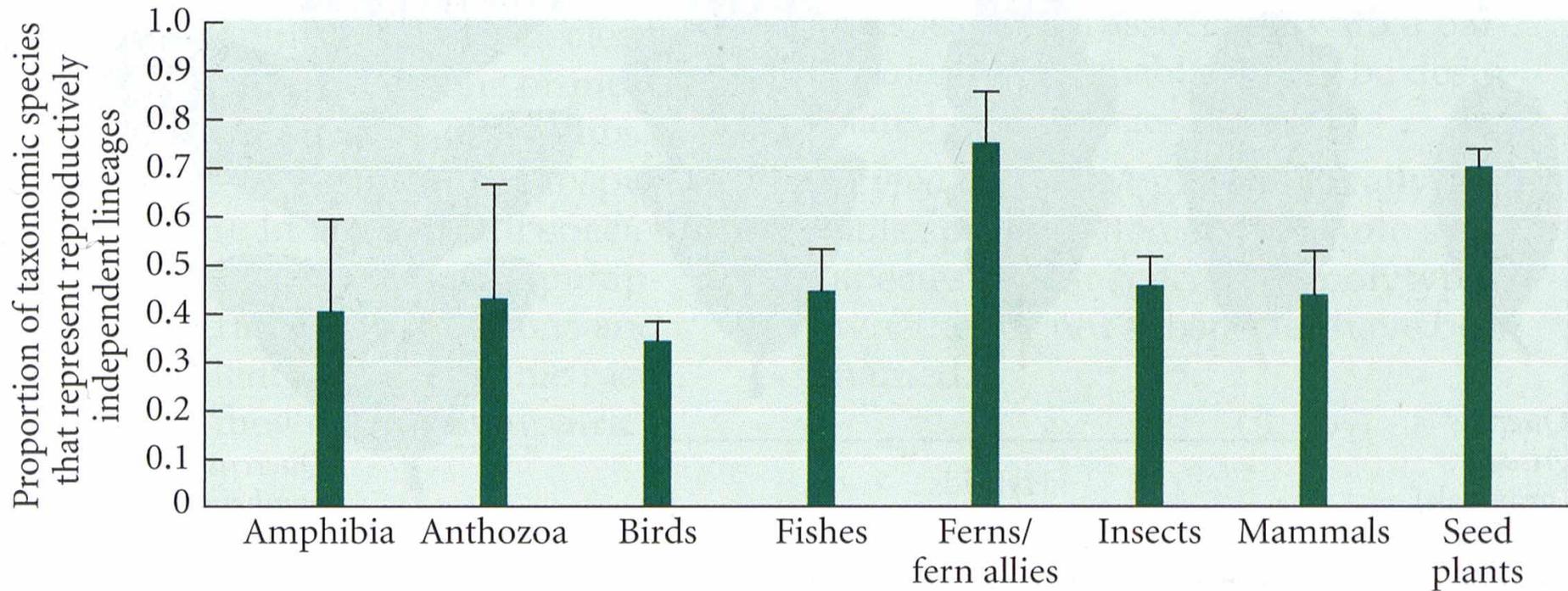


Species concept	Property(ies)	Advocates/references
Biological	Interbreeding (natural reproduction resulting in viable and fertile offspring)	Wright (1940); Mayr (1942); Dobzhansky (1950)
Isolation	*Intrinsic reproductive isolation (absence of interbreeding between heterospecific organisms based on intrinsic properties, as opposed to extrinsic [geographic] barriers)	Mayr (1942); Dobzhansky (1970)
Recognition	*Shared specific mate recognition or fertilization system (mechanisms by which conspecific organisms, or their gametes, recognize one another for mating and fertilization)	Paterson (1985); Masters et al. (1987); Lambert and Spencer (1995)
Ecological	*Same niche or adaptive zone (all components of the environment with which conspecific organisms interact)	Van Valen (1976); Andersson (1990)
Evolutionary	Unique evolutionary role, tendencies, and historical fate	Simpson (1951); Wiley (1978); Mayden (1997)
(some interpretations)	*Diagnosability (qualitative, fixed difference)	Grismer (1999, 2001)
Cohesion	Phenotypic cohesion (genetic or demographic exchangeability)	Templeton (1989, 1998a)
Phylogenetic	Heterogeneous (see next four entries)	(see next four entries)
Hennigian	Ancestor becomes extinct when lineage splits	Hennig (1966); Ridley (1989); Meier and Willmann (2000)
Monophyletic	*Monophyly (consisting of an ancestor and all of its descendants; commonly inferred from possession of shared derived character states)	Rosen (1979); Donoghue (1985); Mishler (1985)
Genealogical	*Exclusive coalescence of alleles (all alleles of a given gene are descended from a common ancestral allele not shared with those of other species)	Baum and Shaw (1995); see also Avise and Ball (1990)
Diagnosable	*Diagnosability (qualitative, fixed difference)	Nelson and Platnick (1981); Cracraft (1983); Nixon and Wheeler (1990)
Phenetic	*Form a phenetic cluster (quantitative difference)	Michener (1970); Sokal and Crovello (1970); Sneath and Sokal (1973)
Genotypic cluster (definition)	*Form a genotypic cluster (deficits of genetic intermediates; e.g., heterozygotes)	Mallet (1995)

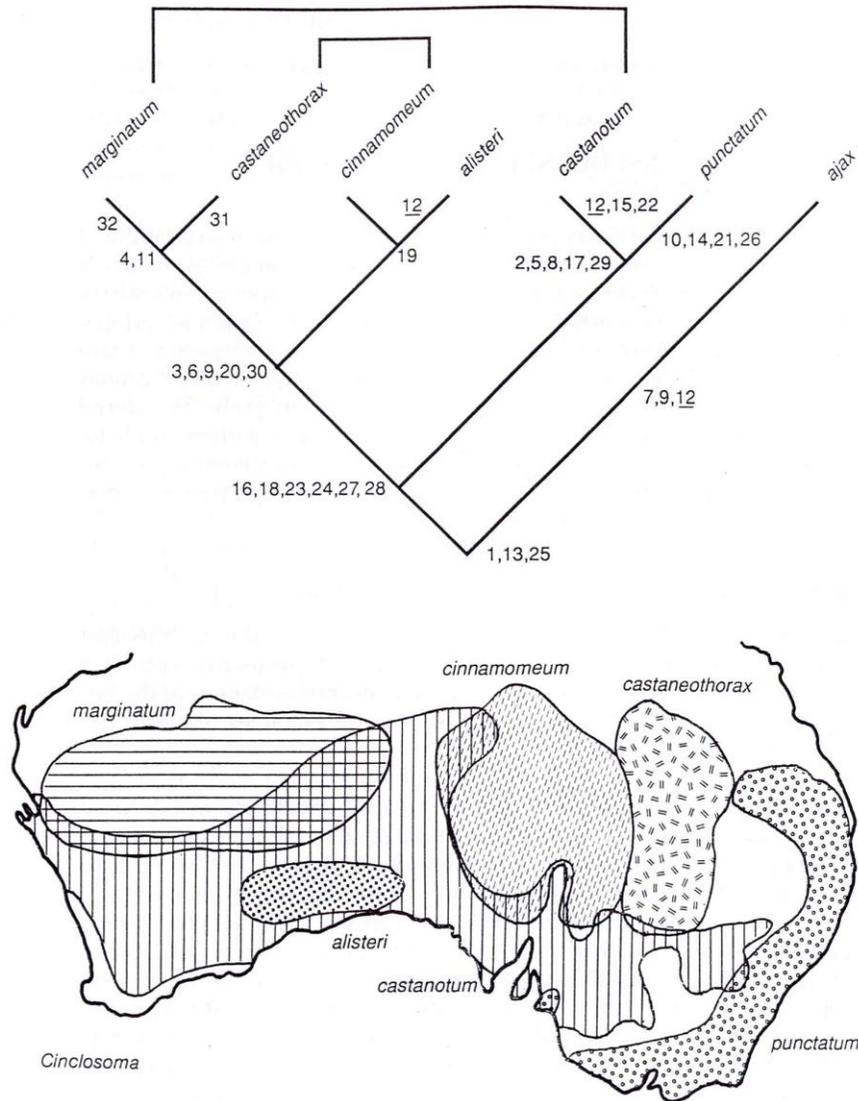
**Biological Species Concept (Mayr, 1991):** A species is a group of interbreeding natural populations that is reproductively isolated from other such groups.

Strengths:

- works for most taxa around us  
Mayr and Short (1970) claims it works for all but one of 607 species of NA birds
- worked for 93.5% of the flora in New Hampshire (Mayr 1992 in AJB)
- operational: can carry out crossing tests
- mechanistic, i.e., a process definition
- “prospective” of sorts



Futuyma (2009): Figure 17.3: The fraction of named species that represent reproductively independent lineages in several major groups of plants and animals. Contrary to widespread impression, taxonomic species are more likely to represent biological species in plants than in animals (After Riesenbergr et al. 2006).



**FIGURE 1.** Distribution and phylogenetic hypothesis for the phylogenetic species of Australian quail-thrushes (*Cinclusoma*). An analysis of 32 ordered characters (Table 2) produced a best-fit tree of 35 steps (consistency index = 0.914). The tree was rooted using the outgroup taxa, *Ptilorhoa castanota* and *P. leucosticta*. Underlined characters identify parallelisms and brackets link taxa that are known to hybridize. Distributions are after Ford (1983).

**Cracraft objected to BSC because the ability to interbreed is often a shared trait(s) inherited by a “bevy” of descendents**

From Cracraft, J. 1989. Speciation and its Ontogeny: The empirical consequences of alternating species concepts... pp. 28-59. In *Speciation and its Consequences*, Otte, D. and J.A. Endler (eds). Sinauer, Sunderland MA.

**Recognition Concept (Paterson, 1985):** Species are the most inclusive population of individual biparental organisms which share a common fertilization system. A species is “a field for gene recombination.”

- a species is a group of organisms sharing a common fertilization system
- focus becomes what holds various populations together (why they will share a common evolutionary fate).
- emphasizes what is holding together a species (as opposed to the isolation)

Shortcomings:

- same as those for BSC
- locked into gene flow as the only evolutionary force holding a species together

Strengths:

- isolation is usually the product of speciation, and not the mechanism that holds a “species or lineage together”
- recognition concept and not BSC tells us about process of speciation
- is "the positive inverse of the BSC " (Templeton 1989)

**Evolutionary Species Concept** (Simpson 1961, Wiley 1978, 1981): A species consists of a population or group of populations that share a common evolutionary fate through time.

Simpson (1961:153): An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary (fate) role and tendencies.

- focus is on describing an observed *pattern*
- species can be held together by many forces:
  - a. gene flow
  - b. natural selection or ecological constraints
  - c. developmental constraints or canalization
  - d. etc.

**Evolutionary Species Concept** (Simpson 1961, Wiley 1978, 1981): A species consists of a population or group of populations that share a common evolutionary fate through time.

Shortcomings:

- what is common evolutionary fate?
- a bit vague since common does not equal identical evolutionary fate
- subjective and difficult to test
- non-mechanistic, i.e., only the pattern matters (both a weakness and a strength perhaps)

Strengths:

- works for asexual taxa
- works for fossils (Simpson was palaeontologist)

\* The ESC seems to sit at the core of other species definitions:

## Unified Species Concept (De Quieroz, 2007)

A species is a separately evolving metapopulation lineage

A **metapopulation** consists of a group of spatially separated populations of the same species which interact at some level. Often used to describe a dynamic set of subpopulations over a landscape that may lack appropriate habitat.

Species concept	Property(ies)	Advocates/references
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## **Phylogenetic Species Concept(s)**

**Diagnosability Camp** (Cracraft, Nixon, Platnik, Wheeler, etc.): The smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent (Cracraft 1983: 170). The smallest detected samples of self-perpetuating organisms that have unique sets of characters (Nelsen and Platnik, 1981:12).

**Monophyly Camp** (Donoghue, Mishler, de Quieroz, etc.): The smallest exclusive monophyletic group. Or “a population or group of populations defined by one or more apomorphous features” (Rosen 1979).

- \* independent of process (pattern-based definition)
- \* testable
- \* apply to asexual taxa, fossils, etc.

# Phylogenetic Species Concept(s)

Diagnosability Camp (Cracraft, Nixon, Platnik, Wheeler, etc.): The smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent (Cracraft 1983: 170). The smallest detected samples of self-perpetuating organisms that have unique sets of characters (Nelsen and Platnik, 1981:12).

- crux: need trait found in all members of a given population/  
taxon that is absent in closely-related ones thus *diagnosable*
  - \* a single fixed, shared trait (trait could be secondarily lost in some members)
- a character-based definition (works for dead organisms (museum specimens, fossils))
- less subjective than evolutionary concept: i.e., it's testable

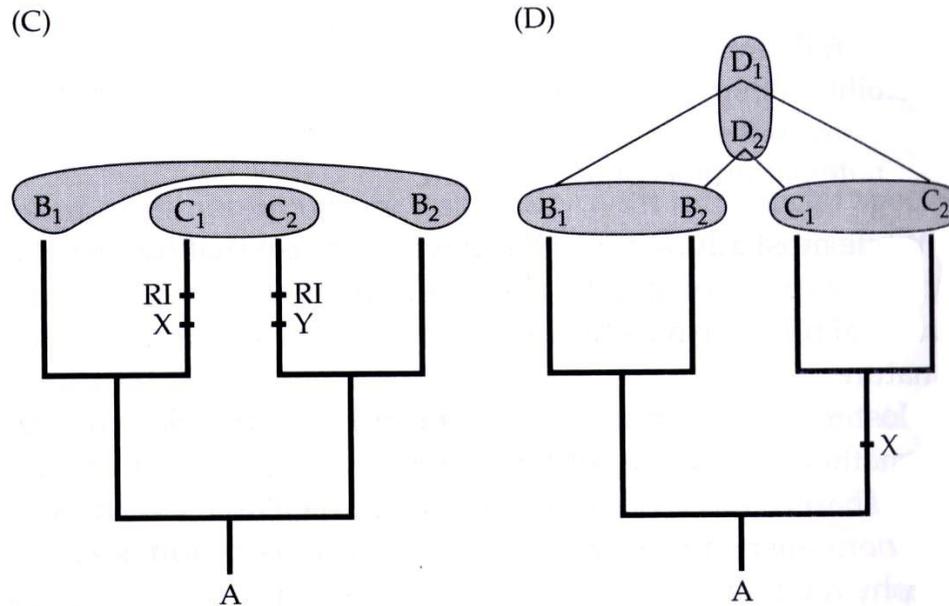
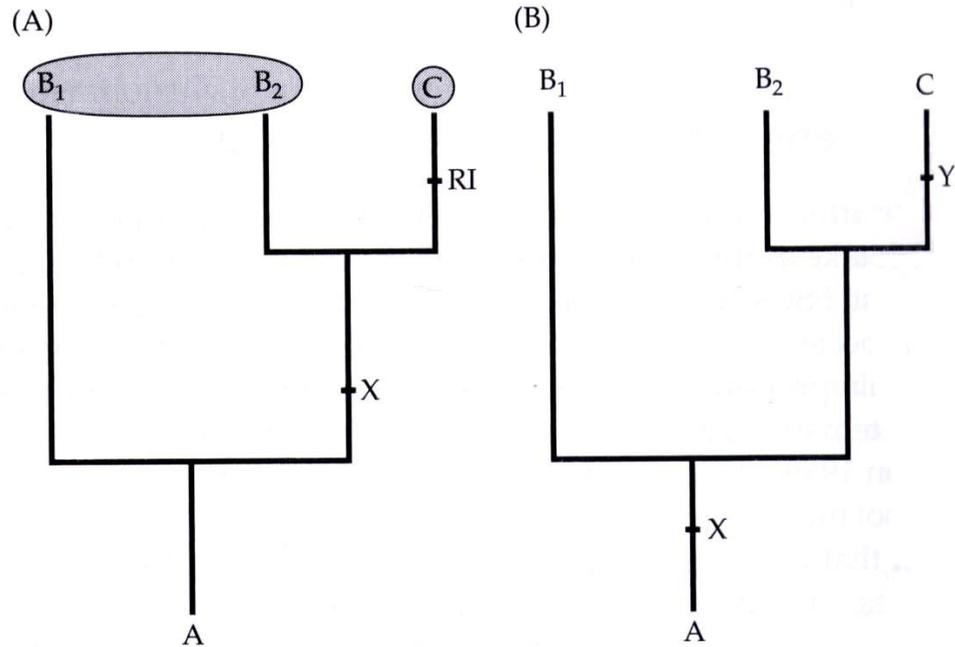
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The smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent (Cracraft 1983: 170). The smallest detected samples of self-perpetuating organisms that have unique sets of characters (Nelsen and Platnik, 1981:12).

Problems:

- \* mother species is often paraphyletic
- \* trivial changes in nucleotides is sufficient for recognition
- \* possible for two populations to be diagnosable yet still be genetic contact



**Figure A.1** Phylogenies showing disparities between evolutionary history and reproductive isolation (see text for discussion). (A) Speciation in a peripheral isolate. (B) Species diagnosed by a trait difference using Phylogenetic Species Concept 1 (PSC 1). (C) Parallel speciation yielding a polyphyletic biological species. (D) Allopolyploidy yielding a polyphyletic biological species.

## **Phylogenetic Species Concept(s)**

Monophyly Camp (Donoghue, Mishler, de Quieroz, etc.): The smallest exclusive monophyletic group. Or “a population or group of populations defined by one or more apomorphous features” (Rosen 1979).

- species comprise all descendants of a common ancestor
- smallest exclusive monophyletic group
- exclusivity: all members must be more closely related to each other, than any is to any outside member
- \* fixes paraphyly problem of diagnosability definition

## **Phylogenetic Species Concept(s)**

Monophyly Camp (Donoghue, Mishler, de Quieroz, etc.): The smallest exclusive monophyletic group. Or “a population or group of populations defined by one or more apomorphous features” (Rosen 1979).

- need phylogeny before you can recognize a species
- can't easily applied to some asexual taxa
- blind to process (and therefore retrospective)
- still tendency to split out trivially differentiated entities

## Prospective vs retrospective species definitions (O'Hara)

- \* prospective definitions: invoke criteria that have implications for future status of populations/species
  - allow one to make predictions about future pattern of variation?
- \* retrospective definitions: examine pattern or end-processes; eventual fate of an entity or pair of entities is irrelevant
- \* prospective definitions are inherently mechanistic
- \* retrospective definitions are inherently historical (pattern-based)

**Cohesion Concept** (Templeton, 1989): A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms. Or a species is the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability.

\* a population geneticist's application of Simpson's Evolutionary Species Concept + Patterson's Recognition Concept

## Cohesion Concept (Templeton, 1989)

\* Templeton argues that:

- gene flow is but one of the principal mechanisms that hold species together (genetic exchangeability)
- other evolutionary forces can hold species together (demographic or ecological exchangeability)
  - e.g., drift sometimes holds taxa together through coalescence
  - e.g., selection sometimes holds populations in a similar evolutionary position
  - e.g., developmental canalization and other constraints could lock populations into a shared fate

“There are two problems with the isolation and recognition concepts ...both caused by sex: too little and too much sex.”

Too little sex

- a. parthenogenetic taxa, apomicts, etc. (note rotifer example)
- b. selfers (barley)
- c. sib-mating (many parasitic Hymenoptera)
- d. gene flow is more restricted than many think (Ehrlich and Raven (1969))

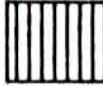
## Too much sex

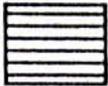
*syngameons*: "the most inclusive unit of interbreeding in a taxon hybridizing species group (Grant, 1981)."

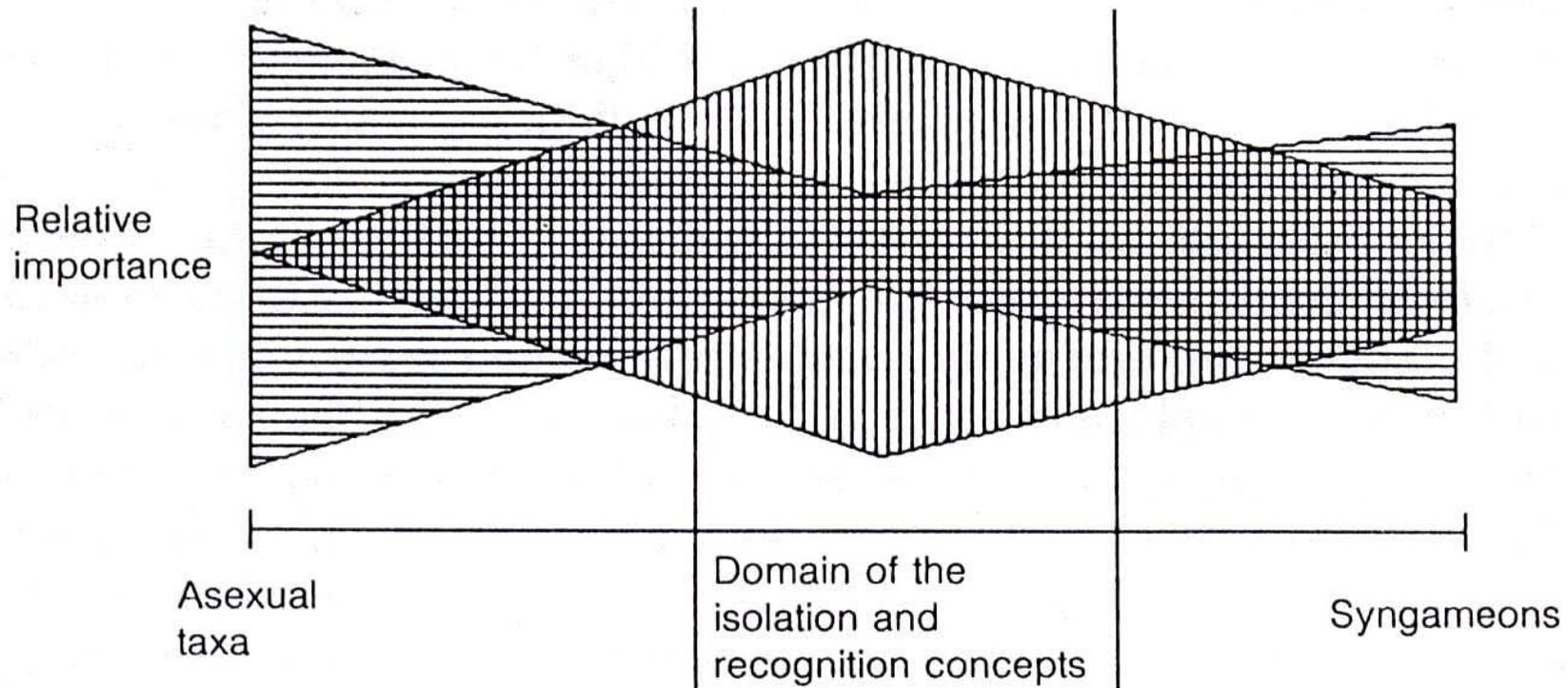
### Examples

- a. *Populus* (Eckenwalder, 1984)  
cottonwoods: separate but hybridizing for last 12 million years
- b. *Quercus* (Van Valen)
- c. *Canis* (Wayne) (wolf and coyote)
- d. *Drosophila*: detailed example with molecular evidence of different DNA haplotypes
- e. baboons, cattle, gophers, rabbits ...

# THE MEANING OF SPECIES AND SPECIATION 21

 Genetic exchangeability

 Demographic exchangeability



**TABLE 2.** Classification of cohesion mechanisms.

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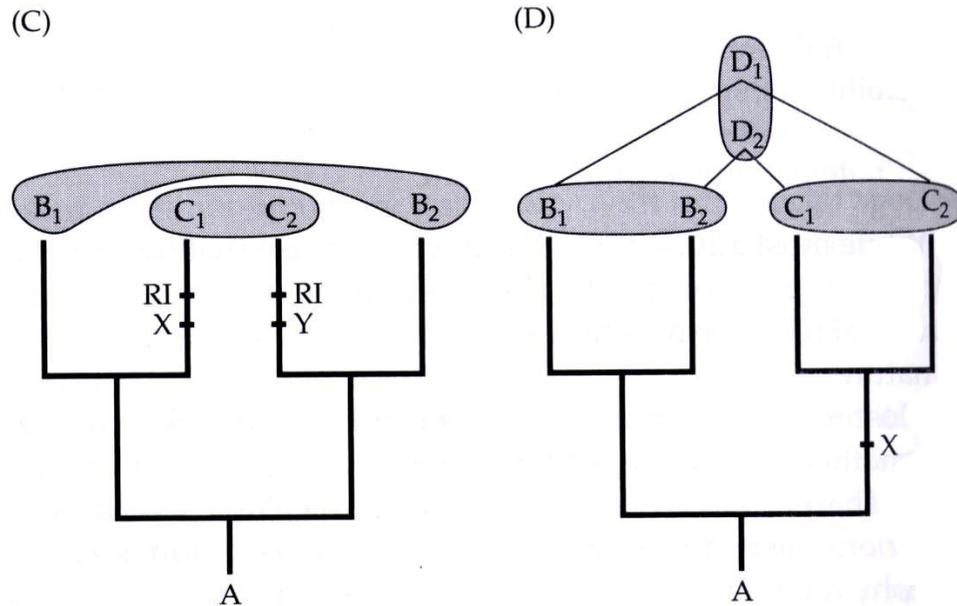
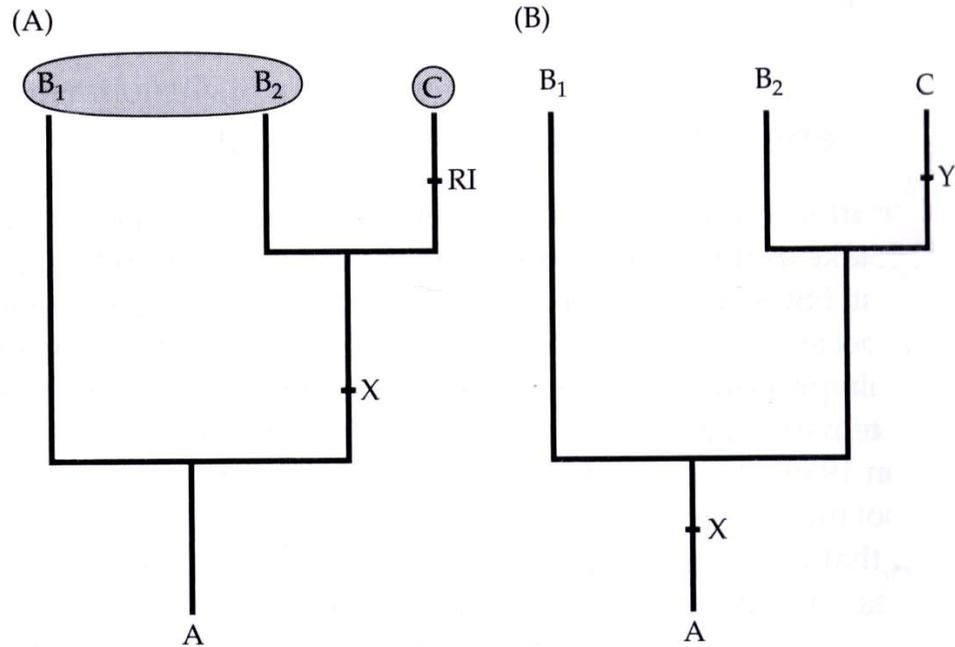
- I. Genetic exchangeability: the factors that define the limits of spread of new genetic variants through *gene flow*
  - A. Mechanisms promoting genetic identity through *gene flow*
    1. Fertilization system: the organisms are capable of exchanging gametes leading to successful fertilization
    2. Developmental system: the products of fertilization are capable of giving rise to viable and fertile adults
  - B. Isolating mechanisms: genetic identity is preserved by the lack of *gene flow* with other groups
- II. Demographic exchangeability: the factors that define the fundamental niche and the limits of spread of new genetic variants through *genetic drift* and *natural selection*
  - A. Replaceability: *genetic drift* (descent from a common ancestor) promotes genetic identity
  - B. Displaceability
    1. Selective fixation: *natural selection* promotes genetic identity by favoring the fixation of a genetic variant
    2. Adaptive transitions: *natural selection* favors adaptations that directly alter demographic exchangeability. The transition is constrained by:
      - a. Mutational constraints on the origin of heritable phenotypic variation
      - b. Constraints on the fate of heritable variation
        - i. Ecological constraints
        - ii. Developmental constraints
        - iii. Historical constraints
        - iv. Population genetic constraints

**Cohesion Concept** (Templeton, 1989): A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms. Or a species is the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability.

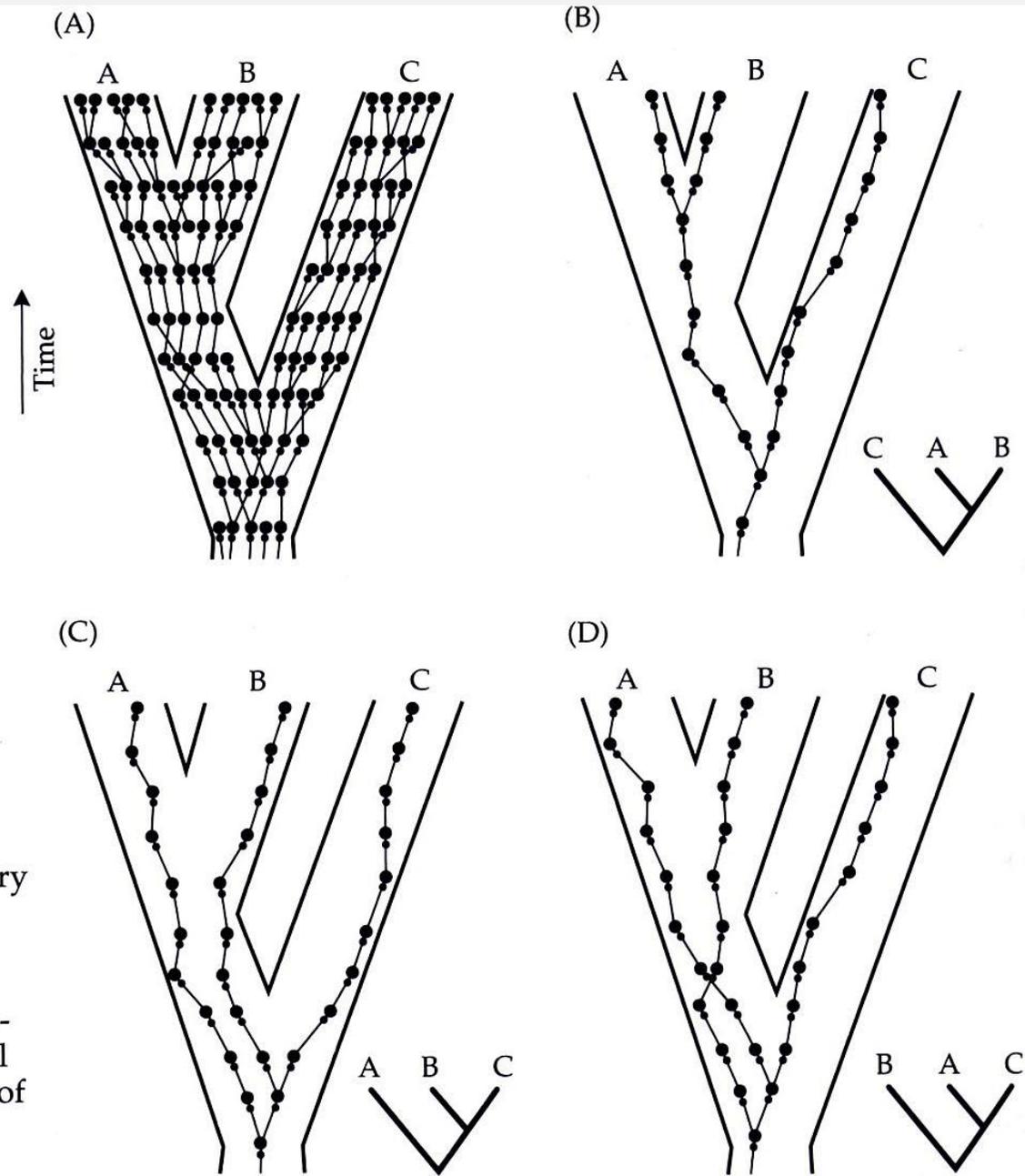
Problems:

\* little vague and thus difficult in application

- When are two populations demographic exchangeable and when are they distinct?
- How exchangeable is exchangeable...
- Not easily testable, not easily disproven

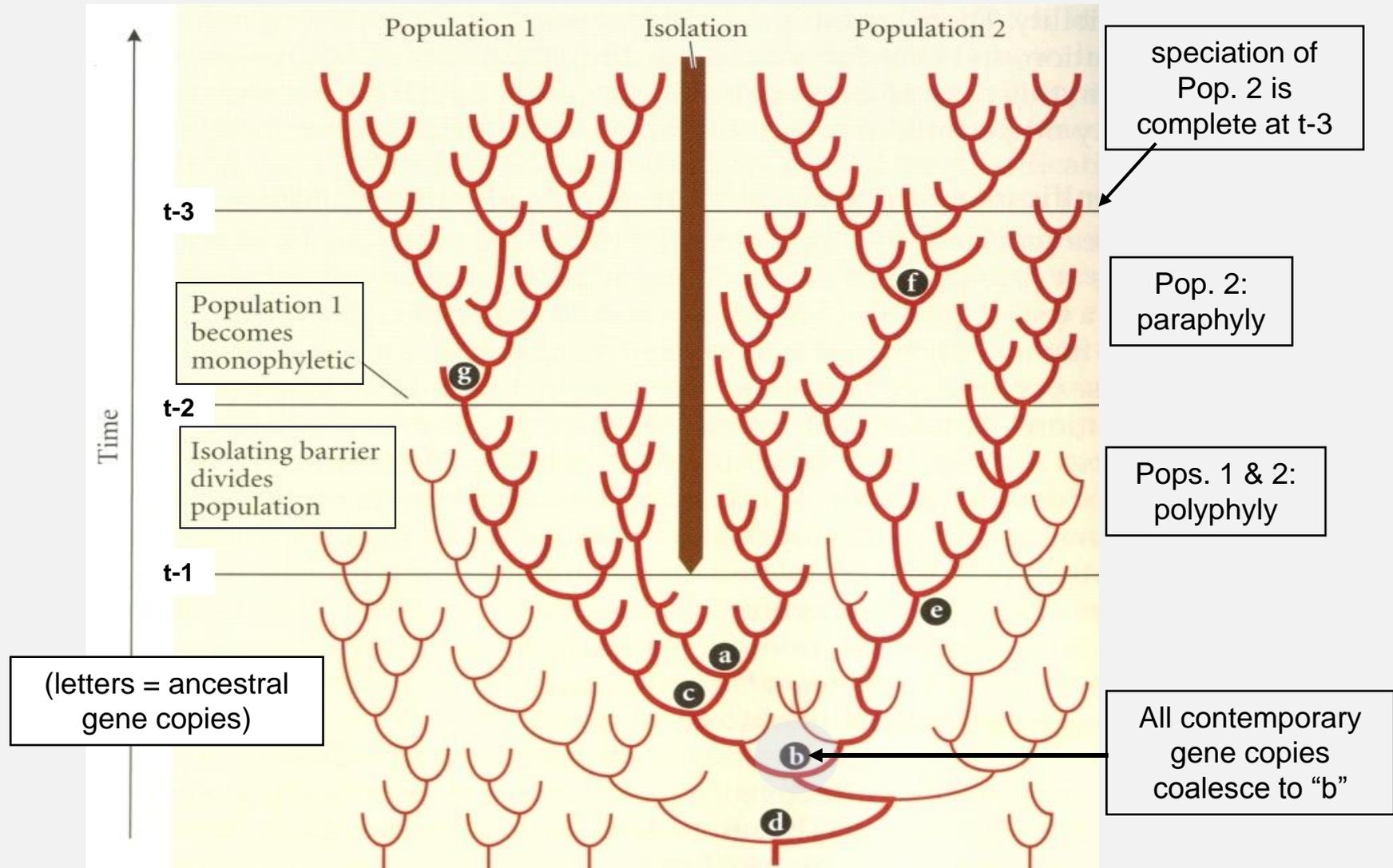


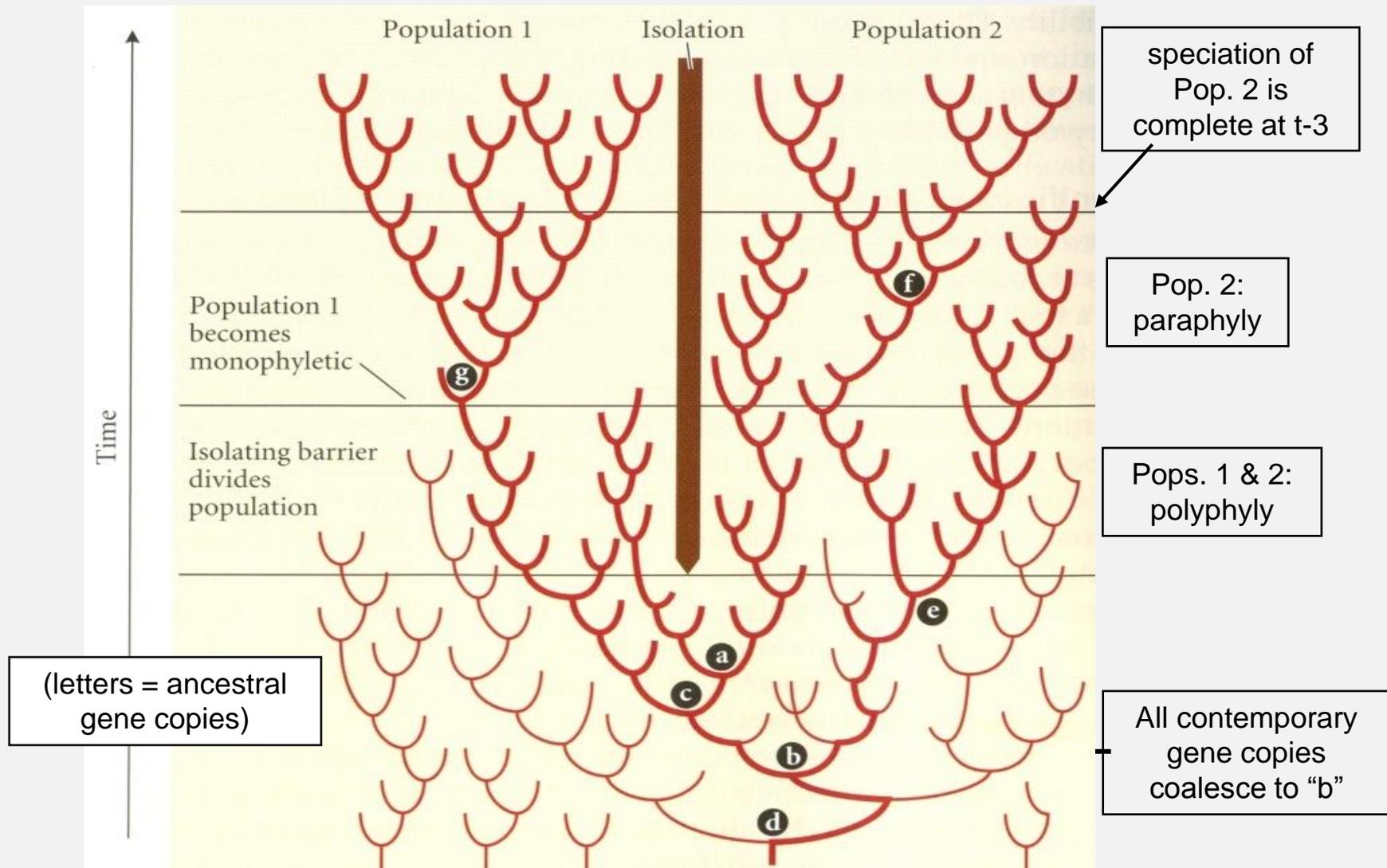
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**Figure A.2** Gene sorting occurring in a phylogeny whose true population history is shown in (A). Depending on which gene copies are picked for analysis, one can derive all three possible phylogenies, shown by the small diagrams to the lower right of diagrams (B), (C), and (D). (After Hey 1994.)

Lineages of haplotypes at a single locus: transition from polyphyly to paraphyly to monophyly during speciation (Avisé & Ball 1990)





Once two populations become separated (by a barrier to gene flow) their genes will go from being polyphyletic to paraphyletic to reciprocally monophyletic (through drift and selection). reciprocally monophyletic = when all copies of a gene within one lineage are all more closely related to one another than any outside (= exclusivity).

**Genotypic Cluster Concept** (Mallet, 1995): “A species is a [morphologically or genetically] distinguishable group of individuals that has few or no intermediates when in contact with other such clusters. Species...are...identifiable genotypic clusters...recognized by a deficit of intermediates, both at single loci (heterozygous deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters).”

- a geneticists pattern concept (independent of processes)
- \* looks for genetic clusters identified by absence of intermediates, deficit of heterozygotes, and or linkage disequilibrium