

Next lecture: [speciation](#).

Today: (1) [nature of species](#)

(2) whether this indicates [speciation](#) differs from [microevolution](#).

- What are species?
- How do species differ from each other?
- How many species are there? We will briefly cover species-level [biodiversity](#).

Species "concepts" - What are species?

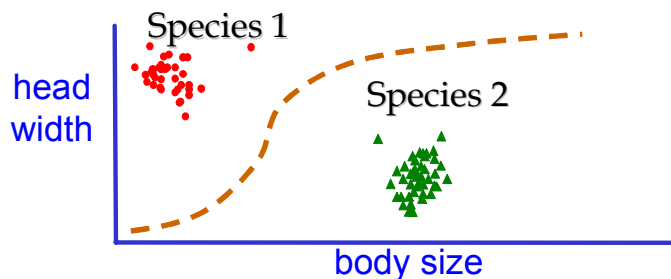
Darwin proved species evolved

But a difficulty:

Species weren't created kinds, with an essence. They gradually evolved from each other.

So where is the dividing line? A pragmatic solution:

Darwin's [view of species](#) -- species differ from races and morphs via gaps. e.g. *Primula* (primrose, oxslip, and cowslip), and human races.



Species concepts

Today: much debate, many "[species concepts](#)".

1) [Morphological species concept](#). Species delimited by gaps in morphology.

e.g. (i) Darwin: *Primula veris* (primrose) and *Primula elatior* (cowslip) are varieties of the same species -- many intermediates or hybrids are found. (ii) Similarly, races of humans: same species.

[In neither case is it easy to find a dividing line.](#)

In 1960s-1970s, [phenetic species concept](#). A multivariate statistical version of Darwin's ideas.

However some [problems with phenetic concept](#):

a) [Morphological gaps within species](#).

e.g. Peppery moth or *Papilio memnon* morphs.

b) [Lack of morphological differences between species](#):

There are often [sibling species](#) which are

(i) morphologically similar, though differ genetically.

(ii) evolve more or less separately

(iii) little or no hybridisation/gene flow:

- willow warbler & chiff-chaff: sing different songs
- *Drosophila* fruitflies: *D. pseudoobscura* and *D. persimilis* differ chromosomally
- *Anopheles* mosquitoes: differ in habitat, biting preference, and malaria-carrying

2) The biological species concept

Species defined by interbreeding (Poulton 1903, Dobzhansky 1937, Mayr 1942).

Gene flow within each species

no hybridization or gene flow between species

Lack of gene flow due to [isolating mechanisms](#)

(Not necessarily "[mechanisms](#)" in any sense, I prefer the term "[reproductive isolation](#)")

Types of reproductive isolation

A) [Pre-mating isolation](#) {or [pre-zygotic isolation](#)}

a) Ecological/seasonal isolation - mates do not meet

b) Behavioural isolation - meet but do not attempt mating

c) Mechanical isolation - attempts at mating do not work!

B) [Post-mating](#) {or [post-zygotic](#)} [isolation](#)

d) Gametic incompatibility - gametes die before fertilization (*note*: post-mating *but* pre-zygotic)

e) Hybrid inviability – hybrid zygotes have reduced fitness:

- genomic factors
- hybrids are not suited ecologically
- reduced mating propensity.

f) Hybrid sterility though may survive & mate as normal).

g) Sexual selection against hybrids.

[Problems with the biological species concept](#)

a) [Does not apply in allopatry](#). Species become less clear over large spans of space (in geography) or time (in the fossil record).

b) [Natural hybridisation/introgression](#) occurs.

10-12% of bird and butterfly species, 6% of mammal spp. hybridise naturally. (Hybrid fraction < 1/1000 in populations). [Introgression](#) common.

Examples: ducks, mammals e.g. blue whale x fin whale, the world's biggest animal, plants (> 20% of species).

Hybridization and introgression are [important topics](#) in conservation and agriculture.

3) [Ecological species concept](#)

Leigh Van Valen (1970s) species concept based on [ecological niche](#).

[Adaptive radiations](#): species evolve to occupy multiple ecological niches, especially on islands. Similar processes undoubtedly occur on the world's major mainlands as well. e.g. the radiation of mammals in the Tertiary (64 million years ago), after the demise of the dinosaurs.

[Problems](#)

a) [Sibling species](#) may have same niches. (Eventually: loss of one species via competition?)

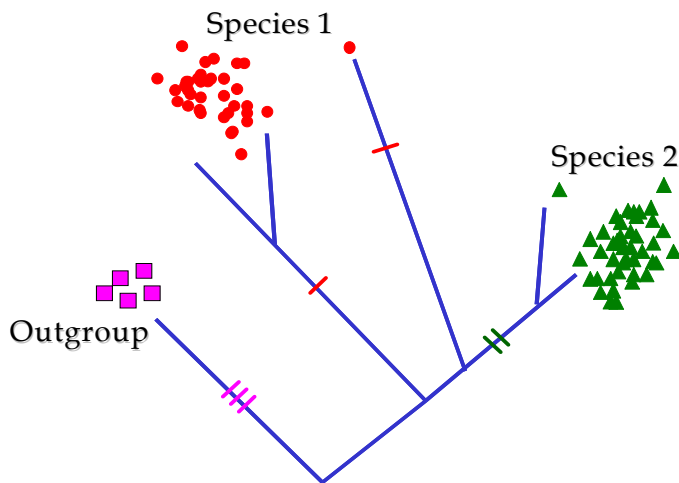
b) Ecological morphs within species. Adaptations often differ in different parts of a species' range (see [Evolution in space and time](#)).

The cichlid fish *Cichlasoma* from Cuatro Ciénegas, Mexico, has multiple morphs that do different things: bottom living mollusc-feeder: grinding teeth
pelagic piscivore: sharp teeth
algae/detritivore: rounded teeth

So hard to say ecology is *the* definition of species.

4) Cladistic and phylogenetic species concepts

Cladistic movement founded by Willi Hennig in the 1950s. If higher taxa are defined by means of phylogeny, then so should species, reasoned *cladists*.



Thus: **phylogenetic** (based on **monophyly**) and **diagnostic species concepts** (based on diagnostic characters, such as morphology or mtDNA bases).

Unfortunately, there are **Problems**:

- a) Apparent **phylogenies are hypotheses**, not necessarily real groups. For example, mtDNA may evolve differently from nuclear genes. So unstable definitions result.
- b) **Many isolated populations may be monophyletic**; but their evolution does not alter their mainland ancestor in any way. Cladistic concepts → many spp., only faintly recognizable.
- c) **Hybridization between branches of a phylogeny**. A phylogeny is really a mass of "**genealogies**" at different loci. So is average phylogeny (sometimes called a "**consensus**" phylogeny) the "true" species phylogeny? Not exactly!
Many alternative **evolutionary** and **phylogenetic** species concepts which attempt to answer these problems. None are (yet) clearly accepted.

5) Rank-free taxonomy, and giving up on species altogether! Do away with species altogether? But then how would we communicate about groups of organisms. My own view: species will remain a convenient naming device to classify animals and plants. There must be a certain validity to species, or bird or plant guides wouldn't be very useful. But we shouldn't take the "reality" of species too seriously.

Why are there so many species concepts?

What should practising evolutionary geneticists like you do, faced with such a diversity of opinion? Evolutionary biologists, often think **biological species concept** is best.

Many taxonomists and systematists prefer some form of **phylogenetic species concept**

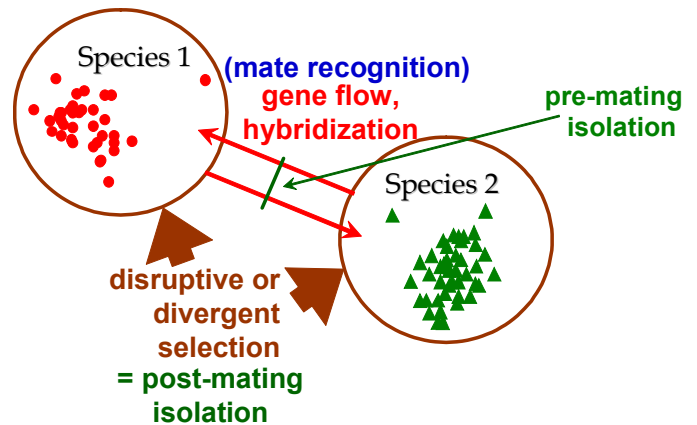
Ecologists often use the **ecological species concept**.

People are partisan to their own expertise!

Which do you prefer?

Genetics and the definition of species

Let's update Darwin's view of species with Mendelian genetics ideas of gene flow (which Darwin did not have).



Species are genetically differentiated populations potentially connected by gene flow. Gene flow may be very low (as in the **biological species concept**), or in geographic isolation. Or: if much gene flow; collapse to a single species.

Species are then clusters of genotypes with discontinuities or gaps separating them. Gene flow (weak **pre-mating isolation**) might break down genetic differences. Therefore: Gene flow, if it exists, must be balanced by disruptive selection -- intrinsic (**post-mating isolating mechanisms**) or extrinsic (as in **ecological concept**). Biological and ecological species concepts are **explanations** of the existence of distinct groups. Species become more phylogenetically "real" (monophyletic) as they emerge from cross-linking caused by hybridization. (But never absolute?).

Genetic differences between species

Studying actual data more fruitful than philosophy. Species differ in ways similar to different races or geographic populations (see previous lecture), only more. Some of the ways in which species differ:

a) **Morphological differences** (Darwin's definition, above). Morphology differs between races and populations as well; as already mentioned.

b) **Genome-level differences**. Francisco Ayala's surveys with enzyme loci on *Drosophila*. Differences: species > sibling species > races.

c) **Chromosomal differences**. For example: humans and chimpanzees (see Chromosomal Evolution) common in many spp.

Again many subspecies and races also differ chromosomally, only somewhat less.

Polyploidy is an exception to gradual differences. Common feature of plant species differences. offspring of diploid (2N) x tetraploid (4N) crosses are triploids (3N), usually completely sterile.

d) **Signals used in mating**. Sexually-selected colours, tail length in birds, pheromones in moths, other insects, and even mammals are all involved in species recognition as well.

Crickets and grasshoppers, as well as frogs, species-specific sounds are required; fireflies, recognize each other by means of coded flashes.

Again, these differences easily derived from mate choice differences within species.

e) Hybrid inviability and sterility - genomic

incompatibility. Mules (donkey x horse hybrids, which are sterile); chromosomal heterozygotes.

However, other species seem to have no hybrid problems: Darwin's finches, ducks

Once again, species differ from races only in degree of hybrid inviability and sterility, not in kind.

Hybrid breakdown: F1 hybrid between two species may be alright, but backcrosses or F2 crosses produce inviability or sterility. Caused by recessive epistatic genes becoming homozygous during these crosses. Genes causing incompatibility must be **epistatic**; can you see why?

Special case of hybrid inviability/sterility: **Haldane's Rule**: "When one sex of F1 hybrid between species is inviable or sterile, that sex is usually the *heterogametic* sex," rather than the *homogametic* sex. Works in mammals, *Drosophila* ($XY\sigma^{\circ}$, $XX^{\circ}\tau$), also in birds, butterflies ($ZZ\sigma^{\circ}$, $WZ^{\circ}\tau$). Probably due to recessive effects of genes causing incompatibility on the X.

f) **Genealogical differences.** Humans and chimps mutually monophyletic at many loci, but not MHC. *Heliconius cydno* and *H. melpomene*:

g) Ecological differences.

For example: **adaptive radiations** on islands. Darwin's finches are well-known.

Hawaiian honeycreepers are even more extraordinary. Finch-like ancestors → nectarivores, insectivores, frugivores, + seed-eating forms.

But once again: no clear dividing line between races and species in the degree of ecological differentiation (see **ecological species concept**).

Genetic differences between species

- multiple loci
- species more different than geographic races
- but not qualitatively more different

Most *parsimonious* (simplest) explanation: usual microevolutionary forces - selection, drift, mutation - explain speciation.

Biodiversity

The sum total of diversity at all levels of the evolutionary hierarchy

- genetic diversity within populations
- genetic diversity between populations & races
- diversity of species
- ... of genera
- ... of ecosystems, biomes etc.

The species traditionally viewed as most important. see E.O. Wilson's *The diversity of life* (1992)

Species diversity

Most of diversity is not mammalian, or even vertebrate.

Beetles make up 20% of all described species!

Insects in general: 53% of described species.

Total described species	1,413,000
Animals	1,032,000
Insects	751,000
Beetles	290,000
Plants and fungi	350,000

Bias of using described species

1) **Entomologists** (Terry Erwin and others):

- Fogged canopies of South American tree species
- Counted unidentified, host-specific beetles
- Calculated may be as much as a 30x more species than currently described.
- 30,000,000 is their estimate.

2) **Bacteriologists**:

- Prokaryotic world is far more diverse DNA
- Maybe more diverse in "species"
- Mostly not discovered (e.g. recent discoveries of "extremophiles" in deep sea vents, in granite)

Genetic diversity (and metabolic diversity) therefore gives a different view to species diversity: most of the genetic diversity is in the prokaryotes.

FURTHER READING

FUTUYMA, DJ 2005. Evolutionary Biology. Chapter 15 (pp. 353-378). Species.

FREEMAN & HERRON 2001. Chapter 12 (or equivalent in 2004 edition)

WILSON, EO 1992. The diversity of life.

Next time: how does all this diversity evolve? The study of speciation.