# Systems Biology Across Scales: A Personal View
# V. Networks: Degree & Reciprocity

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# Local properties of networks: Node degree

*Degree* $k_i$ of a node i in a network is its number of connections

For an undirected network $k_i = \sum^{N}_{j=1} A_{ij}$

The total number of connections in the network $L = (1/2) \sum^{N}_{i=1} k_i$

as the two ends of every connection contribute to the degree of two nodes

The mean degree of a node in an undirected network $\langle k \rangle = 2L/N = (1/N) \sum^{N}_{i=1} k_i$

**Regular** networks: all nodes have the same degree

The maximum possible connections in a network with N nodes is

${}^{N}C_2 = (1/2)N(N - 1)$

$\Rightarrow$ The connection density (connectance) is $\rho = L / ({}^{N}C_2) = 2L/N(N-1) = \langle k \rangle/(N-1)$

The density of any network lies in the range [0,1] (e.g., $\rho = 1 \Rightarrow$ Clique)

**Dense** network: A network whose density $\rho$ tends to a constant > 0 as $N \to \infty$

**Sparse** network: A network whose density $\rho \to 0$ as $N \to \infty$ (e.g., for networks whose average degree tends to a constant as no. of nodes increase)

# Constant degree or constant connectance in Food webs

*Question:* How does the number of trophic links L in a food web vary with the number of trophic species S ?

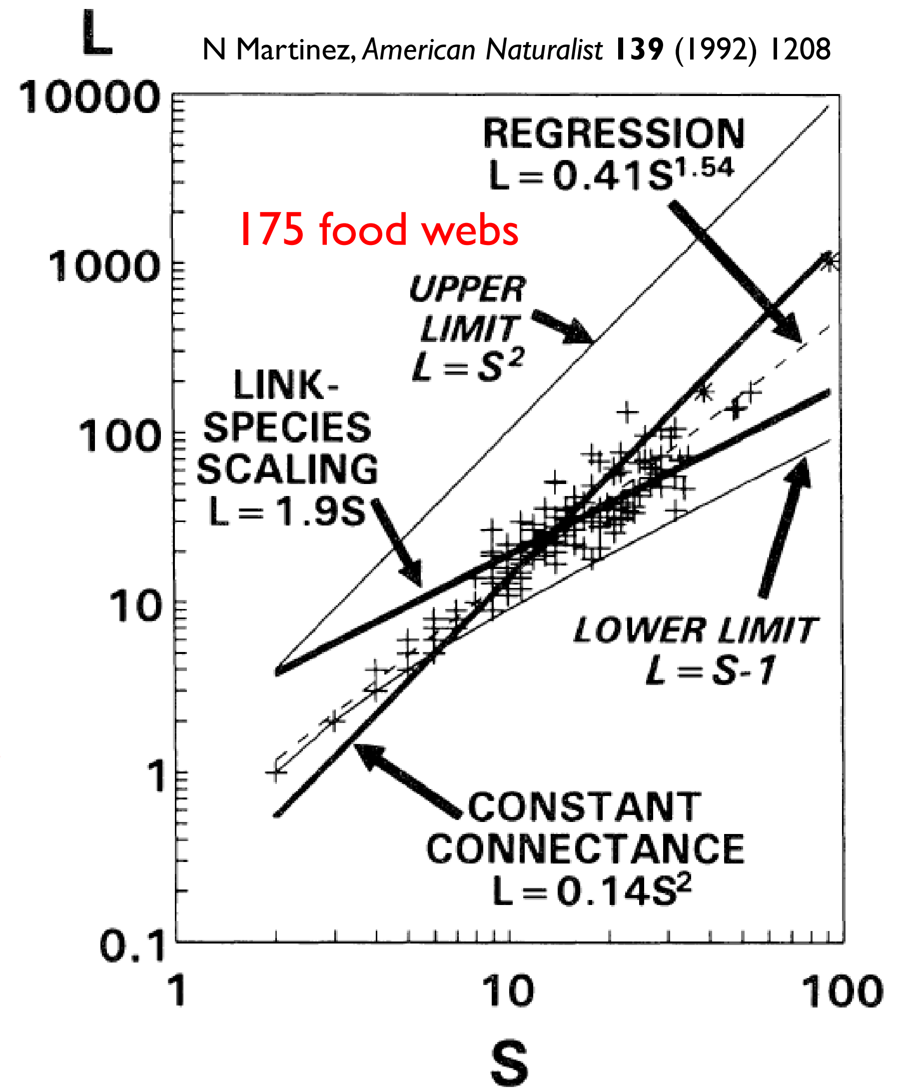
Trophic species: groups of organisms having identical sets of predators & prey

Trophic links: feeding interactions directed from prey to predators

Link-species scaling law: On average the number of links (L) per species (S) in a food web is constant, i.e., species have constant avg degree independent of S

Constant-connectance hypothesis: The number of links (L) increases approximately as the square of functionally distinct species (S) in a web

N Martinez, *American Naturalist* **139** (1992) 1208



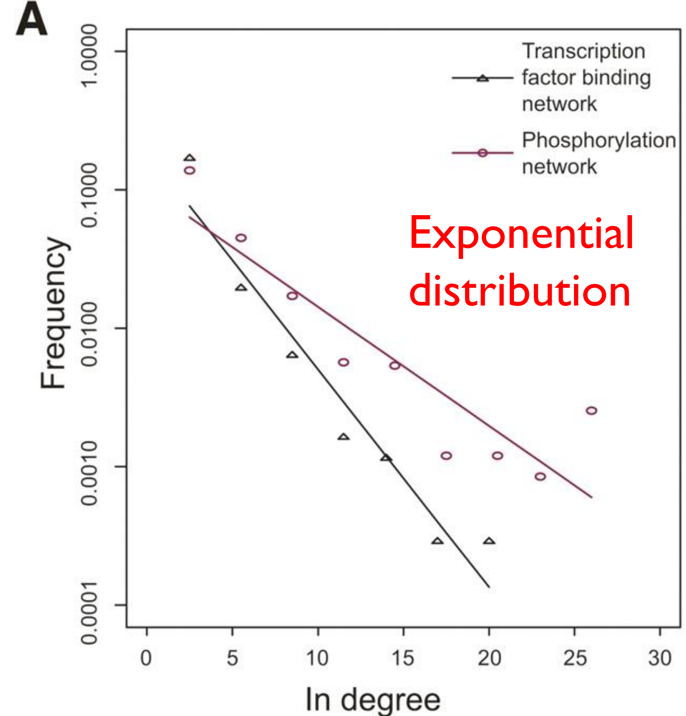
# Degree in directed networks

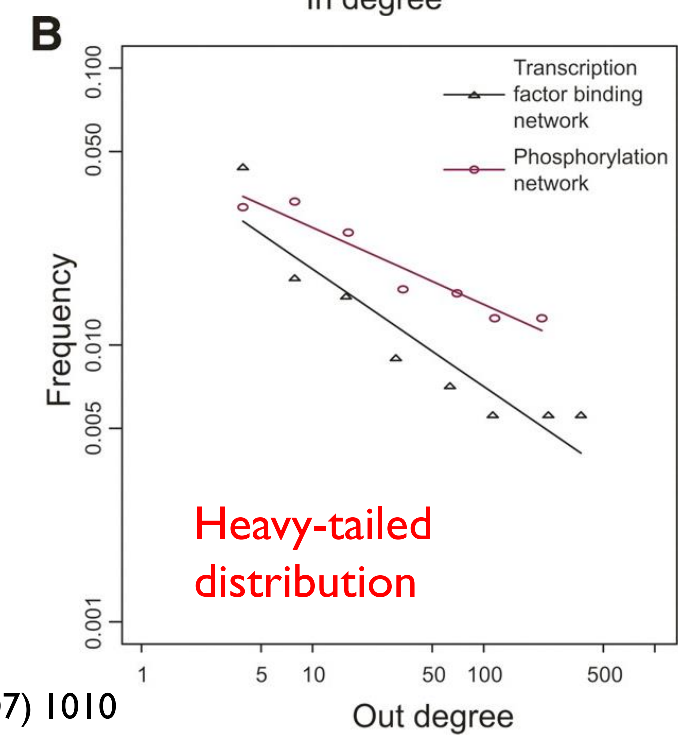
In a directed network each node is associated with two types of degree
**In-degree:** number of incoming connections.
**Out-degree:** number of outgoing connections.

$A_{ij}$ = 1 means there is connection from j to i
In-degree of node i : $k_{i\,(in)} = \sum^{N}_{j=1} A_{ij}$ and
Out-degree of node j: $k_{j\,(out)} = \sum^{N}_{i=1} A_{ij}$

Total number of connections in the network
$L = \sum^{N}_{i=1} k_{i(in)} = \sum^{N}_{j=1} k_{j(out)} = \sum_{i,j} A_{ij}$
as each incoming end of a link is paired with an outgoing end of a link
$\Rightarrow$ Mean in-degree $\langle k_{(in)} \rangle$ = Mean out-degree $\langle k_{(out)} \rangle = \langle k \rangle = L/N$

*Question*: In a network, do the high out-degree nodes also tend to have high in-degree ?
Distributions of in-degree and out-degree may have very different natures

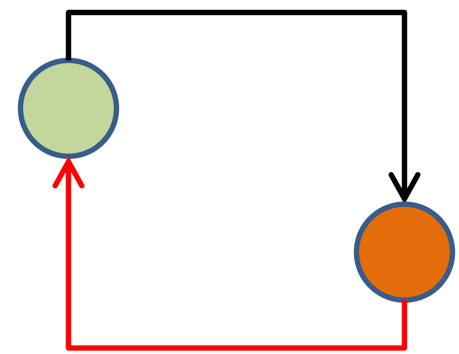



X Zhu et al. *Genes Dev.* **21** (2007) 1010

# Local properties of networks: Reciprocity

Just as we can ask if a node that sends out many links, also receive many connections from other nodes…
we can ask in directed networks that if node i sends a connection to j, whether node j also sends one to i



Example: gene regulation or synaptic contacts

## Question: Are links between a pair of nodes reciprocated ?

The frequency of loops of length 2 is measured by reciprocity, i.e., the fraction of edges that are reciprocated $f_r = (1/L) \sum_{ij} A_{ij} A_{ji} = (1/L)\, \mathrm{Tr}\, A^2$

Alternatively, defined as correlation coefficient between corresponding entries of adjacency matrix

$f_r^{(GL)} = \sum_{i \neq j} (A_{ij} - \langle A \rangle)(A_{ji} - \langle A \rangle) / [\sum_{i \neq j} (A_{ij} - \langle A \rangle)^2]$

where $\langle A \rangle = \sum_{i \neq j} A_{ij} / N(N-1) = L/N(N-1)$ [Garlaschelli & Loffredo, PRL (2004)]

lies within -1 and +1 ($>0 \Rightarrow$ reciprocal, $<0 \Rightarrow$ anti-reciprocal)

If there are no reciprocal edges, $[f_r^{(GL)}]_{min} = -\langle A \rangle / [1 - \langle A \rangle]$

Dispersion of reciprocity among nodes measured by the standard deviation $\sigma_f$ of $f_r^{(GL)}$ in terms of $f_r^{(GL)}(i,j)$ obtained when any link betn (i,j) is removed.

# Reciprocity in the biological world

- Neuronal network (*C. elegans* chemical synapses) shows reciprocity
- Metabolic networks are weakly reciprocal (reciprocity could be linked to potential reversibility of biochemical reactions

Garlaschelli & Loffredo, PRL **93** (2004) 268701

- Food webs are anti-reciprocal

Networks belonging to the same class (e.g., metabolic, neuronal or ecological) appear to have similar values of reciprocity