What is a species?
"the fundamental unit of classification"

but it has proven impossible for biologists to agree upon what is “fundamental” about species

perhaps we need to “get over the species problem”


1. species are “recurrent aspects of nature”

2. to communicate about these, the mind constructs categories and interprets organisms as members of these categories

3. we retain these categories (species) even when our insight into evolution leads us to understand that, although “organisms often constitute real evolutionary groups*”, these groups are often indistinct and change over time

*defined as “groups of replicator molecules, which share competition, genetic drift, and adaptation”

4. paradox: We recognize the pluralism of different kinds of species; but (generally) retain the monism implied by the single term “species”

“our categorical imperative distracts us from understanding species, for it would be nice to develop a richer lexicon about the real entities that we study”

5. real species = “large evolutionary groups with potentially uncertain boundaries”

6. taxonomic species = hypotheses based upon “a unique pattern of biological diversity that we think has been caused by evolution”

unfortunately, these hypotheses are very difficult to test…

7. Biologists need to be cognizant of the difference between categories (taxonomic species) and real entities (evolutionary groups).

Traditional Species Concepts

I. MORPHOLOGY
"species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (A. Cronquist, 1988)

A. Pragmatic

B. Predominant

C. Arbitrary?

considering “lumpers” vs. “splitters” one can ask:

e.g. Levin, 1979: "do species exist"?
populations are real, everything else is artificial

II. BIOLOGY

“New synthesis” = adding genetics to evolution
(Dobzhansky, Mayr, Stebbins, Grant)

Ecogenetic species concept (Levin 2000)

"each species has a unique way of living in and relating to the environment and has a unique genetic system - which governs the intercrossability and interfertility of individuals and populations"

A. Reproductive Isolating Barriers

1. Prezygotic Barriers

a. ecological  [ grow in different habitats ]

b. geographic  [ same habitat, spatial sep. ]

c. reproductive

   i. flower at different times

   ii. different flowers [ different pollinators]

   iii. pollen / pistil incompatibility

2. Postzygotic Barriers

   a. hybrid inviability
   from embryo abortion to mature but sterile adults
b. hybrid sterility
   i. inviable seed (embryo abortion)
   ii. offspring are sterile
   iii. floral isolation

B. problems with the BSC in plants

1. crossing experiments
   a. often impractical
   b. inconsistent results

2. incongruence with morphological species

3. too much sex
   i. hybridization
   ii. introgression

   examples: *Quercus, Lupinus*

4. too little sex
   i. self-compatibility
      limited or no gene exchange across pops.
   ii. chromosomal or genic barriers
      = microspecies or cryptic species
   iii. apomixis
      limited or no gene exchange across individs.

5. agamic complexes
   i. sexual species and their (partially) agamospermous hybrids
   ii. hybrids and introgressants among agamospecies

examples: *Antennaria, Poa, Rubus, Taraxacum*
6. “reproductive compatibility is plesiomorphic”

III. PHYLOGENY
see Goldstein & DeSalle 2000 Cladistics 16:364-84.

“rank of species marks the boundary between reticulate (among interbreeding individuals) and divergent relationships (between lineages with no gene exchange)”

“unfortunately the boundary is often blurred”

Different criteria for a Phylogenetic Species Concept  Process vs. Pattern

A. History based (process) "Harvard school"

1. Monophyly [ = Autapomorphy ]

(Donoghue 1985; Mishler 1985)
problems:
   a. requires cladistic analysis of tokogeny - where it is inappropriate

   b. many species are likely paraphyletic
      (progenitor derivative species) or polyphyletic
      (e.g. multiple origins of polyploids)

2. Genealogy (Baum & Shaw 1995)

   a. determined by gene coalescence (tree-based)

   b. problem: different genes may show different patterns of coalescence

   c. may impose a "tree" on non-hierarchical data

B. Character based (pattern)
"Cornell school"

1. Diagnostic character states
   (Davis & Nixon 1992)
= population aggregation analysis
   "smallest diagnosably distinct clade of individuals in which there is a parental pattern of ancestry and descent"

   a. diagnosability = fixed differences

   problems:
b. fixation may vary over time

c. is one fixed difference enough?

IV. Within species variation
   A. cline
   "gradual morphological variation across a geographic region"

   B. ecotypes
   "populations that have diverged genetically in response to their environments"

   C. may be treated as subspecies and varieties (inconsistently)

V. SPECIATION
   A. Allopatric Speciation
   "different homes"

      1. subdivision
         a. geographic isolation -- non-biological
         b. extinction of intermediate pops.
         c. result: NO GENE FLOW

      2. gradual accumulation of mutations

      3. genetic divergence over time

      4. reproductive isolation [follows divergence]

      5. intercontinental disjunctions
         e.g. Datisca, Platanus

   B. Local Speciation (Progenitor - Derivative)
      Parapatric Speciation

      1. isolation
         a. migration
         b. long distance dispersal
c. peripheral population

2. genetic bottlenecks
   a. population reduction
   b. increased inbreeding & genetic drift
   c. adaptation  ?? maybe, maybe not

   i.e. selection pressure could cause the fixiation of genetic differences,
   but so might random events

   3. fixation of mutations

   4. with or without reproductive isolation

   5. faster than allopatry

   6. reduced genetic diversity in derivative

   7. relatively high genetic identity betw. progenitor & derivative

Examples: *Stephanomeria, Clarkia* (studies of L.D. Gottlieb) *Cirsium*

C. Adaptive Radiation

http://www.botany.hawaii.edu/faculty/carr/silversword.htm

1. open habitats

2. little competition

3. radiation into new ecological niches -

4. often w/o genetic reproductive isolation

5. generally w/o much genetic divergence

6. can result in a “star phylogeny”

D. Sympatric Speciation
1. Polyploidy  [50-80% of angiosperms]
   a. hybrid formed between dissimilar species  “allopolyplody”
   b. sterile due to pairing problems at meiosis
   c. chromosomes doubled
   d. each parental chromosome can now pair with a homologue
   e. fertility restored at the tetraploid level

2. Chromosomal Rearrangements
   a. rearrangement established
      [e.g. translocation]
   b. hybrid sterility
      ex. _Clarkia_ species  (H. Lewis)

3. Mating System Change
   a. self-compatibility arising from self-incompatibility
      ex. _Stephanomeria malheurensis_