

# Adaptive Systems

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Informatics

## Lecture 8: Evolution

## This lecture

- ‡ Origins of evolutionary theory
- ‡ Darwin's Origin of Species
- ‡ Mechanisms of inheritance: neo-Darwinism
- ‡ Evolution and adaptation
- ‡ Evolution of complexity
- ‡ Developmental and non-selective factors
- ‡ Horizontal transmission
- ‡ Metagenomics
- ‡ The Microbial Genetic Algorithm

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## What is the problem?

- ‡ The Earth is filled with millions of distinct kinds of plants and animals - where did they come from?
- ‡ They have forms and behaviour that seems to match the requirements of their habitat and lifestyle (in other words they are adapted) - how did this come about?

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## Towards a solution...

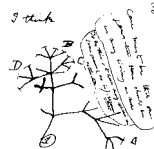
- ‡ Species were unchanging natural kinds that had been independently designed and created. Hmm...
- ‡ Transformism: species do change (Lamarck, 1809) but lineages do not branch or go extinct. Inheritance of acquired characteristics.
- ‡ Malthus's *Essay on Population* (1798): Population tends to grow geometrically, but food resources grow only linearly: winners and losers.
- ‡ Charles Lyell's *Principles of Geology* (1830-33): Big changes can happen incrementally over very long periods of time.
- ‡ Voyage of Beagle (1837-38): Darwin concludes that species are not stable, and begins to think about 'the origin of species'.

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## The Origin of Species (1859)

- ‡ Evolution by common descent  
Species change; they are not independently created, but branch from common ancestors.



The letters A, B, C, D, E, F, G, H, I, J, K, L, M, N, O, P, Q, R, S, T, U, V, W, X, Y, Z  
are placed at the ends of the branches, representing different species or forms that have evolved from a common ancestor.

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## The Origin of Species (1859)

- ‡ Evolution by common descent Species change; they are not independently created, but branch from common ancestors.
- ‡ They do so by a process of natural selection. In a non-uniform population, those variants that have characteristics resulting in a reproductive advantage will increase their representation in future generations, provided those characteristics are inheritable.
- ‡ Explains both the variety of species, and their apparent adaptation.

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## All you need for change is...

- ✦ **The principle of variation:** individuals within a species differ in physiology, morphology, and behaviour
- ✦ **The principle of heredity:** the variation is heritable, so (on the average) individuals resemble their parent(s) more than they resemble other individuals.
- ✦ **The principle of natural selection:** different variants leave different numbers of offspring either immediately or in remote generations

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## ...but for adaptation you also need:

- ✦ **The principle of the struggle for existence:** Variations that favour an individual's survival in competition with other organisms and in the face of environmental stress tend to increase reproductive success and so tend to be preserved.

(Treatment taken from Lewontin, 1978 - see seminar reading list)

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## The twist in the (peacock's) tail

- ✦ 12 years after the appearance of *The Origin of Species*, Darwin published *The Descent of Man, and Selection in Relation to Sex*.

In sexually reproducing species, the number of offspring left by an individual depends not only the individual's survival to maturity, but also on its ability to secure a good mate in competition with others - a quality that would itself be heritable. He called this sexual selection, and regarded it as being as important as natural selection, especially in relation to humans. (See G. Miller's *The Mating Mind*)

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## The twist in the (peacock's) tail



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## Darwinian innovations

- ✦ **Importance of populations**
  - From Malthus
- ✦ **Importance of long time spans**
  - From Lyell
- ✦ **Variation is the key**
  - From Darwin
- ✦ **Selection is the mechanism - not design**
  - A powerful idea - more later...

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## Inheritance

- ✦ Darwin lacked a good theory of heredity. (He tried inventing one - pangenesis - but experiments on transfusing blood between rabbits by his cousin Francis Galton suggested it was incorrect.)
- ✦ **Blending heredity:** Offspring show characteristics somewhere "in between" its parents'. In the absence of selection, variation is cut by half each generation if inheritance is blending. So adaptive variations would be progressively blended away...
- ✦ **Gradualism:** whilst gradual changes could be accounted by natural selection, it was difficult to imagine it explaining the origin of novel traits.

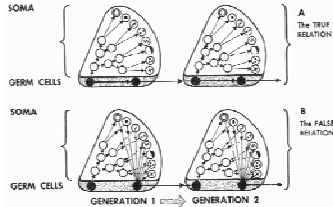
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## Inheritance

Are acquired characteristics heritable? Darwin thought they probably were.

But Weismann produced evidence against the idea (*Weismann's barrier*, the intellectual product of cutting the tails of 1,592 mice).

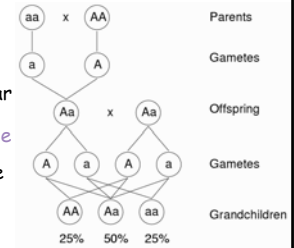


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## Particulate inheritance: Mendel

- ✦ *Experiments in Plant Hybridization* (1865).
- ✦ Differential traits that disappear in first generation can re-appear in the next.
- ✦ In *Mendelian inheritance* characters are transmitted by discrete "factors". Beneficial mutations are not blended away. With no selection, variation is constant.



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## The modern synthesis

- ✦ In the first half of the twentieth century a series of theoretical works, most importantly in the area of population genetics, unified gradual natural selection and Mendelian genetics. This is the basis of the current view, which is known variously as the modern evolutionary synthesis, the modern synthesis, and (among some) as Neo-Darwinism.
- ✦ In the second half of the century, the idea of the gene as the unit of selection - "gene-centric evolution" - was strongly emphasised by some, and probably reached a peak with Dawkins' *The Selfish Gene*.

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## The attack on adaptationism

- ✦ This point of view didn't go down too well with some evolutionary theorists, notably Stephen Jay Gould, who attacked what he called "the adaptationist programme".
- ✦ "Because of the excellence of his essays, he [Gould] has come to be seen by non-biologists as the preeminent evolutionary theorist. In contrast, the evolutionary biologists with whom I have discussed his work tend to see him as a man whose ideas are so confused as to be hardly worth bothering with." John Maynard Smith

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## The attack on adaptationism

- ✦ Gould & Lewontin (1979) *The Spandrels of San Marco and the Panglossian Paradigm*. Complexity does not imply adaptation. If an adaptationist hypothesis fails, it is replaced by another: "Just So" story.



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## The adaptationist programme

- ✦ Evolution is a process of natural selection among randomly produced variations.
- ✦ The unit of selection is the individual organism or its genes. Genotype determines fitness. Weismann's barrier cannot be crossed.
- ✦ Organism is clearly divisible into traits. These are adaptive because they are the solution to environmental problems.
- ✦ Suboptimality in individual traits comes from tradeoffs.
- ✦ Environments are fixed, or change independently.
- ✦ Non-selective effects play a minimum role.

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## Types of evolutionary adaptation

- ✦ *Adaptation as fit*: harmony between parts, congruence between structures, behaviours and environment.
- ✦ *Adaptation as solution to a problem*: adaptations have functions, and all functions are adaptations arising via natural selection.
- ✦ *Adaptation as conservation*: maintenance of viable organism/ niche relation. Makes sense in macroevolutionary contexts. Adaptation of different species cannot be compared meaningfully. Non-adapted means extinct.

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## Challenges to adaptationism

- ✦ Other factors play an important role in evolution: developmental and historical constraints, allometry, genetic drift.
- ✦ Environments are not independent of organisms. They are *co-defined*: life changes the physical constitution of the environment (Brandon, 1990, *Adaptation and Environment*).
- ✦ Dividing integrated organisms into traits is controversial.

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✦ In the seminar paper *Optimisation theory in evolution* (1978) Maynard-Smith defends adaptationist thinking as the first alternative in the explanation of a biological trait. We find out what the optimum situation should be and when it does not compare with Nature, we have reasons to suspect that other factors may have intervened.

✦ The optimality assumption is not under test. But he recognises the poor science in rescuing failed adaptationist hypothesis with further *ad hoc* adaptationist hypotheses.

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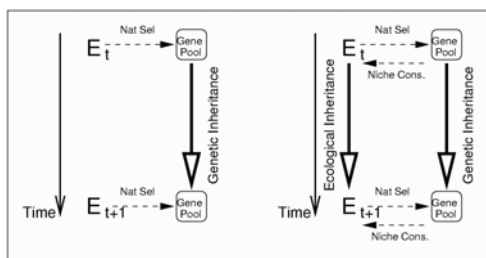
## Niche construction

- ✦ Organisms select and actively affect their environments, both during their lifetime and from one generation to the other. Selective "problems" are not independent of current "solutions".
- ✦ Birds and insects build nests, rabbits and rats dig burrows and tunnel systems, beavers create ponds and alter local water levels, leaves accumulate under high plants, etc. On longer timescales, oxygen in the atmosphere and the seas is constantly being renewed by life (algae, plankton, trees, etc.)

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Niche construction contradicts the basic premises of the adaptationist programme.



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## Frequency-dependence

- ✦ The fitness of a trait depends on the current pool of traits in the population. For example:
  - ✦ **Co-evolution**: Two or more species influence each other's niches. (Predator/prey, host/parasite, +- symbiosis ++, resource competition --). Can lead to arms races: runaway evolution
  - ✦ **Sexual selection**: A special case of co-evolution, also leads to runaway selection (peacock tails and, perhaps, human brains)
  - ✦ **Density dependence**: Fitness depends on the number and distribution of individuals. All social behaviour is, by definition, frequency dependent.

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## Evolutionarily Stable Strategies

✦ A game-theoretic approach (Maynard-Smith & Harper, 1973)

✦ An Evolutionarily Stable Strategy (ESS) is one that cannot be invaded once it has been adopted by most of the population.

✦ It may not exist. Cyclic solutions are possible. Strategy *A* may be the best if most of the population uses strategy *B*, but be beaten by *C* once it has invaded the whole population. Side-blotched lizards: Male phenotype has a period 3 cycle.

		Player B	
		Cooperate	Defect
Player A	Cooperate	Mutual cooperation 3	Winner = 5 Sucker = 0
	Defect	Winner = 5 Sucker = 0	Mutual defection 1



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## Evolutionary "progress"

✦ Do organisms become "more adapted" or complex with time?

✦ "There is no theoretical reason to expect evolutionary lineages to increase in complexity with time, and no empirical evidence that they do so" (Szathmáry & Maynard-Smith, 1995)

✦ S.J. Gould's argument: a random walk process bounded on one end would look as if it were directed towards the other, but it is not. So even the null-hypothesis of undirected change produces increased complexity over time. (Don't take this as a *model* of complexity!)

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## Major transitions

However we can observe transitions in complexity that some claim "redefine" the evolutionary process, and especially the "unit" of evolution:

✦ Replicating molecules	Molecules in compartments
✦ Independent replicators	chromosomes
✦ RNA as gene and enzyme	DNA and proteins
✦ Prokaryote	Eukaryote
✦ Asexual clones	Sexual populations
✦ Protists	Animals, Plants, Fungi
✦ Solitary Individuals	Colonies
✦ Primate Societies	Human Societies, Language

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## Transitions to new entities

✦ A common theme in many of these transitions is the passing from entities that reproduce independently to entities that reproduce by forming part of a larger whole - for example, groups. May appear difficult to explain from a gene-centred view, but explanation is not impossible.

✦ **Kin selection**: (Hamilton, 1964); individuals within many kinds of groups tend to be more genetically related than individuals from different groups. This linkage allows standard individual genetic mechanisms to support apparent group selection.

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## Transitions to new entities

✦ **Group selection**: Competition between groups of unrelated individuals may overcome intragroup competition if pressures are sufficiently high, or because of other ecological factors (e.g. D.S. Wilson). Biased sex-ratios can be good evidence of group selection - they reduce local competition. Group selection provoked bitter controversies in the 60s but it has become more acceptable in a modern form thanks to convincing modelling and evidence.

✦ **Kin selection and group selection** can sometimes be shown to be formally equivalent (M.J. Wade)

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## Multilevel evolution

✦ Selection can act at different levels in a hierarchy (gene, organism, group, colony, etc.) Particular traits may sometimes be explained as the tradeoff of selective pressures at different levels.

✦ Michod (*Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*, 1998) explores the mathematics of the formation of composite reproductive entities, and the different meanings of fitness.

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## Non-selective factors

- ‡ **Self-organisation:** Kauffman: intrinsic structural stability of genetic regulatory networks, order for free. Bak-Sneppen model of coevolution between interacting species shows self-organised criticality, ecologies poised at a critical state, and power laws for extinction events, independent of selection.
- ‡ **Neutral evolution:** (Kimura, Ohta). Most molecular changes in genes are neutral, and so substantial drift can take place without affecting fitness. This may form most evolutionary change in the genome, but does not involve selection. Nearly Neutral Networks can provide paths between fitness peaks, and speciation can arise from percolation in "holey" landscapes (Gavrilets).

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## Modelling tools

- ‡ **Game Theory:** looks for ESSs in frequency-dependent conditions. Interactions between individuals modelled as games, fitness = payoff.
- ‡ **Individual-based models:** Pitched at the level of individuals but observed at population level and evolutionary timescales. If carefully constructed they can extend the above tools, by exploring evolution in *finite* and *variable* populations, subject to *stochasticity* and *spatial variation*, by studying the effects of *discreteness*, and integrating *environmental factors* as variables.

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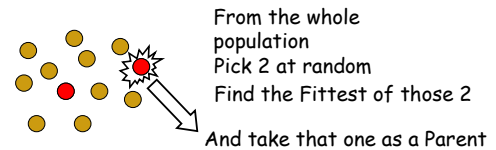
## Horizontal Transmission

- ‡ It has only been recognised fairly recently that a lot of genetic transfer - particularly bacterial - is *horizontal* within generations, rather than *vertical* between generations
- ‡ Metagenomics
- ‡ Lead up to Microbial Genetic Algorithm

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## Tournament selection

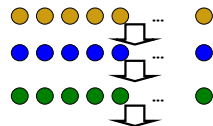


It turns out that if you repeat this n times (with replacement) everyone has same expectation of parenthood as with Linear Rank Selection

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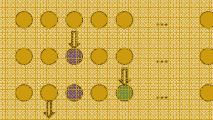
## Steady State Genetic Algorithm

Instead of a Generational GA, replacing all n at the same time



You can just produce one new offspring at a time, replacing one.

Repeat n times for the equivalent of one generation



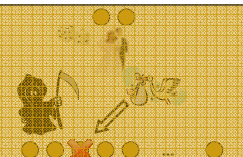
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## Select who dies

Typically, many GAs select positively ('greater fitness') for who is to be a parent

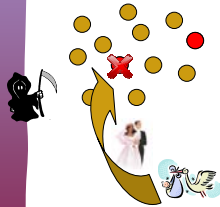


But it works just as well to select parents at *random*, then select negatively (less fitness) to choose who makes way for the offspring.



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## Combine these with Tournament Selection



From the whole population  
Pick 2 at random as parents  
Generate an offspring

Then select *negatively* which parent dies ('less fitness')

To make way for the baby

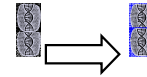
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## Without Death — Horizontal Transmission

Normally we think of Vertical Transmission of genes, from one generation to the next

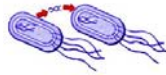
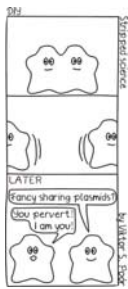


But Microbes can achieve the same end, without dying!



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## Microbial Sex

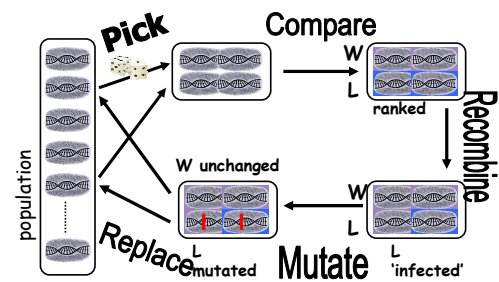


Instead of "Let's make babies!"

It is  
"Want to share some of my genes?"

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## The Microbial GA



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## The code

```

void microbial_tournament(void) {
    int A,B,W,L,i;
    Pick      A=P*rnd(); B=P*rnd();    // Choose A, B randomly
    Compare   if (eval(A)>eval(B)) {W=A; L=B;} // W=Winner
             else {W=B; L=A;}           // L=Loser
             for (i=0;i<N;i++) {        // walk down N genes
    Recombine if (rnd()<REC)             // REComb rate
             gene[L][i]=gene[W][i];    // Copy from Winner
    Mutate    if (rnd()<MUT)             // MUTation rate
             gene[L][i]^=1;           // Flip a bit
             }
}
    
```

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## Final comments

✳ Organisms are to a greater or lesser extent *adapted*, and evolution is the main *adaptive* process.

So does that mean Darwin was right?

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