Topics in philosophy of biology: species

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Plan

1. The nature of species
   - The reality and origin of species
   - Three families of species concepts
2. Applying the species concept
   - The tree of life and systematics
   - Species selection

Species realism vs antirealism

Kim Sterelny and Paul E Griffiths (1999). *Sex and Death: An Introduction to the Philosophy of Biology*. Chicago: University of Chicago Press.

Question

Are biological species a result of the way we humans conceptualise and structure the world (antirealism) or are they an objective feature of the world as it exists largely independently of us (realism)?

Sterelny and Griffiths (1999, 182)—short SG 182:

> *In our view, evolutionary theory lends no support to the idea that our species classifications do not reflect objective features of the living world. The division of organisms into species is an objective feature of the living world.*

Species do explandatory work

- Species have important role in biology as ‘score-keeping devices’, i.e., as “indices of the effects of evolutionary and ecological processes” (Sterelny and Griffiths 1999, 183)

Example: species-area effect

- species-area effect: the biodiversity of a region is linked to its area in that diversity falls disproportionately with decreasing area

$\Rightarrow$ two small national parks contain less biodiversity than large park of the same total size

- biodiversity of a region = number of species present in the region
- If species are just projections of our own limitations, this (controversial) effect would not have objective implications.

The received view of the origin of species

Thesis (The received view of the origin of species)

"New species originate when isolated fragments of a population differentiate from the paternal population as a result of selection and chance." (SG 183)

Limitations of the received view:

- does not explain patterns in species formulation:
    - the frequency of speciation or the number of species
    - the phylogenetic structure (why are there so many beetles, yet few horseshoe crabs)
- fits some organisms better than others
- does not entail a species concept—there may be different concepts in the kingdoms of plants, animals, bacteria, etc
- may understate the evolutionary importance of species (species are merely seen as a result of evolution, does not account for crucial link between speciation and adaptive shifts); in fact, species themselves may be units of selection

Sterelny and Griffiths on species

1. identification of species: what are species?
2. What is the place of species in the overall tree of life?
3. Does selection also operate at the level of species (rather than just of individuals)?

A threat to objectivity: temporality of species

- If we accept evolutionary gradualism, then (phenotypic) changes along evolutionary paths are smooth and almost continuous.
- This seems to imply, for example, that there is no fundamental difference between Homo erectus and Homo sapiens: had we discovered members of a H. erectus alive on a remote islands, we would have considered a distinct species—but is this justified for ancestors linked by continuous changes?
- Future hominids may consider us just as an intermediate gradation between Homo future sapiens and Homo past erectus.

$\Rightarrow$ Unless phenotypic change proceeds by 'saltations' (= large jumps), then species are not objectively identifiable over time.

- Furthermore, saltations are extremely rare, as large mutations almost never lead to viable organisms.

$\Rightarrow$ Gradualism seems to lead to a temporality of species which undermines their objective standing.

Not so fast: species defined at the level of populations

- This implication does not hold: even if phenotypic change between generations is small, there may be rapid change at the level of populations: species can go extinct suddenly, change their genetic diversity, change their range, or their role in the ecosystem.
- For instance, such change may be caused by geographic changes (from volcano eruptions to changing courses of rivers), the new presence of a predator or an epidemic (from sabre tooth tigers to viruses; Ex: Australian rabbits after the myxomatosis epidemic), etc.

SG 181:

So if populations are species by virtue of population-level properties, speciation need not be smooth, gradual, and seamless.

- The important biological species concept (more on this in a moment) identifies species by reproductively isolated populations, so a potentially quickly acquired population-level property.

Further evidence: punctuated equilibrium

Thesis (Punctuated equilibrium)

"[T]he typical life of a species involves a relatively sudden appearance followed by a comparatively long period of stasis, terminated either by extinction or by splitting into daughter species." (SG 182)

- If this is right (it is controversial), then species emerge relatively rapidly over geologically short periods upon divisions of lineages (and not upon the transformation of an entire lineage).

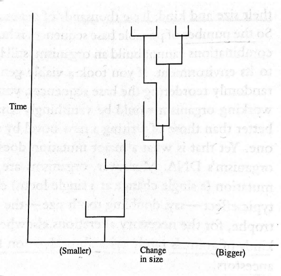
⇒ A species can be identified as it involves relatively well-defined origins and terminations.

- The punctuated equilibrium is also an example of a population-level property.

Cope's rule

SG 182:

Figure 9.1 An example of punctuated equilibrium. Cope's rule is a rule of thumb stating that descendant species tend to be larger than the founding species of a lineage. In the evolutionary history depicted here, we have an instance of Cope's rule: the surviving species are all larger than their common ancestor. Yet individual species phenotypes do not change over time, even though there has been phenotypic change in the species lineage as a whole. For once speciation takes place, the members of daughter species have phenotypes distinct from those of the parent species. In this case, differential species survival shifts the phenotype to the right of the graph.



(1) Phenetic species concepts

Position (Phenetic conception of species)

A species is defined in terms of an overall morphological, genetic, or behavioural similarity as given by some measure of similarity. Species are groups of similar organisms. Phylogenetic relationships are not relevant.

- This conception has "slid from favor" (SG 184).
- A main reason is the difficulty to find an objective measure of similarity, which is necessary to maintain a realist stance on species but nearly impossible to get.
- Even if we did have such a measure, individuals of same species may be very different: females vs males vs juveniles; polytypic species, whose members vary strikingly.
- Box 9.1 in SG: what is genetic similarity?

(2) Biological species concepts

SG 186

> *All the alternatives to phenetic definitions accept some version of the proposal [...] that particular species are defined by their history. No intrinsic genotypic of phenotypic property is essential to being a member of a species [...] the essential properties that make a particular organism a platypus, for example, are historical or relational. An animal is a platypus by virtue of its place in a pattern of ancestry and descent (its phylogeny). But to say that species are historical kinds is one thing; to say just which historical kinds is another. [...] Phylogeny is the correct grouping criterion for organisms, but it does not provide any obvious ranking criteria to determine which groups are species.*

Position (Biological conception of species)

A species is defined by reproductive isolation, meaning that a species is a group of individuals in which genes can flow freely.

- received species concept
- Species are defined by processes that create and sustain species, here reproductive processes.

(2) Biological species concepts: advantage

- By taking reproductive community to be central, it provides evolutionary units for adaptation and speciation, which both require some isolating mechanism for small populations to preserve evolutionary advantages.

Example: Adaptation to '1080' (poison) of population of New Zealand rabbits

- This adaptation can spread through isolated population.
- But this adaptive shift is lost if they interbreed with members of the nonimmune parent population.

⇒ Until reproductive isolation has been established, adaptive changes remain fragile.

⇒ Biological species concepts identify a grouping of populations that can evolve distinctively and so play an important role in evolution.

Note

On this view, species are real evolutionary units, in contrast to higher taxa (genus, family, etc), which are merely convenient groupings of species.

(2) Biological species concepts: problems

1. There is no good, or obvious way to segment a lineage over time.

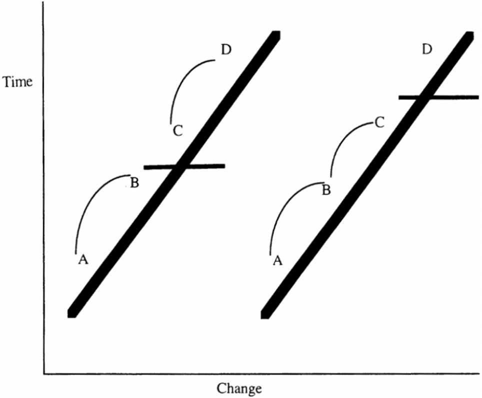


Figure 9.2 Tracking species over time. If we attempt to apply the interbreeding criterion over time, we lose the objectivity of our species distinctions. The left bar shows the species distinctions we might make if we choose A as our baseline individual, and hence define a species by including all and only A's potential mates. A would recognize B as a potential mate, but gradual change in the traits through which mates recognize one another means that C would have changed beyond A's recognition threshold. So the lineage is divided into two species, one including both A and B; the other, C and D. On the right, we see the species distinctions consequent on choosing B to be our baseline individual and defining as a species all and only B's potential mates. B would recognize both A and C as potential mates, since both are similar enough—about equally similar—to B. But D is beyond B's recognition threshold. So we get two species, one of which has A, B and C as members, and the other with D as a member.

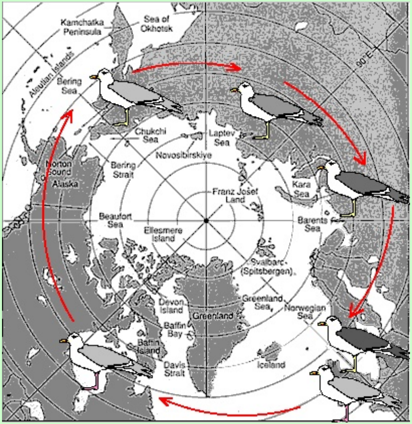
⇒ interbreeding criterion cannot be applied to organisms at different times

⇒ supplementation by speciation criterion needed

(2) Biological species concepts: problems

2. It is hard to distinguish real from pseudo-divisions of a lineage (the Queen's corgis are not a separate species).

Example: ring species, such as black-backed gulls



- ring species: chains of populations where each link can breed with its neighbour, but populations separated by several links cannot even if they come into contact

(2) Biological species concepts: problems

3. Lineages can be genuinely separate despite some gene flow across the boundary.

Example: mallard ducks and Pacific grey ducks

Are cases such as the mallard ducks introduced to Australia and New Zealand, which freely hybridize with native Pacific grey duck instances of a single species (since they interbreed) or not (since it was only through accidental human intervention that there separate evolutionary tracks meshed)?

SG 189

> *There is no objective count of protected gene pools. Gene flow really does come in degrees.*

(2) Biological species concepts: problems

4. These may all be signs of a deeper problem: the biological species concepts fits multicellular organisms much better than other forms of life.

Examples

- Lineage crossing is common among plants, and so gene flow across species boundaries easier.
- In many single-celled organisms, gene exchange is not connected to reproduction and happens across species boundaries (e.g. in bacteria).
- Asexual organisms escape the biological species concept altogether.

SG 190

Phyologeny, shared environment, and exposure to a common selective regime must all be part of the cohesiveness of a species.

(3) Phylogenetic species concepts

Position (Phylogenetic conception of species)

A species is identified through patterns in evolutionary history rather than through causal processes that generate those patterns (such as reproductive isolation). Specifically, phyolgenetic species concepts identify a species with a segment of a phylogenetic tree between two speciation events (or between speciation and extinction).

⇒ relies on concept of speciation event, and may so depend on the biological species concept (which delivers a causal process for speciation), inheriting its problems (such as that of asexually reproducing organisms)

- There are different proposals for solving the problem of identifying dividing lineages: cohesion species concept, ecological species concept

(3) Phylogenetic species concepts

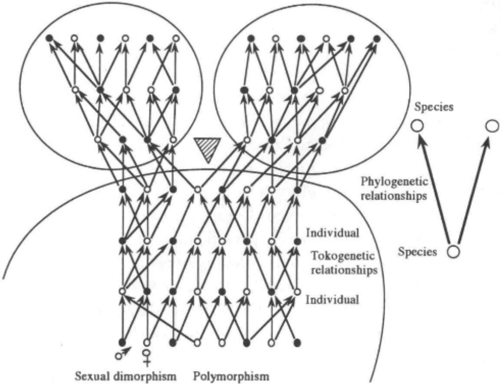


Figure 9.4 Phylogenetic species concepts base relationships between species, the *phylogenetic* relationships shown on the right of the diagram, on the actual family relationships between individual organisms, as shown on the left of the diagram. Here we see seven generations of sexual reproduction. During this period the descendants of the initial generation become separated into two streams that no longer interbreed with each other. If it becomes permanent, this splitting of the lineage into two parts will have been a speciation event. The single *stem species* will have been replaced by two *daughter species*. Cladists have yet another neologism for the individual relationships between one organism and another: *tokogenetic relationships*. (Adapted from Hennig 1966.)

Supplementing the phylogenetic species concepts

Position (Cohesion species concepts)

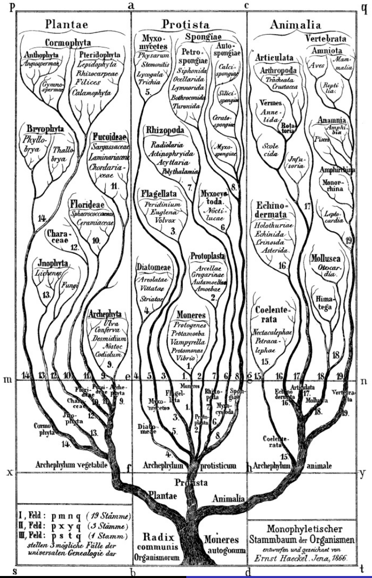
Cohesion species concepts generalize the biological species concept by recognizing that gene flow is not the only factor that holds one population together and makes it recognizably different from others, and by including ecological or demographic factors.

Position (Ecological species concepts)

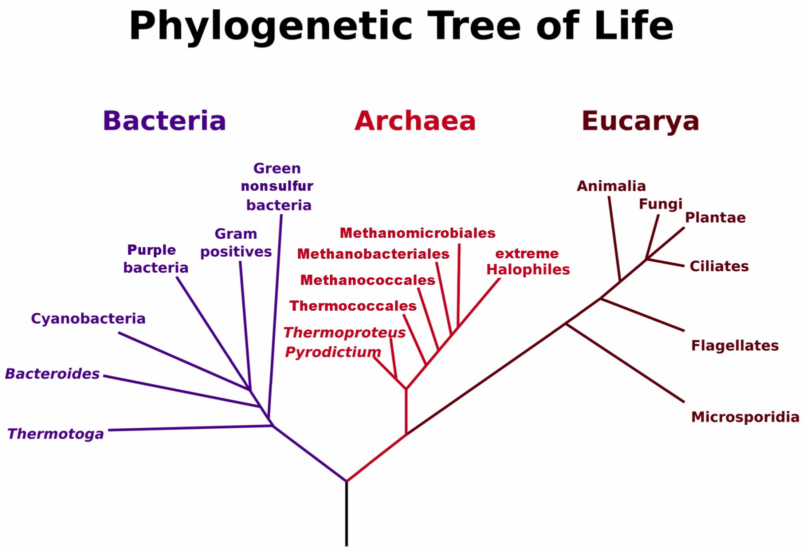
"Ecological species concepts define species by appealing to the fact that members of a species are in competition with one another, since they need the same resources. A species is a group of organisms whose members share an adaptive niche and can replace one another's descendants if they find more efficient ways to occupy that niche. Species are ecologically isolated by their distinctive niches." (SG 193)

The tree of life

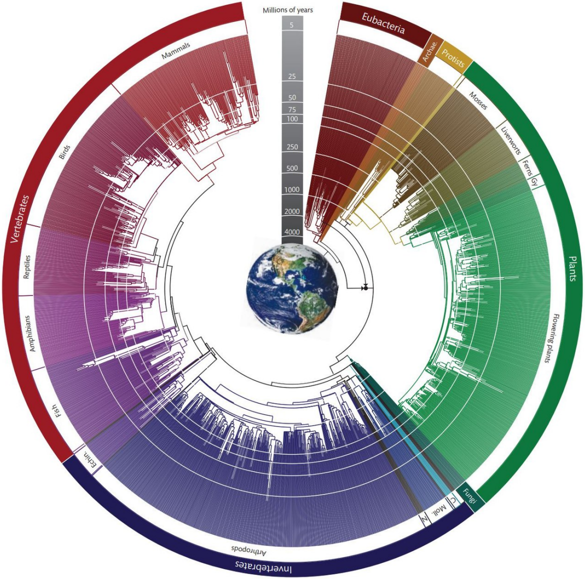
Ernst Haeckel, *Generelle Morphologie der Organismen* (1866)



The tree of life now

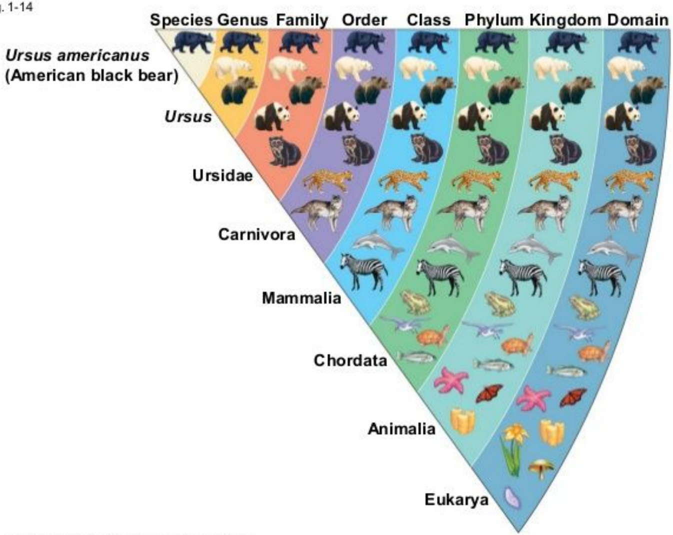


The tree of life now



The bigger picture: systematics
The strict nesting of the taxonomic ranks

Fig. 1-14



The cladistic conception of systematics

The emerging cladistic conception of systematics has resulted from a controversy attempting to have biological classification respect three different goals at once:

1. Information storage: it should maximally efficiently store information about the organism, allowing us to recover a rich array of typical features (this is demanded by a movement called ‘phenetics’ or ‘numerical taxonomy’)
2. Disparity capturing: it should reflect the biological disparity of organisms and the extent of their evolutionary change compared to others (demanded by ‘evolutionary taxonomy’, who do not recognize birds as dinosaurs)
3. Cladistic structure: it should describe the branching (and fusing) pattern through which the tree of life has grown, resulting in the phylogenetic systematics (AKA cladistics, from clade = ‘branch’) which views systematics as history

These goals generally make inconsistent recommendations:

E.g. two evolutionary lineages which the same number of species but in one of which species are very similar whereas in the other they diverge significantly will likely be treated very differently by both evolutionary as well as phenetic taxonomy, but may be treated the same by cladistics if the branching structure is the same.

⇒ We need to make a selection, which is in general in favour of cladistics.

Problems with the phenetic conception

- The information-storage conception relies on a notion of similarity across groups of organisms, but similarity depends on which traits one considers (ex: pigs and oysters are both forbidden food to orthodox Jews, neither has ten legs, and neither eats spiders exclusively).
- This conception is supposed to be independent of theory, particularly of evolutionary theory, but "phenetic taxonomy needs a theoretically principled way of deciding what to measure" (SG 196).

⇒ not clear we can have a well-defined notion of biological similarity

Problems with the evolutionary conception

- The idea of disparity so central to evolutionary taxonomy rests on little more than educated guesses on the part of the biologists.

⇒ not very scientific

The cladistic conception in detail

- Lineage branching is objective (though not always straightforwardly determined), history has an objective structure.

⇒ There are objective facts about who is more closely related to whom, i.e., who shares a more recent common ancestor.

- Cladistics combines three central ideas:
  1. Systematics discovers and represents evolutionary history.
  2. The only 'real' groups in nature are monophyletic groups, i.e., species groups that consist of a species and all, and only, its descendants.

Example: reptiles

- Reptiles are not such a group, since there is no species that is ancestral to all reptiles that is not also an ancestor of the birds.

⇒ Contemporary cladistic systems either redefine *Reptilia* as a clade (i.e,, monophyletic group) to include birds, or else introduce the larger clade *Sauropsida*, which includes all amniotes more closely related to reptiles than to mammals.

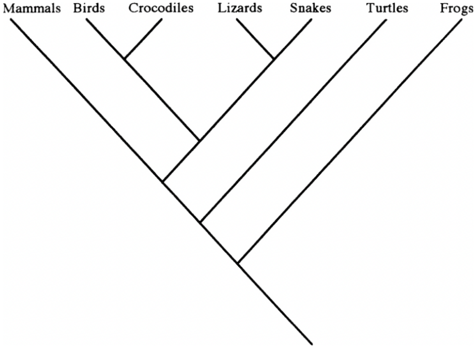
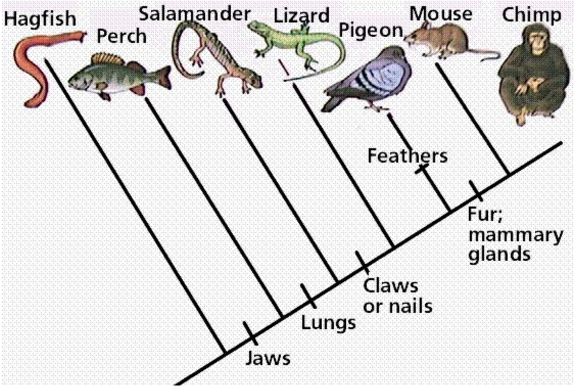


Figure 9.5 A cladogram. If the history of descent represented here is correct, then the group birds/crocodiles/lizards/snakes is a natural group.It is *monophyletic*—that is, it consists of all, and only, the descendants of a particular ancestral species. In contrast, the snake/lizard/crocodile group is not a natural group. It is *paraphyletic*, since it contains only the descendants of a single ancestral species, but does not contain all of them; birds are left out. A group containing only birds and mammals would be even less natural. It would be a *polyphyletic group*, one containing species with no recent common ancestor. Cladists argue that only monophyletic groups are real.

The cladogram

Definition (Cladogram)

A cladogram is a branching diagram that groups taxa by shared descent. The branches are referred to as 'clades', where each clade shares common traits not shared with other clades.



The cladistic conception in detail

3. There is a detailed methodology for identifying cladistic relations.

Without going too much into the details or being exhaustive, some examples:

- Unique traits are uninformative: a trait that only the platypus bears tells us nothing about its relation to others.
- Primitive traits are irrelevant: traits shared by all mammals are silent on their relationships.
- Only derived traits, i.e., traits varying within the group, are informative: platypus's egg laying, electrolocation place it with the two echidnas.

Definition (Sister species)

Sister species are most closely related species such that they share an ancestor that is ancestor to no other species.

Cladistics: methodology

- How to determine whether two species are sister species, how closely they are related, etc? Use derived traits!
- If species A and B alone share a derived trait, they are sister species.
- If A, B, and C share a derived trait and D does not, then they are more closely related to one another than to D.
- Etc.
- Difficulty: pseudo-present (i.e., evolved independently) and pseudo-absent (i.e, lost) traits
- parsimony analysis: method of reconstructing evolutionary history based on overall parsimony

Example: are bats mammals or aves (birds)?

The most parsimonious hypothesis, i.e., the one requires the fewest possible evolutionary changes, groups bats as mammals, not as birds.

Parsimony analysis

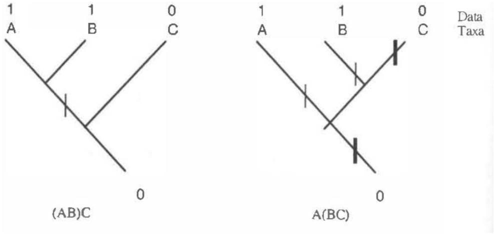


Figure 9.6 Resolving a phylogenetic tree by parsimony analysis. Under consideration are two hypotheses about the relationships among three taxa. One hypothesis groups A and B together: (AB)/C. The other groups B and C together: A/(BC). The primitive state of the character of interest (ascertained independently) is represented as 0, and the derived state as 1. How do these two hypotheses compare as explanations of the character's distribution? The left-hand tree, representing the first hypothesis, is more parsimonious, as it requires only one change to explain the current distribution of the trait. The right-hand tree, and the second hypothesis, requires one or the other of two pairs of changes. The first possibility (heavy bars) is that 0 changed to 1 before the divergence of A, B, and C, and then changed back to O after C had diverged from B. The other possibility (light bars) is that 0 changed to 1 twice, first in the lineage leading to A after the (BC) lineage had diverged, and again in the lineage leading to B after this had diverged from C. (Redrawn from Sober 1988b, 246.)

Systematics: in sum

- Although overall more convincing, cladistics comes at the price that the traditional taxonomic hierarchy (species, genus, family, etc) makes little sense: when to call a monophyletic group a genus or family or order etc is not well defined.
- To repeat: only monophyletic groups are well defined.
- However, scepticism regarding the traditional taxonomic hierarchy has long existed.
- Reminder:

Definition (Monophyletic group)

A monophyletic group is a group of taxa consisting of a species and all, and only, its descendants.

Species selection

- Evolutionary trends operate at the level of single species (red kangaroos shrinking in size), intermediate trends in lineages (teeth size and toes in horse lineage, brain size in homo lineage), all the way to mega-trends involving thousands of species (defensive structures in shelled marine vertebrates).

What mechanism might explain evolutionary trends such as these?

- Some trends are 'passive', a result of statistical artefacts (such as the growth of horses, which went near extinct, and the survivors just happened to be larger). These need no further explanation.
- What explains 'driven' trends?

Two potential explanations of evolutionary trends

1. Similar response: the trend might have arisen as a result of a correlated evolutionary change within a cluster of species which each responds in similar ways to the same evolutionary challenge (Ex: leave change in many Australian plants as response to hotter and drier climate).
2. Punctuated equilibrium (see slide 9-10): evolutionary trends might be produced by differential generation and extinction of species (Ex: Australian acacias becoming more fireproof because climatic conditions 'punctuate' equilibrium and force speciation and extinction events).

Species selection vs species sorting

Elizabeth Vrba makes an important distinction:

1. species selection: differential success of species by virtue of features of the species themselves
2. species sorting: differential success of species by virtue of features of their member organisms

Example: New Zealand kakapo (endangered flightless nocturnal parrot)

- May go extinct as a result of "countless, sadly one-sided" interactions with stoats, an introduced predator species.
- Enough bad news for individuals in a population amounts to bad news for the population...

$\Rightarrow$ extinction may be result of 'species sorting'

Necessary conditions for species selection

Species selection requires...

1. "an account of the distinction between a species trait and the traits of its component organisms;"
2. "a demonstration that species traits are causally salient;"
3. "a case for thinking that species properties can be built or maintained by some type of feedback process, so that species traits result from cumulative selection." (SG 204)

- Let's look at some examples...

Example of species trait (condition 1)

- common European cuckoo: a generalist nest parasite
- Individual cuckoos often specialize on particular hosts, but the species as a whole attacks a wide range of hosts and so is generalist.

⇒ property of being a generalist is a species trait, not a property of its members

Example of causally salient species trait (condition 2)

- If a population is small and dispersed, survivors may find it hard to find mates. If a population is small and concentrated, it is vulnerable to local catastrophes.

⇒ The size and concentration of a population may be population-level properties which are causally salient for its survival.

- But: these properties are generally not heritable enough from one species to another for it to underwrite cumulative selection on a lineage.

Candidate for inherited species trait: species distribution (condition 3)

- Bat lineage is geographically and ecologically widespread.
- Distribution (or range) is causally salient for survival of species, and may be heritable: surviving mass extinction event may lead to daughter species becoming even more widespread.

Condition (3): the evolution of sex

SG 206f

> *Sex is a puzzle for evolutionary theory, for it is expensive, both for individual organisms and the genes they replicate. Sex has obvious costs: the cost of sexual ornamentation and the time, trouble, and danger involved in finding a partner. It also has a more subtle, but more pervasive cost. Imagine an isolated stream that is home to ten platypuses... Asexual reproduction increases the number of tickets in the survival lottery without increasing the number of winners. But it reserves the extra tickets for the asexuals. So unless their tickets are much worse, asexuality should sweep through the population.*

- ⇒ There is a very serious cost to sex, yet it is prevalent among multicellular organisms.
- ⇒ What is the evolutionary explanation of sex?

The benefits of sexual reproduction

Muller's ratchet

Asexuality is selected against in the sufficiently long run because of the accumulation of irreversible disadvantageous mutations.

- Since random mutations are generally deleterious, an asexually reproducing population will increase its 'genetic load' of mutations over time.
- A sexually reproducing species can avoid Muller's ratchet.
- Moreover, they may respond to environmental change by maintaining (or increasing) its fitness through gene flow and its ability to recombine its genetic material.

⇒ It is possible that sexual reproduction is maintained by species selection. (But see SG 208-210 for challenges.)

- Sex may be just one instance of phylogenetic plasticity, i.e., the capacity of a lineage to change over evolutionary time.