Species and Speciation
Microevolution – evolutionary processes within species

Macroevolution – evolutionary processes at or above the species level

the distinction is irreversible but the processes are the same

Cladogenesis – splitting of one lineage into two or more

Anagenesis – morphological change in a single lineage through time resulting in diagnosably distinct chronospecies
species may be the only biologically natural taxonomic unit

“Speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances. Without speciation, there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution” - Ernst Mayr
Phyletic Gradualism versus Punctuated Equilibrium

Punctuated equilibrium asserts that the only significant evolutionary changes that occur are the result of speciation.
Punctuated Equilibrium – after Eldredge and Gould

"very rapid rates of change"

stasis
Phyletic Gradualism – after Gingerich
Species Concepts

If species are the only biologically-real taxonomic unit, then why are species so difficult to define?

1) differences in reproductive mechanisms among taxonomic groups

2) philosophy

3) speciation is a process that may not be complete
“ring species” California salamander (Ensatina escholtzii)

(from Hickman et al. 1993)
Biological Species Concept

– a species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (Dobzansky 1935)

- species are groups of actually or potentially interbreeding populations that are reproductively isolated from other such groups (Mayr 1942)
Evolutionary Species Concept

– a species is a single lineage (an ancestral-descendant sequence) of populations of organisms that maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley 1978)

Phylogenetic Species Concept

– a phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent (Cracraft 1989)
"phylogenetic species" - monophyletic

"biological species" - paraphyletic

Reproductive isolation
The problem with speciation is “how two different populations can be formed without intermediates?”
Geographic Modes of Speciation

(A) Allopatric speciation by vicariance

(B) Peripatric speciation (founder effect)

(C) Parapatric speciation

(D) Sympatric speciation
Snapping shrimp - allopatric speciation
Tanisyptera kingfishers - peripatric speciation
California salamander (Ensativa escholtzii) -
Parapatric speciation

(from Hickman et al. 1993)
Apple maggot fly (*Rhagoletis pomonella*)
Sympatric speciation
Genetic models of speciation
(not mutually exclusive of geographic models)
  Natural Selection
  Sexual Selection
  Drift
  Transilience
  Cytoplasmically Induced or Endosymbiotic Incompatibility
  Hybrid species
  Polyploids
Cytoplasmic Incompatibility

*Wolbachia* – a vertically transmitted (i.e., by females) cytoplasmic Rickettsial endoparasite/endosymbiont

Present in most if not all orders of insects (and others)

Rapidly becomes widespread in populations by excluding males

1) Feminization of males
2) Female parthenogenesis
3) Male lethality

Promotes reproductive isolation of populations by Cytoplasmic Incompatibility (infected sperm lethal to uninfected eggs or eggs infected with different strain)

*e.g., Nasonia* - parasitoid wasp and endosymbiont *Wolbachia* induced Cytoplasmic Incompatibility
Genetic models of speciation

*Potentially Instantaneous Speciation*

Autopolyploids (4N of one parental species)

e.g., four-wing saltbush (*Atriplex canescens*)
Genetic models of speciation

*Potentially Instantaneous Speciation*

Hybrid Species

Homoploids (diploid)

House Sparrow

(Passer domesticus)

\( \times \)

Spanish Sparrow

(P. hispaniolensis)

= Italian Sparrow

(Passer italicae)
(more) Homoploids

Coyote (*Canis latrans*)

Gray Wolf (*Canis lupus*)

Red Wolf (*Canis rufus*)
Genetic models of speciation

*Potentially Instantaneous Speciation*

Hybrid Species

Allopolyploids (4N or more)

reversed chirality in hybrid snails (*Partula spp.*)
Allopolyploids

Pool Frog  
(*Rana ridibunda*)

Marsh Frog  
(*Rana lessonae*)

Edible Frog  
(*Rana esculenta*)

2N, 3N, or 4N all-female species
Genetic models of speciation

Potentially Instantaneous Speciation

Hybrid Species

Allopolyploids (4N or more, some secondarily homoploids)

“Polyplody, often referred to in the genomics literature as whole-genome duplication (WGD), has played a dramatic role in the diversification of most, if not all, eukaryotic lineages, perhaps most impressively within the angiosperms (Soltis et al 2009 Am J Bot 96 336-348).”
Angiosperms

An estimated 30 to 80% of angiosperms are of hybrid origin
“The world is not a formless mass of randomly combining genes and traits, but a great array of gene combinations which are clustered on a large but finite number of adaptive peaks. The gene combinations whose adaptive value has been vouchsafed by natural selection must be protected from disintegration by barriers to gene exchange, termed *isolating mechanisms*” (Theodosius Dobzansky)
Barriers to Gene Flow (either during speciation or upon Secondary Contact)

Prezygotic isolating mechanisms – anything that evolves (i.e., is selected for in the species themselves) specifically to prevent hybrid or inter-populational fertilization

Postzygotic isolating mechanisms (secondary contact only) – anything that evolves (i.e., is selected for in the species themselves) specifically to diminish hybrid (zygote or organism) fitness
Prezygotic isolating mechanisms

Habitat, spatial, or host

Temporal or phenological

Behavioral

Mechanical

Gametic inviability or incompatibility
Allopatry is not a “prezygotic isolating mechanism” because it is not something that has evolved specifically to prevent gene flow between species.
character displacement – any trait with greater interspecific phenotypic difference in sympatry than in allopatry, often a prezygotic isolating mechanism.
Character Displacement in song of African *Pogoniulus* tinkerbirds

in coloration of dewlaps in Haitian *Anolis* lizards

Kirschel et al. PNAS 2009;106:8256-8261
Postzygotic isolating mechanisms

Hybrid zygote death or inviability

Hybrid sterility

Reduced hybrid fitness

Haldane’s Rule – in hybrids, the heterogametic sex is more likely to be absent, rare, or sterile than the homogametic sex
Definitions

Polytypic species – a species with recognizably different populations

Subspecies – a recognizably distinct population (a matter of degree)

Semispecies – hybridizing species

Superspecies – a collection of semispecies

Sibling species – sister species

Cryptic species – unrecognizably (to humans) distinct species

Chronospecies – recognizably distinct populations of a single lineage separated in time