visiting any number of nodes in between.

# Reminder: multiplying matrices

- Only *square* matrices can be raised to an exponent (Exercise: What of bipartite rectangular networks?)
- $(\mathbf{AB})_{ij} = \sum_{p=1}^{m} A_{ik} B_{jk}$
- $\mathbf{A}^0 = \mathbf{I}$
- $\mathbf{A}^2 = \mathbf{AA}$
- $(r\mathbf{A})^k = r^k \mathbf{A}^k$
- $\det(\mathbf{A}^k) = \det(\mathbf{A})^k$ because $\det(\mathbf{AB}) = \det(\mathbf{A})\det(\mathbf{B})$

# Number of paths

The number of paths of length $2$ between $i$ and $j$ is given by

$$N_{ij}^{(2)} = \sum k = 1^n A_{ik} A_{kj}$$

.

This is generalized for paths of length $n$ to

$$N_{ij}^{(n)} = (\mathbf{A}^n)_{ij}$$

.

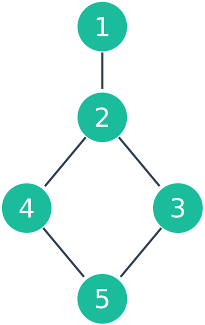
# Number of paths

## A little bit of programming

### Exercise

Write this undirected network as an adjacency matrix, and calculate the number of paths of length 1, 2, $\ldots$, between species $1$ and $3$, and between species $1$ and $5$.

Reminder: $\mathbf{A} \times \mathbf{B}$ = `A %*% B`



## Number of paths

### A little bit of programming

```
matPow = function(A,n)
{
    for(i in c(1:(n-1))) A = A%*%A
    return(A)
}

A = matrix(0, ncol=5, nrow=5)
A[1,2] = A[2,4] = A[2,3] = A[4,5] = A[3,5] = 1
A[2,1] = A[4,2] = A[3,2] = A[5,4] = A[5,3] = 1
for(pathLength in c(0:5)) print(matPow(A, pathLength))
```

Exercise: What happens if the edges are directed (*e.g.* from lower to higher numbers)?

# Number of paths

## Find the number of cycles

Based on the previous result, we can identify the number of paths of size $n$ from one node to itself, $(\mathbf{A}^n)_{ii}$.

Because for square matrices, $\mathrm{Tr}(\mathbf{A}) = \sum \mathrm{diag}(\mathbf{A})$, the *total number of cycles of length* $n$ is given by $L_n = \mathrm{Tr}(\mathbf{A}^n)$.

# Identify the shortest path

A **very crude** way to find the shortest path between $i$ and $j$ is to find the *smallest value of* $n$ for which $(\mathbf{A}^n)_{ij} > 0$.

The shortest path is called the **geodesic** path.

This method in inefficient, and modern software implements much better search strategies.

# Other remarkable paths

An **Eulerian path** visits each *edge* once. The graph is Eulerian (unicursal) if this path is a cycle, and semi-Eulerian (traversable) if not.

A **Hamiltonian path** visits each *node* once. A graph with a Hamiltonian path is traceable.

Exercise: Prove that for a complete undirected graph with $n$ nodes, there are $(n-1)!/2$ Hamiltonian paths.

# Where is the ecology in all that?

**graph** The whole community, *i.e.* the populations and their interactions

**vertices** The composition of the community (species present)

**edges** The interactions between the populations

# Where is the ecology in all that?

## Example of “networkable” systems

- Trophic systems
- Plant–pollinators
- Hosts–parasites
- Mutualism
- Social interactions

Any system in which the **same ecological interaction** happens several time in a community can (should) be studied using network theory

## Connectance

Connectance is the *proportion of possible interactions realized* (also called the density $\rho$ in graph theory)

The order of an ecological network is usually called $S$, and its size $L$

Ecologists often define connectance as $Co = L/S^2$.

Exercise: What do you think of this definition based on results about the maximal order of a graph or size $S$?

## Number of partners

The number of (*e.g.*) preys of a predator is its **generality** (number of successors)

The number of (*e.g.*) predators of a prey is its **vulnerability** (number of predecessors)

## Number of partners

```
web = read.table('web.dat')
generality = rowSums(web)
vulnerability = colSums(web)
degree = generality + vulnerability
```

# Null models

## The ecological use

Even just *by chance*, networks will have statistical properties. The truth is in the residuals.

**Null models** allow to disentangle the random and non-random properties of networks.

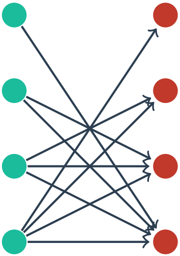
Example of a question: is a given network more or less nested than expected by chance?

# Null models

## WTF is nestedness?

In a *nested* network, a species with a degree $d_i$ interacts with a subset of the species with a degree $d_j$ so that $d_j > d_i$.

The more this is true, the more a network is nested.



```
library(vegan)
web = read.table('matrix.txt')
nestednodf(web)
```

# Null models

## The basic approach

We want to simulate *pseudo-random* networks that reproduce *some* features of the empirical (observed) network.

For any empirically measured property $X$, we will have a distribution of $\mathcal{X}$.

We might want to test that $\sum(X - \mathcal{X})/n = 0$, *i.e.* the observed property is not significantly different from the random expectation.

This is formally called a *Erdös–Renyi graph*. Each pair of nodes has a probability $\rho$ of being connected.

Exercise: write a function in R filling a matrix with 0 and 1 at random.

# Null models

## Controlling for node degree

We want each node to receive and establish interactions (almost) as in the original network.

$$P(i \rightarrow j) = \frac{1}{2}\left(\frac{g_i}{d_i} + \frac{v_j}{d_j}\right)$$

Exercise: Using operations on matrices, write a function to generate a random network in R, conserving either the connectance, or the degrees.

# The niche model of food webs


- Small stuff produces stuff
- Large stuff east smaller stuff
- Sometimes that’s not entirely true

Each species has parameters $n_i, r_i, c_i$, and $\mathbf{A}(i,j) = 1$ when $c_i - r_i \leq n_j \leq c_i + r_i$.

When done for all $(i,j)$, we have a food web!

# The niche model of food webs

1. Draw $n$ uniformly from $[0;1]$
2. Draw $r'_i$ from a $\beta$ from $[0;1]$ with expected value $2 \times C$
3. $r_i = r'_i \times n_i$
4. Species with the lowest $n_i$ have $r_i = 0$
5. Draw $c_i$ uniformly from $[r_i/2; n_i]$

# The niche model of food webs

## Exercice

Program a R version of the NMFW.

Your function will

1. take $C$ (connectance) and $S$ (number of species) as inputs
2. return a matrix $S \times S$, with 0 and 1
3. return the species traits ($r$, $c$, $n$)

We'll use this function this afternoon. . . !