What is coevolution? Coevolution is:
Evolution in two or more evolutionary entities brought about by reciprocal selective effects between the entities.

from Ehrlich and Raven (1964): "Butterflies and plants: a study in coevolution"

Examples we have already encountered:

Sex and recombination may have evolved because of:

- a coevolutionary arms race between organisms and their parasites

sexual selection:

- potentially a coevolutionary phenomenon between female choice and male secondary sexual traits.
- i.e. coevolution within a single species.

Here we deal with interspecific coevolution only.

Coevolution might occur in any interspecific interaction.

For example:

- Interspecific competition for food or space
  - Parasite/host interactions
  - Predator/Prey interactions
  - Symbiosis
  - Mutualisms

Mimicry, for example potentially coevolutionary, can be:

- parasite/host interaction (in Batesian mimicry)
- mutualism (Müllerian mimicry).

Batesian mimicry

- however, model finds it hard to escape its parasite.

So coevolutionary chase unlikely.

Müllerian mimicry

- the more abundant and noxious species trapped by its own pattern;
- the rarer or less noxious species gains by mimicking the more common or noxious species,

Thus: mutual convergence is unlikely.

Types of coevolution

"How likely is coevolution?"

- depends what you mean by “coevolution”!

Various types:

Specific coevolution = coevolution (narrow sense)

One species interacts closely with another
Changes in one species induce changes in the other
Either polygenic or gene_for_gene coevolution.

Concordant speciation or cospeciation

Speciation in one form causes speciation in another
Cospeciation doesn't necessarily require coevolution

Diffuse coevolution = guild coevolution

Groups of species interact in non-pairwise fashion
- e.g. Group of plant species may be fed on by a particular family of insects
- c.f. Ehrlich & Raven’s original idea

Escape_and_radiate coevolution

- evolutionary innovation enables adaptive radiation, i.e. speciation due to availability of ecological opportunity.

Concordant and non_concordant phylogenies

If the phylogenies are concordant (see overheads), this may imply:

- That cospeciation has occurred, or
- That one of the groups (often the parasite) has "colonized" the other (the host). Here, the host shifts may well correspond to phylogeny because closely related hosts are more similar.

In other cases, phylogenies may not be concordant, because the parasite may be able to switch between host lineages fairly frequently (see examples on overheads).

Host/parasite and predator/prey coevolution

Concordant phylogenies does not prove coevolution
We must look at individual adaptations of the exploiter and the exploited.

Examples:

Defences of plants against herbivores

- "Secondary chemistry"
  - e.g. tannins and other phenolic compounds, alkaloids like nicotine and THC, or cyanogenic glycosides
  - Often toxic
  
  Animals, such as insects, have obviously adapted to feeding on plants
  
  If plants have evolved defensive chemistry, ? plant/insect coevolution. Argument of Ehrlich & Raven

Critics argue that:

- phytophagous insects are usually rare, and therefore do not pose a threat to their host plants
- secondary chemistry may be a byproduct of normal metabolic processes, rather than necessarily defensive

Evidence for insect/plant coevolution

Central American plant "bullshorn Acacia"

- Large spines against mammalian herbivores
- Lacks cyanogenic glycosides.
- Thorns are particularly large, hollow, provide shelter to a species of Pseudomyrmex ant
- Plant also provides proteinaceous food bodies (Müllerian bodies) on the tips of the leaflets; ants eat
- Ants are nasty! Defend against caterpillars, even mammals and plant (vines) competitors.
- Plants not occupied by ants are heavily attacked.
Related *Acacia* species
- Lack hollow thorns, food bodies
- Have no specific associations with ants
- Many cyanogenic glycosides in their leaves
  - bullshorn *Acacia* has evolved a close, mutualistic association with the ants to protect from herbivores (and plant competitors).
  - cyanogenic glycosides that are found in other species have a defensive role; a role which has been taken over by *Pseudomyrmex*.

*Egg mimicry in Passiflora*
Defenses of cyanogenic glycosides, alkaloids breached by *Heliconius*

*Predator–prey coevolution*

*Predator offensive evolution*
e.g. Mammalian predators must be fast, strong, cunning

*Prey defence*
- Large size and strength
- Protective coverings such as shells or hard bony plates
- Defensive weapons, such as stings or horns
- Defensive coloration (see mimicry lecture)
- Unpalatability and nastiness
  - examples of coevolution

As we have seen, *mimics* may not coevolve with their *models*, but do coevolve with their *predators*

*Highly coevolved pollination systems*

*Yucca* and *Yucca* moths (*Tegeticula*)
Figs and figwasps
  - Larvae are seed/flower eaters
  - Plant is dependent on herbivore for pollination
  - Tightly coevolved mutualism

*Yucca* and *Yucca* moths
- Sometimes the mutualism has breaks down
- Moth reverts to a parasitism; does not pollinate.
  - In fig wasps, and most *Yucca* moths, these mutualisms have become very specific, and essential to both species.

Similar to ancient prokaryotic mutualisms:
Mitochondria & chloroplasts with archaeobacterial cells producing eukaryotes

*Coevolutionary competitive interactions and adaptive radiation*

“Gause’s principle”
If two species have identical resources
  - competitive exclusion
    - less well adapted species will go extinct

*Ecological release* (the reverse of Gause’s principle)
- A species colonizes area where no competitors
- May experience *ecological release*
- Grows to very large population sizes
- Disruptive selection to evolve apart
  - Adaptive radiation

Often on islands:
e.g. Darwin’s finches of the Galapagos islands
e.g. Hawaiian honeycreepers

Sometimes on “ecological islands”
e.g. lakes in the North temperate zone in last 10,000 years

*Sticklebacks (Gasterosteus) in Canada*
*benthic* (deep water) and *limnetic* (shallow water) forms keep to their own habitat, mate assortatively

*Trout family*
- Atlantic char (*Salvelinus*), Thingvallavatn, Iceland
- FOUR different trophic forms

*Cichlids in African Lakes*
- 300 spp. in the last 12,400 years in Lake Victoria
- Partly sexual selection, partly ecological divergence

*Adaptations leading to ecological release; “escape and radiate” coevolution*

*Possession of a unique adaptation*
may also allow adaptive radiation
  - Brian Farrell: herbivory on flowering plants
  - massive amounts of speciation (overhead).
  - Resin_ or latex_bearing canals in plants
  - Latex and resin is a physical defence against herbivorous insects.
  - more rapid speciation rate

*Conclusions*

*Coevolution*
An area where genetics, ecology, phylogeny interact
(A general theme we have stressed in this course!)

Majority of diversity of life and life forms
not just due to adaptation to static environments instead, due to *biotic* interactions

Biotic environment itself constantly evolving
  - orders of magnitude more diversity than by simple, static adaptations