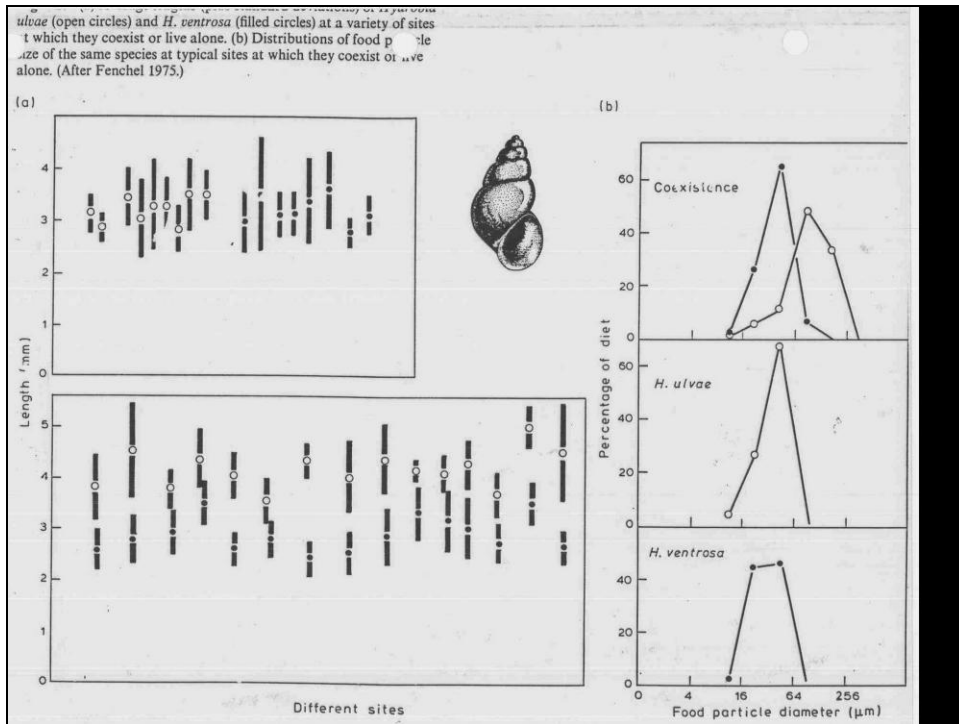
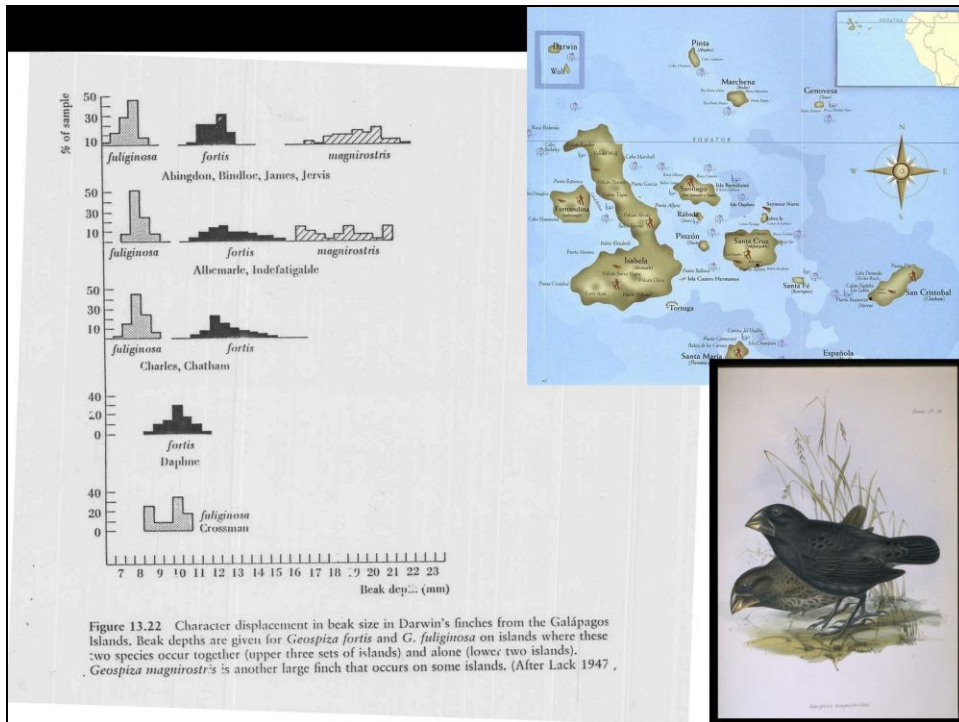


To review: even fundamental niche dimensions can vary within a species. Here are distributions of mandible sizes for a single species of desert seed-eating ant for four different areas/populations. Mandible size is pretty much genetically determined (and therefore *heritable*) and determines what seed sizes an ant *can* eat – i.e., mandible size would seem to be an indicator of *fundamental* niche. So fundamental niche seems to vary among these populations. The arrows show the *average* mandible sizes for species of coexisting (sympatric) seed-eating ants. This seems to suggest a minimization of fundamental niche overlap...

Think about it.



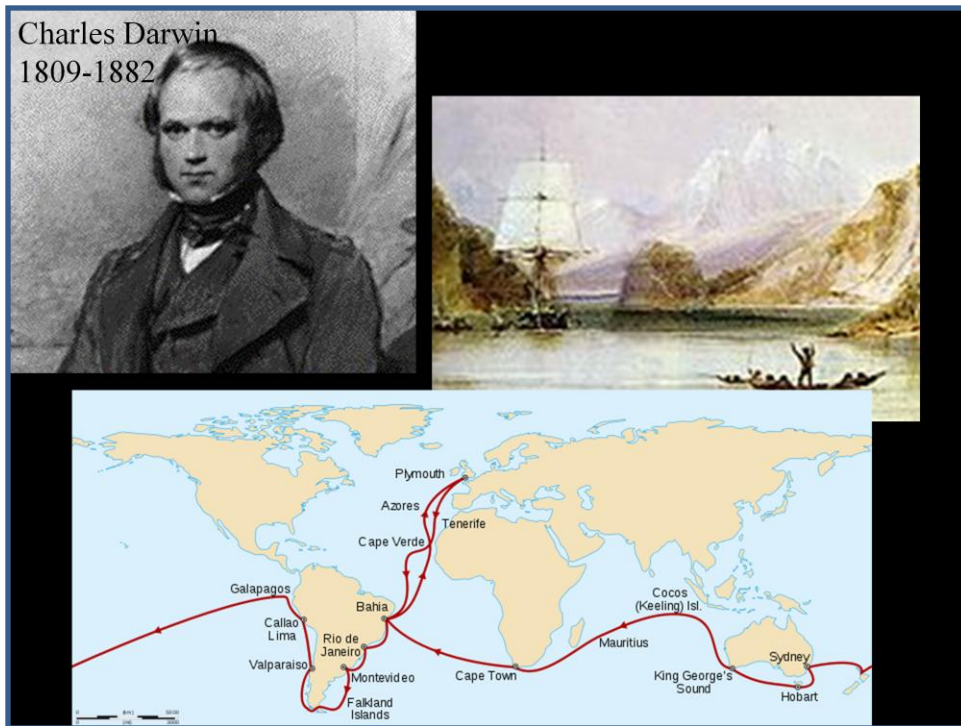
A similar scenario with snails in lots of different water bodies. Graphs to left show average (and range of) shell sizes for populations of two snail species *Hydrobia ventrosa* and *H. ulvae*. The upper graph shows populations where each species occurs by itself (i.e., they are allopatric – not overlapping in distribution); one species is symbolized by solid dots, one by open dots). The lower graph shows shell sizes where populations of the two species coexist (where they are sympatric). Again, there appears to be a 'separation' of traits where populations are likely to compete.



Finally, Darwin's finches. Look at beak depth distributions for *Geospiza fortis* – the darkest curves -- on different islands where it co-occurs with 0 (4th down), 1 (3rd down), or 2 (top and 2nd) other species of finches. As with ants and snails, presence of 'adjacent' members of similar guild (they're all seed-eaters) seems to be associated with a narrow range of beak depths in finch populations (but less so in 2nd graph than top). Where there are no *sympatric* (spatially co-occurring) potential competitors, *fortis* and *fuliginosa* actually have very similar beak size distribution. Again, beak size is strongly heritable (*how would you assess this?*), so seems like a reasonable index of some dimension of fundamental niche.

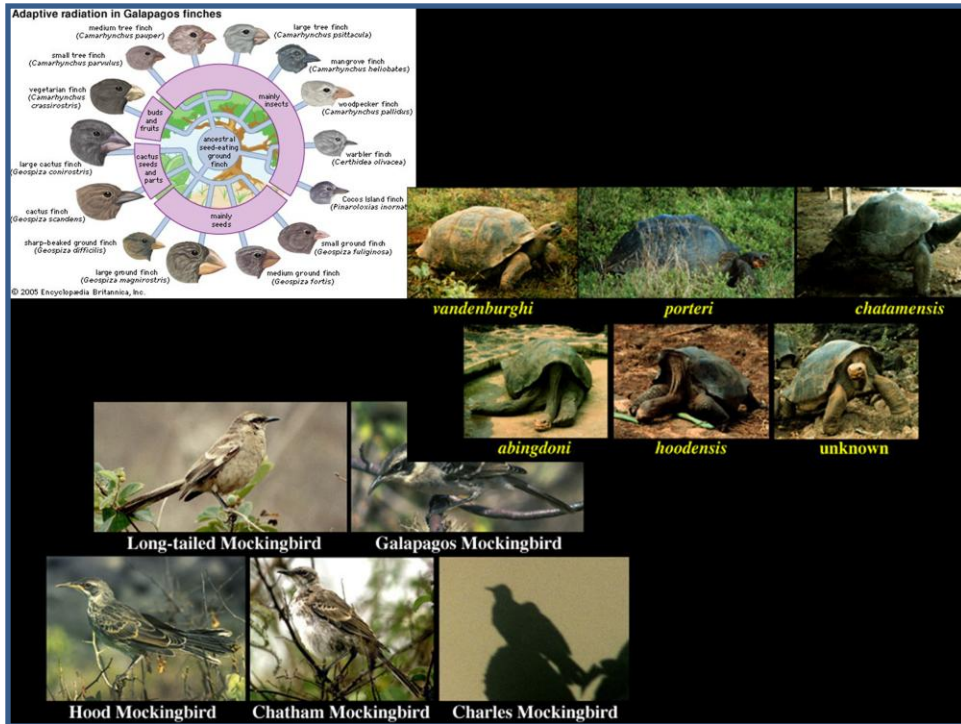
This sort of pattern is taken to suggest that there've been *changes in beak size* over time – shifts in *fundamental niche*. Consider what would happen if an island like Daphne (4th line) were colonized by *G. fuliginosa* from Crossman. Which individuals would compete most or least intensively with the other species? What would be results of such competition? Think in terms of a) resources individuals can 'claim', how they might allocate resources to survival and to reproduction, and which individuals will have more offspring as a result. What will those offspring look like?

Consider differences between top two lines; could they be a result of different histories?

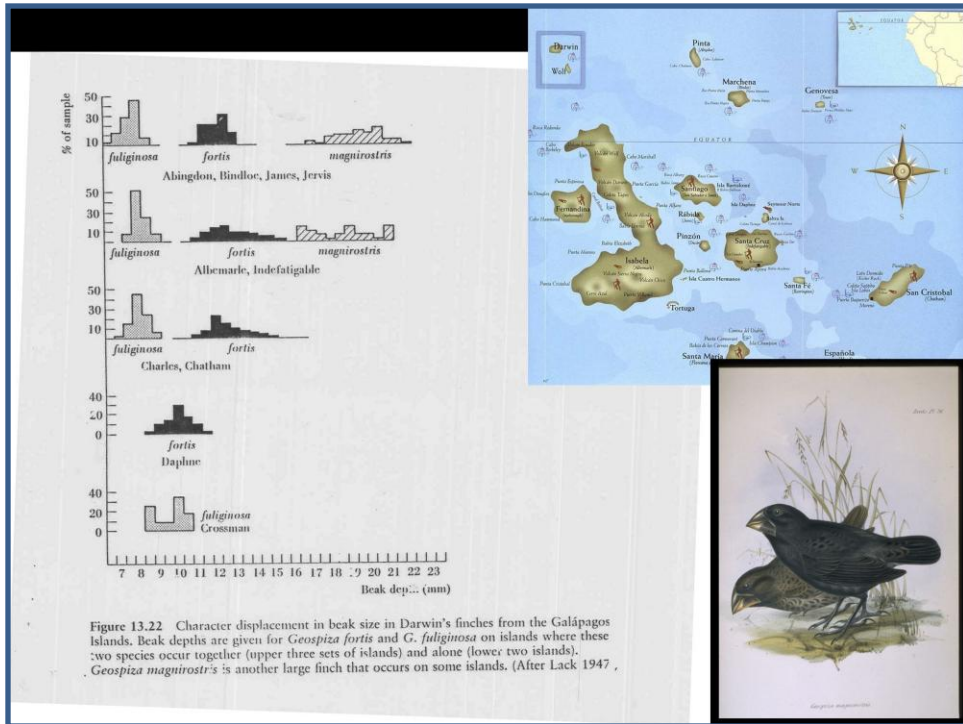


The basic framework of natural selection as constructed by C.D (published in 1859, more than 20 years after his trip around the world) emerged from considering such scenarios (though not, in fact, the finches...). His basic reasoning:

1. IF entities reproduce (as anything we call 'living' tends to do)
2. AND there is heredity (offspring are more like parents than 'average' properties of the population: also basic to things that are 'alive'?),
3. AND there is variation among individuals in terms of heritable traits
4. AND populations tend to grow so long as conditions permit (Malthus and exponential growth)
5. AND resources are finite (OR the world somehow constrains numbers: density-dependence)
6. THEN there will be competition (OR some form of limitation on a growing population)
7. AND it is likely that individuals possessing specific *heritable forms* of a variable phenotypic 'trait' will be BETTER AT CAPTURING resources or dealing with constraints
8. SO THAT they'll be more likely to reproduce than individuals possessing other forms of the trait
9. AND that more 'adaptive' trait will increase in frequency until it replaces others, changing the genetic make-up of the population at issue

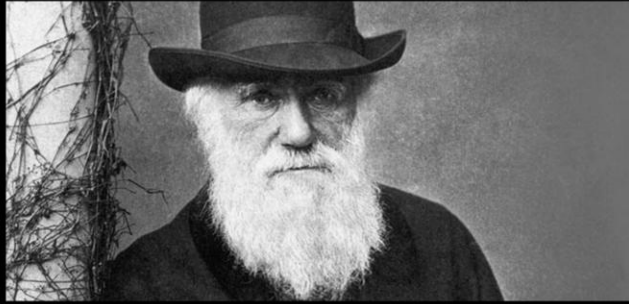


In fact, Darwin failed to keep records of which islands specific finch collections came from, so he wasn't able to assess how finch populations might have diverged – but he did note that sailors could tell which island a tortoise came from by shell shape, size, neck length, etc. (vegetation varies among islands...). Several species of mockingbirds are also endemic to the Galapagos, but only one per island; this pattern influenced Darwin's thinking strongly (he wondered why there would be different species on each island, even though they were doing essentially the same thing; why not just one species found on all the islands if organisms were 'created' specifically for their habitat/job?).



Darwin's Finches continued: NOW, think about:

- if you mixed the populations from Daphne and Crossman, individuals of *fuliginosa* with smaller beaks and of *fortis* with larger beaks might face less competition with the other species, thus gain more resources than their conspecifics in the 'overlap' zone, thus leave more descendants, so that the whole populations 'shift' beak size (and fundamental niche)
- The narrower distribution of *fortis* beak sizes in the top graph where a larger-beaked species, *G. magnirostris*, is present. This might result from competition disfavoring genes for big beaks AND genes for small beaks.
- FINALLY, think about a historical selective scenario that might explain difference between top two lines.

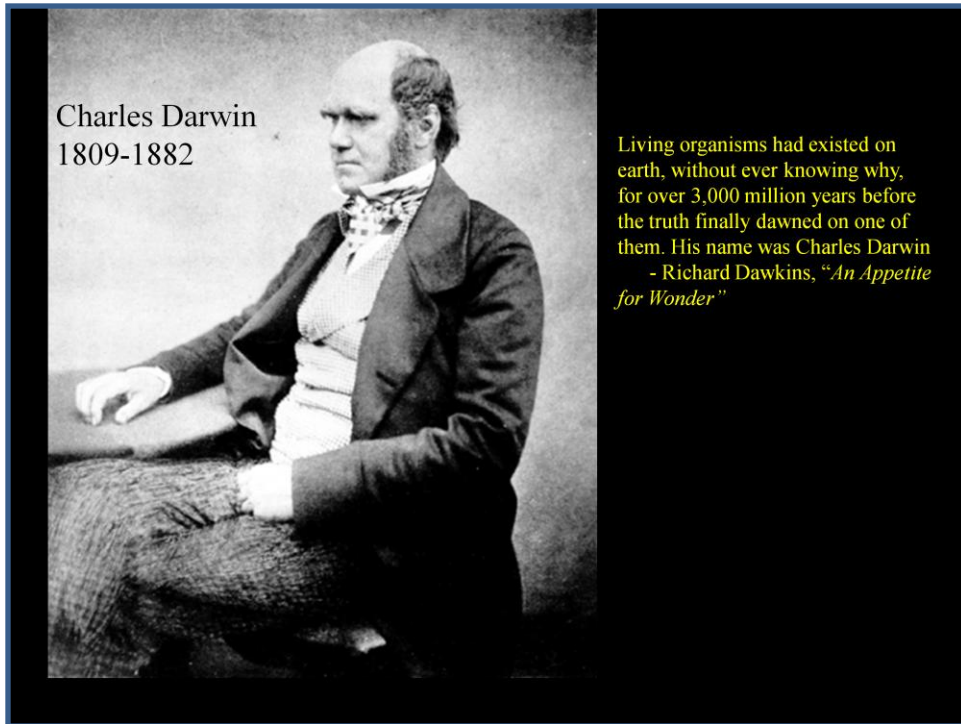


*I have called this principle, by which each slight variation, if useful, is preserved, by the term **Natural Selection**.*

*- Charles Darwin, **The Origin of Species***

SO – Natural Selection is NOT ‘survival of the fittest’; Darwin liked to call it ‘descent with modification’, and this quote comes close to pointing out the actual mechanism he proposed in a few words. Replace ‘if useful’ with ‘if it contributes to reproductive success’, and you have the basic idea in more current framing. Darwin lacked understanding of genetic mechanisms of inheritance (Mendel was a contemporary, but his discoveries never really made their way into Darwin’s awareness). Modern evolutionary thought combines Mendelian genetics with Darwin’s notion of selection. You could equally well describe natural selection at the genetic level: “genetic variations (mutations/alleles) that contribute to the reproductive success of their host organism will increase in frequency in the population (gene pool) until other versions are replaced.”

Finally, modern evolutionary theory adds the concept of **FITNESS**, which, strictly speaking, is simply *relative reproductive success* of an individual. It is NOT the same thing as **ADAPTATION**. Any trait that helps an organism cope with its environment is an adaptation; it may enhance fitness, but so may other things (like greater success in finding mates).



SO: *Natural selection* is simply changes in frequency (*proportional* abundance) of **heritable** phenotypic traits (or of homologous **alleles** for a gene) **due to the effects of those traits or alleles on the individual organism's reproductive success** compared to other individuals in a population.

FIVE IMPORTANT THINGS TO REMEMBER:

- It OPERATES ON differences among *individuals* (not properties of species or populations)
- But what EVOLVES/changes is the genetic (and phenotypic) make-up of POPULATIONS.
- It works ONLY on variation that is available within the population; it can't make new variations and the 'best' possibilities may not occur
- It works **ONLY** through differences in individual's contribution of descendants or relatives to future generations; other things (like survival) only matter if they influence this; see definition of FITNESS below...
- It is driven **ONLY** by CURRENT CONDITIONS; there is no means by which natural selection can work towards FUTURE benefits (think about 'altruism' in this context).

Natural selection =

-changes in frequency or proportion of a heritable trait (allele) within a population

- due to the effect of that trait (allele) on the holder's reproductive success compared to other individuals in a population.

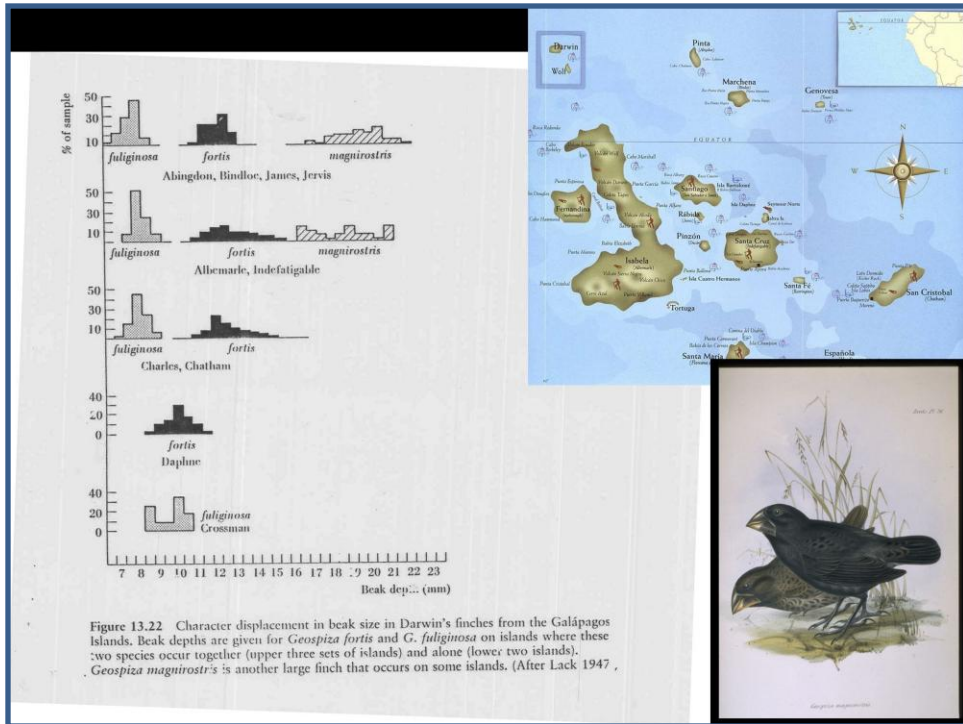
“Natural selection will operate wherever there is heredity, variation (and that will almost inevitably follow given you have got heredity), competition (and that will almost inevitably follow given you have got heredity and variation). So I suspect that the conditions for natural selection to work are very minimal indeed: namely, the existence of the phenomenon of heredity.” -- Richard Dawkins



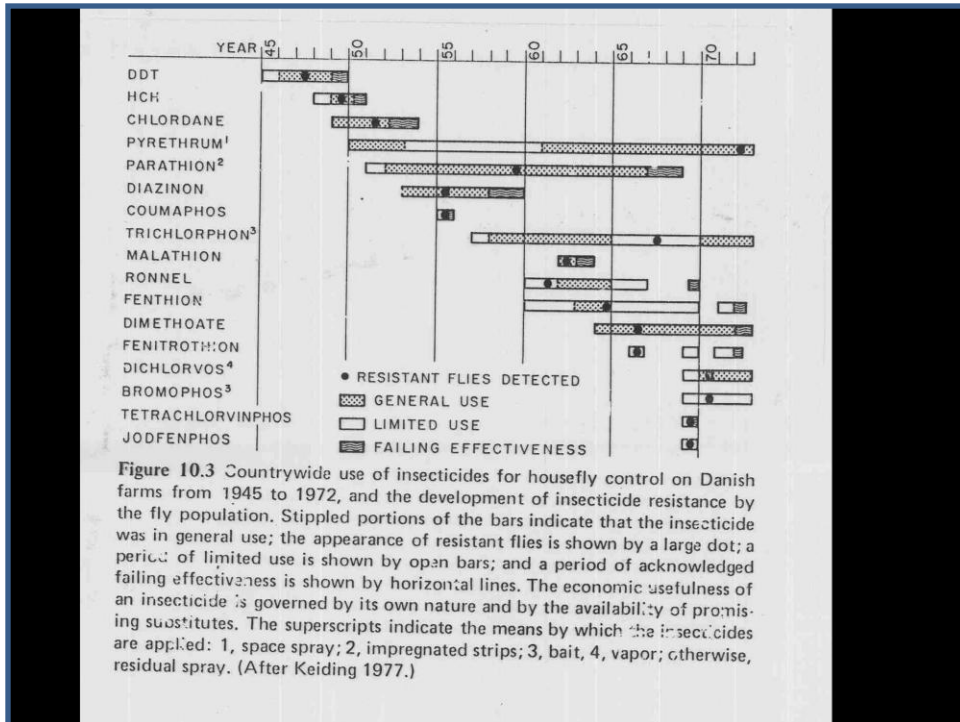
There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Charles Darwin, "On the Origin of Species", 1859

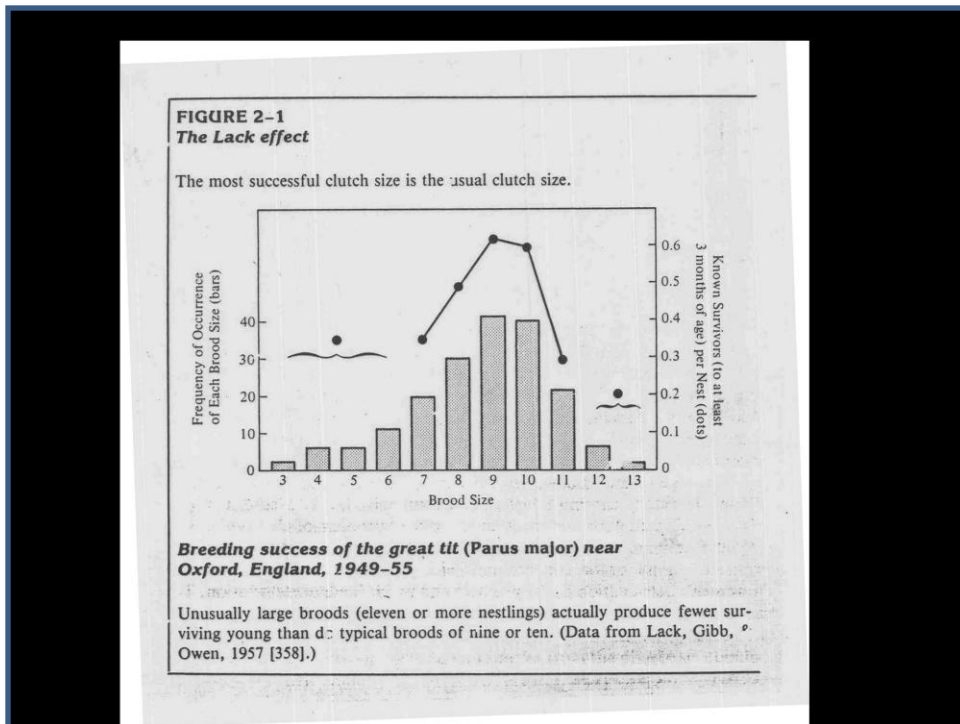
All of this seems very powerful. Natural selection is the only mechanism we know of that can produce ADAPTATION in organisms, and we often marvel at the intricacies and precisions of adaptation to environment (as did Darwin) – indeed, it may well be that this 'adaptive complexity' is what's most fascinating to us about living organisms. BUT it's often not this simple, as we will see...



The scenarios here present a mix of *directional selection* (eg., third line; larger-beaked *fortis* experience less competition so might have higher fitness, at least for a time), and *stabilizing selection* (top two lines; larger- and smaller-beaked *fortis* BOTH experience more competition, so selection will tend reduce variation and maintain an intermediate beak size). A third mode -- *disruptive selection* -- is when the most frequent phenotype is less favored by selection than rare phenotypes; in this case selection would tend to maintain or increase genetic variation within a population; think about when this might happen.



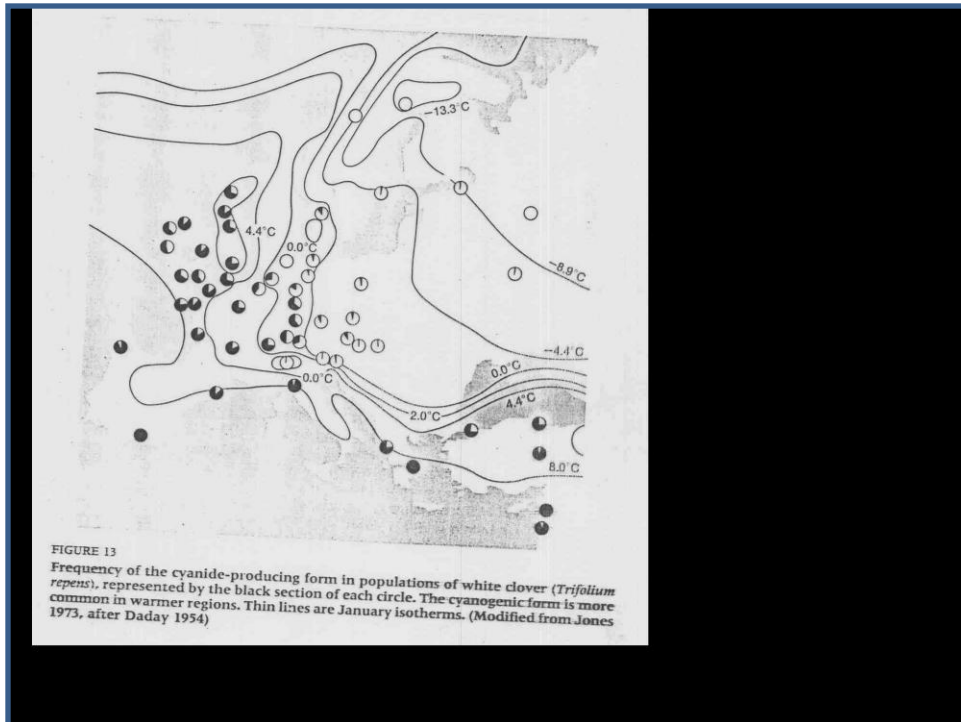
Here's an example of a common sort of *directional selection* – where more pronounced values for a 'trait' confer progressively higher fitness. Here the trait under selection is insecticide resistance in flies in Danish cattle barns. Once an insecticide is brought into use, there is *directional* selection for resistance; any (more) resistant mutant will have higher fitness, all else being equal (although there are will generally be limits; see later slide...). Similar dynamics apply to the evolution of resistance to antibiotics by pathogens.



FITNESS is a central concept in modern thinking about evolution by natural selection. *FITNESS* is strictly defined as the *relative reproductive success of different individuals or genotypes within a population*. It is NOT the same thing as 'adaptation' which is a measure of how well-engineered a phenotype is to environmental circumstances. Differences in adaptation may certainly influence fitness, but fitness must ALWAYS and ONLY be defined only in terms of differences in reproductive success. A genotype or allele that, on average, leaves more descendants than other genotypes/alleles, has *RELATIVELY* highest fitness. An individual that has more offspring than another generally has higher *individual fitness* (there are fine points here that we won't get into right now). And so on. Here, *clutch size*, the number of eggs per brood/nest/female, for a European song-bird is shown to affect *fitness*. We know clutch size to be strongly genetically determined – i.e., *heritable* – so selection can act on it. Birds with clutches of 9 or 10 have higher *fitness* (here measured as number of known survivors from the clutch at 3 months of age) than birds with either larger or smaller clutches. (NOTE that this assumes a number of things – e.g., that mature females with different clutch-size-genes have similar survival over years, that survivorship at 3 months is indicative of long-term survival, etc.). This is a case of *stabilizing selection*; selection will tend to REDUCE variation and produce an 'optimal' state of the trait in question. BUT, A PROBLEM: If this scenario played out over a few generations, the genes for smaller and larger clutches would be 'selected out' of the population! Why are there still such variants in the population? Hint: Think about WHY larger and smaller clutches would confer reduced fitness, and then think about how selective factors might change over time...



Think about how selection might act on the TIMING of leaf senescence in deciduous trees. Why do they change when they do and not earlier? Or later? What are the FITNESS-RELATED costs and benefits? Would this be another example of STABILIZING selection? *How would this change if climate were to change slowly (say warmed) over decades?* THEN, the optimal timing might change, and genetic variants that senesced later than the norm would have higher fitness. This would amount to *directional selection* , at least for a time...



Some clover populations have a gene that allows them to produce cyanide as a defence against (mammalian) herbivores. That gene is more frequent in populations in southern and western Europe (the black slices of pie charts), and completely absent in far northeast. Think about selective benefits AND COSTS (mainly, perhaps, energetic costs of producing cyanide). What might cause the balance between costs and benefits (to FITNESS) to shift? Think climate/growing-season...

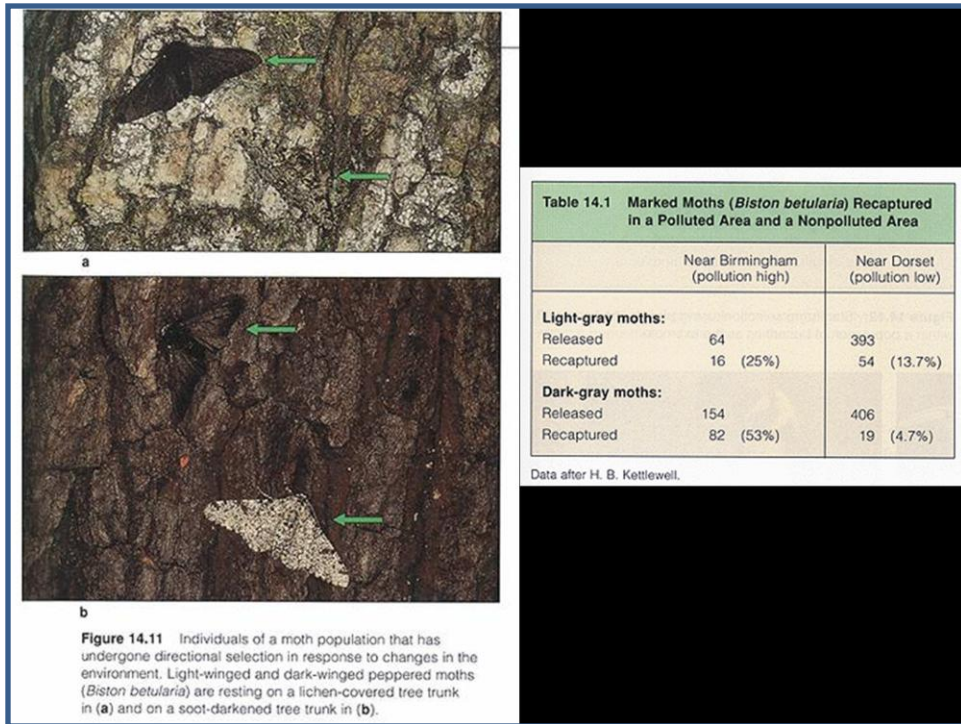
The point here: the overall fitness contribution of most traits has to be thought of as the balance of fitness costs and fitness benefits – i.e., there are TRADE-OFFS, and the ‘best’ trade-off will depend on circumstances.

TABLE I
Fitness of insecticide-resistant homozygotes in two species of *Anopheles* mosquitoes relative to that of susceptible homozygote (fitness = 1)^a

<i>Anopheles</i> species	Insecticide	Fitness in environment with insecticide	Fitness in environment without insecticide
<i>culifacies</i>	DDT	1.3–1.5	0.62–0.97
	Dieldrin	2.9–6.1	0.44–0.79
<i>stephensi</i>	Malathion	1.3–1.6	—
	Dieldrin	1.7–2.7	—
	DDT	—	0.96

(From Wood and Bishop 1981)
^aFitness estimated from the change in frequency of resistant genotypes in natural populations during insecticidal control and after termination of control. It was assumed that there was no immigration of susceptible mosquitoes. *A. culifacies* was studied in villages in India, *A. stephensi* in villages in India and Iran.

Insects quickly evolve resistance to insecticides (toxins are powerful selective factors!). These data are measured reproductive output of mosquito genotypes resistant to two insecticides (fitness of the non-resistant, 'wild' genotype, is set at 1, so all of these values are proportional to that). Resistant genotypes show much higher fitness – reproductive rates often several times higher -- in environment with insecticide (not surprising). BUT, in environments *without* the insecticide, their reproductive output – or fitness – is actually *lower* than that of the wild type. This suggests that insecticide resistance involves some form of *trade-off*. This is a general pattern. Think about consequences for evolution of populations with and without exposure to insecticide.

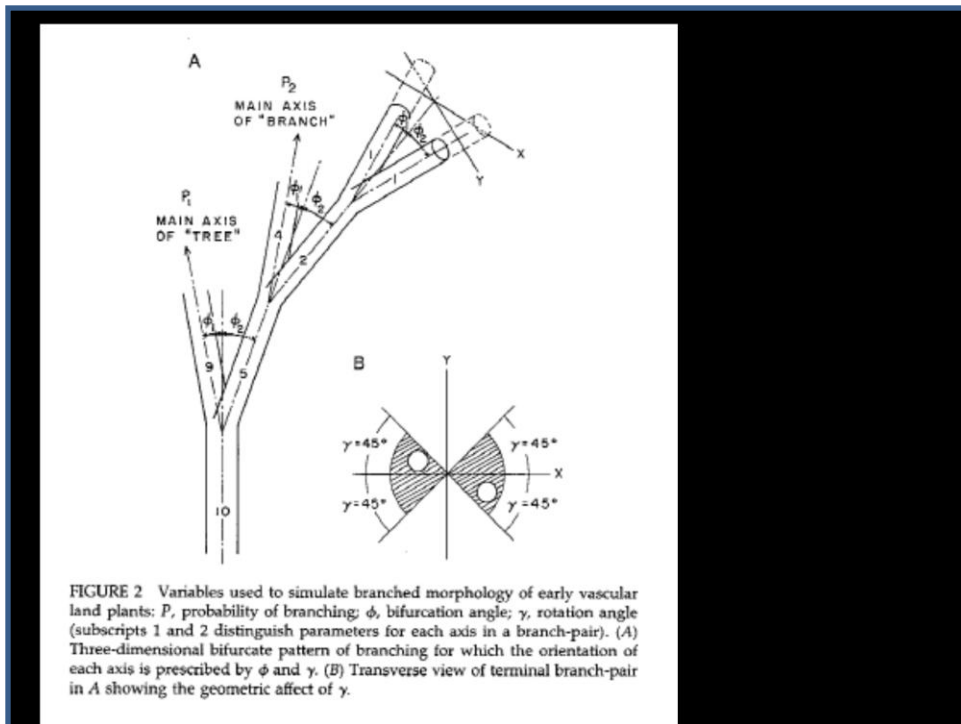


A classic real-world analysis of fitness: Moths roost on tree trunks during the day. In Britain before industrialization, tree trunks were lichen-covered (top photo), and pale, mottled moths were dominant, with only very rare 'melanic' (uniformly dark) mutants (they were highly valued by collectors!). With industrialization, air pollution killed lichens leaving tree-trunks dark gray-brown. Dark-colored moths rapidly increased to dominance in the population. This is consistent with the notion that predation imposes differential selection on these two phenotypes; the hypothesis would be that more camouflaged individuals survive predation to reproduce with greater frequency. Kettlewell tested part of this hypothesis by releasing marked moths of both types in both polluted woodlands and unpolluted ones (where trees were still lichen-covered) and then recapturing as many as possible; in both cases, recapture rates were higher for the genotype predicted to be better able to avoid predation



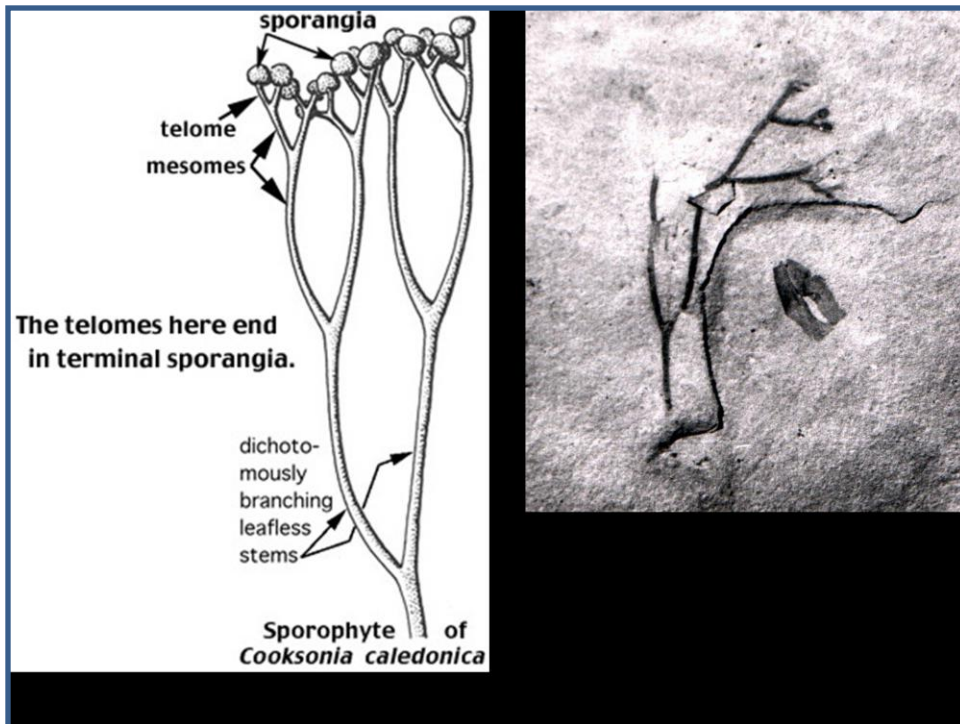
TRADE-OFFS abound in selective dynamics. We've talked about differences among plants in 'shade-tolerance'. Consider what it takes to design a leaf that's particularly good at operating in low light. In high light. Can you 'optimize' for both tasks simultaneously? Think about a) the energetic cost of building a leaf, b) it's efficiency at using available light, and c) it's 'yield' in sugar (energy) gain from photosynthesis. A leaf that doesn't pay it's construction costs is a really poor design, but so is a leaf that could have made a much greater 'profit' if a bit more had been 'invested' in its building...

A leaf with a thick layer of photosynthetic cells will capture more photons when there are a lot of photons coming in (i.e., fewer are allowed to pass through without being captured), but it costs more to build. A thin leaf is cheap and will capture most available light when light levels are low, but will waste a lot of photons when they are abundant. Which of these (left) is a 'sun-leaf', which a 'shade-leaf'? Again, the concept of trade-offs that is embedded in our thinking about 'life-histories'. This is a good example of how many evolutionary/selective trade-offs can be cast in economics-like terms – but, ultimately, they only matter IF the costs and benefits end up manifesting in differences in reproductive success. This adaptive trade-off in leaf structure is a bit more complicated than some because some types of plants (many shade-tolerant trees) are capable of growing leaves of different structure on same tree depending on environment; a large tree might have broad, thin 'shade leaves' in the lower part of its canopy, smaller but thicker (and often more lobed) 'sun leaves' in its upper canopy.



Because evolution by natural selection is fundamentally a very simple *algorithmic* (what does this mean?) mechanism, it is easily simulated. Here is an ‘artificial’ digital life-form that might be used as a model to better understand evolution and adaptation in real life forms. *Karl Niklas* – a paleobotanist, used the shapes of very early land plants (see next page) to come up with simple, branching ‘plant-like’ shapes defined by four shape parameters (think of them as genes). These control 1) frequency of branching (or distance between branches), 2) angle of bifurcation at each branching event, 3) rotation of branching plane from one branching event to the next, and 4) total number (or length) of branches before growth stops. There were some more complexities in the end, but this is the basic plan. At the tip of each ‘final’ branch, the ‘plant’ produces a reproductive organ (spore-case in his model).

Now, think of each of these growth/shape parameters as a ‘gene’. For any individual ‘plant’ it has some numeric value. Let your plant reproduce; shape ‘genes’ are mostly the same for offspring as for parents. BUT you can let the values for these genes mutate a little bit with some low probability (most offspring don’t mutate, and mutations are always small). Now ‘create’ your plants in the computer as a few lines of computer code written to generate shapes determined by the values of these parameters.

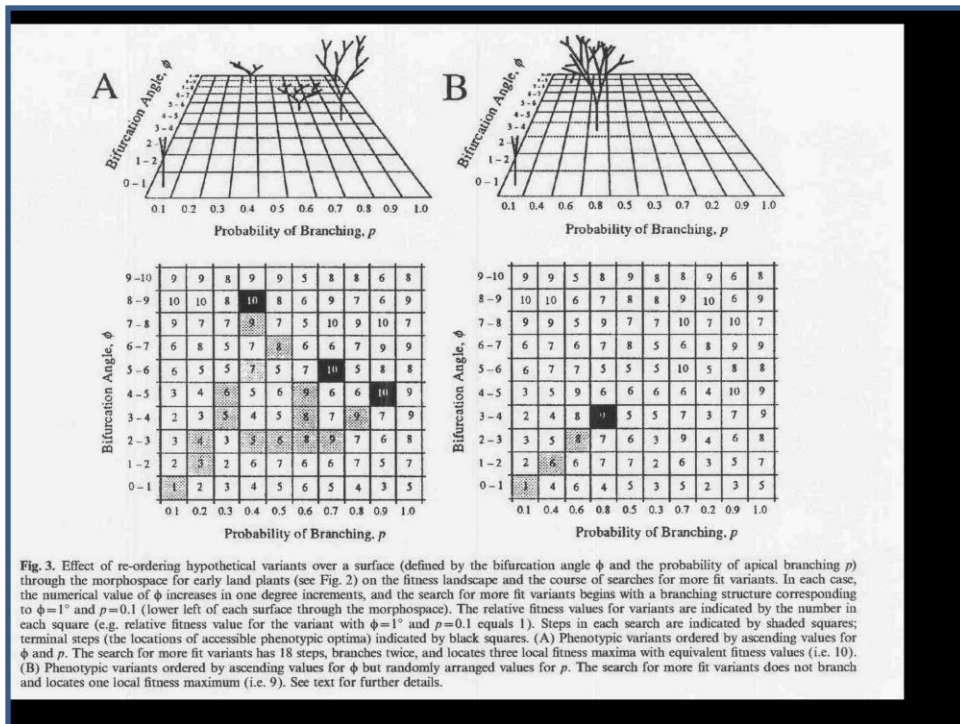


Right panel is an actual fossil of one of the earliest land plants; left panel is a reconstruction of what it might have looked like. They were only a few cm high, and look very much like the shapes generated by Niklas's code (simple branching stems, presumably green...).

Now consider *adaptive properties* of these plants/shapes. Niklas considered four ways in which he could assess the 'quality' or 'adaptedness' of a shape:

- 1) light-capture effectiveness: simply the total surface area facing upward ('projected' area);
- 2) Water-use efficiency: since plants lose water through surfaces, Niklas simply calculated total surface area (all surfaces). Smaller surface area equals higher water-use efficiency
- 3) Structural strength: Assuming constant properties of the materials used to build the shapes, strength (resistance to being blown over or broken) is a simple engineering calculation based on mass, angles of branches, height, etc.)
- 4) Reproductive success: Niklas assumed wind-blown spores and based reproductive success on the number of spore-cases (stem-tips) and how high they were (for good dispersal).

All obviously simplistic, but remember that 'modeling' and theory approaches try to start with simple models and see how realistically they behave, making them more complicated as needed to make behavior sufficiently 'real'.



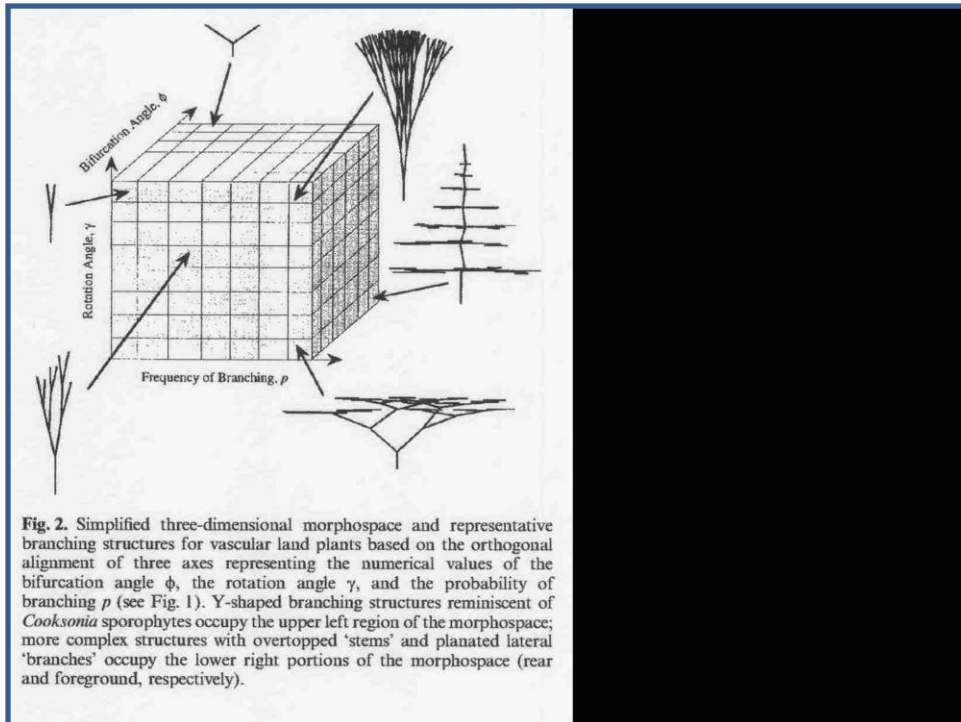
Imagine all the shapes that could be produced by varying just two of the 'genes'; these can be arranged on a two-dimensional space/plane (phenotype space) as at top; a few of the shapes corresponding to values of 'genes' are shown as example.

Using the 'adaptedness' measurements (previous slide), each shape (combination of two gene values) can be assigned a synthetic adaptation score; treat this, for now, as equivalent to fitness.

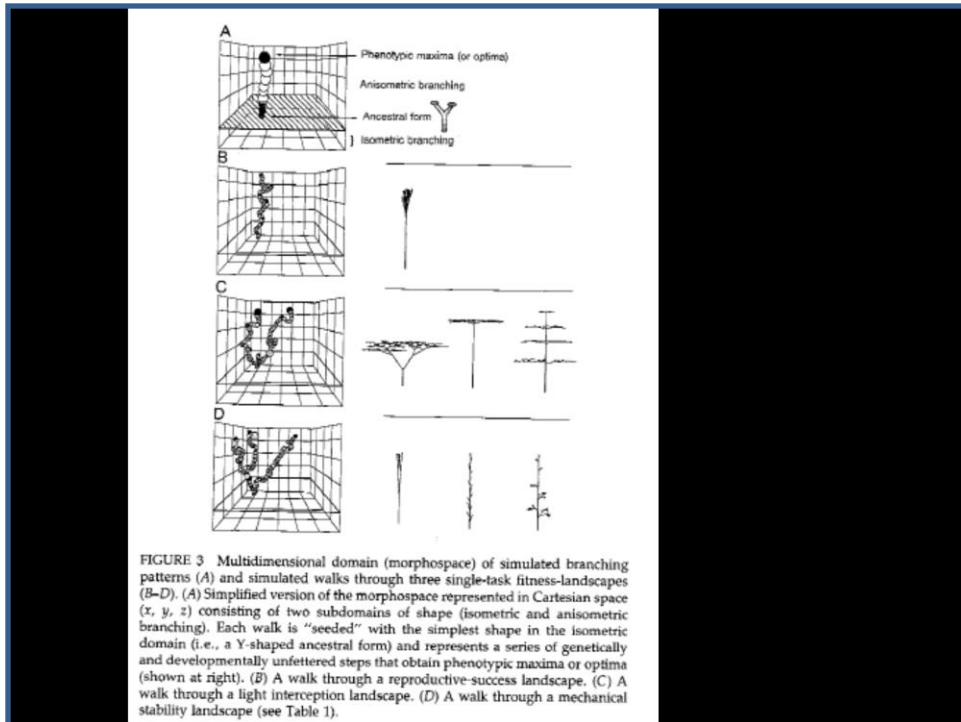
Now, start with simplest shape (lower left). Allow it to reproduce and mutate, but 'mutations' can only change either gene by one step, so 'offspring' shapes are never more than one square from the parent.

Each generation, choose the 'offspring' with highest fitness to produce the next generation. Over time, the descendant population of shapes will tend to move, one step at a time to, combinations of gene-values with higher fitness. Niklas calls this a 'walk through fitness space'. (Here, a walk over a fitness 'surface'; think of the plane as a topographic map with values representing elevation; selection will tend to move the 'population' up-slope.)

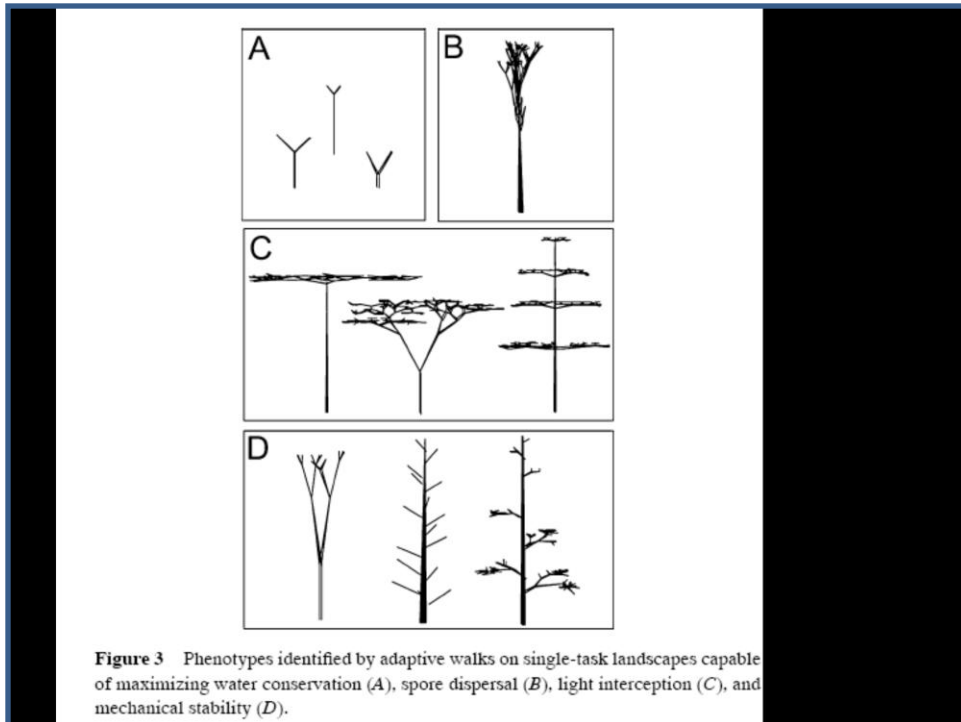
Note important correspondences to selective processes: a) Selection can only act on variations available – there may be 'better' combinations out there, but we're only allowed to move one step at a time. B) there's a chance element that determines which 'branch' history might take; it depends on which random mutation happens, c) Once population finds a 'peak' – a square surrounded by lower values – it is 'fixed' by stabilizing selection. SO different outcomes *might* happen in different runs, and there may be several 'peaks' to which population CAN evolve (and not all of them are equally 'good'!)



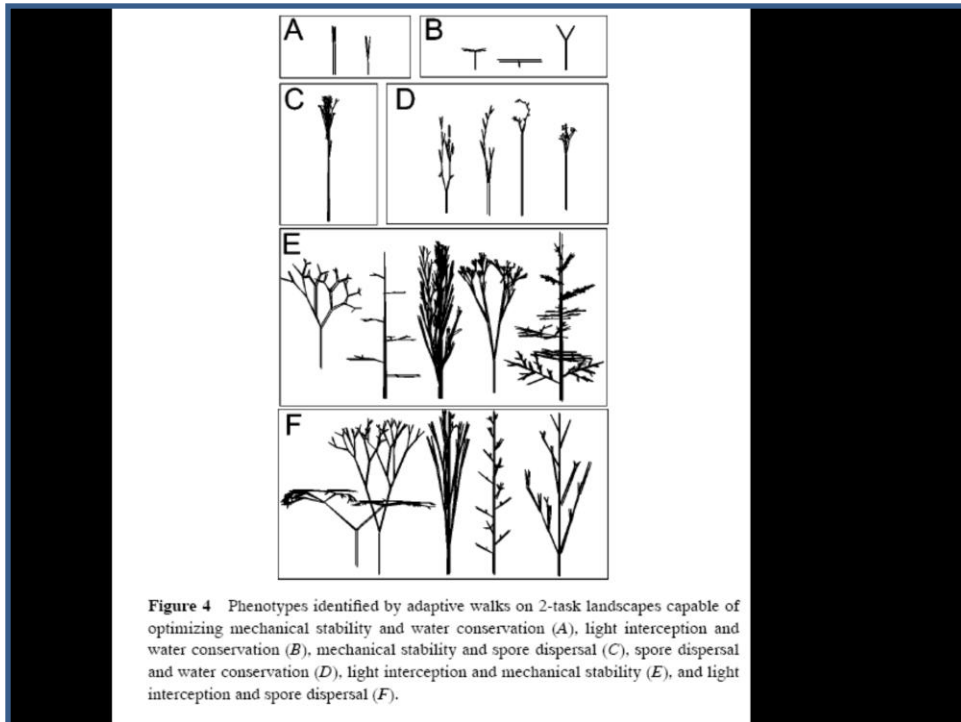
Same sort of concept in three dimensions – using three of the ‘genes’ for shape.
 Now, just generalize to 4-gene space – or as many dimensions as there are genes for
 any type of organism (for humans that’s about 25,000 dimensions)



So, Niklas simulates walks through ‘morphospace’ – the universe of possible shapes – with ‘fitness’ for each shape calculated on the basis of some combinations of the adaptive aspects discussed earlier. These are some ‘real’ runs showing the path of selective change in the 3D space, and the final forms reached to the right...



If fitness is based on just ONE of those adaptive tasks, these are the ‘peaks’ achieved by selection acting in morphospace on each task in turn (in *A* selection is only about water conservation; in *B*, spore dispersal; in *C*, light interception; and in *D*, mechanical stability) – there may be better designs, but they can’t be reached. In three selective scenarios there are multiple ‘local adaptive peaks’ in morphospace. Selection for spore dispersal alone, however, always leads to the same shape.



It's possible to 'combine tasks' – create an adaptedness (fitness) score that combines 'tasks'. These are the shapes produced by adaptive 'walks' in fitness landscapes defined by combinations of two of the adaptive needs. Note that combining scores for mechanical stability and spore dispersal again always leads to convergence on one shape – the same shape as spore-dispersal selection alone. All other combinations of 'tasks' produce multiple 'solutions' that are better than any small variations on them (i.e., local optima in the 'fitness space'). Which 'solution' is achieved depends on which chance mutations occurred first. Combining light interception task with either mechanical stability (E) or spore dispersal (F) tends to produce relatively realistic tree-shapes. Does this suggest that a large part of the evolution of plant shapes can be explained this simply?

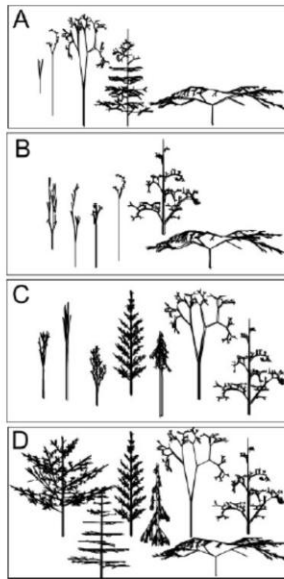


Figure 5 Phenotypes identified by adaptive walks on 3-task landscapes capable of optimizing light interception, mechanical stability, and water conservation (*A*); light interception, spore dispersal, and water conservation (*B*); mechanical stability, spore dispersal, and water conservation (*C*); light interception, mechanical stability, and spore dispersal (*D*).

Similar results, now combining THREE adaptive tasks in calculating fitness scores. Some of these pseudo-plants (cyber-plants?) are looking pretty realistic...

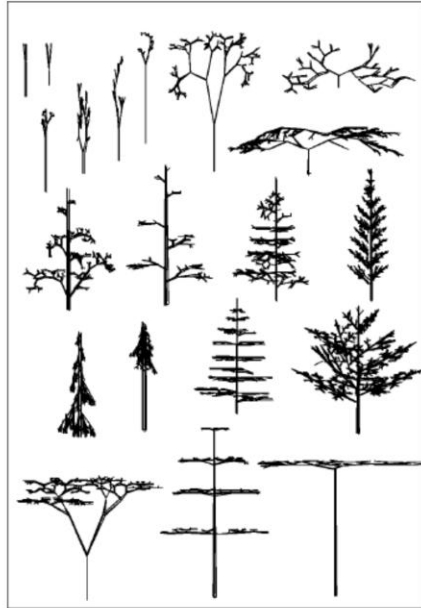
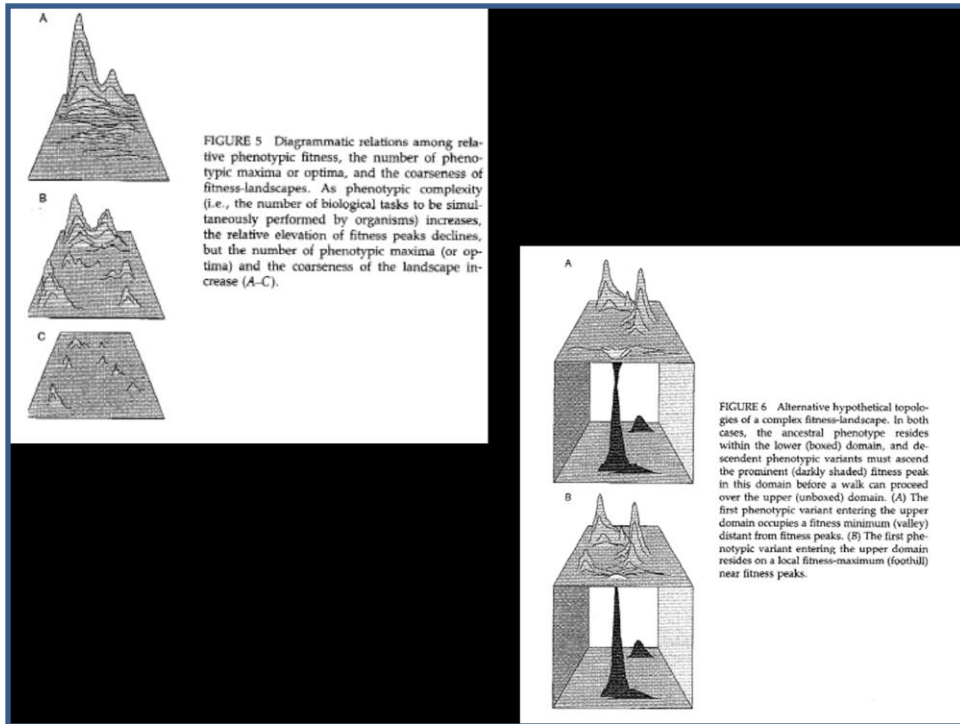
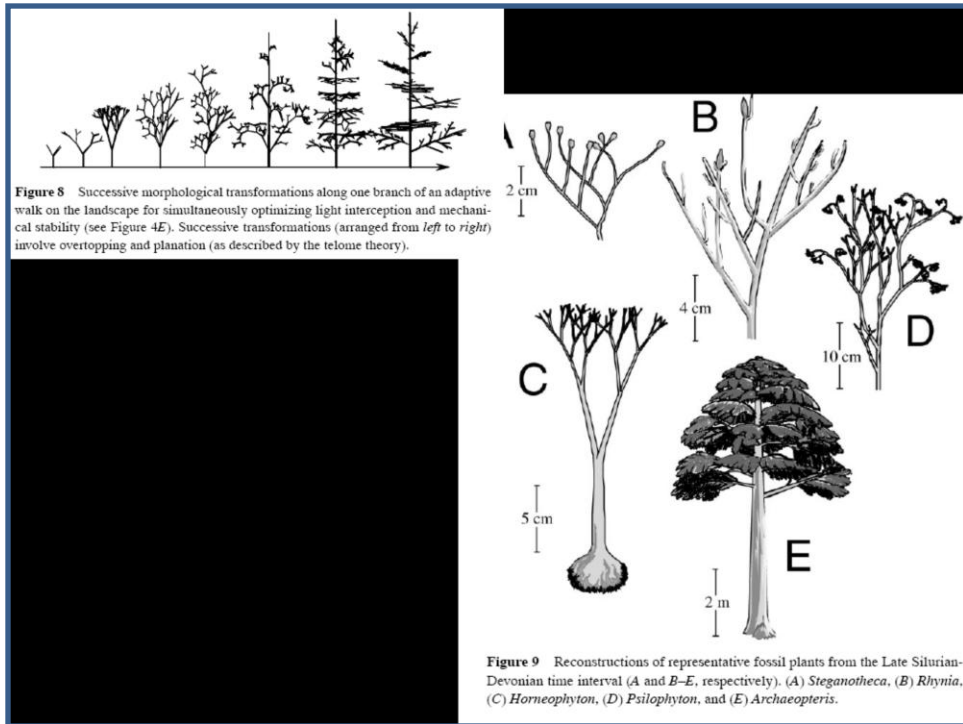


Figure 6 Phenotypes identified by adaptive walks on the 4-task landscape capable of optimizing mechanical stability, water conservation, light interception, and spore dispersal.

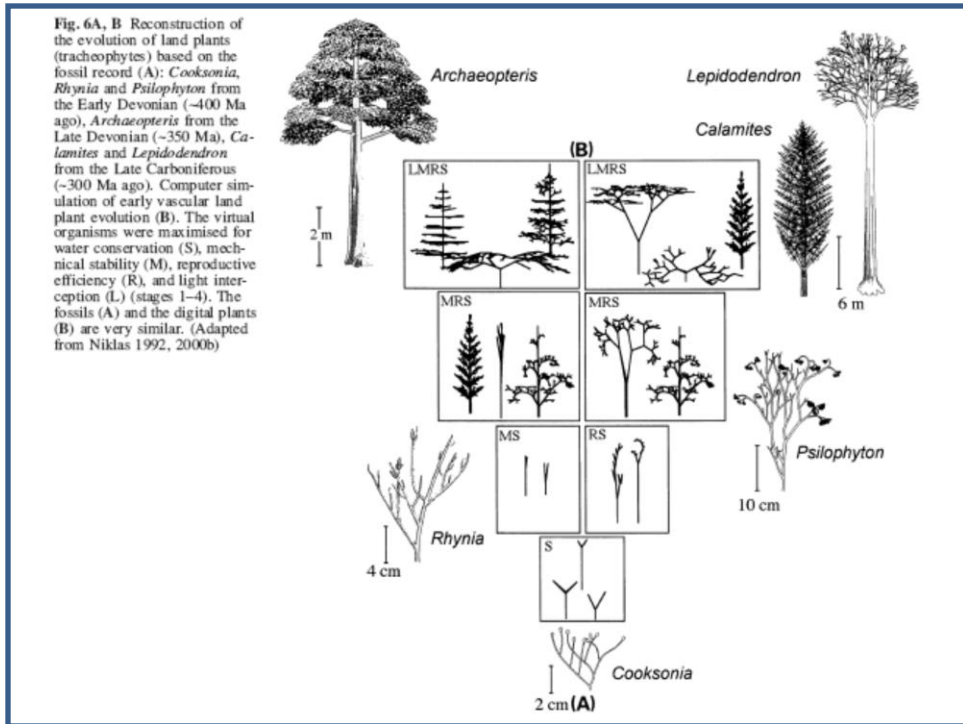
And, finally, combining all four adaptive tasks. Now there are quite a few 'local peaks' on the landscape – about 20 stable designs. Consider how this model successfully reproduces 'real-world' patterns and where it doesn't. What does all this mean? Does it say anything about why there are diverse types of trees? Why there's no single 'best-design' tree that out-competes all others? An important concept to consider is notion of TRADE-OFFS. Might doing one thing make you inherently *less effective at doing another*?



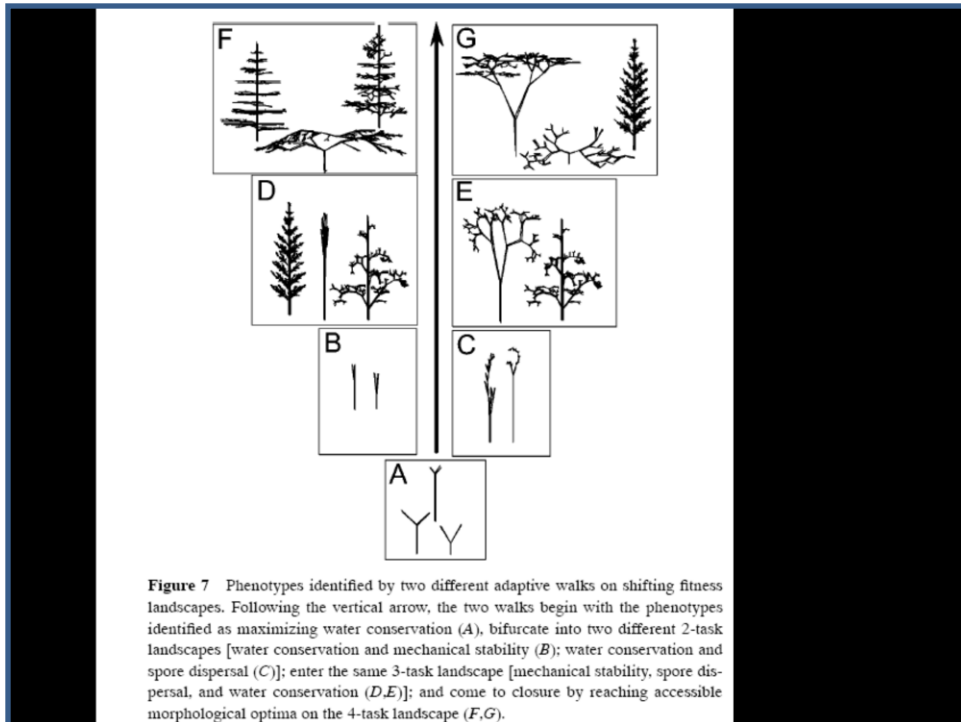
Left-hand figure shows some 2-D simplifications of possible ‘fitness landscapes’; think of the peaks as ‘local optima’ for adaptive design. Each peak is better – has higher fitness – than surrounding points. Some peaks are higher than others – but if a single ‘evolving’ population becomes isolated on one of the lower peaks, it may not be possible for it to ‘find’ the higher peaks through incremental/small-effect mutations – no small change will produce an individual of higher fitness. **Natural selection does not necessarily produce the best/optimal design**: THIS IS AN IMPORTANT POINT!



Here's an actual sequence of shapes (left) from one of Niklas's 'walks'. The right-hand figure shows some actual fossil plants.



Some more examples of plants reconstructed from fossil remains, compared with plants 'grown' by the computer simulation...



Finally (for now), Niklas explored the possibility of changing the rules during the game. What would happen if conditions changed part way through the simulation? This is simulated by changing the ‘weight’ – the relative importance – of the four adaptive ‘tasks’. While selection can only respond to what enhances fitness in the ‘here and now’, the available possibilities may be conditioned or constrained by the past.



Compare to some real trees





These are reconstructions of trees that were important in the Mesozoic; they belong to lineages that are now either extinct or exist only as small, herbaceous plants.



These are tree-ferns.

