Robustness

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Contenido

Coping with Complexity

- **Adaptation** (learning, evolution; feedback control). The system changes to cope with the change.
- **Anticipation**(cognition; feedforward control). The system predicts a change to cope with, and adjusts accordingly. This is a special case of adaptation, where the system does not require to experience a situation before responding to it.
- **Robustness** (buffering). A system is robust if it continues to function in the face of perturbations (Wagner, 2007).

Robustness

- Present in many biological systems at multiple scales (from molecules to ecosystems).
- Not so much in engineered systems...
- Understand better phenomenon to build robust systems.
- More general than stability...
- How would you relate it to Ashby's concept of a machine?
- Perturbations can be functional, structural, material, etc...

Questions about Robustness (Jen, 2005 + my spoon)

- What are its origins? How does it evolve?
- What are the organizational principles (redundancy, modularity, neutrality, hierarchy, degeneracy, spatial structure, diversification) that characterize robust entities? How are these related? What is their cost?
- What is the effect of robustness on evolvability, adaptability, and fitness?
- When is robustness desirable and when not?

Robustness Below Gene Level

- Neutral landscapes are characterized by large domains where changes in sequence have no effect on phenotype.
- RNA folding:
  - Neutral networks percolate the entire genotype space (there are always neutral point mutations)
  - All phenotypes are present around a relatively small neighbourhood of a given sequence.
- Protein folding:
  - Proteins modular and robust
  - similar to RNA...
  - universal principles? (we'll see next class!)

Robustness Above Gene Level

- Development
- Metabolic pathways
- Metabolic networks

Robustness Beyond Organism

- Ecology (resilience, stability)
    - Food webs
    - Keystone species
    - Homeostasis
    - Weak links (Csermely, 2006).

Robustness in Artificial Systems

- WWW, TCP/IP
- P2P systems
- *Ad hoc* networks
- Robust social systems???
- Can there be a robust economy???

Robustness in Networks

- Scale-free networks are robust to random attacks but fragile to directed attacks to hubs.
- How can you improve robustness?
- Link all hubs?
- Duplicate hubs?
- Shift or hide hubs?

Robustness in RBNs (Gershenson, Kauffman & Shmulevich, 2006)

- Random Boolean networks (RBNs), being general models, can be used to explore theories of how evolution can take place in rugged landscapes; or even change the landscapes.
- What happens when redundant nodes are added?
- Redundancy consists on having more than one copy of an element type.
    - Diploidy.
    - Growth in GRN seems to be via duplication + mutation.
- Redundancy is a way of “smoothening” fitness landscapes.
- Too much redundancy could reduce the rate of adaptation of an evolutionary process.

Kauffman's Conjecture (2000, p. 195)

1-bit mutations to a minimal program will change drastically the output of the program, making it indistinguishable from noise.

- The conjecture points to the necessity of having some redundancy to allow smooth transitions as a program changes in an evolutionary search.
- How to obtain a minimal program?
- How to measure redundancy or compressibility (Kolmogorov, Chaitin, Solomonoff)?
- Let's better compare more and less redundant networks.

Redundant Links

- Redundant links are fictitious links, i.e. functionality does not change.
- Check sensitivity to initial conditions (similar states converge or diverge?)
- Check damage spreading: 1 bit mutations of lookup tables, then compare overlap of the state space transitions using normalised Hamming distances (Equation 1).
- Result: no difference, fictitious links do not affect stability of networks.

$$H(A,B) = \frac{1}{n}\sum_{i}^{n} |a_i - b_i| \tag{1}$$

Redundant Nodes

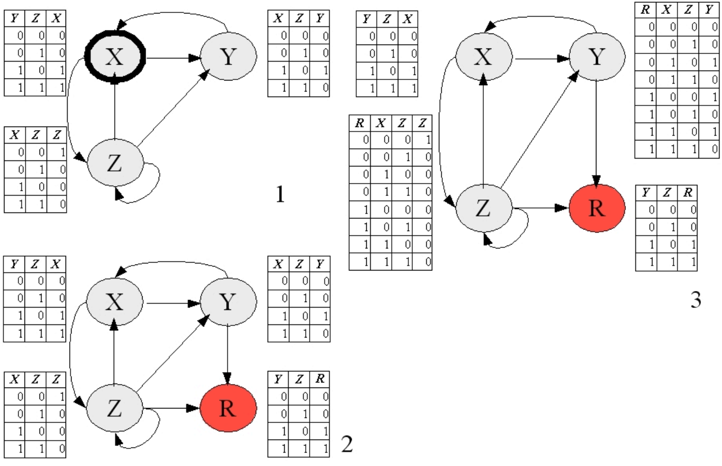
1. Select randomly a node X to be “duplicated”.
2. Add a new node R to the network ($N^{new} = N^{old} + 1$), with the same inputs and lookup table as X (i.e. $k_R = k_X$, $f_R = f_X$), and outputs to the same nodes of which X is input:

$$k_i^{new} = k_i^{old} \cup k_{i_R} \quad if\ \exists k_{i_X}, \forall i \tag{2}$$

3. Double the lookup tables of the nodes of which X is input with the following criterion: When $R = 0$, copy the old lookup table. When $R = 1$, and $X = 0$, copy the same values for all combinations when $X = 1$ and $R = 0$. Copy again the same values to the combinations where $X = 1$ and $R = 1$. In other words, make an inclusive OR function in which X OR R should be one, to obtain the old outputs when only X was one

$$\left.\begin{array}{l}
f_i^{new}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 0, \sigma_{i_R} = 0 \cdots, \sigma_{i_{k_i}}) = f_i^{old}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 0, \cdots, \sigma_{i_{k_i}}) \\
f_i^{new}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 0, \sigma_{i_R} = 1 \cdots, \sigma_{i_{k_i}}) = f_i^{old}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 1, \cdots, \sigma_{i_{k_i}}) \\
f_i^{new}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 1, \sigma_{i_R} = 0 \cdots, \sigma_{i_{k_i}}) = f_i^{old}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 1, \cdots, \sigma_{i_{k_i}}) \\
f_i^{new}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 1, \sigma_{i_R} = 1 \cdots, \sigma_{i_{k_i}}) = f_i^{old}(\sigma_{i_1}, \cdots, \sigma_{i_X} = 1, \cdots, \sigma_{i_{k_i}})
\end{array}\right\} \quad if\ \exists k_{i_X}, \forall$$

Example RBN $N = 3$, $K = 2$



1

Y	Z	X
0	0	0
0	1	0
1	0	1
1	1	1

X	Z	Y
0	0	0
0	1	0
1	0	1
1	1	0

X	Z	Z
0	0	1
0	1	0
1	0	0
1	1	0

2

Y	Z	X
0	0	0
0	1	0
1	0	1
1	1	1

X	Z	Y
0	0	0
0	1	0
1	0	1
1	1	0

X	Z	Z
0	0	1
0	1	0
1	0	0
1	1	0

Y	Z	R
0	0	0
0	1	0
1	0	1
1	1	1

3

Y	Z	X
0	0	0
0	1	0
1	0	1
1	1	1

R	X	Z	Z
0	0	0	1
0	0	1	0
0	1	0	0
0	1	1	0
1	0	0	0
1	0	1	0
1	1	0	0
1	1	1	0

R	X	Z	Y
0	0	0	0
0	0	1	0
0	1	0	1
0	1	1	0
1	0	0	1
1	0	1	0
1	1	0	1
1	1	1	0

Y	Z	R
0	0	0
0	1	0
1	0	1
1	1	1

Simulation Experiments

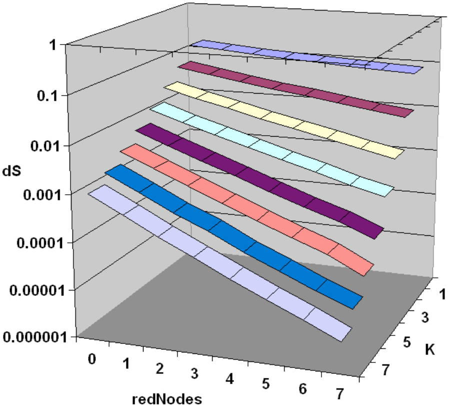
- Implemented in RBNLab `http://rbn.sourceforge.net`
- Measure the overlaps of state space transitions of 1-bit mutant nets with “original” ones as red nodes are added.
- The mutations consist in flipping a random bit from the lookup table of a randomly selected node.
- We used normalised Hamming distances (1) to measure the difference dS between state spaces:

$$dS = \frac{1}{2^n} \sum_{i}^{2^n} H(A_i^{t+1}, M_i^{t+1}) \tag{3}$$

Effect of Mutations

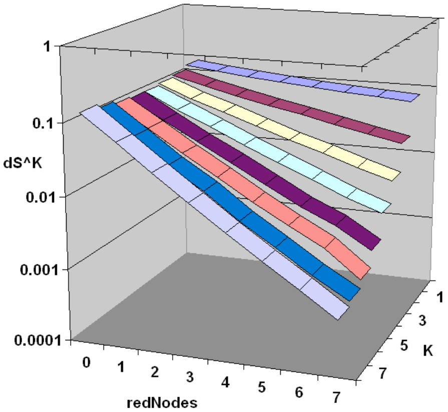
- If $dS = 0$, there is no difference between state spaces, and thus the mutation had no effect.
- A higher dS reflects a greater effect of the mutation in the state space.
- There is no correlation of state spaces, i.e. a mutation is maximally catastrophic, when $dS \simeq 0.5$
- Disadvantage: restricted to small networks (state space doubles for each node added).

Results $N = 7$, $p = 0.5$



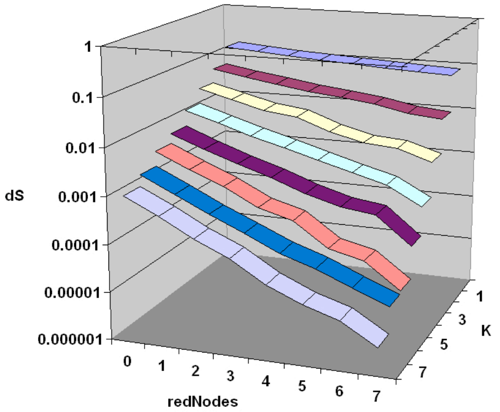
Note that the *dS* for RBNs without red nodes decreases as *K* increases. This is because the lookup tables are doubled each time *K* is incremented. Thus, a one-bit mutation will have less effect on a network with higher connectivity.

Results $N = 7$, $p = 0.5$, dS^K



1-bit mutation makes $dS^K \simeq 0.1$ for networks without red nodes. Adding red nodes increases the network robustness. The effect of red nodes is more evident for higher K values, where the network dynamics are more chaotic.

Results $N = 10$, $p = 0.5$



A network with 7 white + 3 red nodes has a lower dS than a network with ten white nodes, especially for high values of K.

More experiments

- Similar results with scale-free topologies.
- Similar results with different updating schemes (deterministic asynchronous, non-deterministic asynchronous, etc.)

Discussion

- Mutations in redundant nodes do not propagate through the network, whereas mutations in fictitious inputs do.
- "Useful" vs. "useless" redundancy.
- Useful redundancy *smoothens* rough fitness landscapes.
- Useful redundancy increases neutrality.
- Too much redundancy can make evolutionary search slow.
- No need to add redundancy in smooth landscapes.

On Kauffman's Conjecture

- A random mutation on a "minimal" RBN should produce a $dS \simeq 0.5$.
- But you cannot prove that a RBN is minimal (independently of a fixed universal model of computation).
- "Less compressible" RBNs, i.e. with no red nodes, have always a higher dS.
- As we add more red nodes, the RBN becomes more compressible, and dS decreases, showing an increase in robustness.
- The compressibility is directly proportional to the robustness of a network to random mutations.
- Positive evidence in favour of conjecture.

Redundancy vs. Degeneracy

- Evidence showed that robustness in molecular and genetic networks is due to degeneracy, not redundancy (Wagner, 2007).
- Maybe different types of robustness with different mechanisms?

Conclusions (you tell me)

- What is redundancy?
- Why is it useful?
- What are examples of robust systems?
- How can we achieve robustness in systems?
- What is the effect of redundant nodes in RBNs?

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