Self-organization and emergence in networked systems

René Doursat & José Halloy
Common features of complex systems

- Large number of elements
- Individual behavior rules
- Local interactions
- Node / link diversity & dynamics
- Hierarchy of levels, heterogeneity, reproducibility
Common features of complex systems

Large number of elements

<table>
<thead>
<tr>
<th>System</th>
<th>Nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td>BZ reaction</td>
<td>molecules</td>
</tr>
<tr>
<td>slime mold</td>
<td>amoebae</td>
</tr>
<tr>
<td>animal coats</td>
<td>cells</td>
</tr>
<tr>
<td>insect colonies</td>
<td>ants, termites</td>
</tr>
<tr>
<td>flocking, traffic</td>
<td>animals, cars</td>
</tr>
<tr>
<td>swarm sync</td>
<td>fireflies</td>
</tr>
</tbody>
</table>
### Common features of complex systems

#### Individual behavior rules

<table>
<thead>
<tr>
<th>System</th>
<th>Nodes</th>
<th>Rules</th>
</tr>
</thead>
<tbody>
<tr>
<td>BZ reaction</td>
<td>molecules</td>
<td>react, diffuse</td>
</tr>
<tr>
<td>slime mold</td>
<td>amoebae</td>
<td>diffuse, sync, move</td>
</tr>
<tr>
<td>animal coats</td>
<td>cells</td>
<td>activate, inhibit</td>
</tr>
<tr>
<td>insect colonies</td>
<td>ants, termites</td>
<td>carry, deposit, follow</td>
</tr>
<tr>
<td>flocking, traffic</td>
<td>animals, cars</td>
<td>steer, adjust speed</td>
</tr>
<tr>
<td>swarm sync</td>
<td>fireflies</td>
<td>reset phase/freq</td>
</tr>
</tbody>
</table>

- always do A
- if B then C
- sometimes do D
- etc.

- limited repertoire of fixed and reactive behavior

- note: elements are not intrinsically “simple”, only functionally at the level of description of the studied process
Common features of complex systems

*Local interactions: geometric, regular*

<table>
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<tr>
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<th>Nodes</th>
<th>Edges</th>
</tr>
</thead>
<tbody>
<tr>
<td>BZ reaction</td>
<td><em>molecules</em></td>
<td><em>collisions</em></td>
</tr>
<tr>
<td>slime mold</td>
<td><em>amoebae</em></td>
<td><em>cAMP</em></td>
</tr>
<tr>
<td>animal coats</td>
<td><em>cells</em></td>
<td><em>morphogens</em></td>
</tr>
<tr>
<td>insect colonies</td>
<td><em>ants, termites</em></td>
<td><em>pheromone</em></td>
</tr>
<tr>
<td>flocking, traffic</td>
<td><em>animals, cars</em></td>
<td><em>perception</em></td>
</tr>
<tr>
<td>swarm sync</td>
<td><em>fireflies</em></td>
<td>*photons <em>long-range</em></td>
</tr>
</tbody>
</table>

- interactions inside a local neighborhood in 2-D or 3-D geometric space
- limited “visibility” within Euclidean distance
- one-to-one messaging or one-to-many broadcasting

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Common features of complex systems

*Local interactions: Semi-geometric, irregular*

<table>
<thead>
<tr>
<th>System</th>
<th>Nodes</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Internet</td>
<td>routers</td>
<td>wires</td>
</tr>
<tr>
<td>brain</td>
<td>neurons</td>
<td>synapses</td>
</tr>
<tr>
<td>WWW</td>
<td>pages</td>
<td>hyperlinks</td>
</tr>
<tr>
<td>Hollywood</td>
<td>actors</td>
<td>movies</td>
</tr>
<tr>
<td>gene regulation</td>
<td>proteins</td>
<td>binding sites</td>
</tr>
<tr>
<td>ecology web</td>
<td>species</td>
<td>competition</td>
</tr>
</tbody>
</table>

- local neighborhoods can also contain “long-range” links:
  - either “element” nodes located in space
  - or “categorical” nodes not located in space
- still limited “visibility”, but not according to distance

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## Common features of complex systems

### Node diversity

<table>
<thead>
<tr>
<th>System</th>
<th>Node diversity</th>
<th>Node state/dynamics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internet</td>
<td>routers, PCs, switches ...</td>
<td>routing state/algorithm</td>
</tr>
<tr>
<td>brain</td>
<td>sensory, inter, motor neuron</td>
<td>electrical potentials</td>
</tr>
<tr>
<td>WWW</td>
<td>commercial, educational ...</td>
<td>popularity, num. of visits</td>
</tr>
<tr>
<td>Hollywood</td>
<td>traits, talent ...</td>
<td>celebrity level, contracts</td>
</tr>
<tr>
<td>gene regulation</td>
<td>protein type, DNA sites ...</td>
<td>boundness, concentration</td>
</tr>
<tr>
<td>ecology web</td>
<td>species traits (diet, reprod.)</td>
<td>fitness, density</td>
</tr>
</tbody>
</table>

- Nodes can be of different subtypes: ●, ○, ▲, ▼, ...
- Nodes have variable states of activity: ●, ○, ▲, ▼, ○...
Common features of complex systems

Node dynamics: individual nodes

- if each node in the network obey some diff equation, e.g.: $\frac{dx}{dt} = f(x)$
- then generally, three possible behaviors in phase space:

  - fixed point attractor
  - limit cycle attractor
  - chaotic attractor
Common features of complex systems

Node dynamics: coupled nodes

- a complex system is a set of coupled nodes obeying:
  \[ \frac{dx_A}{dt} = f(x_A) + \sum_{A \leftarrow B} g(x_A, x_B) \]
- generally, three types of node network dynamics:
  - fixed point node network
  - limit cycle node network
  - chaotic node network

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Pattern retrieval in Hopfield memory: full graph with Ising-type interactions

Common features of complex systems

Node dynamics: attractors in full networks

- fixed point nodes
- fully connected network
→ a few fixed patterns
\[ \approx 0.14 \, N \]
Common features of complex systems

*Node dynamics: attractors in lattice networks*

- fixed point nodes
- regular lattice network
  → a great number of new patterns

*Pattern formation in animal pigmentation:*

*2-D lattice with stationary reaction-diffusion*

(NetLogo simulation, Uri Wilensky, Northwestern University, IL)
Common features of complex systems

Node dynamics: sync in full networks

- limit cycle nodes
- fully connected network → global synchronization

Spontaneous synchronization in a network of limit-cycle oscillators with distributed natural frequencies

(Strogatz, 2001)

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Common features of complex systems

Node dynamics: sync in full networks

Spontaneous synchronization in a swarm of fireflies:
(almost) fully connected graph of independent oscillators

(NetLogo simulation, Uri Wilensky, Northwestern University, IL)
Common features of complex systems

Node dynamics: waves in lattice networks

- limit cycle nodes
- regular lattice network
→ traveling waves

BZ reaction or slime mold aggregation:
2-D lattice with oscillatory reaction-diffusion

(NetLogo simulation, Uri Wilensky, Northwestern University, IL)

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Common features of complex systems

Node dynamics: epidemics in complex networks

- Understand of beneficial or nefarious activity/failures spread over a network:
  - Diseases
  - Power blackouts
  - Computer viruses
  - Fashions, etc.

- Susceptible-infected-susceptible (SIS) epidemiological model:
  - Two node states: infected or susceptible
  - Susceptible nodes can get infected with probability \( \nu \)
  - Infected nodes heal and become susceptible again with proba \( \delta \)

\[ \text{Spreading rate: } \lambda = \frac{\nu}{\delta} \]
Common features of complex systems

Node dynamics: epidemics in complex networks

Epidemic on exponential and scale-free networks

(Pastor-Satorras & Vespignani, 2001)

- exponential network
  → spread with threshold

- scale-free network
  → spread WITHOUT threshold
# Common features of complex systems

## Link diversity & dynamics

<table>
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<tr>
<th>System</th>
<th>Link diversity</th>
<th>Link state/dynamics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internet</td>
<td>bandwidth (DSL, cable) ...</td>
<td>--</td>
</tr>
<tr>
<td>brain</td>
<td>excit., inhib. synapses ...</td>
<td>synap. weight, learning</td>
</tr>
<tr>
<td>WWW</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Hollywood</td>
<td>theater movie, TV series ...</td>
<td>partnerships</td>
</tr>
<tr>
<td>gene regulation</td>
<td>enhancing, blocking ...</td>
<td>mutations, evolution</td>
</tr>
<tr>
<td>ecology web</td>
<td>predation, cooperation</td>
<td>evolution, selection</td>
</tr>
</tbody>
</table>

- Links can be of different subtypes: /, /, / ...
- Links can also have variable weights: /, /, /, /
the state of a network generally evolves on two time-scales:
- fast time scale: node activities
- slow time scale: connection weights

examples:
- neural networks: activities & learning
- gene networks: expression & mutations

the structural complexity of a network can also evolve by adding or removing nodes and edges

examples:
- Internet, WWW, actors, ecology, etc.

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Common features of complex systems

Hierarchy of levels

- each complex system can become a “simple” component in a higher organization
Complex networks within complex systems

• Three network metrics
• Random & regular networks
• Small-world & scale-free networks
• Case studies
Complex networks

2D, 3D spatial range

Non-spatial, hybrid range

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Complex networks

✓ complex networks are the backbone of complex systems
  ▪ every complex system is a network of interaction among numerous smaller elements
  ▪ some networks are geometric or regular in 2-D or 3-D space
  ▪ other contain “long-range” connections or are not spatial at all
  ▪ understanding a complex system = break down into parts + reassemble

✓ network anatomy is important to characterize because structure affects function (and vice-versa)

✓ ex: structure of social networks
  ▪ prevent spread of diseases
  ▪ control spread of information (marketing, fads, rumors, etc.)

✓ ex: structure of power grid / Internet
  ▪ understand robustness and stability of power / data transmission

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Complex networks

Three metrics: average path length

- the path length between two nodes $A$ and $B$ is the smallest number of edges connecting them:
  \[
  l(A, B) = \min l(A, A_i, \ldots A_n, B)
  \]
- the average path length of a network over all pairs of $N$ nodes is
  \[
  L = \langle l(A, B) \rangle = \frac{2}{N(N-1)} \sum_{A,B} l(A, B)
  \]
- the network diameter is the maximal path length between two nodes:
  \[
  D = \max l(A, B)
  \]
- property: $1 \leq L \leq D \leq N-1$
Complex networks

*Three metrics: degree distribution*

- The *degree* of a node $A$ is the number of its connections (or neighbors), $k_A$
- The *average degree* of a network is
  \[ \langle k \rangle = \frac{1}{N} \sum_A k_A \]
- The *degree distribution* function $P(k)$ is the histogram (or probability) of the node degrees: it shows their spread around the average value

The degree of $A$ is 5
Complex networks

Three metrics: clustering coefficient

- the neighborhood of a node $A$ is the set of $k_A$ nodes at distance 1 from $A$
- given the number of pairs of neighbors:
  \[ F_A = \sum_{B,B'} 1 \]
  \[ = k_A (k_A - 1) / 2 \]
- and the number of pairs of neighbors that are also connected to each other:
  \[ E_A = \sum_{B\leftrightarrow B'} 1 \]
- the clustering coefficient of $A$ is
  \[ C_A = E_A / F_A \leq 1 \]
- and the network clustering coefficient:
  \[ \langle C \rangle = 1/N \sum_A C_A \leq 1 \]

The clustering coefficient of $A$ is 0.6
Complex networks

Regular networks: fully connected

- In a fully (globally) connected network, each node is connected to all other nodes.
- Fully connected networks have the lowest path length and diameter:
  \[ L = D = 1 \]
- The highest clustering coefficient:
  \[ C = 1 \]
- And a peak degree distribution (at the largest possible constant):
  \[ k_A = N-1, \quad P(k) = \delta(k - N+1) \]
- Also the highest number of edges:
  \[ E = \frac{N(N-1)}{2} \sim N^2 \]
Complex networks

Regular networks: lattice

- A lattice network is generally structured against a geometric 2-D or 3-D background.
- For example, each node is connected to its nearest neighbors depending on the Euclidean distance:
  \[ A \leftrightarrow B \iff d(A, B) \leq r \]
- The radius \( r \) should be sufficiently small to remain far from a fully connected network, i.e., keep a large diameter:
  \[ D \gg 1 \]
Complex networks

Regular networks: lattice: ring world

- in a ring lattice, nodes are laid out on a circle and connected to their $K$ nearest neighbors, with $K \ll N$

- **HIGH** average path length:
  \[ L \approx \frac{N}{2K} \sim N \quad \text{for } N \gg 1 \]
  (mean between closest node $l = 1$ and antipode node $l = N / K$)

- **HIGH** clustering coefficient:
  \[ C \approx 0.75 \quad \text{for } K \gg 1 \]
  (mean between center with $K$ edges and farthest neighbors with $K/2$ edges)

- **PEAK** degree distribution (low value):
  \[ k_A = K, \quad P(k) = \delta(k - K) \]

A ring lattice with $K = 4$
Complex networks

Random networks

- In a random graph each pair of nodes is connected with probability $p$
- LOW average path length:
  \[ L \approx \frac{\ln N}{\ln \langle k \rangle} \approx \ln N \quad \text{for } N \gg 1 \]
  (because the entire network can be covered in about $L$ steps: $N \sim \langle k \rangle^L$)
- LOW clustering coefficient (if sparse):
  \[ C = p = \frac{\langle k \rangle}{N} \ll 1 \quad \text{for } p \ll 1 \]
  (because the probability of 2 neighbors being connected is $p$, by definition)
- PEAK (Poisson) degree distribution (low value):
  \[ \langle k \rangle \approx pN, \quad P(k) \approx \delta(k - pN) \]
Percolation in a random graph
(Wang, X. F., 2002)

- Erdős & Rényi (1960): above a critical value of random connectivity the network is almost certainly connected in one single component

- Percolation happens when “picking one button (node) will lift all the others”

- The critical value of probability $p$ is

$$p_c \approx \frac{\ln N}{N}$$

- And the corresponding average critical degree:

$$\langle k_c \rangle \approx p_c N \approx \ln N$$

NetLogo model: /Networks/Giant Component
Complex networks
Small-world networks

- a network with *small-world EFFECT* is ANY large network that has a low average path length:
  \[ L \ll N \quad \text{for} \quad N \gg 1 \]

- famous “6 degrees of separation”

- the *Watts-Strogatz (WS) small-world MODEL* is a hybrid network between a regular lattice and a random graph

- WS networks have both the LOW average path length of random graphs:
  \[ L \sim \ln N \quad \text{for} \quad N \gg 1 \]

- and the HIGH clustering coefficient of regular lattices:
  \[ C \approx 0.75 \quad \text{for} \quad K \gg 1 \]
Complex networks
Small-world networks

Ring Lattice
- large world
- well clustered

Watts-Strogatz (1998)
- small world
- well clustered

Random graph
- small world
- poorly clustered

- the WS model consists in gradually rewiring a regular lattice into a random graph, with a probability $p$ that an original lattice edge will be reassigned at random

$p = 0$ (order)

$0 < p < 1$

$p = 1$ (disorder)
Complex networks
Small-world networks

- the clustering coefficient is resistant to rewiring over a broad interval of $p$
  - it means that the small-world effect is hardly detectable locally: nodes continue seeing mostly the same “clique” of neighbors

- on the other hand, the average path length drops rapidly for low $p$
  - as soon as a few long-range “shortcut” connections are introduced, the original large-world starts collapsing
  - through a few bridges, far away cliques are put in contact and this is sufficient for a rapid spread of information
Complex networks
Small-world networks

Modeling & simulation

- setup:
  - number of nodes
  - each node is connected to its 2+2 nearest neighbors

- rewire ONCE:
  - rewire *one* ring lattice *incrementally* (ignoring the rewiring probability)

- rewire ALL:
  - rewire *several* ring lattices *in one shot* under a certain rewiring probability

- calculate 2 metrics for each network:
  - average path length
  - clustering coefficient

NetLogo model: /Networks/Small Worlds
on the other hand, the WS model still has a PEAK (Poisson) degree distribution (uniform connectivity)

in that sense, it belongs to the same family of exponential networks:
- fully connected networks
- lattices
- random graphs
- WS small-world networks

$P(k)$

$(k)$
A schematic scale-free network

Complex networks
Scale-free networks

- in a *scale-free network* the degree distribution follows a POWER-LAW:
  
  \[ P(k) \sim k^{-\gamma} \]

- there exists a small number of highly connected nodes, called *hubs* (tail of the distribution)

- the great majority of nodes have few connections (head of the distribution)
Typical aspect of a power law
(image from Larry Ruff, University of Michigan, http://www.geo.lsa.umich.edu/~ruff)
Complex networks

Scale-free networks

U.S. highway system

U.S. airline system

(Barabási & Bonabeau, 2003)

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Effect of failures and attacks on scale-free networks

(Barabási & Bonabeau, 2003)

- Regular networks are not resistant to random node failures: they quickly break down into isolated fragments.

- Scale-free networks are remarkably resistant to random accidental node failures . . .

- . . . however they are also highly vulnerable to targeted attacks on their hubs.
Complex networks

Scale-free networks

- in a random graph the average path length increases significantly with node removal, then eventually breaks down
  → for a while, the network becomes a large world

- in a scale-free network, the average path length is preserved during random node removal
  → it remains a small world

- however, it fails even faster than a random graph under targeted removal

Albert, Jeong & Barabási, 1999
Complex networks

Scale-free networks

- the Barabási-Albert model, reproduces the scale-free property by:
  - growth and
  - (linear) preferential attachment

- growth: a node is added at each step
- attachment: new nodes tend to prefer well-connected nodes (“the rich get richer” or “first come, best served”) in linear proportion to their degree

NetLogo model: /Networks/Preferential Attachment

Growth and preferential attachment creating a scale-free network
(Barabási & Bonabeau, 2003)
Complex networks

Scale-free networks

NetLogo model: /Networks/Preferential Attachment

Modeling & simulation

➢ setup:
  ▪ 2 nodes, 1 link

➢ step:
  ▪ a new node is added to the network and preferentially attached to one other node

➢ calculate 1 metric:
  ▪ degree distribution (displayed as histogram and in log-log coordinates)
Complex networks

Case studies: Internet

- the Internet is a network of routers that transmit data among computers
- routers are grouped into domains, which are interconnected
- to map the connections, “traceroute” utilities are used to send test data packets and trace their path

Schema of the Internet

(Wang, X. F., 2002)
Complex networks

Case studies: Internet

Map of Internet colored by IP address
(Bill Cheswick & Hal Burch, http://research.lumeta.com/ches/map)

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Complex networks

Case studies: Internet

- The connectivity degree of a node follows a power of its rank (sorting out in decreasing order of degree):
  \[
  \text{node degree} \sim (\text{node rank})^{-\alpha}
  \]

- The most connected nodes are the least frequent:
  \[
  \text{degree frequency} \sim (\text{node degree})^{-\gamma}
  \]
  \[
  P(k) \sim k^{-\gamma}
  \]

→ The Internet is a scale-free network

Two power laws of the Internet topology
(Faloutsos, Faloutsos & Faloutsos, 1999)
Complex networks
Case studies: World Wide Web

- the World Wide Web is a network of documents that reference each other
- the nodes are the Web pages and the edges are the hyperlinks
- edges are directed: they can be outgoing and incoming hyperlinks

Schema of the World Wide Web of documents
Complex networks
Case studies: World Wide Web

Hierarchical topology of the international Web cache
Complex networks

Case studies: World Wide Web

➤ WWW is a scale-free network:

\[ P(k) \sim k^{-\gamma} \]

with \( \gamma_{\text{out}} = 2.45 \) and \( \gamma_{\text{in}} = 2.1 \)

➤ WWW is also a small world:

\[ L \approx \alpha \ln N \]

with \( L \approx 11 \) for \( N = 10^5 \) documents

Distribution of links on the World-Wide Web

(Albert, Jeong & Barabási, 1999)
Complex networks

Case studies: actors

“The Oracle of Bacon”
http://www.cs.virginia.edu/oracle

- A given actor is on average 3 movies away from Kevin Bacon ($L_{\text{Bacon}} = 2.946$, as of June 2004) . . . or any other actor for that matter.

- Hollywood is a small world.

- . . . and it is a scale-free small world: a few actors played in a lot of movies, and a lot of actors in few movies.

Path from K. Kline to K. Bacon = 3 (as of 1995)
(http://collegian.ksu.edu/issues/v100/FA/n069/fua-making-bacon-fuqua.html)
Complex networks

Case studies: scientists

“The Erdős Number Project”
http://www.oakland.edu/enp

Co-authors of Paul Erdős have number 1, co-authors of co-authors number 2, etc.

Mathematicians form a highly clustered 
\((C = 0.14)\) small world \((L = 7.64)\)
High-Quality Binary Protein Interaction Map of the Yeast Interactome Network

Haiyuan Yu,1,2* Pascal Braun,1,2* Muhammed A. Yildirim,1,2,3* Irma Lemmens,4
Kavitha Venkatesan,1,2 Julie Sahalie,1,2 Tomoko Hirozane-Kishikawa,1,2 Fana Gebreab,1,2
Na Li,1,2 Nicolas Simonis,1,2 Tong Hao,1,2 Jean-François Rual,1,2 Amélie Dricot,1,2
Alexei Vazquez,5 Ryan R. Murray,1,2 Christophe Simon,1,2 Leah Tardivo,1,2 Stanley Tam,1,2
Nenad Svrzikapa,1,2 Changyu Fan,1,2 Anne-Sophie de Smet,4 Adriana Motyl,6
Michael E. Hudson,6 Juyong Park,1,7 Xiaofeng Xin,8 Michael E. Cusick,1,2 Troy Moore,9
Charlie Boone,8 Michael Snyder,6 Frederick P. Roth,1,10 Marc Vidal1,2†

Albert-László Barabási,1,7

3 OCTOBER 2008 VOL 322 SCIENCE www.sciencemag.org

Designed by René Doursat & José Halloy
Current yeast interactome network maps contain several hundred molecular complexes with limited and somewhat controversial representation of direct binary interactions. We carried out a comparative quality assessment of current yeast interactome data sets, demonstrating that high-throughput yeast two-hybrid (Y2H) screening provides high-quality binary interaction information. Because a large fraction of the yeast binary interactome remains to be mapped, we developed an empirically controlled mapping framework to produce a “second-generation” high-quality, high-throughput Y2H data set covering ~20% of all yeast binary interactions. Both Y2H and affinity purification followed by mass spectrometry (AP/MS) data are of equally high quality but of a fundamentally different and complementary nature, resulting in networks with different topological and biological properties. Compared to co-complex interactome models, this binary map is enriched for transient signaling interactions and intercomplex connections with a highly significant clustering between essential proteins. Rather than correlating with essentiality, protein connectivity correlates with genetic pleiotropy.
Correct Identification of nodes and links is a difficult task that presents numerous experimental technical.
NETWORK BIOLOGY: UNDERSTANDING THE CELL’S FUNCTIONAL ORGANIZATION

Albert-László Barabási* & Zoltán N. Oltvai‡

A key aim of postgenomic biomedical research is to systematically catalogue all molecules and their interactions within a living cell. There is a clear need to understand how these molecules and the interactions between them determine the function of this enormously complex machinery, both in isolation and when surrounded by other cells. Rapid advances in network biology indicate that cellular networks are governed by universal laws and offer a new conceptual framework that could potentially revolutionize our view of biology and disease pathologies in the twenty-first century.
Complex networks
Case studies: ecological food webs

Food web patterns and their consequences
Stuart L. Pimm, John H. Lawton & Joel E. Cohen

A food web is a map that describes which kinds of organisms in a community eat which other kinds. A web helps picture how a community is put together and how it works. Although webs were often initially reported in despair at ever understanding ecological complexity, recently discovered widespread patterns in the shapes of webs, and theoretical explanations for these patterns, indicate that webs are orderly and intelligible, and have some foreseeable consequences for the dynamics of communities.

NATURE • VOL 350 • 25 APRIL 1991
Complex networks
Case studies: ecological food webs
FIG. 4 Prey overlap graph derived from the *Nepenthes* web and the ‘topological hole’ formed by connecting the various prey species that share a particular predator (see Box 2).
Complex networks

Case studies: mutualistic networks

Mutualistic Webs of Species

John N. Thompson

Asymmetric relationships. Part of an interaction web from a montane forest in southeast Spain. Each interaction between frugivore and fruit illustrates two dependence values (green and yellow arrows). The relative frequency of the interaction is shown by the thickness of the arrows.

Quantitative analysis of a network of plant-animal interactions reveal new organizing principles, including how asymmetric relations stabilize the coevolution of the whole network.
Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance

Jordi Bascompte, Pedro Jordano, Jens M. Olesen

The mutualistic interactions between plants and their pollinators or seed dispersers have played a major role in the maintenance of Earth’s biodiversity. To investigate how coevolutionary interactions are shaped within species-rich communities, we characterized the architecture of an array of quantitative, mutualistic networks spanning a broad geographic range. These coevolutionary networks are highly asymmetric, so that if a plant species depends strongly on an animal species, the animal depends weakly on the plant. By using a simple dynamical model, we showed that asymmetries inherent in coevolutionary networks may enhance long-term coexistence and facilitate biodiversity maintenance.
Non-random coextinctions in phylogenetically structured mutualistic networks

Enrico L. Rezende¹, Jessica E. Lavabre¹, Paulo R. Guimarães Jr¹², Pedro Jordano¹ & Jordi Bascompte¹

The interactions between plants and their animal pollinators and seed dispersers have moulded much of Earth’s biodiversity¹–³. Recently, it has been shown that these mutually beneficial interactions form complex networks with a well-defined architecture that may contribute to biodiversity persistence⁴–⁸. Little is known, however, about which ecological and evolutionary processes generate these network patterns⁹. Here we use phylogenetic methods¹⁰,¹¹ to show that the phylogenetic relationships of species predict the number of interactions they exhibit in more than one-third of the networks, and the identity of the species with which they interact in about half of the networks. As a consequence of the phylogenetic effects on interaction patterns, simulated extinction events tend to trigger coextinction cascades of related species. This results in a non-random pruning of the evolutionary tree¹²,¹³ and a more pronounced loss of taxonomic diversity than expected in the absence of a phylogenetic signal. Our results emphasize how the simultaneous consideration of phylogenetic information and network architecture can contribute to our understanding of the structure and fate of species-rich communities.
Complex networks
Case studies: mutualistic networks
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Network motifs in the transcriptional regulation network of *Escherichia coli*

Shai S. Shen-Orr¹, Ron Milo², Shmoolik Mangan¹ & Uri Alon¹,²

*nature genetics • volume 31 • may 2002*
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Gene Regulatory Networks and the Evolution of Animal Body Plans

Eric H. Davidson¹* and Douglas H. Erwin²

Development of the animal body plan is controlled by large gene regulatory networks (GRNs), and hence evolution of body plans must depend upon change in the architecture of developmental GRNs. However, these networks are composed of diverse components that evolve at different rates and in different ways. Because of the hierarchical organization of developmental GRNs, some kinds of change affect terminal properties of the body plan such as occur in speciation, whereas others affect major aspects of body plan morphology. A notable feature of the paleontological record of animal evolution is the establishment by the Early Cambrian of virtually all phylum-level body plans. We identify a class of GRN component, the “kemels” of the network, which, because of their developmental role and their particular internal structure, are most impervious to change. Conservation of phyletic body plans may have been due to the retention since pre-Cambrian time of GRN kemels, which underlie development of major body parts.

10 FEBRUARY 2006 VOL 311 SCIENCE
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