Coevolution

Solé & Goodwin (2000), ch 9
Kauffman (1993), ch 2 & 6

CS 790R, March 2005

presented by Jeff Wallace

Burgess Shale Fossils

- Cambrian explosion
- Well-organized communities
- Predator/prey species
- Range of sizes and morphologies
- Complex food web
- Ecological niches
- Conclusion: basic rules that organize a complex community today were present in first communities

Why the Cambrian Explosion?

- Special conditions?
- Inevitable?
- Did history influence it?
- Were there universal “laws” at work? Or was it totally contingent?

The other side of Explosion: Extinction

- During Cambrian explosion
- 99.9% of all species ever to appear are extinct
- 5 large-scale events (possibly due to large external events — meteors)
- Smaller events on all scales

Evolution/Extinction Paradox

- Probability of a species going extinct is independent of its length of existence
- But if evolution leads to improvement through adaptation, why aren’t “newer” species more durable than ancestors?
- Or, if adaptation improves species progressively through time, why aren’t older species more durable?

Red Queen hypothesis

- Species do not evolve to become better at avoiding extinction
- Species adapt to each others changes
- Species change just to stay in the evolutionary game
- Extinctions occur when no further changes are possible
- “Here, you see, it takes all the running you can do, to keep in the same place.”

Amplification Processes and Scaling Laws

- Extinction rate patterns may have fractal features
- Distribution of extinctions follows power law
- Lifetime distributions of family longevity follows power law
- “Tree of Life” exhibits fractal branching

Rugged Fitness Landscapes (Kauffman)

- Each genotype can be assigned a fitness
- Distribution of fitness values over space of genotypes is a fitness landscape
- Fitness landscape may be flat (correlated fitness values) or mountainous (uncorrelated)
- Adaptive evolution is a hill-climbing process

Complexity Catastrophes

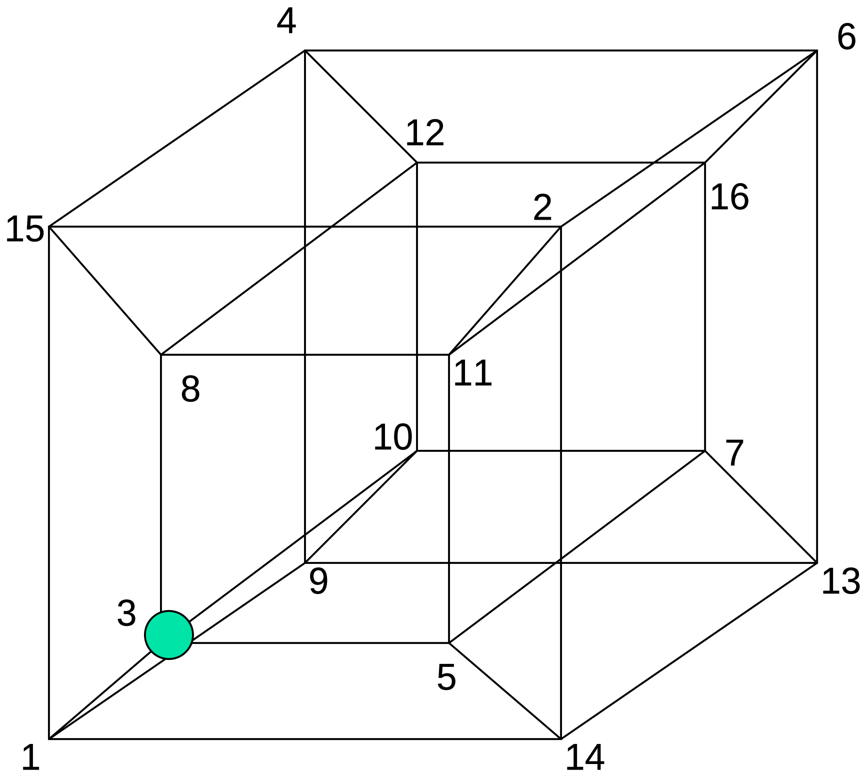
1. If selection is too weak to hold a population around single peaks of high fitness

— or —

2. As landscapes become rugged, fitness walks get trapped on local peaks

- One or the other occurs as the complexity of the entities being selected increases, thus limiting the power of selection

Adaptive Walks



NK Model

- N = number of parts in a system
    - genes in a genotype
    - amino acids in a protein
- K = number of epistatic connections to each gene
    - inter-connectedness
    - fitness contribution of one gene depends on K other genes
- Genotype fitness = average contributions of all loci (gene expressions)

NK Model

- K = 0 corresponds to highly correlated smooth landscape with single peak
- K = N-1 corresponds to fully random (uncorrelated) mountainous landscape with many peaks

Large K (relative to N)

- conflicting constraints lead to more rugged multipeaked landscapes
- number of local fitness optima is large
- lengths of adaptive walks are short
- any genotype can only reach a small fraction of local optima
- Only a small fraction of genotypes can reach a given optimum

Third Complexity Catastrophe

- As complexity increases:
  - accessible optima become poorer
  - the heights of accessible peaks fall toward the mean fitness

- Result: Power of selection is limited

Mean Fitness of Local Optima

K \ N	8	16	24	48	96
2	0.70	0.71	0.71	0.71	0.71
4	0.68	0.71	0.71	0.72	0.72
8	0.66	0.69	0.69	0.70	0.71
16		0.65	0.65	0.67	0.68
24			0.63	0.65	0.66
48				0.60	0.62
96					0.58

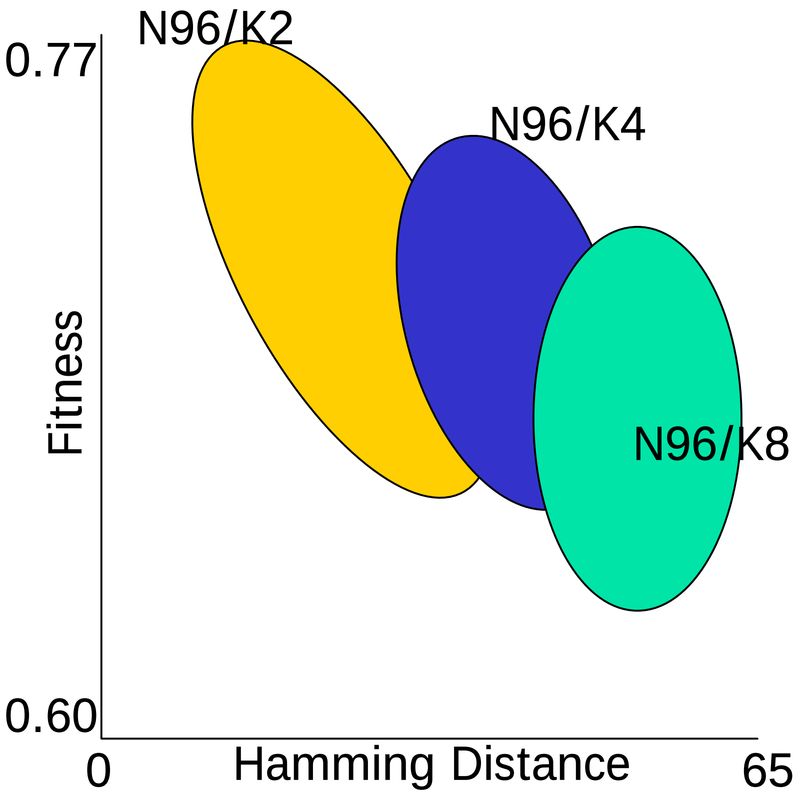
- optima do not fall if K fixed while N increases
- small values of K higher than K=0 (not shown)
- if K increases with N, fitness falls towards mean

Number of Optima

N K	8	16
2	5	26
4	15	184
7	34	
8		1109
15		4370

- exhaustive search (or until 10K optima)
- optima with small basins of attraction may be missing

Plateau in K=2 Landscapes



- local optima not randomly distributed
- highest optima near one another
- optima located further from highest optimum are less fit
- global structure to fitness landscape

Coevolving Systems

- Adaptive landscape of one species deforms the landscapes of others
- May not have a potential function, therefore, may not have local optima
- Not clear that coevolving systems are optimizing anything
- NKC Model, where C works like K, except it’s between species

NKC Results

- As K increases relative to C, waiting time to hit NE decreases
- When K > C, NE found quickly
- K=C demarcates these regimes
- When C > 1, fitness at NE is higher than when system is oscillating
- As C increases, initial fitness for both species decreases during oscillation phase

NKC Results (CONT’D)

- When C is high (20), high-K results in higher mean fitness during oscillation phase
- In this situation, the high-K also helps “partner” species.
- When C = 1, the opposites are true
- Average fitness is highest when K and C are matched

Open Questions

- Are there a few fundamental families of correlated landscapes?
- If so, it might be possible to measure a few parameters, determine which family it is in, then optimize for the landscape family.
- Are parameters (K and C) evolvable?