

A (not so) gentle introduction to networks in ecology

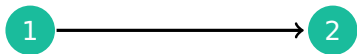
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August 29, 2013

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...



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

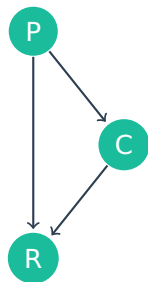
In an omnivory scenario, one top predator P consumes both an intermediate consumer C and a primary producer R . The intermediate consumer also consumes the producer.

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?

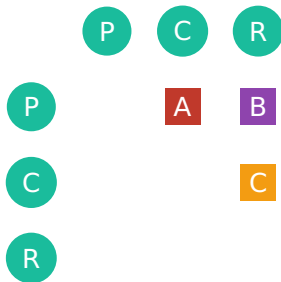
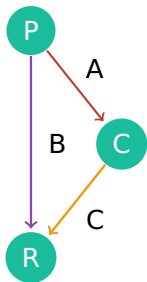
The adjacency matrix

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

The adjacency matrix **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



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 **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.

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

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

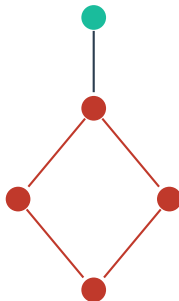
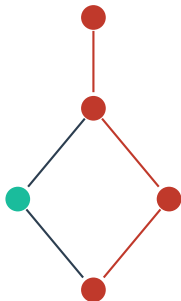
A **path** is a sequence of nodes, so that every consecutive pair of nodes are connected through an edge. You can “walk” along edges from the first to the last node along a path.

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?)
- ▶ $(\mathbf{AB})_{ij} = \sum_{p=1}^m A_{ip} B_{pj}$
- ▶ $\mathbf{A}^0 = \mathbf{I}$
- ▶ $\mathbf{A}^2 = \mathbf{AA}$
- ▶ $(r\mathbf{A})^k = r^k \mathbf{A}^k$
- ▶ $\det(\mathbf{A}^k) = \det(\mathbf{A})^k$ 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

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

.

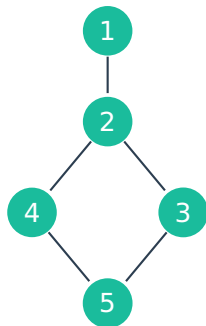
Number of paths

A little bit of programming

Exercise

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

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



Number of paths

A little bit of programming

```
1  matPow = function(A,n)
2  {
3      for(i in c(1:(n-1))) A = A%%*%A
4      return(A)
5  }
6
7  A = matrix(0, ncol=5, nrow=5)
8  A[1,2] = A[2,4] = A[2,3] = A[4,5] = A[3,5] = 1
9  A[2,1] = A[4,2] = A[3,2] = A[5,4] = A[5,3] = 1
10 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, $\text{Tr}(\mathbf{A}) = \sum \text{diag}(\mathbf{A})$, the *total number of cycles of length n* is given by $L_n = \text{Tr}(\mathbf{A}^n)$.

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 is 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 ρ 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

```
1 web = read.table('web.dat')
2 generality = rowSums(web)
3 vulnerability = colSums(web)
4 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?

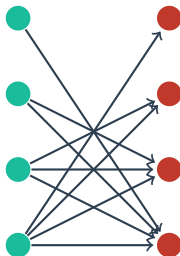
Null models

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.

```
1 library(vegan)
2 web = read.table('matrix.txt')
3 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.

Null models

Controlling for mean degree

This is formally called a *Erdős–Renyi graph*. Each pair of nodes has a probability ρ 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 eat 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

Exercise

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...!