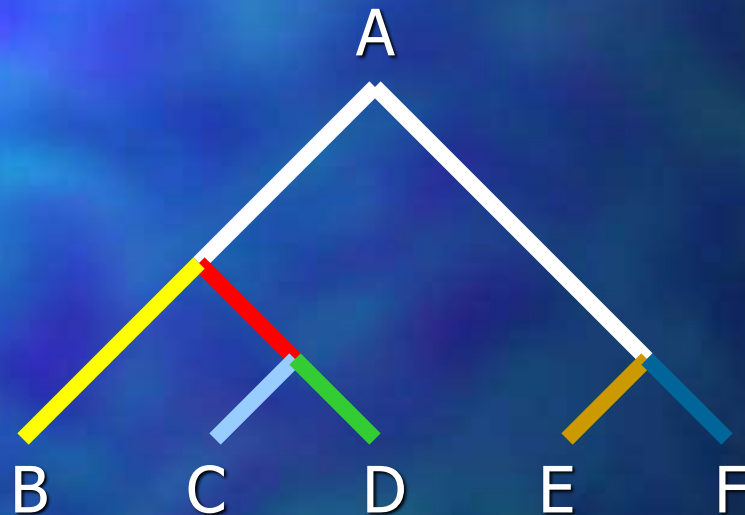


Species Concepts

SPECIATION

- **Speciation**, or the origin of new species, is central to macroevolution since all higher taxa originate with a new species which is novel enough to be the first member
- Fossil record provides evidence for two patterns of speciation:
 - ✦ **Anagenesis (phyletic evolution)** – transformation of an unbranched lineage of organisms to a different state (the new species)
 - ✦ **Cladogenesis (branching evolution)** – budding of one or more species from a parent species that continues to exist

Anagenesis and cladogenesis



What is a species?



- **Species** = Latin for “kind” or “appearance”
- **Linnaeus** described species in terms of their morphology
- Modern taxonomists also consider **genetic makeup and functional and behavioural** differences when describing species

How many species currently exist?

- 1. Many groups are **poorly studied**.
 - notably microorganisms and parasites.



- 2. Many environments are **poorly sampled**.
 - tropical environments - both terrestrial and aquatic



- 3. Molecular approaches are identifying more and more **“cryptic species”**.
 - a cryptic species is indistinguishable from another species at the morphological level, but is distinguishable genetically.

Morphospecies Concept (Typological species concept)

- (TSC, Linnaeus) Plato, Aristotle,
- Species are groups of individuals that are **morphologically similar** and clearly distinguishable from individuals of other groups
- Species had traditionally been defined by reference to a morphological type
- Usually any **geographic variation among members of the group was not detected** or simply ignored



-
- observed diversity consists of a **limited number** of "universals" or types
 - species consist of **similar individuals** sharing the same essence
 - -each species is separated from all others by a **sharp discontinuity**
 - -each is **constant** through time

Problems with the TSC

- It became apparent that what appeared to be distinct morphological species at the **local level** were merely one in a series of morphologically intergrading populations on a broader geographic scale



- 1. Individuals of the same species can be **very different on the basis** of sexual dimorphism, age differences, polymorphisms, and other forms of variation.

- 2. **Geographic variation** among populations

- 3. **Sibling or cryptic species**

sibling species are **reproductively isolated** groups that are **morphologically indistinguishable**.

Nominalistic Species Concept

- This concept denies the existence of "real" universals.- Only individual organisms exist and species are **man-made abstractions**.
- -Thus, we have only names that apply to similar type things.
- -Popular in the 18th century. **Lamarck, Buffon**
- -"**Nature produces individuals** and nothing more- species have no actual existence in nature. They are **mental concepts** and nothing more.... Species have been invented in order that we may refer to great numbers of **individuals collectively**."

Problems with nominalistic species concept

- Summarized by **Mayr** (1969) *"any naturalist ... knows that this is simply not true." "Species ... are not human constructs, nor are they types.... They are something for which there is no equivalent in the realm of inanimate objects."*
- 2. It is clear that there are discontinuities in biological diversity. This is demonstrated by both morphological, genetic, ecological, and behavioral data (as well as others)

The biological species concept emphasizes reproductive isolation

- In 1942, Ernst Mayr proposed the **biological species concept** "**Mayr** (1940): species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups.
- **Dobzhansky** (1937): species are the largest and most inclusive reproductive community of sexual and cross-fertilizing individuals that share a common gene pool.
- It places the taxonomy of natural species within the conceptual scheme of **population genetics**
- For example, a community of interbreeding organisms is, in population genetic terms, a gene

- Mayr states that: members of a species form
- a reproductive community :members recognize and seek each other for the purpose of reproduction.
- an ecological unit they interact as a unit and with other species with which it shares an environment.
- a genetic unit ; large intercommunicating gene pool and the individual is merely a temporary vessel holding a small portion of the gene pool for a short period of time

Gene pools of biological species are isolated by pre- and post-zygotic barriers

- Any factor that impedes two species from producing viable, fertile offspring contributes to reproductive isolation:
 - ✦ Most species sequestered from others by **multiple barriers**
 - ✦ Reproductive barriers prevent interbreeding between closely related species
- Various barriers classified by whether they function before or after zygote formation:
 - ✦ **Pre-zygotic barriers** impede mating between species of hinder fertilisation of the ova by sperm from another species
 - ✦ If fertilisation does occur, **post-zygotic barriers** prevent the hybrid zygote from developing into a viable, fertile adult

Pre-zygotic barriers: habitat isolation



- Two species living in different habitats may not encounter each other:
 - ✦ Two species of garter snake (*Thamnophis*) occur in the same area but one species lives in **water and the other is terrestrial**
 - ✦ Since they live in separate habitats, the two seldom come into contact as they are ecologically isolated

Pre-zygotic barriers: behavioural isolation

- Species-specific signals and elaborate behaviour to attract mates e.g different flashing patterns in fireflies
- Many animals recognise mates by sensing pheromones:
 - ✦ Female **Gypsy moths emit a volatile compound** to which olfactory organs of male gypsy moths are specifically tuned
 - ✦ Males of other moth species do not recognise this chemical as a sexual attractant
- Other behavioural isolating mechanisms:
 - ✦ Eastern and western meadowlarks only recognise **songs of the same species**
 - ✦ Specific **courtship rituals**

Other pre-zygotic isolating mechanisms

● Temporal isolation:

- ✦ Two species that breed at different times of the day, seasons or years cannot mix gametes
- ✦ Brown trout breed in the **autumn** whereas rainbow trout living in the same streams breed in the **spring**

● Mechanical isolation:

- ✦ Anatomical incompatibility may prevent sperm transfer
- ✦ Clasp appendages in dragonflies
- ✦ Floral anatomy corresponding to specific pollinator

● Gametic isolation:

- ✦ Sperm of one species may not survive internal environment of female reproductive tract in another species
- ✦ Lack of gamete recognition in external-fertilising species

Post-zygotic isolating mechanisms

● Reduced hybrid viability:

- ✦ Genetic incompatibility may abort development at embryonic stage
- ✦ Several species of the frog *Rana* live in the same habitats but hybrids do not complete development

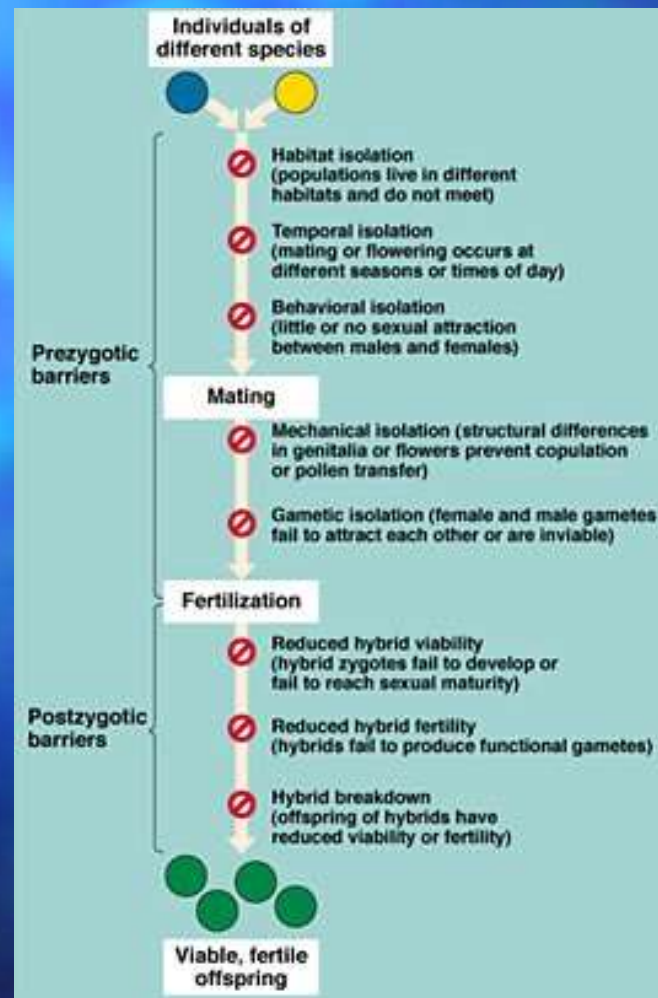
● Reduced hybrid fertility:

- ✦ Species mate and hybrid is viable but sterile e.g. mule
- ✦ If chromosome numbers are different, meiosis cannot produce normal gametes

● Hybrid breakdown:

- ✦ First generation hybrids are fertile but subsequent generations are defective

Reproductive barriers – a summary



Relationship between Morphological and Biological Species

A justification for defining species morphologically is that the morphological characters shared between individuals are indicators of interbreeding. Problems can, however, arise:

Members of a species are by no means all uniform - biological species are regarded as **polytypic** - they have many (or perhaps no) morphological types

Also, it is possible for a species to differ reproductively but not morphologically- **sibling species**

The biological species concept is not always applicable

- The biological species concept cannot be applied to organisms that are **completely asexual** e.g. some protists and fungi, some plants (bananas), many bacteria:
 - ◆ Asexual reproduction effectively produces a series of clones
 - ◆ Asexual organisms can only be assigned to species by grouping clones with the same morphology / biochemistry
- Cannot be applied to **extinct organisms** represented only by fossils (obviously): must be classified morphologically

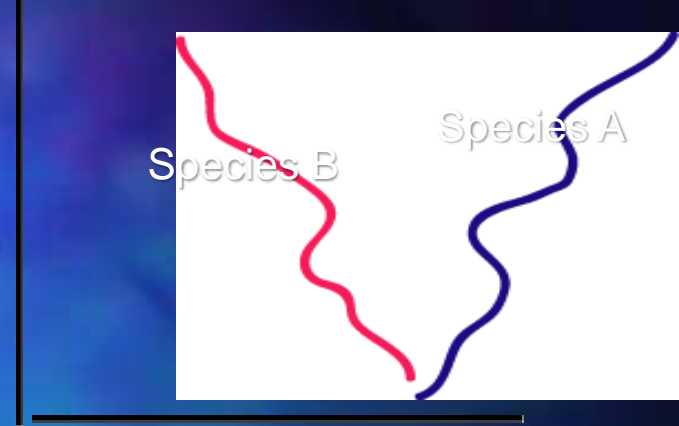
The biological species concept is not always applicable

- Four phenotypically distinct populations (**subspecies**) of deer mouse (*Peromyscus maniculatis*) are geographically isolated in the Rocky Mountains
- Populations **overlap** at certain locations and some interbreeding occurs: same species by BSC criteria
- Two subspecies (*P. m. ssp. artemisiae* and *P. m. ssp. nebrascensis*) do not interbreed, but can breed with other neighbouring subspecies
- **Very limited gene flow** between the two does occur, even though it is via populations of other subspecies

- the absence of a lineage perspective
- its **nondimensionality**
- its **exclusion of non-sexually** reproducing organisms
- most speciation has been shown to occur in allopatry
- **Reproductive isolation is often incomplete**
 -
 - • hybridization is common among many groups (waterfowl, terrestrial plants, freshwater fishes).
- **Multidimensional concept difficult to verify**
 -
 - • how do we assess the “potential to interbreed”?

The Evolutionary Species Concept

Time



A species is an entity composed of organisms

- ◆ maintaining its identity from other such entities through **time and space**
- ◆ and having its own independent evolutionary fate and historical tendencies.
- ◆ **Definition: Simpson, 1961** "an evolutionary species is a lineage (an ancestral descendant sequence of populations) evolving separately from others with its own unitary evolutionary role and tendencies." • "
- ◆ initially developed to define fossil species.

-
- *"a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate"* (Wiley 1978).
 - A lineage concept that avoids many of the problems of the biological species concept without denying that interbreeding among sexually reproducing individuals is an important component in species cohesion.
 - It is compatible with a broader range of reproductive modes and with all speciation models

Problems with evolutionary species concept

- **Is arbitrary.** • how do you define “independent roles and tendencies”?
- **Does not provide a mechanism**
- Operationalism absent
- Use fixed diagnostic differences

The Recognition Species Concept

- According to **Patterson** (1993), species have a **specific mate recognition system (SMRS)**
- Species can be defined as a set of organisms with a common method of recognizing mates
- Advantages:
 - ◆ SMRSs are **easier** to observe than interbreeding in nature
 - ◆ The recognition species concept may more **accurately represent** what happens when a new species originates

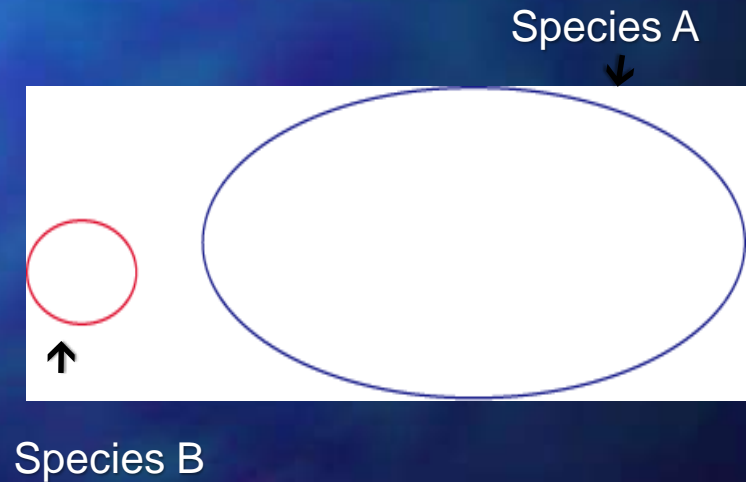
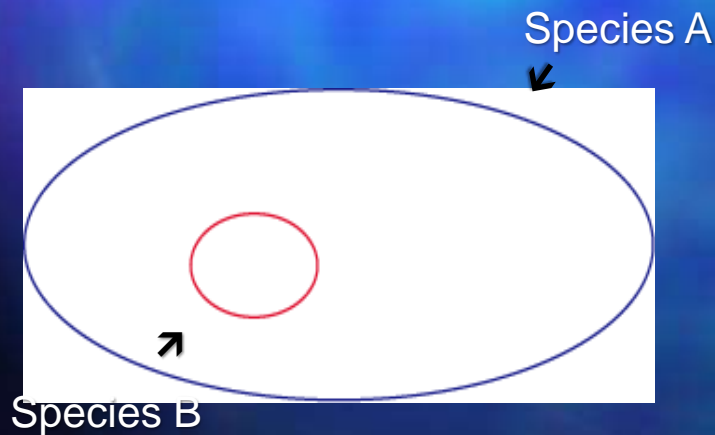
Limitations of Reproductive Species Concepts

- The criterion of interbreeding is **useless for asexual populations**
- Reproductive species concepts cannot be applied to **fossils**
- It is difficult to know whether **geographically isolated** populations potentially can interbreed

- Mayr divided the BSC into the “**nondimensional**” and the “**multidimensional**” species concept:

- **Nondimensional**

- **Multidimensional**



Non dimensional and dimensional species concept

- Concepts of this type have **limited spatial and no temporal dimension** of species in question.
- Thus, there is no evolutionary, phylogenetic, or lineage perspective with which one can view, perceive, or interpret descent of the taxa or their attributes (*eg* shared plesiomorphies or apomorphies, distances), including the ability or propensity to interbreed.

Cohesion species concept

- The **cohesion species concept** relies on mechanisms that maintain species as discrete **phenotypic entities**
- Templeton, 1989
- **broaden the biological species concept** by including asexual organisms and downplaying interbreeding in sexually reproducing organisms. A **species**, in this view, is a population, or series of populations, that has genetic or demographic **cohesion**.
- Fully gene centred: species determined by gene flow
- Process oriented

-
- a cohesion species is the most inclusive population of individuals having the **potential for phenotypic cohesion** through intrinsic cohesion mechanisms; no matter whether populations can hybridize successfully, they are still distinct cohesion species if the amount of hybridization is insufficient to completely mix their respective gene pools

Other species concepts

- The **morphological species concept** defines species based on measurable physical features
- In the **recognition species concept**, a species is defined by a set of characteristics that maximise successful mating
- The **cohesion species concept** relies on mechanisms that maintain species as discrete phenotypic entities
- The **ecological species concept** defines species on the basis of where they live and what they do (adaptation)
- The **evolutionary species concept** defines species in terms of ancestral and descendent populations that are evolving independently of other such groups

- In biological classification, **subspecies** (abbreviated "**subsp.**" or "**ssp.**"; plural: "subspecies") is either a taxonomic rank subordinate to species, or a taxonomic unit in that rank. A subspecies cannot be recognized independently: a species will either be recognized as having no subspecies at all or at least two (including any that are extinct).
- In zoology, under the International Code of Zoological Nomenclature, the subspecies is the only taxonomic rank below that of species that can receive a name.

- When geographically separate populations of a species exhibit recognizable phenotypic differences, biologists may identify these as separate subspecies; a subspecies is a recognized local variant of a species.
- **When zoologists disagree** over whether a certain population is a subspecies or a full species, the species name may be written in parentheses. Thus *Larus (argentatus) smithsonianus* means the American herring gull; the notation within the parentheses means that some consider it a subspecies of a larger herring gull species and therefore call it *Larus argentatus smithsonianus*, while others consider it a full species and therefore call it *Larus smithsonianus* (and the user of the notation is not taking a position)

- **Parapatric** – different forms **meet & interbreed**
- **Sympatric** – different forms “**meet**” but **don’t breed**
- **Allopatric** – **geographically separated** ...never get the chance to mate
- **Polytypic species** – spp. with several defined subspecies (geographic races)
- **Superspecies** – monophyletic group of closely, mostly allopatric species (i.e. used to be one spp., usually post-mating isolation) **E. Mayr and by B. Rensch.**

- The concept of "superspecies," as applied to a monophyletic group of **allopatric** or nearly allopatric taxa that are known or believed to have evolved to the species level,
- **E. Mayr and by B. Rensch.**
- The use of superspecies has been somewhat **retarded by the absence of any formalized notation** for them in Linnaean nomenclature. It is here proposed that brackets (= square parentheses) enclose the first named species of a superspecies: thus, superspecies Bubo [bubo], or Bubo [bubo] virginianus to indicate that the species virginianus is a member of the superspecies Bubo [bubo].