SPECIES

Read: Futuyma Chap. 15 pp. 447-454
Table 15.1: Ignore the Internodal Species Concept, which has disappeared almost entirely from consideration.

Good general source: Coyne & Orr (2004) Speciation Sinauer

Terminology
• Species concept = theoretical model of species.
• Species criterion or definition = operational criterion by which an individual is assigned to one or another species.

How do we know species are real biological units, vs. arbitrary constructs?
• Non-scientists identify same species as taxonomists.
• Statistical identification of clusters. This has been enshrined as the phenetic species definition but seems to be purely empirical with no underlying species concept.
• Species are successfully treated as fundamental units of population and evolutionary genetics.

Species concepts in rough historical order

Phenotypic clusters: phenomenon to be explained, probably the first species definition.

Common descent: parent and offspring belong to same species; common to all concepts.

Typological Species Concept Linnaeus to 20th century: morphological characters possessed by all members of a species. Tradition enshrined in type specimens placed in museums.

Biological Species Concept (BSC) T. H. Dobzhansky, H. J. Muller, Ernst Mayr: species as most inclusive group of individuals that actually or potentially interbreed. Have cohesion as result of shared gene pool (sex as glue that holds a species together). Mayr called BSC to contrast with typological species. Population genetics emphasized species as populations of individuals that are similar but not necessarily identical. Criterion: breeding tests, or definitive evidence that organisms couldn't interbreed even if given the chance. Dominates thinking and research on speciation. Research on speciation is research on the origin of reproductive isolation.

Recognition SC (RSC): most inclusive group of individuals that share common fertilization mechanism. Flip side of BSC, not significantly different.

Pluses:
Theoretically applicable to many or most sexual organisms; works well in practice for many. Informed by population genetics.

Minuses:
Irrelevant to asexual organisms, problematic with organisms like plants that have clear phenotypic clusters with lots of hybridization. (Templeton: BSC fails with organisms that have too little or too much sex.)
Criterion often hard to apply, so use surrogate evidence like phenotypic similarity.

**Evolutionary SC (EvSC)** George Gaylord Simpson: Species as lineage that evolves independently of other Lineages
Plus:
Applicable to any organism.
Implicit or a consequence of many other concepts or criteria.
Minus:
Original form vague, without clear criteria.

**Ecological SC (EcSC)** Leigh Van Valen: Species as lineages that are adapted to different niches. Note that this provides evolutionary cohesion. Criterion: sympatric coexistence of clusters.
Plus:
Applicable to any organism.
Can be grounded in population genetic theory.

Application of molecular data led to new species concepts inspired by population genetics:

**Cohesion SC (CSC)** (Alan Templeton): Inclusive groups of individuals that are cohesive due to shared gene pool and/or adaptation to different niches. Criteria: various. Gedankenexperiment: mix individuals from two populations in equal numbers, many replicates; if belong to same species, over time each population will replace the other in half the populations; if different, one will replace the other more often.
Plus:
Applicable to any organism.
Can be grounded in population genetic theory.
Minus:
Calls species while they are still poly- or paraphyletic, if they are adapted to different niches. I'd prefer to call these subspecies.

**Genotypic Cluster SC (GCSC):** Species are phenotypic or genotypic clusters with few or no intermediates.
Plus:
Focus on clusters and gaps.
Applicable to any organism.
Minus:
Vague about how to define clusters.
Really a vague criterion, not an SC.

**Ecotype SC (EctpSC)** (Fred Cohan): Bacteria form clusters as a result of periodic selection for adaptation to a particular ecotype (ecological niche?). A special case of EvSC emphasizing role of periodic selection in producing clusters.
Plus:
Grounded in population genetic theory.
Improvement over arbitrary division by 2.5% or other amount of rRNA sequence divergence.
Rise of phylogenetic methods and concepts and of cladistics produced several **Phylogenetic Species Concepts (PSCs)**. Multiple versions; Coyne and Orr distinguish two as follows:

**Phylogenetic SC 1 (PSC1)** Joel Cracraft: Basal cluster of organisms diagnosably distinct from other such clusters.

**Plus:**
- ?

**Minus:**
- Basically typological. Would allow any clade distinguished by any shared trait from other clades but shared traits don’t necessarily reflect history.
- Could subdivide biological species into trivial species that are clustered on the basis of one or a few morphological traits.
- Can create species in which some individuals are more closely related to individuals from other species.
- Maybe not applicable to asexuals.

**Phylogenetic SC 2 (PSC2)**. Kevin de Queiroz and Michael Donoghue: Smallest exclusive monophyletic group.

**Plus:**
- Applies to all organisms.
- Solves problem with PSC1 by requiring synapomorphies (shared derived traits) to distinguish reciprocally monophyletic clades.

**Minus:**
- Lacks ranking criterion, so one could have reciprocally monophyletic populations created by drift.

**Genealogical Species Concept (GSC)** (also called PSC3 by Coyne & Orr). Brent Mishler et al: Group in which in which all genes belong to same monophyletic group.

**Plus:**
- Applies to most organisms.

**Minus:**
- Can have lineage separated from rest of species that becomes monophyletic; it is then a species but the original species is now paraphyletic and hence no longer a species.
- In sexual organisms, having all genes be monophyletic is impossible if any locus shows balanced polymorphism. Not a problem with asexual organisms.
- Takes very long time for all loci to become reciprocally monophyletic, long after populations have become reproductively isolated because genes controlling reproductive isolation have already become reciprocally monophyletic. Not a problem with asexual organisms.

**General Lineage SC (GLSC)** Kevin de Quieroz: Species are segments in time of different evolutionary lineages. Other SCs are special cases of the GLSC.

**Plus:**
Very general, applicable to all organisms in principle, incorporates most other SCs as special cases.  
Minus:  
Too general, doesn’t specify when one lineage becomes two lineages and two species.

**Evolutionary Genetic SC (EvSC)** Birky, based on theory developed independently by Birky and by Tim Barraclough & Austin Burt. See below.

**General properties seen in many SCs:**
- Common descent (all)
- Monophyletic
- Phenotypic and/or genotypic clusters
- Evolutionary units and lineages
- Reciprocally monophyletic

**Systematics is a contentious field, especially where species are concerned**

E.g. debate over DNA barcoding.
“The tone and content of this submission reflects the *ad hominem* nature of the debate …”
“We would be astonished if any credible scientists would accept the diversity of *cox1* haplotypes sampled from an area as a valid or meaningful measure of biodiversity.”
“Even among the three of us there is little consensus as to the best species concept, or even the importance of species as a taxonomic rank, a situation that mirrors the broader biological community.”

**Blatantly biased editorial comment: barriers to progress in defining species**
- Confusing philosophy and science
- Birders
- Extreme cladists
- Ignorance of, or just ignoring, population genetics
- Bias toward sexual organisms

**My Approach to Species Concepts and Criteria**

**Principles:**
- Asexual organisms form clusters similar to those in sexuals, so SC must apply to asexual species.
- We need to be able to compare species in asexual and sexual organisms, so SC must apply to sexual species or define units comparable to those defined by BSC.
- Species are populations, so SC must be grounded in population/evolutionary genetic theory.
- If there were only one cluster, there would be no species, so SC must explain gaps as well as clusters.
- SC must not allow gaps due to drift.
- SC must define evolutionarily independent lineages; species must be independent arenas for mutation, selection, and drift. This requires that speciation events be completed and the species be reciprocally monophyletic.
Read Barraclough, Birky, and Burt (2003 *Evolution*) for theory; pdf is on web site.

This theory it could be considered a more explicit version of the EvSC. But it goes further so I think it can be considered a new species concept, the Evolutionary Genetic Species Concept or EGSC.

Disclaimer: Tim doesn’t want to call it a species concept.

For asexual organisms the theory is as follows:

Asexual gene or organism tree with synchronous reproduction and no extinction (A); with stochastic reproduction and extinction (drift) (B); drift plus truncating selection (C); and drift plus diversifying selection (D).

Phylogenetic trees with extinction, random drift, and diversifying selection (top); observed tree based on extant survivors (bottom).
Species criterion involves identifying reciprocally monophyletic populations. If samples are reciprocally monophyletic and \( d \geq 4\pi \), \( \geq 96\% \) of populations are reciprocally monophyletic, when sample sizes \( \geq 3 \).

We used this criterion to identify reciprocally monophyletic populations in monogonont rotifers and two sets of data from bacteria. We found few or no borderline cases, perhaps because periodic selection keeps \( N_e \) low.

For sexual organisms, two populations would be independent evolutionary arenas if they were 95% reciprocally monophyletic for the gene or genotype that makes them reproductively isolated. This is identical with the BSC except that it requires evidence that the majority are reproductively isolated.
This method has been applied to asexual bdelloid and sexual monogonont rotifers and to tiger beetles. In sexual organisms, the species so identified correspond well to species identified under the BSC.

Summary: It is possible to have a species concept (theoretical model) that is informed by population genetics and captures widely (but not universally) accepted features of species, and is potentially applicable to all organisms.