PLANT OF THE DAY!

Stevia rebaudiana, commonly known as sweetleaf

Close relative of sunflower native to South America

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

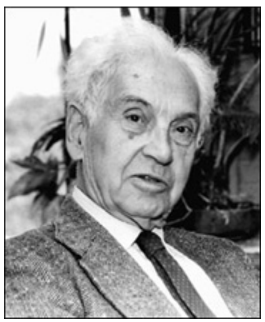
Big Questions

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?

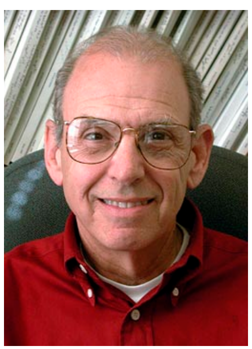
If plant species are real, then what causes plant diversity to be apportioned into clusters separated by gaps?

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)

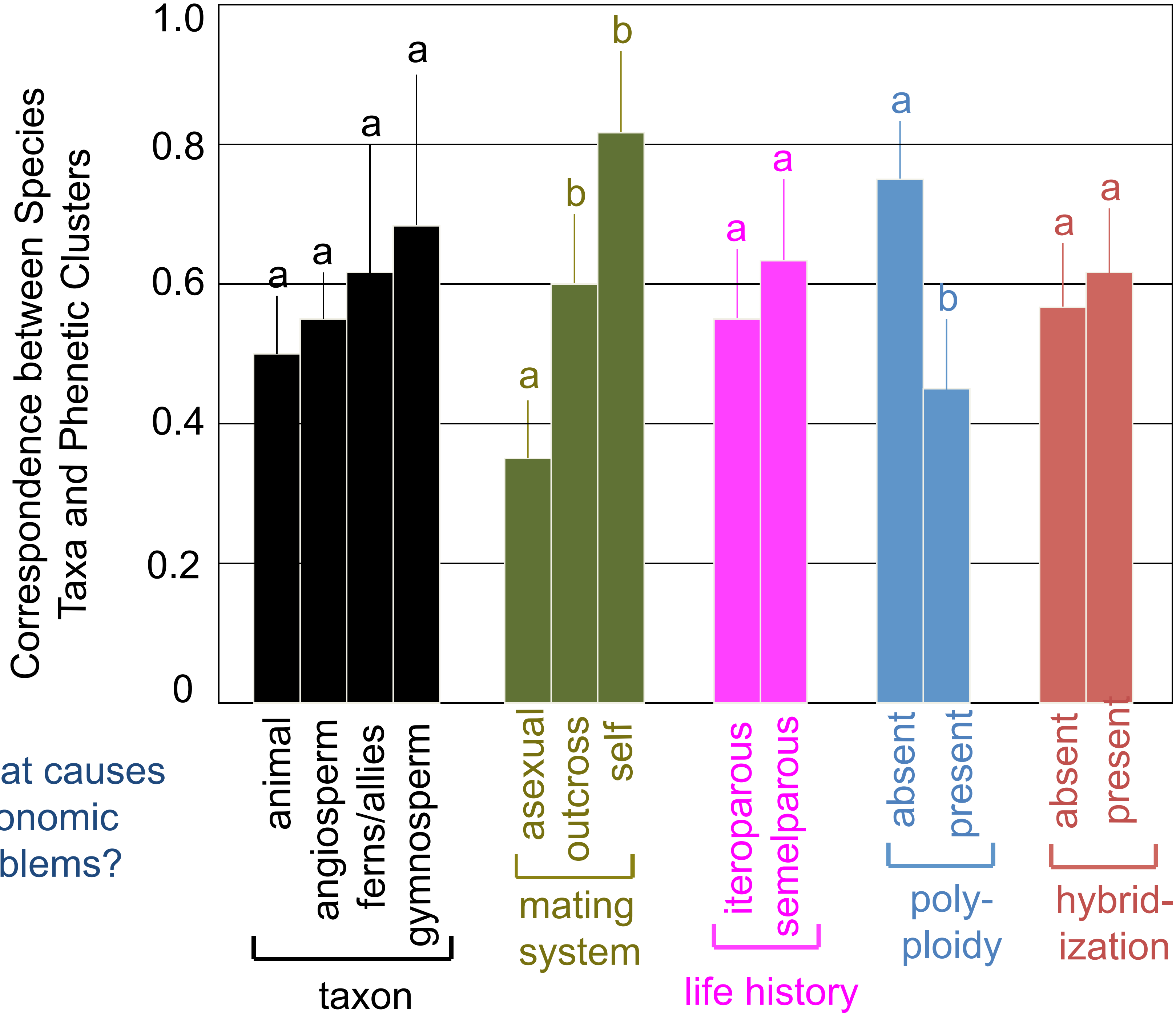


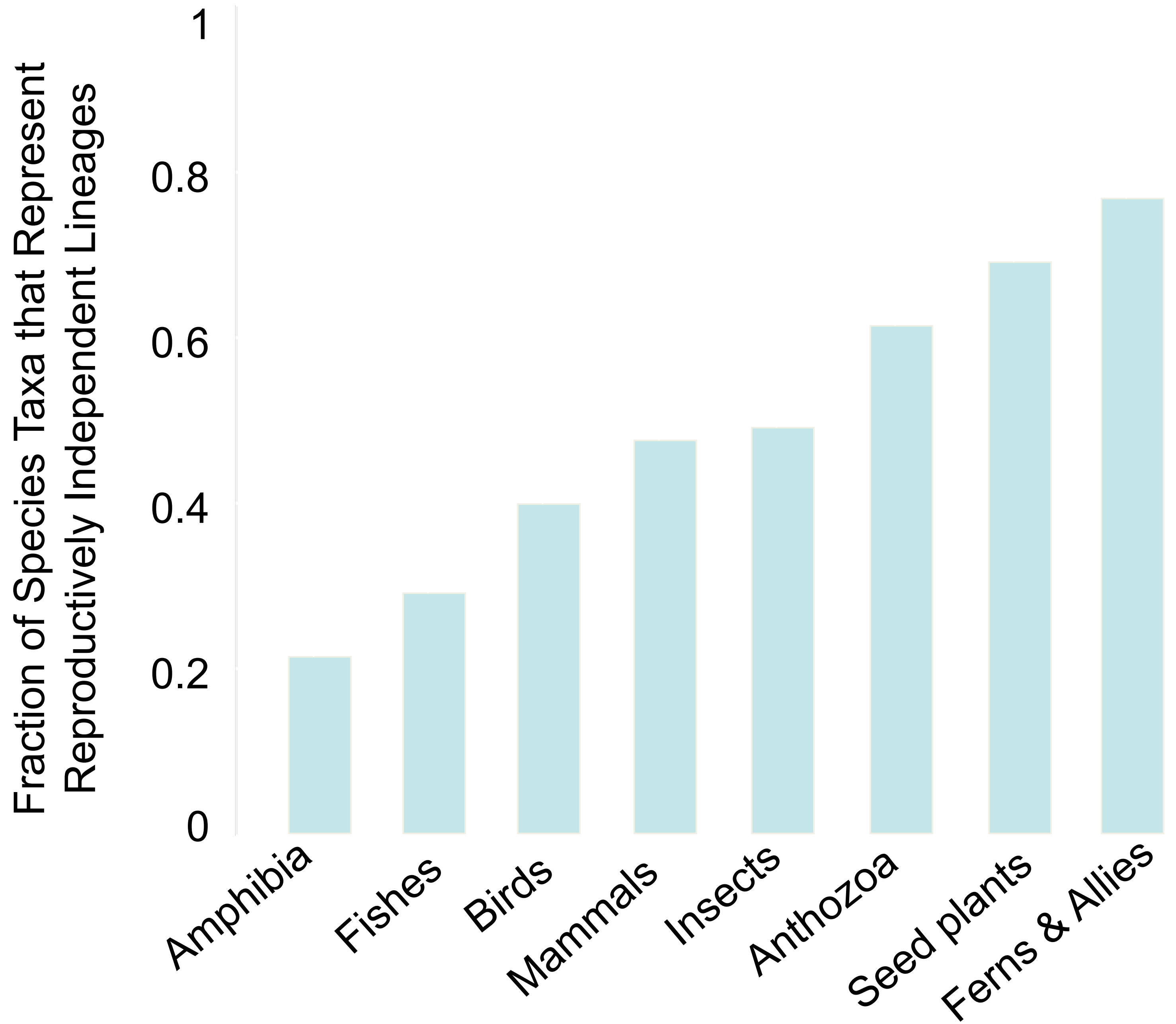
“The non-arbitrariness of the biological species is the result of … the internal cohesion of the gene pool… (Mayr, 1963, p. 21)



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

What causes taxonomic problems?





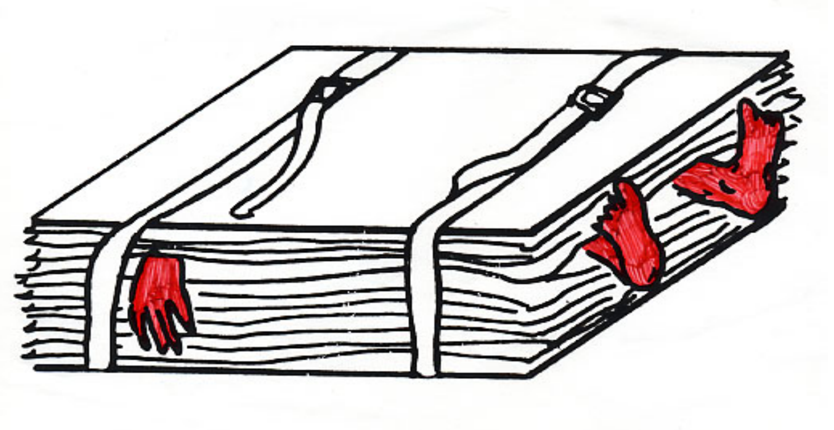
Fraction of Species Taxa that Represent Reproductively Independent Lineages
1
0.8
0.6
0.4
0.2
0
Amphibia
Fishes
Birds
Mammals
Insects
Anthozoa
Seed plants
Ferns & Allies

Conclusions about plant species

Most plant species are real entities, but….

•Botanists are overly influenced by "taxonomic horror stories"

•Taxonomists over-differentiate

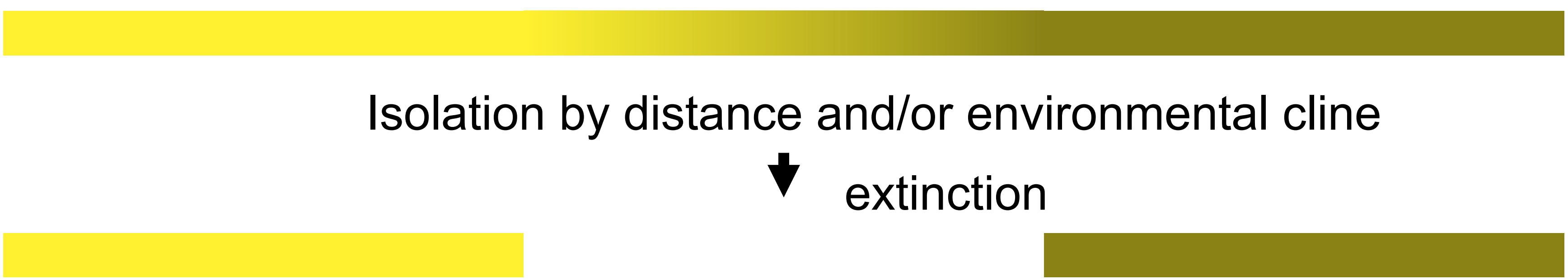


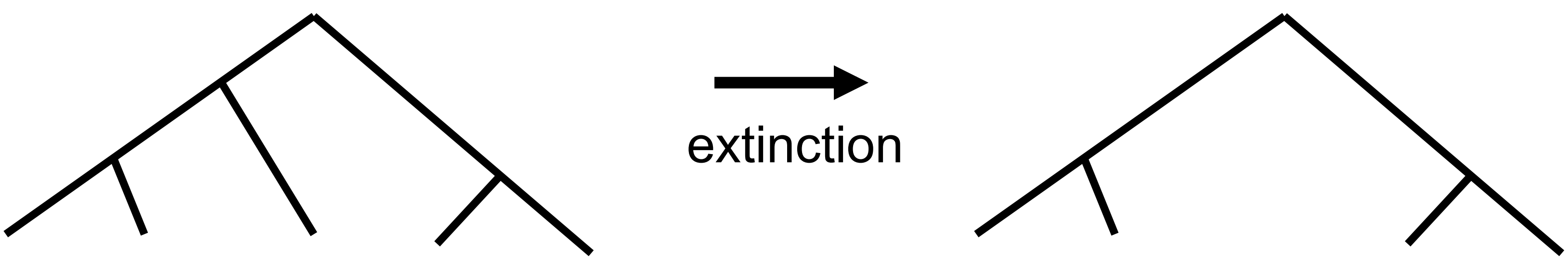
II. WHY ARE THERE SPECIES?

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





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

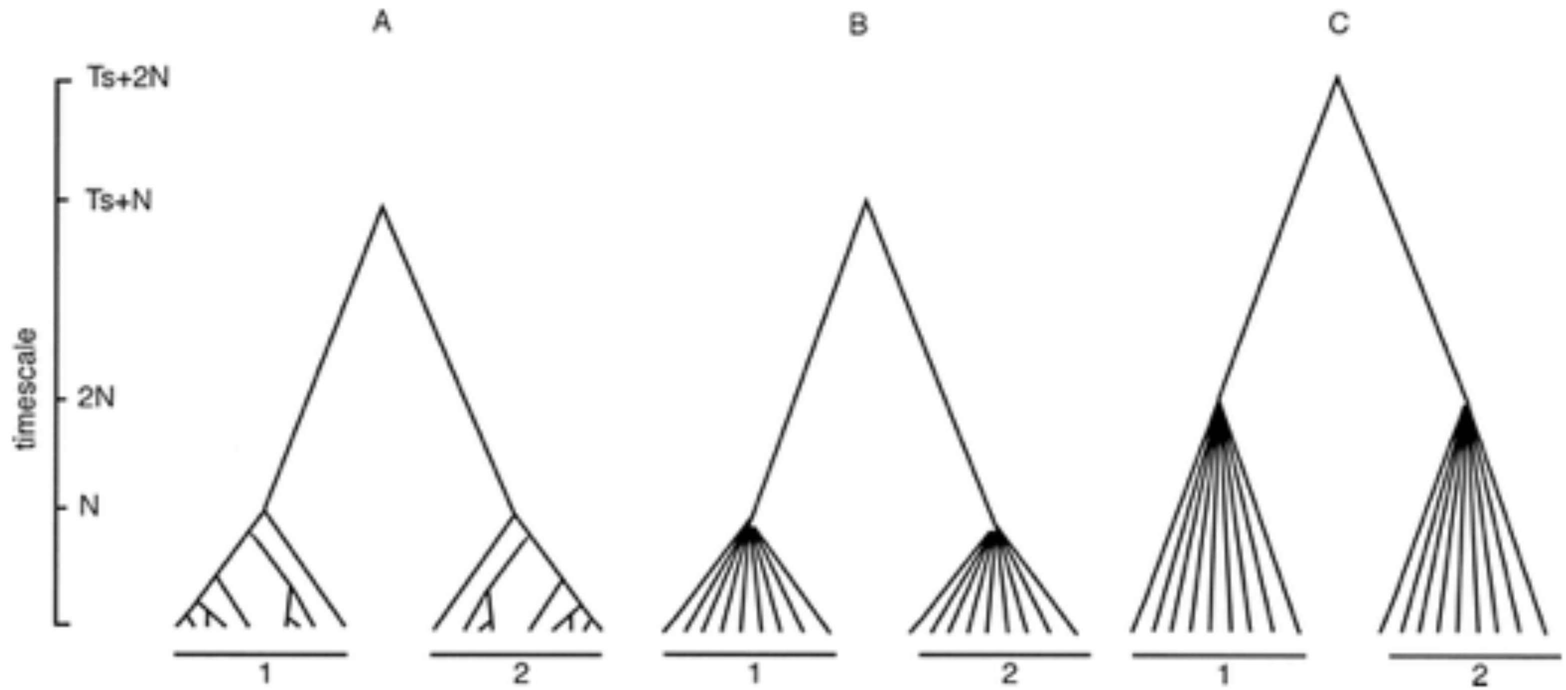


Fig. 3. Consensus gene trees from multiple loci sampled across two populations geographically isolated at time T_s, each with population size $N/2$. (A) Asexual haploid population. Assuming neutral coalescent, the Tmrca within each population is N generations. (B) Sexual haploid population. Same as (A) 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

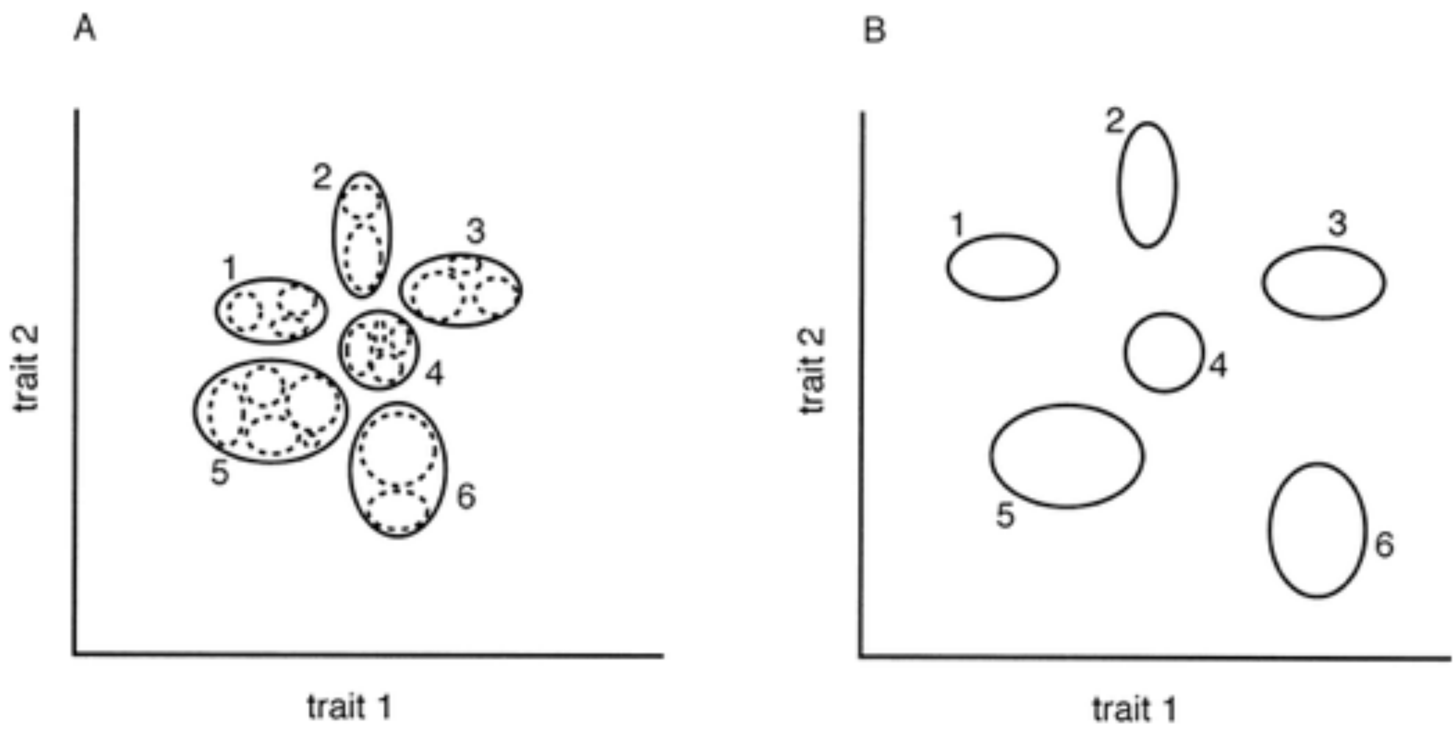


Fig. 4. Expected variation among clusters for two adaptive characters coded by multiple loci in (A) asexual and (B) sexual cases. Each ellipse represents the range of values observed within a single recognizable cluster. Note that the asexuals display further discreteness within each major cluster, due 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

<u>Alice explains why we name things:</u>

"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

<u>Darwin's other view of species:</u>

"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)

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) <u>vs</u> prospective (species as evolutionary units)

Mechanistic (process) <u>vs</u> historical (pattern)

Character-based (characters only) <u>vs</u> history-based (genealogy)

Theoretical <u>vs</u> operational

Relational (species defined in comparison to other species) <u>vs</u> non-relational

What features do we want in a species concept?

Class activity:

1) Think of features or things you want a species concept to do.
2) Rank the features on http://allourideas.org/speciesconcept
3) In groups of 3-4, pick your four most and least important features
4) Pick a species concept based on your ranking

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.

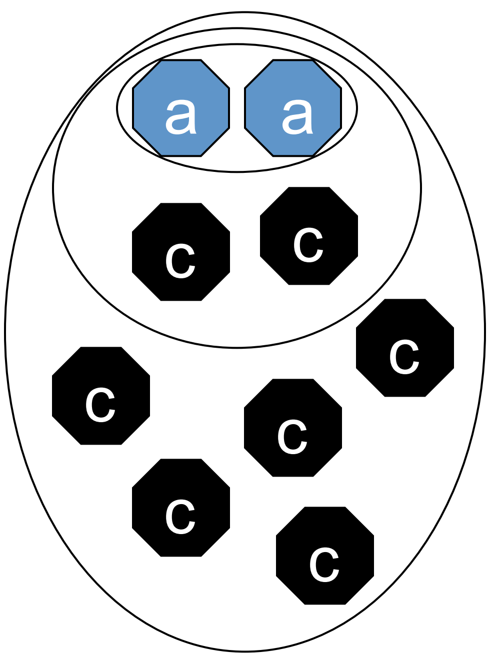
Problems: (1) requires huge amount of data to implement
(2) it takes a very long time for many genes to achieve monophyly
(3) would lead to lumping of evolutionary units

Species Concepts (a subset)

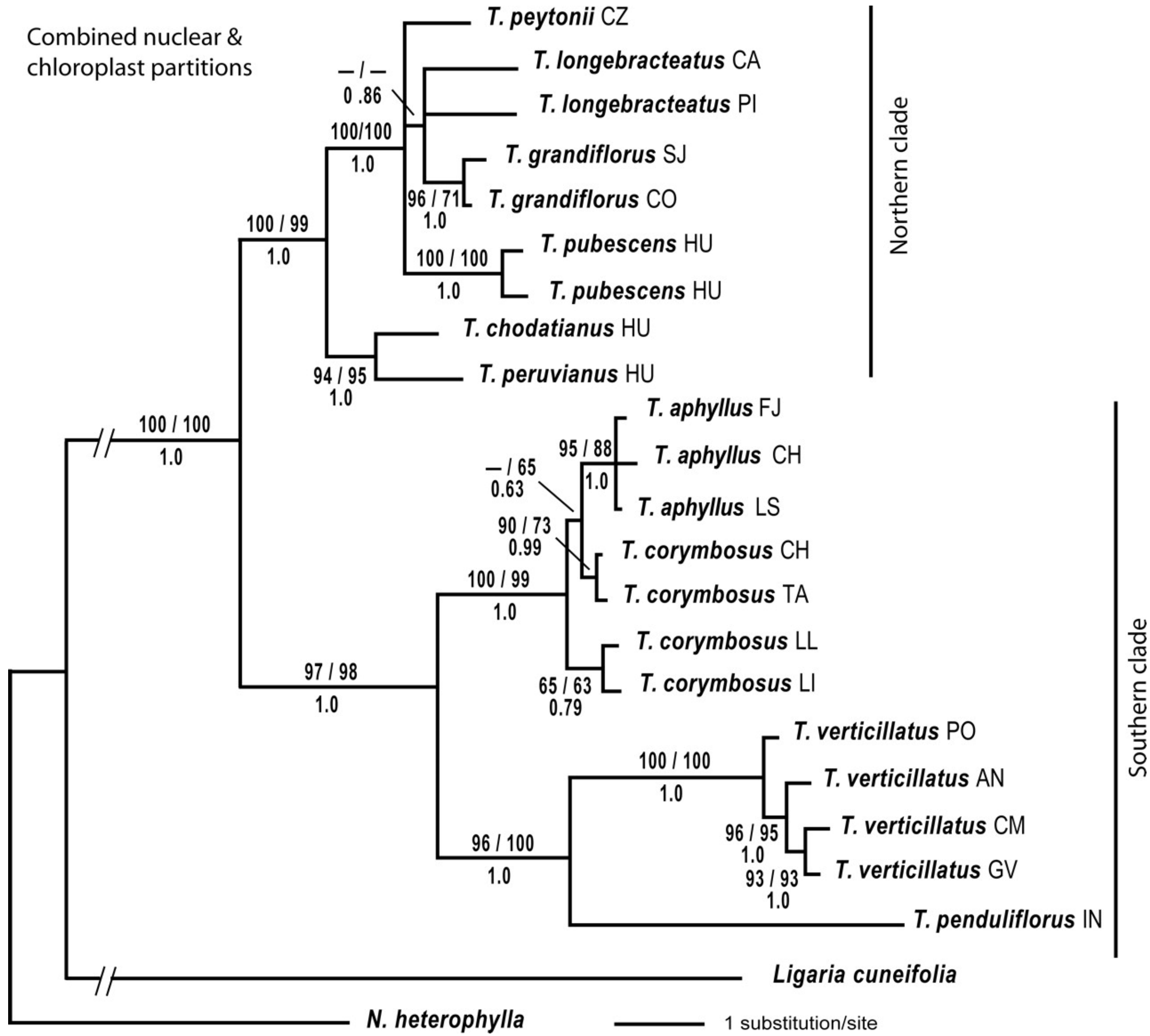
Biological Species Concept (BSC)
Evolutionary Species Concept (EvSC)
Recognition Species Concept (RSC)
Cohesion Species Concept (CSC)
Genotypic Cluster Species Concept (GCSC)
Ecological Species Concept (EcSC)
Phylogenetic Species Concept (PSC)
Genealogical Species Concept (monophyletic species concept)

SHOULD SPECIES BE CONSISTENT WITH RECOVERGED EVOLUTIONARY HISTORY?

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

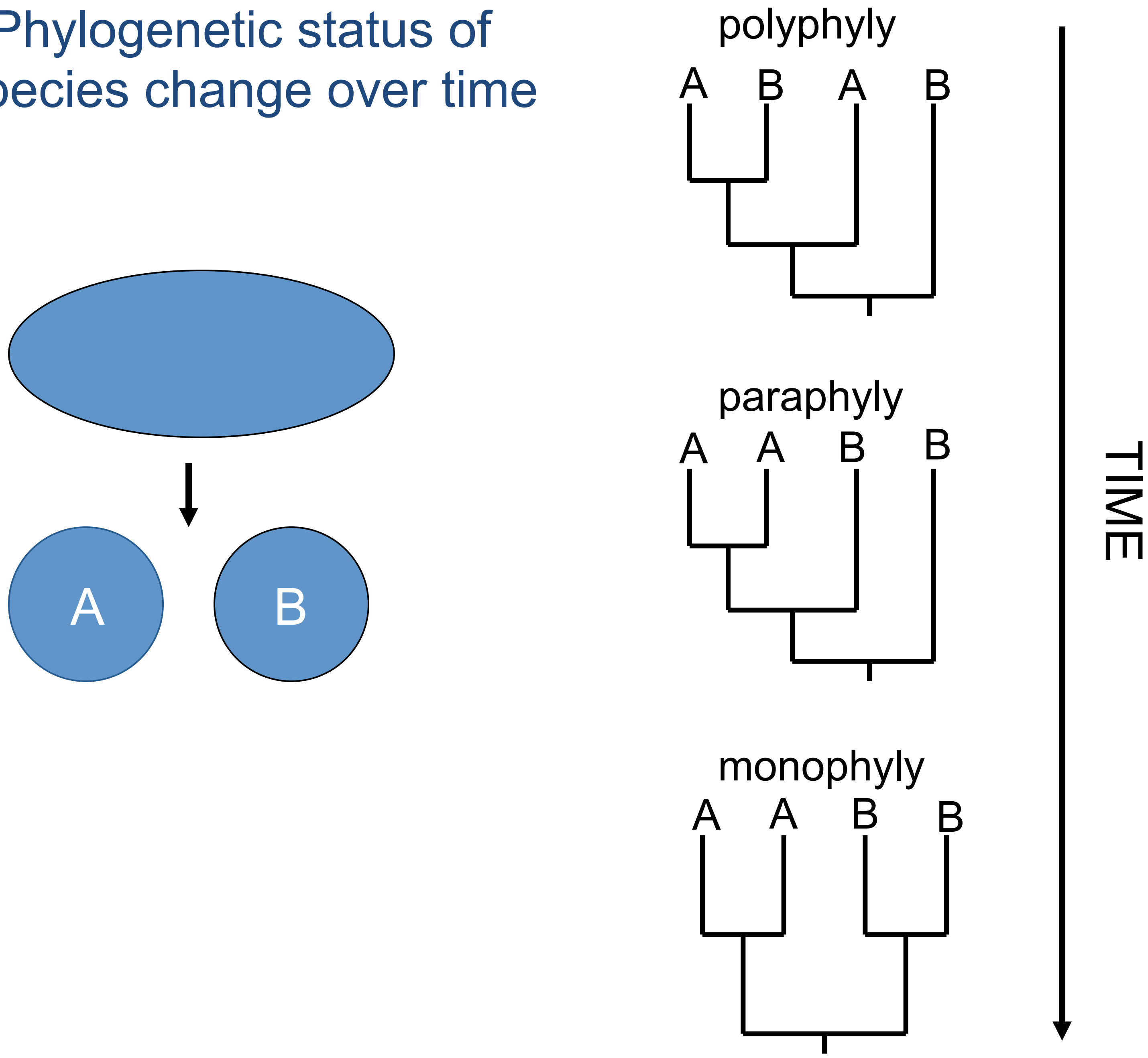


Fear of paraphyly



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

Phylogenetic status of species change over time



Time

population

↓ unique character states

Phylogenetic and genotypic cluster species

↓ barriers to gene exchange
new cohesion mechanisms

biological/recognition/cohesion species

↓ exclusivity

Genealogical/evolutionary species

Species Life Histories (Harrison 1998)

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?