

PLANT OF THE DAY!

*Stevia
rebaudiana*,
commonly
known as
sweetleaf

Close relative
of sunflower
native to
South America

Steviol
glycosides are
circa 300x the
sweetness of
sugar, but no
effect on blood
glucose

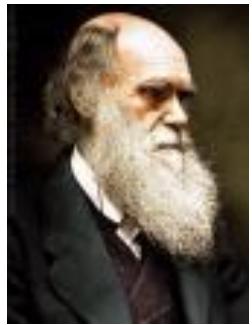


Big Questions

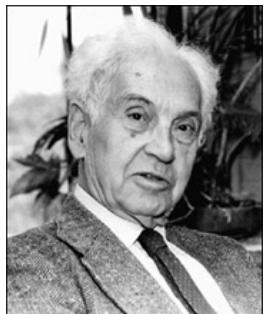
Are plant species real? Is there a phenotypic and reproductive continuum connecting the different forms of plants or do discontinuities exist that can be used to partition diversity into groups?

If plant species are real, then what causes plant diversity to be apportioned into clusters separated by gaps?

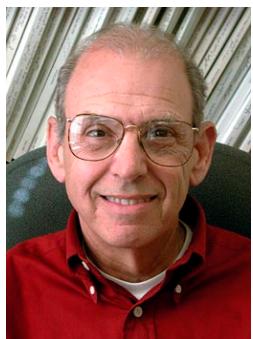
I. ARE SPECIES BIOLOGICALLY REAL ENTITIES?



“From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.” (Darwin, 1859, p. 52)



“The non-arbitrariness of the biological species is the result of ... the internal cohesion of the gene pool... (Mayr, 1963, p. 21)

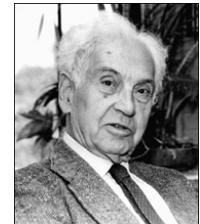


“Plant species are utilitarian mental constructs” (Levin, 1981, p.381)

Evidence from floras and monographs:

- 697 of 838 of named species (83.1%) in Concord Township flora were “morphologically well-defined, relatively uniform, and sharply set off against all other species”

(Mayr 1992, p. 236)



- 120 of 1,790 species (7%) from 104 botanical monographs reported as problematic.

(McDade 1995)

Criticisms: assessments are subjective
human mind adept at classification



Evidence from folk taxonomies:

Animals:

Birds of New Guinea (70-90%)

Frogs of New Guinea (80%)

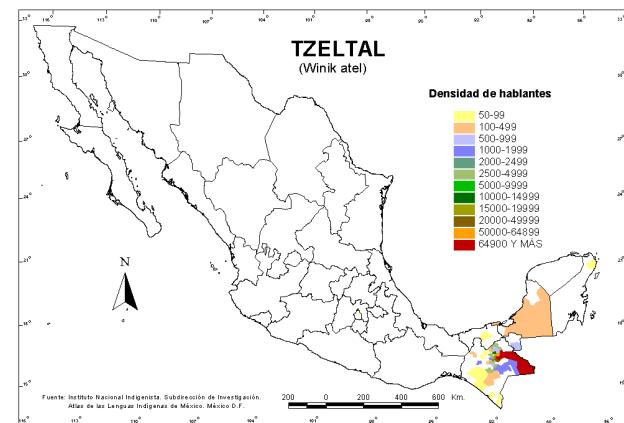
Reptiles of New Guinea (95%)

reviewed in Coyne & Orr (2004)

Plants:

-61% of Tzeltal (S. Mexico) species correspond 1:1 with Linnaean species (Berlin et al. 1974)

-87.7% of Dai (Yunnan, China) taxa have Linnaean equivalent (Wang et al. 2004)



Criticism: all humans share similar neurological processes

Statistical tests: -literature survey

218 numerical taxonomy studies

25% animals

70% flowering plants

4% ferns and fern allies

1% gymnosperms



Troy Wood

Eric Baack

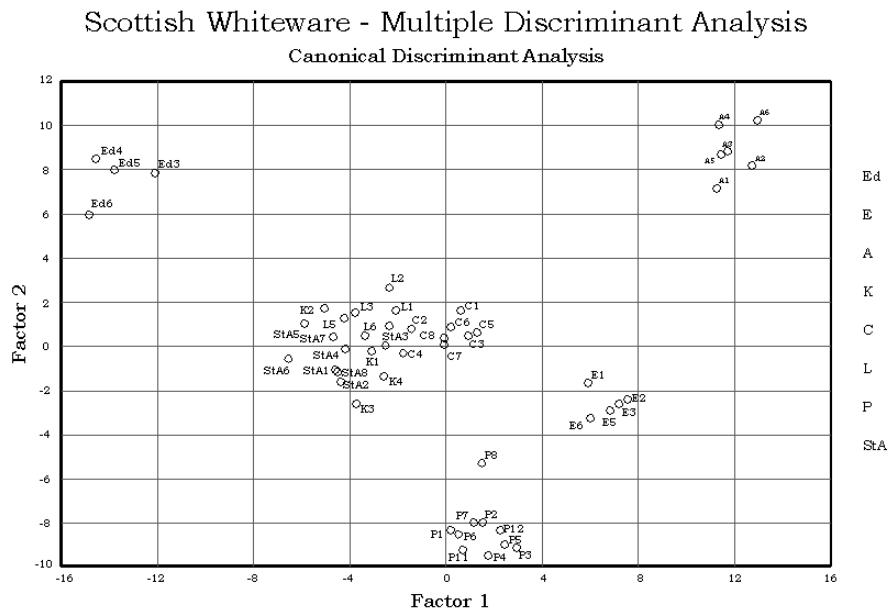
-analyses

number of discrete phenotypic clusters within groups

proportion of species taxa that correspond directly
with phenetic clusters



Scottish medieval gritty
white ware



Key

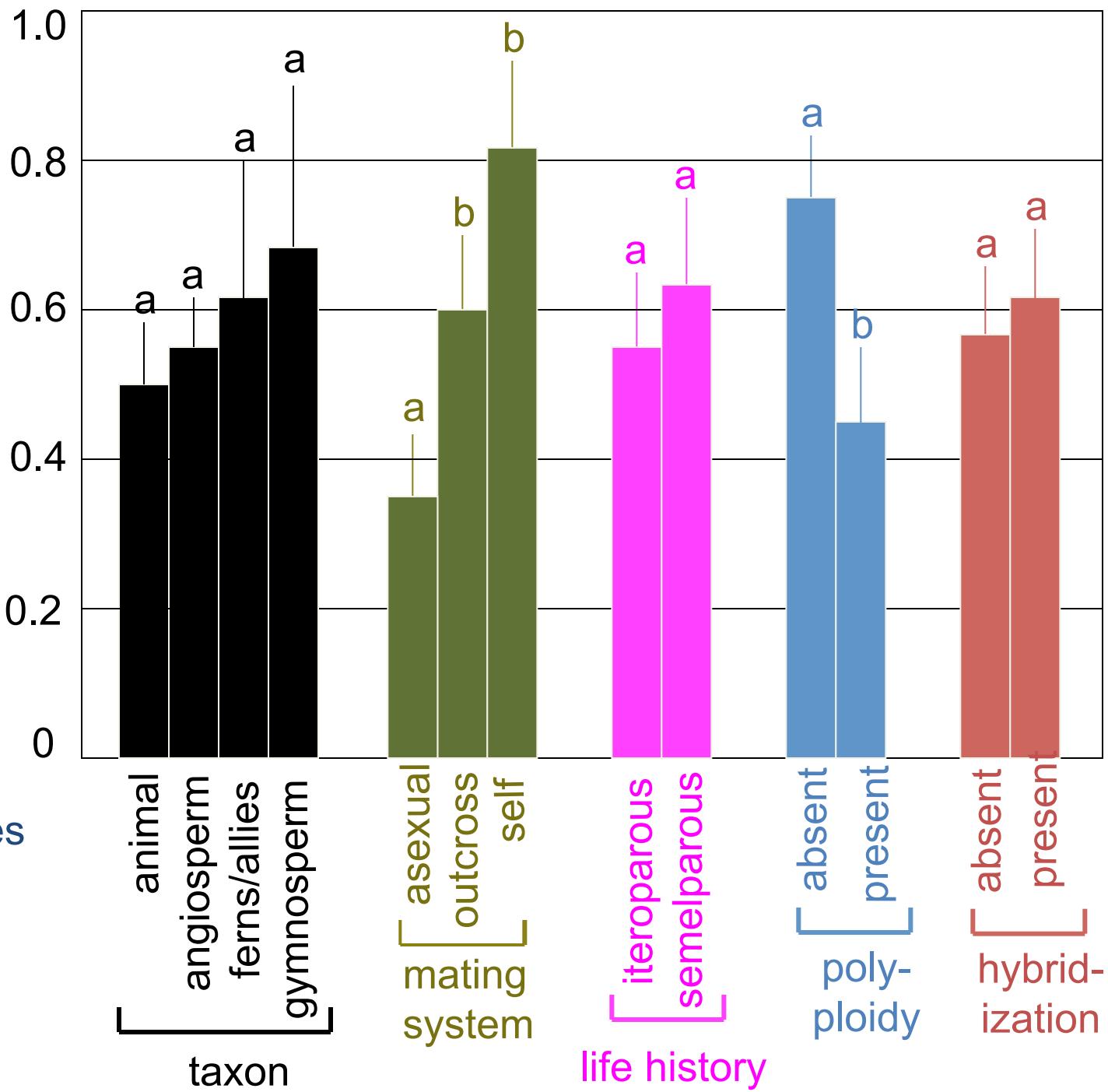
- Ed Edinburgh
- E Elgin
- A Ayr
- K Kelso
- C Colstoun
- L Leith
- P Perth
- StA St Andrews

Results:

- discrete phenetic clusters found in > 80% of taxa studied
- correspondence between species taxa & phenetic clusters was low (54%; 66% if problematic taxa are removed)
- mostly due to over-differentiation or splitting (87.4%) by taxonomists

What causes
taxonomic
problems?

Correspondence between Species Taxa and Phenetic Clusters



Correspondence between species taxa and reproductively independent lineages

That is, do morphological discontinuities correspond closely to reproductive discontinuities?

Literature Survey:

137 plant genera

170 animal genera

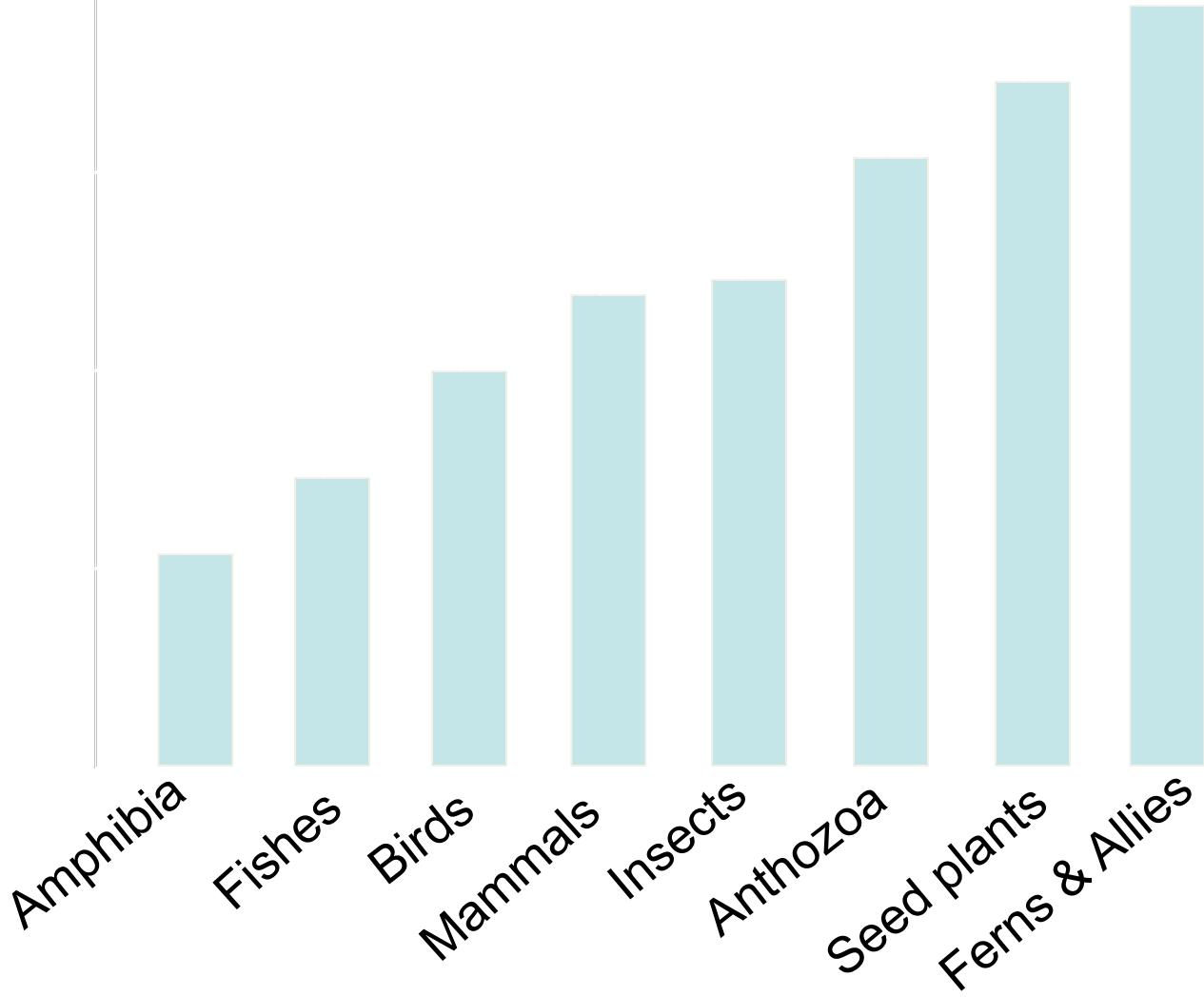
Compatibility index (CI) = $\frac{\text{interspecific compatibility}}{\text{intraspecific compatibility}}$

CI of 1 = no isolation

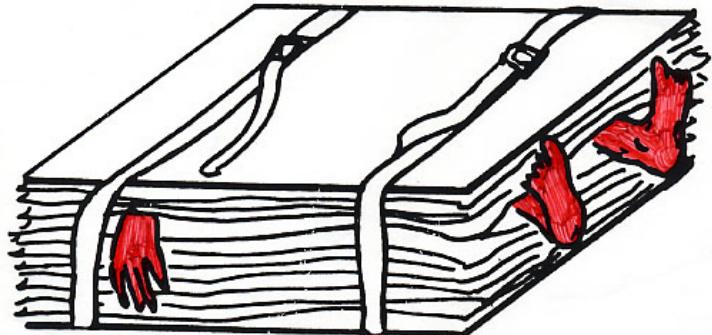
CI < ~0.8 = significant isolation

Correspondence between species taxa and reproductively independent lineages requires that a species be isolated from all relatives.

Fraction of Species Taxa that Represent
Reproductively Independent Lineages



Do phenotypic clusters correspond more closely with reproductively independent lineages than species taxa?



taxonomists

vs



raw statistics

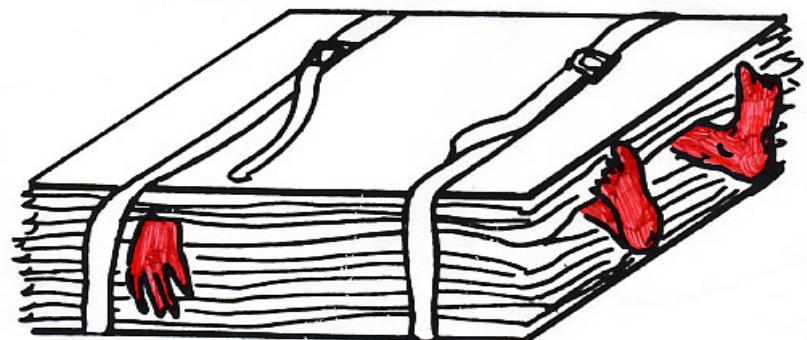
Compared 34 genera that had been subjected to both phenetic and crossability studies

IT'S A DRAW: 75.2 % for clusters vs. $71.2 \pm 7.1\%$ for species taxa ($P = 0.58$)

Conclusions about plant species

Most plant species are real entities, but....

- Botanists are overly influenced by “taxonomic horror stories”
- Taxonomists over-differentiate



II. WHY ARE THERE SPECIES?

Why are organisms apportioned into clusters separated by gaps?

- 1) Inevitable consequence of population or lineage extinction
(geographic speciation via the extinction of intermediate populations in a chain of races)

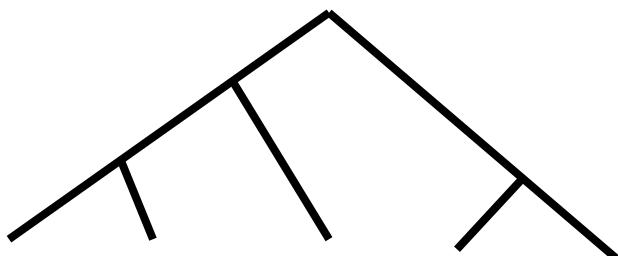
Population or lineage extinction



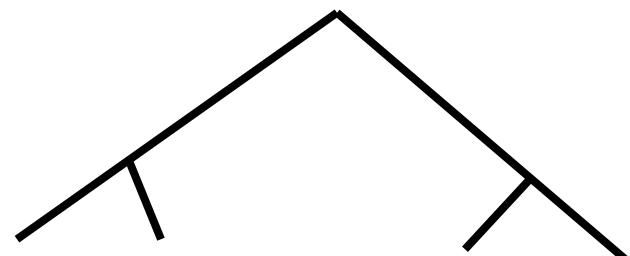
Isolation by distance and/or environmental cline



extinction



extinction



II. WHY ARE THERE SPECIES?

Why are organisms apportioned into clusters separated by gaps?

- 2) Adaptation to different niches
(ecological speciation)
- 3) Inevitable result of mutation order divergence in populations that are either allopatric or reproductively isolated
(mutation order speciation, but through either drift or selection)

Clustering in asexuals versus sexuals

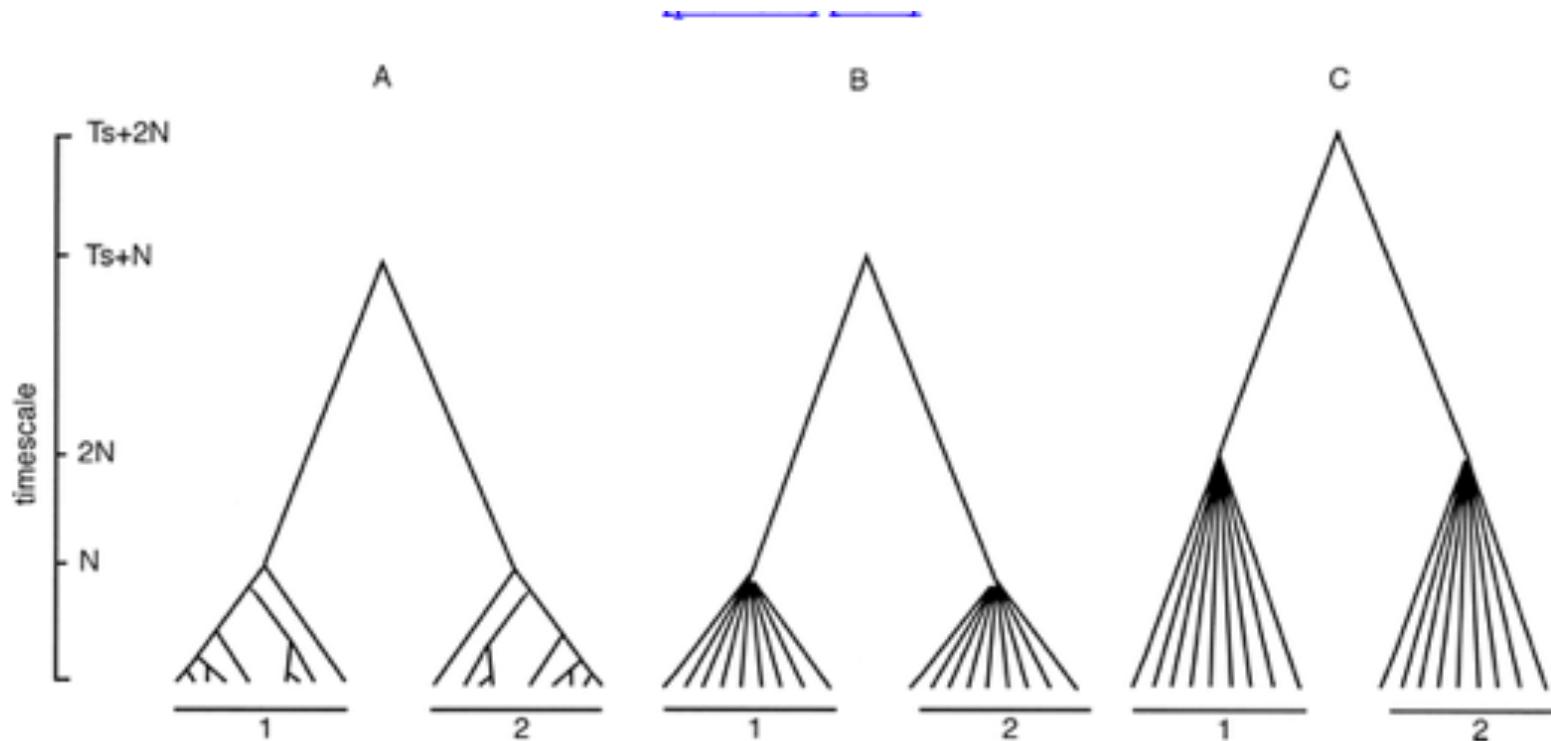


Fig. 3. Consensus gene trees from multiple loci sampled across two populations geographically isolated at time T_s , each with population size $N/2$. (A) Asexual haploid population. Assuming neutral coalescent, the *Tmrca* within each population is N generations. (B) Sexual haploid population. Same as (A) except for lack of resolution in consensus trees. (C) Sexual diploid population. Assuming neutral coalescent, the *Tmrca* within each population is $2N$ generations. Note we assume that $T_s \gg 2N$; that is, that coalescence within populations is complete at time of sample

Consensus gene trees in geographically isolated populations
(Barraclough et al. 2004)

Clustering in asexuals versus sexuals

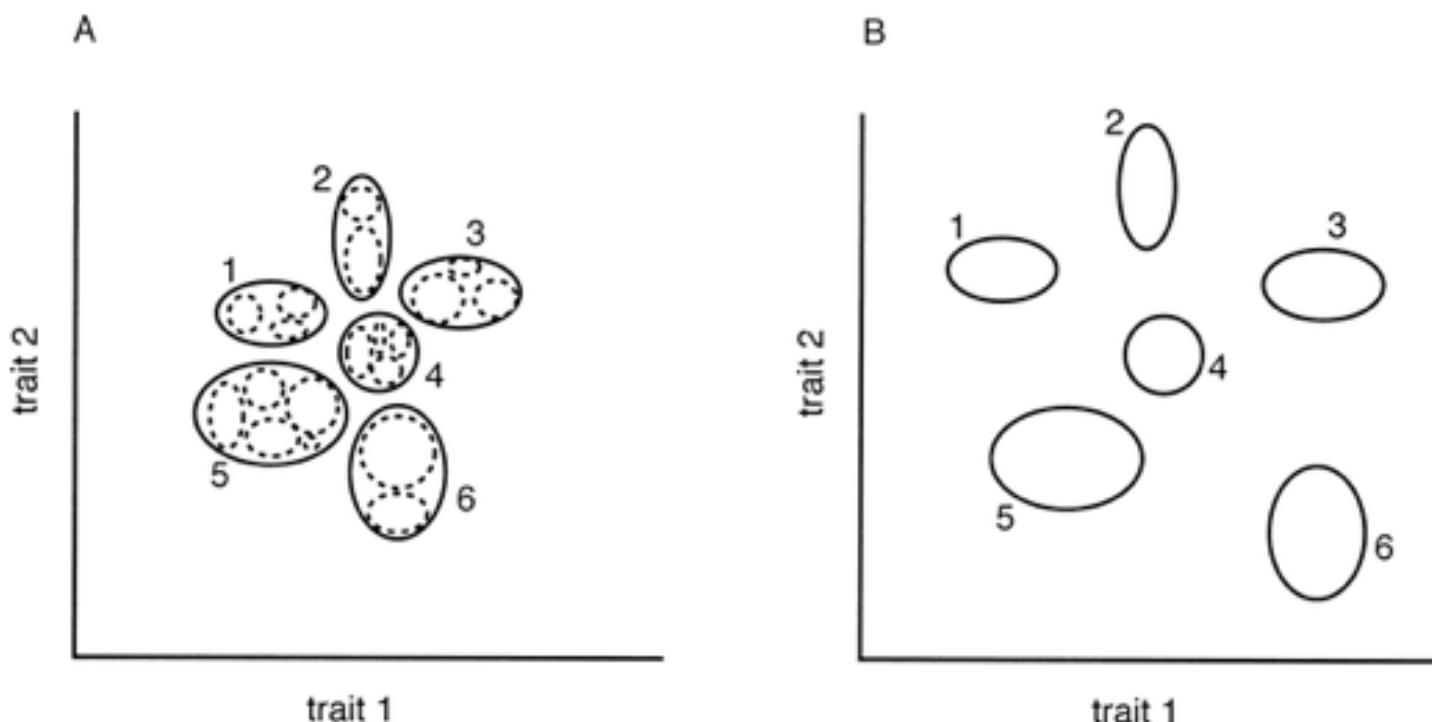


Fig. 4. Expected variation among clusters for two adaptive characters coded by multiple loci in (A) asexual and (B) sexual cases. Each ellipse represents the range of values observed within a single recognizable cluster. Note that the asexuals display further discreteness within each major cluster, due to the inherent tree structure of quantitative variation in asexual populations. The traits could be morphological measures or the first two principal components from a principal components analysis of a set of morphological characters. The number of clusters is the same in the sexual and asexual case, but the magnitude of differences among clusters (disparity) is greater in sexuals

Clustering of adaptive traits in ecologically divergent populations
(Barraclough et al. 2004)

III. SPECIES CONCEPTS

Alice explains why we name things:

"What's the use of their having names," the Gnat said, "if they don't answer to them?"

"No use to them," said Alice, "but it's useful to people that name them, I suppose. If not, why do things have names at all?"

- Lewis Carroll, Through the Looking Glass

Darwin's other view of species:

"Firstly, why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion instead of species being, as we see them, well defined?"

- Charles Darwin, The Origin of Species

Species Concepts A-Z:

Agamospecies Concept
Biological Species Concept
Cladistic Species Concept
Cohesion Species Concept
Composite Species Concept
Ecological Species Concept
Evolutionary Significant Unit
Evolutionary Species Concept
Genealogical Concordance
Genetic Species Concept
Genotypic Cluster Concept
Hennigian Species Concept

Internodal Species Concept
Morphological Species Concept
Non-dimensional Species Concept
Phenetic Species Concept
Phylogenetic Species Concept I
Phylogenetic Species Concept II
Phylogenetic Species Concept III
Polythetic Species Concept
Recognition Species Concept
Reproductive Competition
Successional Species Concept
Taxonomic Species Concept

Mayden (1997)

“It is clear that arguments [about species concepts] will persist for years to come, but equally clear that, like barnacles on a whale, their main effect is to retard slightly the progress of the field.”

Coyne (1992)

“Given the recent pace of new proposals, each evolutionary biologist may soon have his or her own definition of species.”

Schemske (2000)

THINK - PAIR – SHARE

What is an important feature of a species concept and why?
What is the most important feature?

Goals of Species concepts

Species are "tools that are fashioned for characterizing organic diversity"
- Levin (1979)

"different species concepts are best for different purposes"
-Erhlich (1989)

Taxonomy of Species Concepts

Retrospective (species as end products of evolution) vs prospective (species as evolutionary units)

Mechanistic (process) vs historical (pattern)

Character-based (characters only) vs history-based (genealogy)

Theoretical vs operational

Relational (species defined in comparison to other species) vs non-relational

Biological Species Concept (BSC): "species are groups of interbreeding natural populations that are reproductively isolated from all other such groups" (Mayr 1969).

Comment: Most influential concept for sexual species

Problems:

1. Too much sex
2. Too little sex
3. Difficult to apply to allopatric populations

Evolutionary Species Concept (EvSC): "a lineage evolving separately from others and with its own unitary evolutionary role and tendencies." (Simpson, 1951).

Comment: Applicable to living and extinct groups, and to sexual and asexual organisms

Problems: vague operationally in what is meant by “unitary evolutionary role and tendencies

Recognition Species Concept (RSC): "the most inclusive population of biparental organisms that share a common fertilization system" (Paterson, 1985).

Comment: Similar to BSC in viewing conspecific populations as a field for recombination, but focuses on reproduction facilitating mechanisms within species rather than on reproductive barriers.

Problems: similar to those of BSC

Cohesion Species Concept (CSC): "the most inclusive population of individuals having the potential for cohesion through intrinsic cohesion mechanisms." (Templeton, 1989).

Comment: Attempts to incorporate strengths of BSC, EvSC, EcSC, and RSC, and avoid their weaknesses. The major classes of cohesion mechanisms are genetic exchangeability (factors that define the limits of spread of new genetic variants through gene flow) and demographic exchangeability (factors that define the fundamental niche and the limits of the spread of new genetic variants through genetic drift and natural selection).

Problems: difficult operationally in that different scientists may choose to emphasize different cohesive mechanisms

Genotypic Cluster Species Concept (GCSC): A species is a distinguishable group of individuals that has few or no intermediates when in contact with other such clusters (Mallet 1995).

Comment: Allows for low levels of hybridization between species and makes no statement about the mechanism of speciation.

Problems: Difficult to apply to allopatric populations

Ecological Species Concept (EcSC): “A species is a lineage which occupies an adaptive zone minimally different from any other lineage in its range and which evolves separately from all lineages outside its range.” (Cracraft, 1983).

Comment: Proposed as a solution to the problem of ecologically differentiated entities that still exchange genes. The use of the term minimally different excludes higher taxa. Maybe useful for classifying asexual species

Problems: (1) difficult operationally
(2) ecologically identical species may be able to co-exist

Phylogenetic Species Concept (PSC): “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.” (Cracraft, 1983).

Comment: Explicitly avoids all reference to reproductive isolation and focuses instead on phylogenetic histories of populations.

Problems:

- (1) confuses histories of traits with histories of organisms
- (2) classifications change with more data
- (3) creates taxonomic inflation

Genealogical Species Concept (monophyletic species concept): Exclusive group of organisms, were an exclusive group is one whose members are all more closely related to each other than to any organisms outside that group (Baum and Shaw 1995, p. 290).

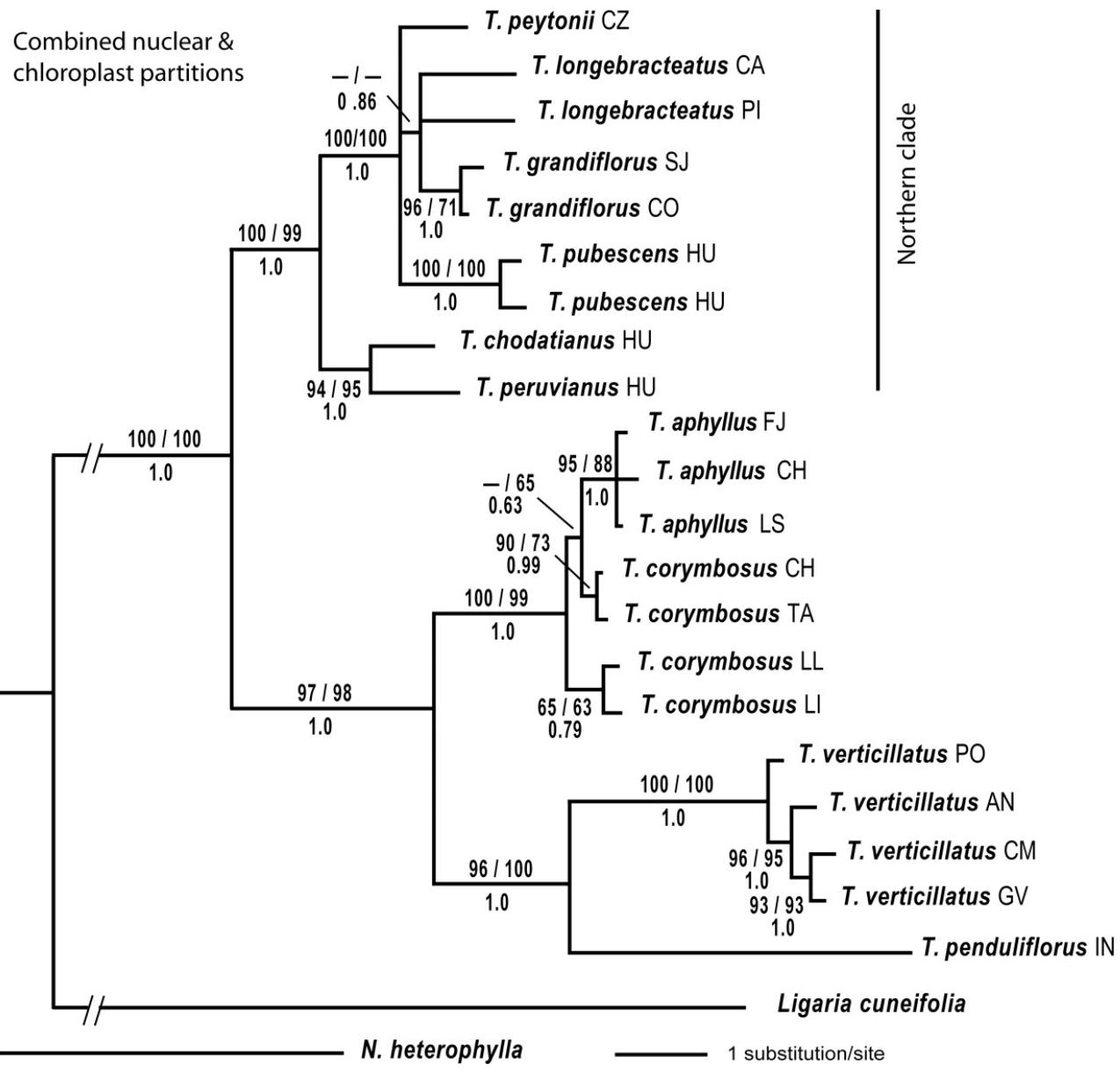
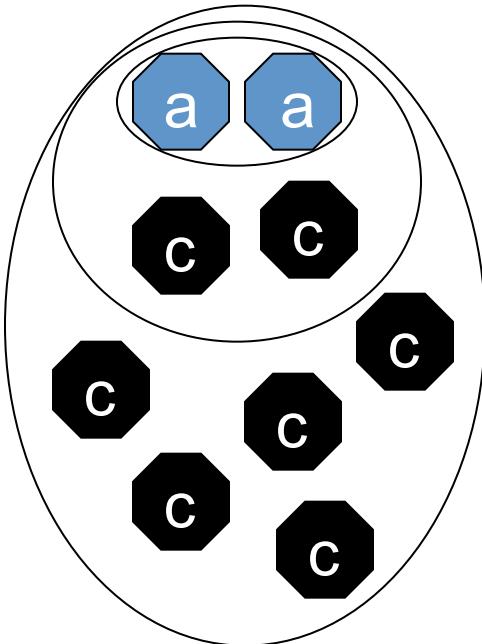
Comment: Character-based approach -- requires concordance of gene genealogies.

Problems:

- (1) requires huge amount of data to implement
- (2) it takes a very long time for many genes to achieve monophyly
- (3) would lead to lumping of evolutionary units

SHOULD SPECIES BE CONSISTENT WITH RECOVERED EVOLUTIONARY HISTORY?

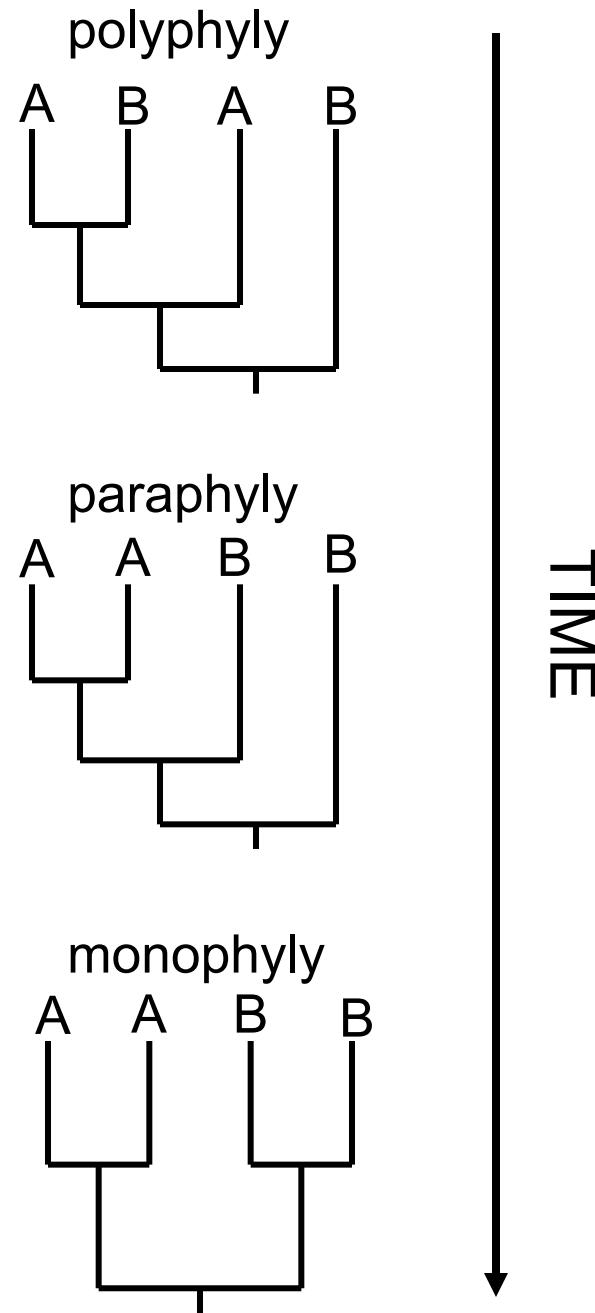
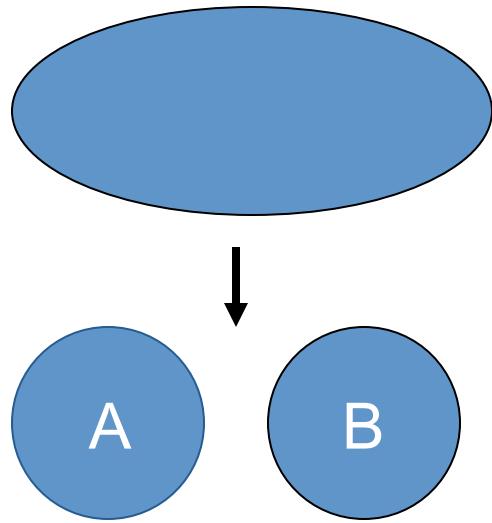
Multiple, independent origins (polyphyly) common for hybrid, polyploid, and ecological speciation

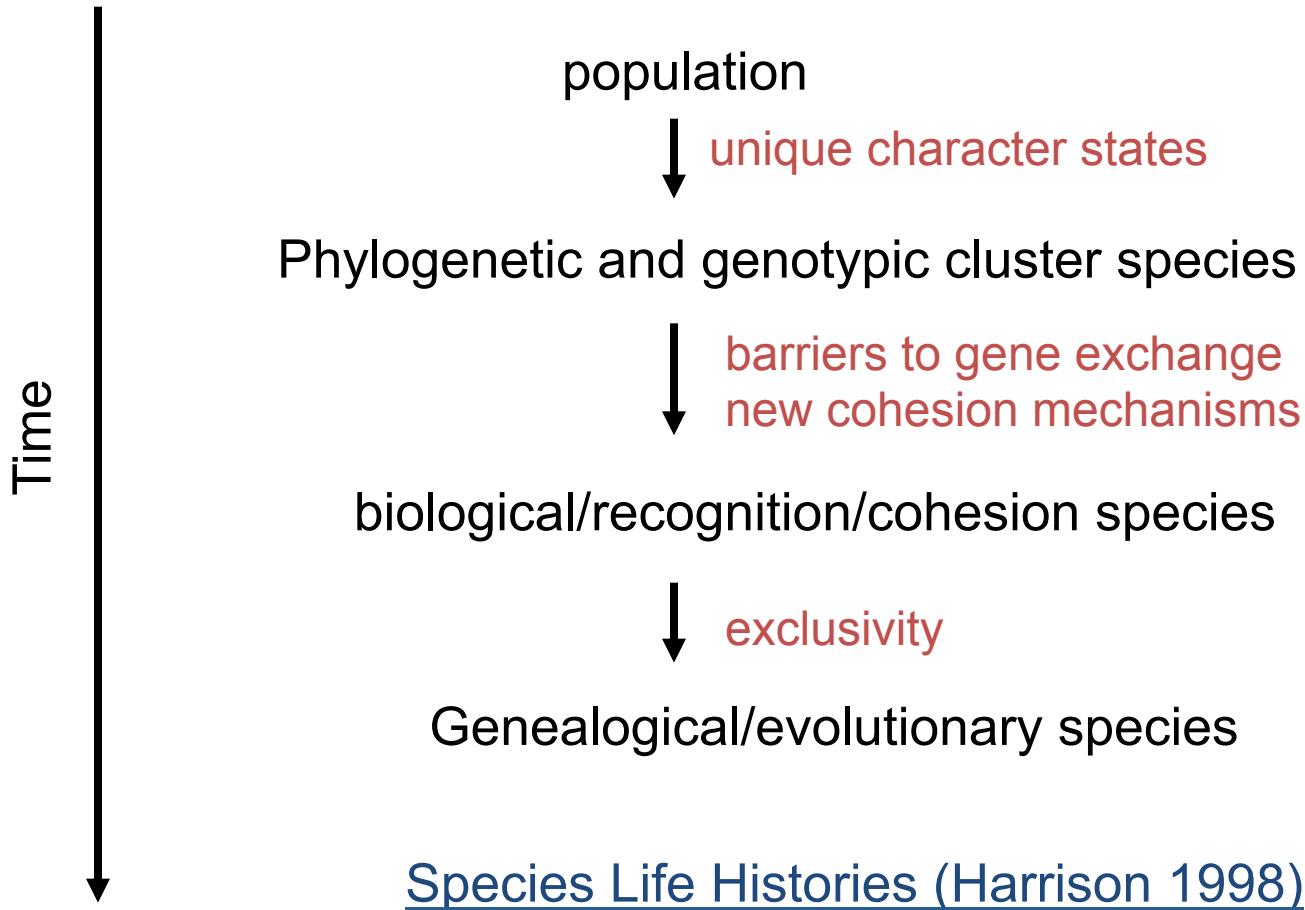


Mistletoe (*Tristerix*) Phylogeny, Amico et al. 2007, AJB

Fear of paraphyly

Phylogenetic status of species change over time





Unanswered Questions

Does hybridization enhance or erode phenotypic and reproductive discontinuities?

Do organisms that exhibit a mixture of sexual and asexual production form discrete clusters?

Do populations of a species evolve collectively? If so, how?