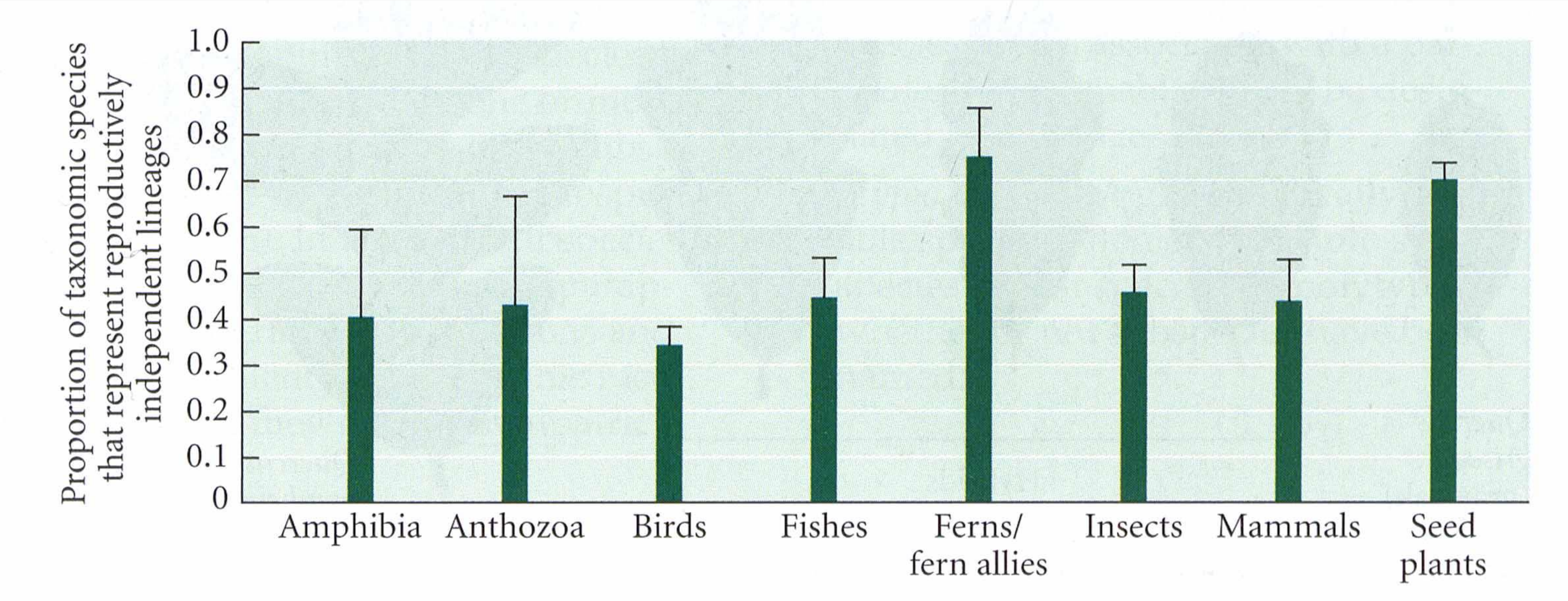
Species concept	Property(ies)	Advocates/references
Biological	Interbreeding (natural reproduction resulting in viable and fertile offspring)	Wright (1940); Mayr (1942); Dobzhansky (1950)
Isolation	*Intrinsic reproductive isolation (absence of interbreeding between heterospecific organisms based on intrinsic 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 Riesenberg et al. 2006).

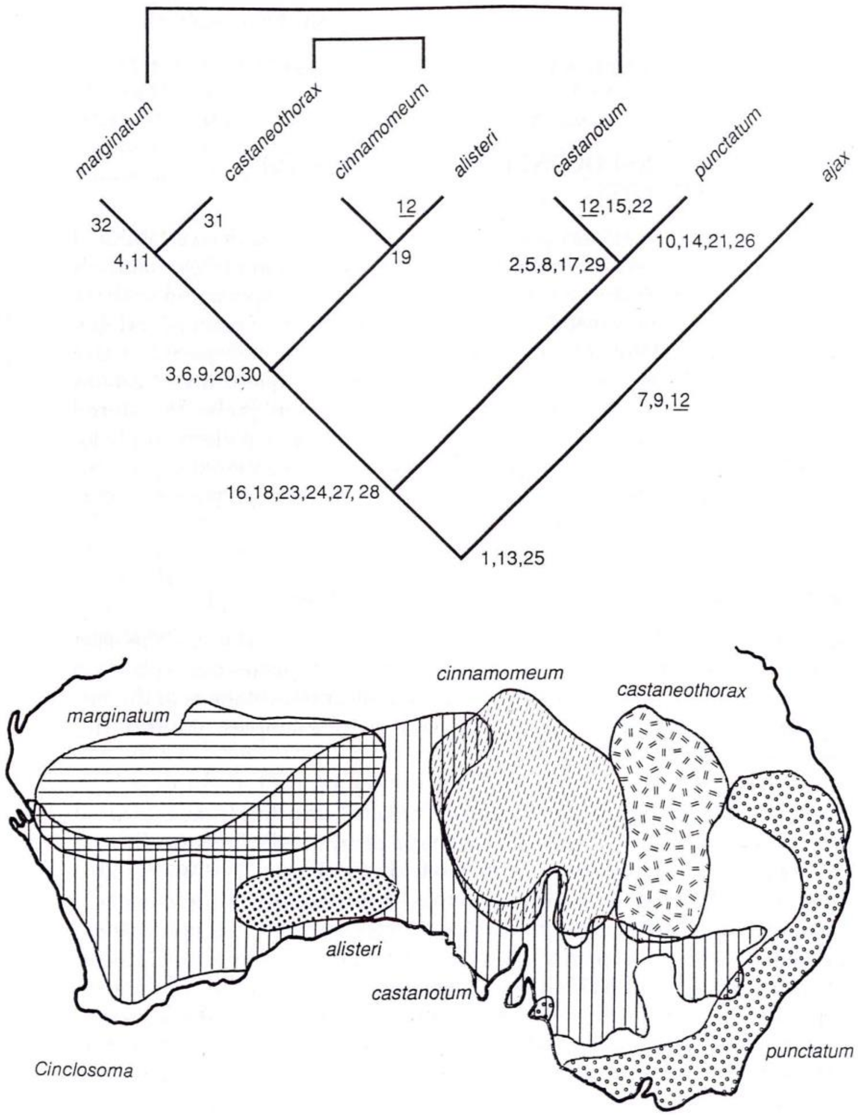


FIGURE 1. Distribution and phylogenetic hypothesis for the phylogenetic species of Australian quail-thrushes (*Cinclosoma*). An analysis of 32 ordered characters (Table 2) produced a best-fit tree of 35 steps (consistency index = 0.914). The tree was rooted using the outgroup taxa, *Ptilorrhoa castanota* 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 palaeonologist)

* The ESC seems to sits 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
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)

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

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).

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

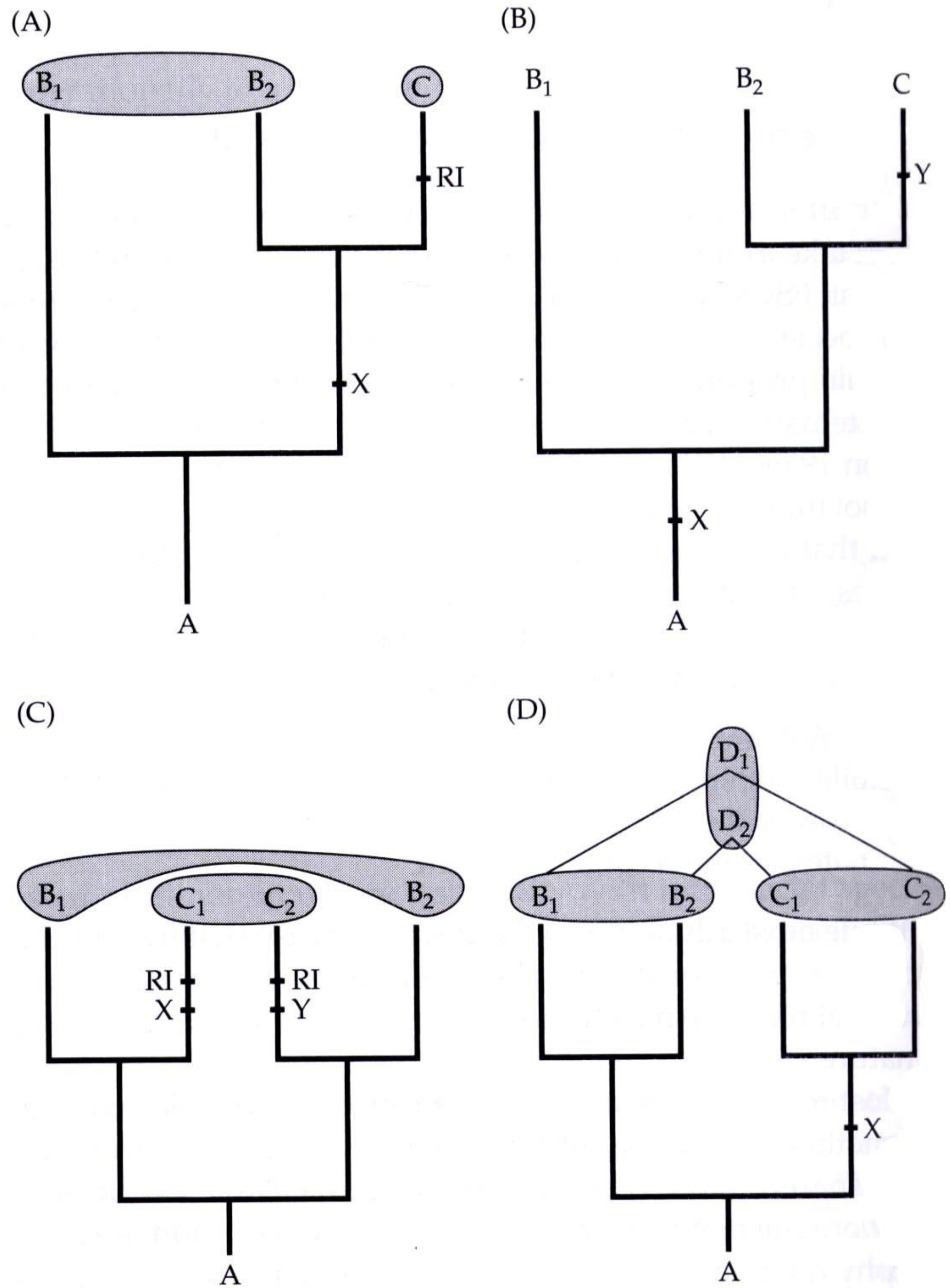


Figure A.1 Phylogenies showing disparities between evolutionary history and reproductive isolation (see text for discussion). (A) Speciation in a peripheral isolate. (B) Species diagnosed by a trait difference using Phylogenetic Species Concept 1 (PSC 1). (C) Parallel speciation yielding a polyphyletic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

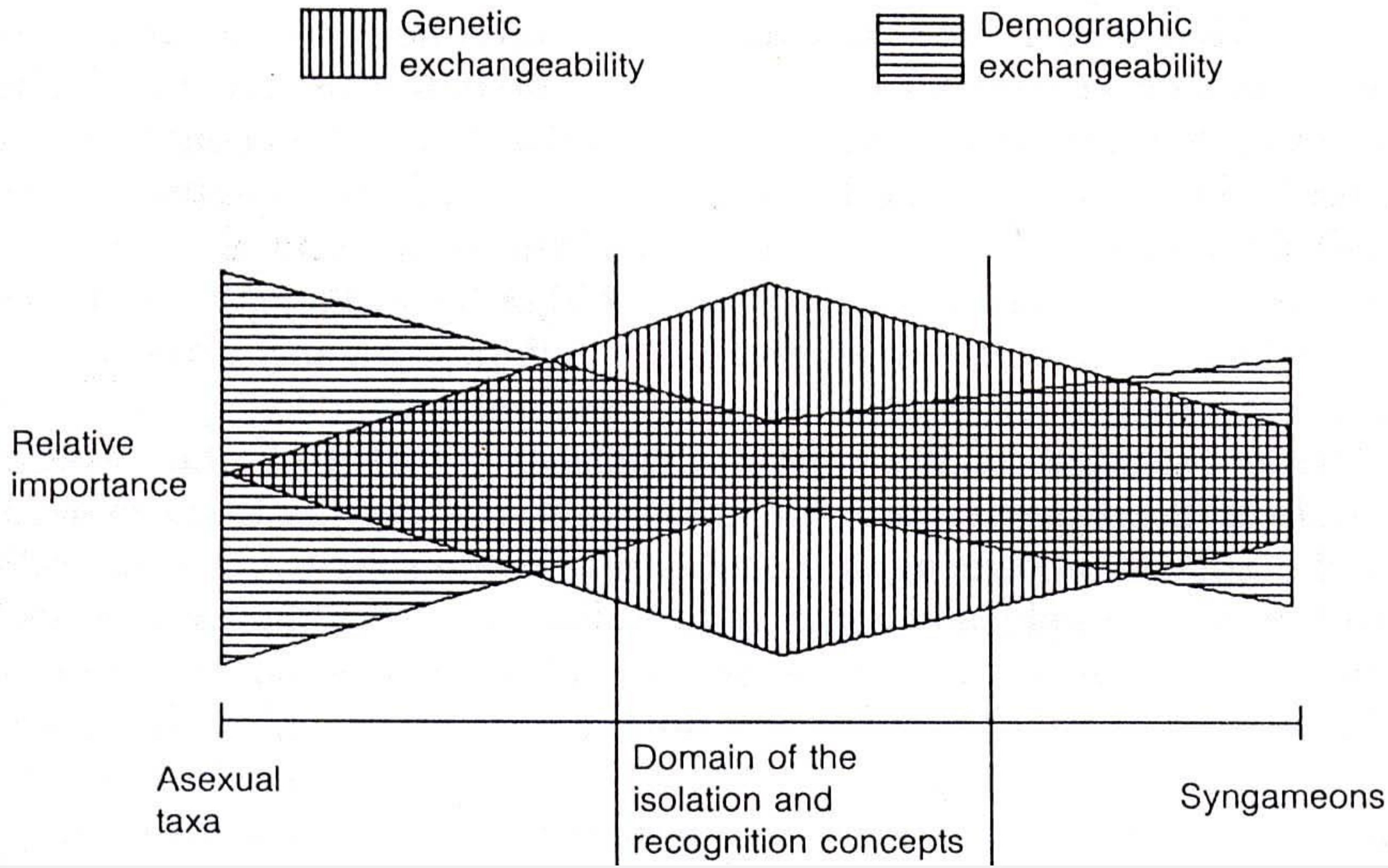

Genetic exchangeability
Demographic exchangeability
Relative importance
Asexual taxa
Domain of the isolation and recognition concepts
Syngameons

TABLE 2. Classification of cohesion mechanisms.

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

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

De Queiroz (2007): “Unified Species Concept”

* a separately evolving metapopulation lineage
* species are (segments of) separately evolving metapopulation lineages

* seeks agreement among definitions
* De Quirioz claims all other definitions employ criteria as lines of evidence (operational criteria) relevant to assessing lineage separation

"…differences in emphasis are to be expected, because the various properties are of greatest interest to different subgroups of biologists. For example, reproductive incompatibilities are of central importance to biologists who study hybrid zones, niche differences are paramount for ecologists, and diagnosability and monophyly are fundamental for systematists. Similarly, morphological differences are central for paleontologists and museum taxonomists, whereas genetic ones are key for population geneticists and molecular systematists."

de Queiroz (2007)

“Thus, as the lineages diverge, they (or their component organisms) become phenetically distinguishable. They become diagnosable in terms of fixed character states. Their genitalia, gametes, and developmental systems become incompatible. Their mate recognition systems diverge to the point where the organisms no longer recognize one another as potential mates. They evolve distinctive ecologies. And they pass through polyphyletic, paraphyletic, and monophyletic stages in terms of their component genes. The problem is that these changes do not all occur at the same time, and they do not even necessarily occur in a regular order.” de Queiroz (2007)

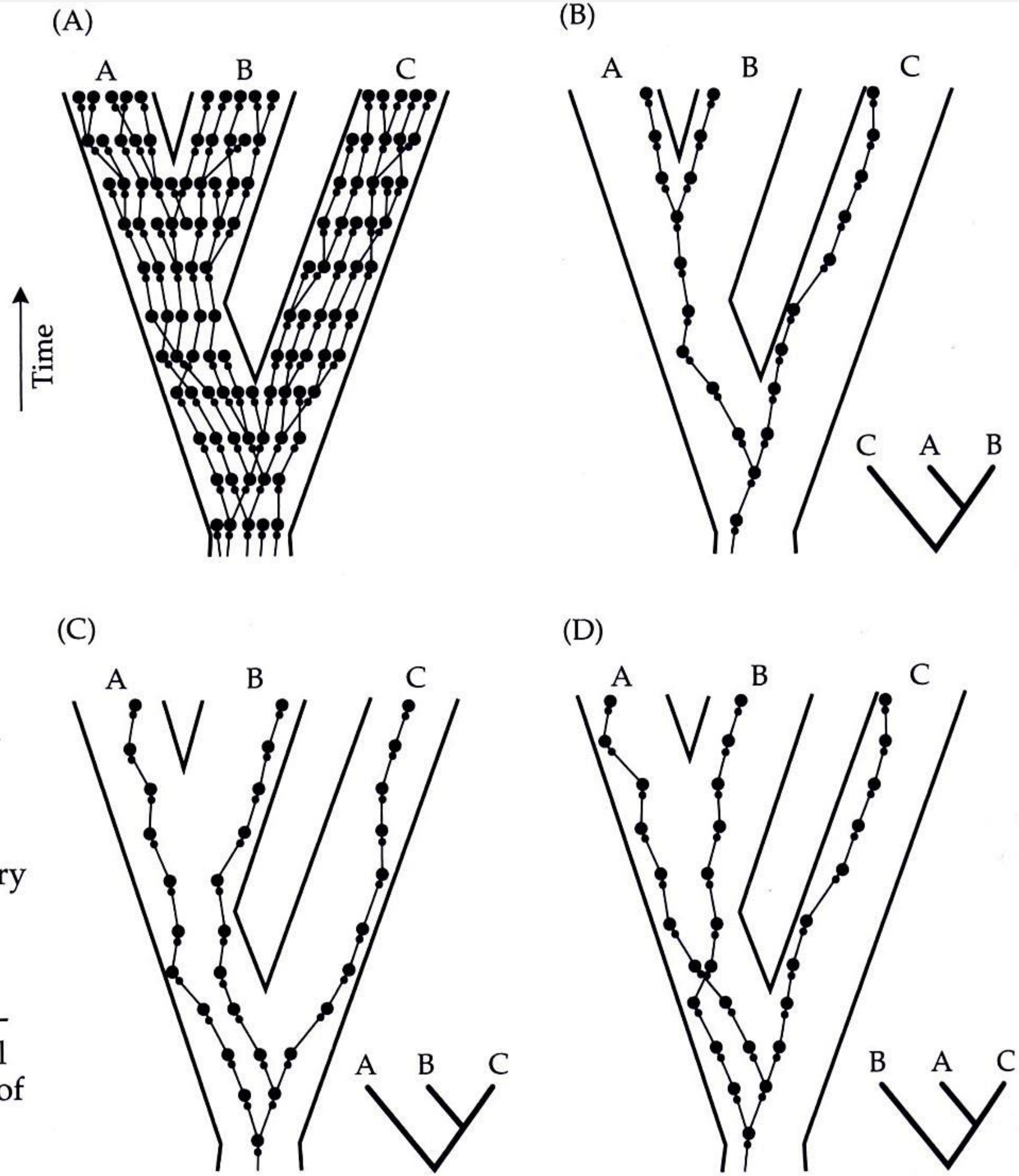
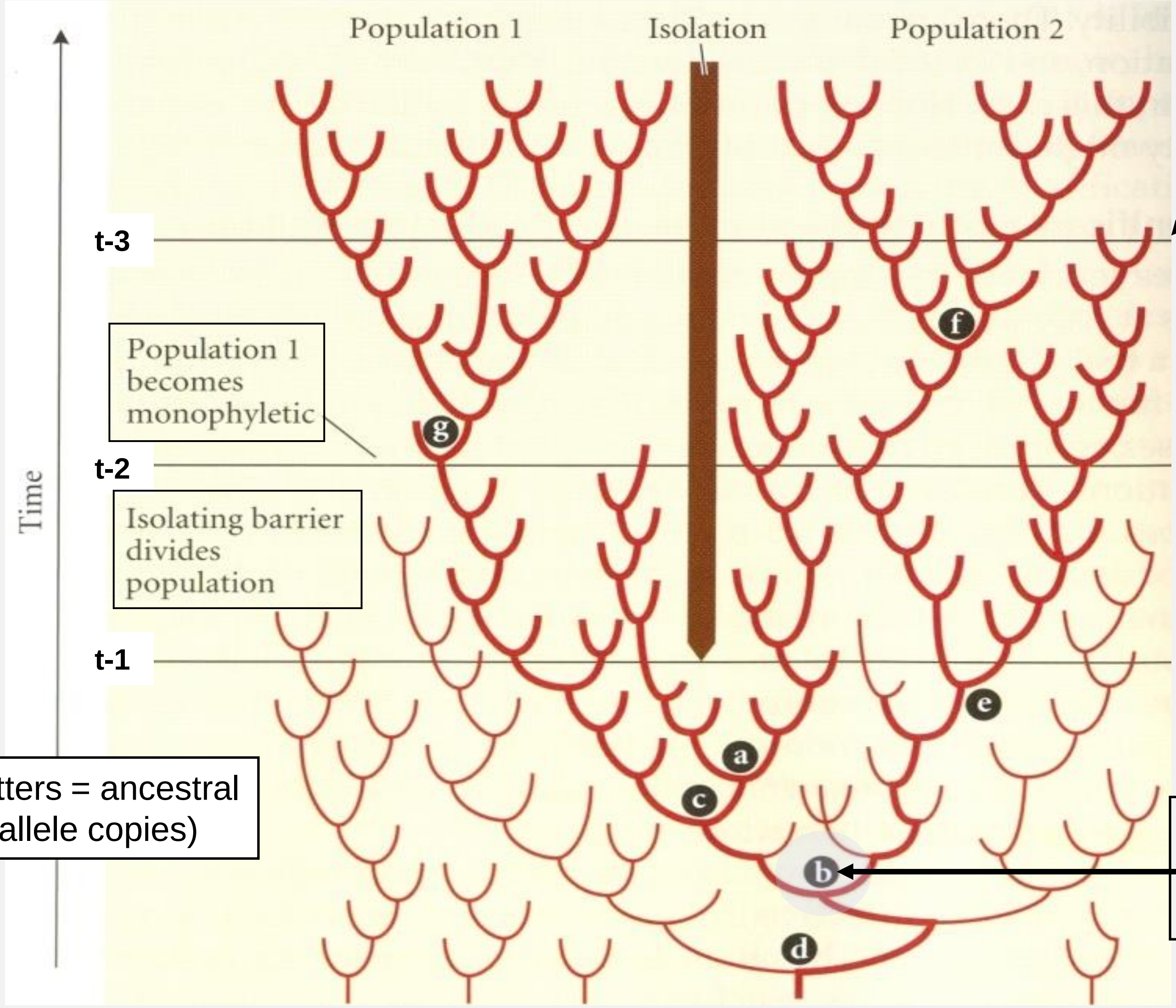


Figure A.2 Gene sorting occurring in a phylogeny whose true population history is shown in (A). Depending on which gene copies are picked for analysis, one can derive all three possible phylogenies, shown by the small diagrams to the lower right of diagrams (B), (C), and (D). (After Hey 1994.)

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



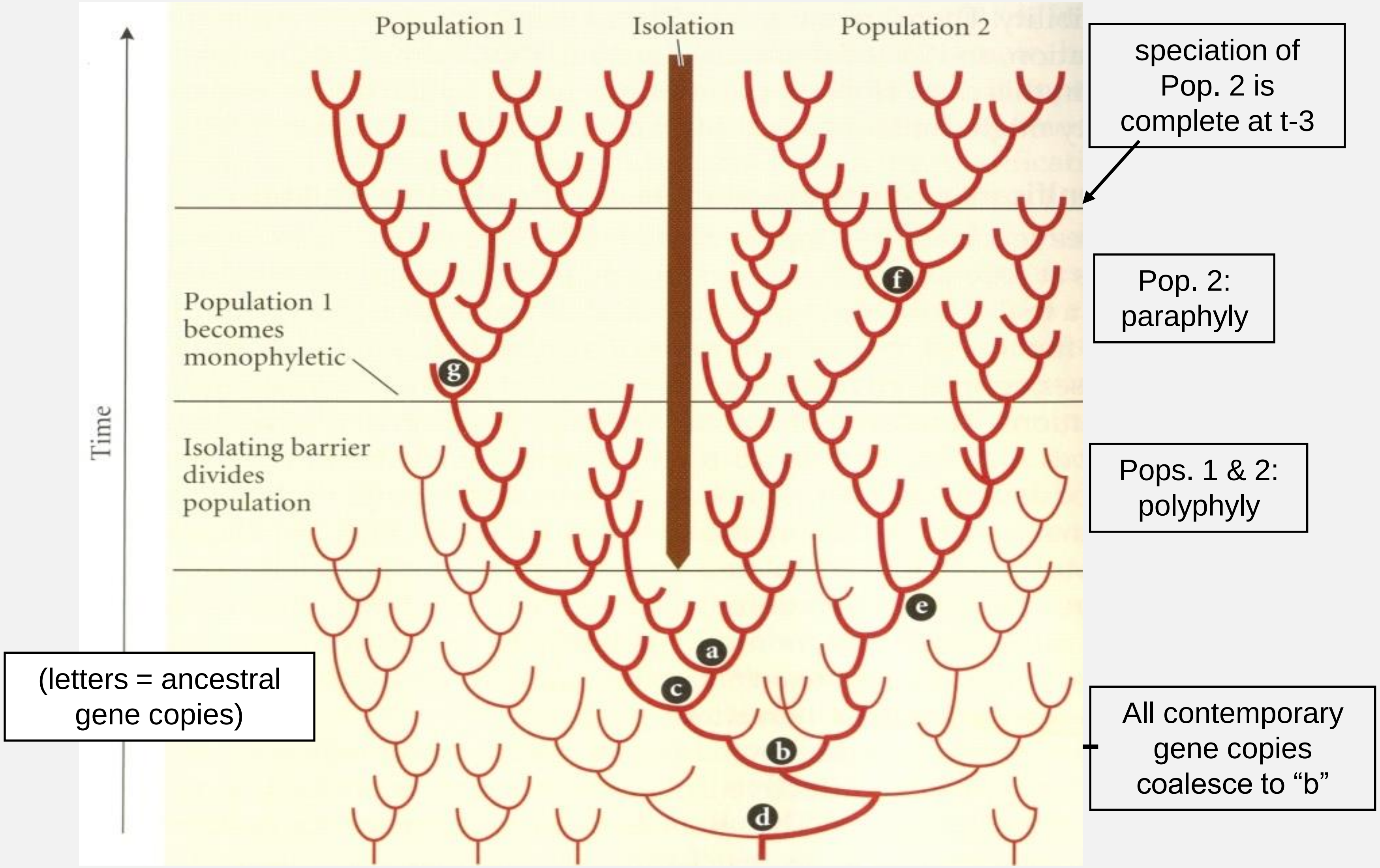
speciation of Pop. 2 is complete at t-3

Pop. 2: paraphyly

Pops. 1 & 2: polyphyly

All contemporary gene copies (alleles) coalesce to “b”

(letters = ancestral allele copies)



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).

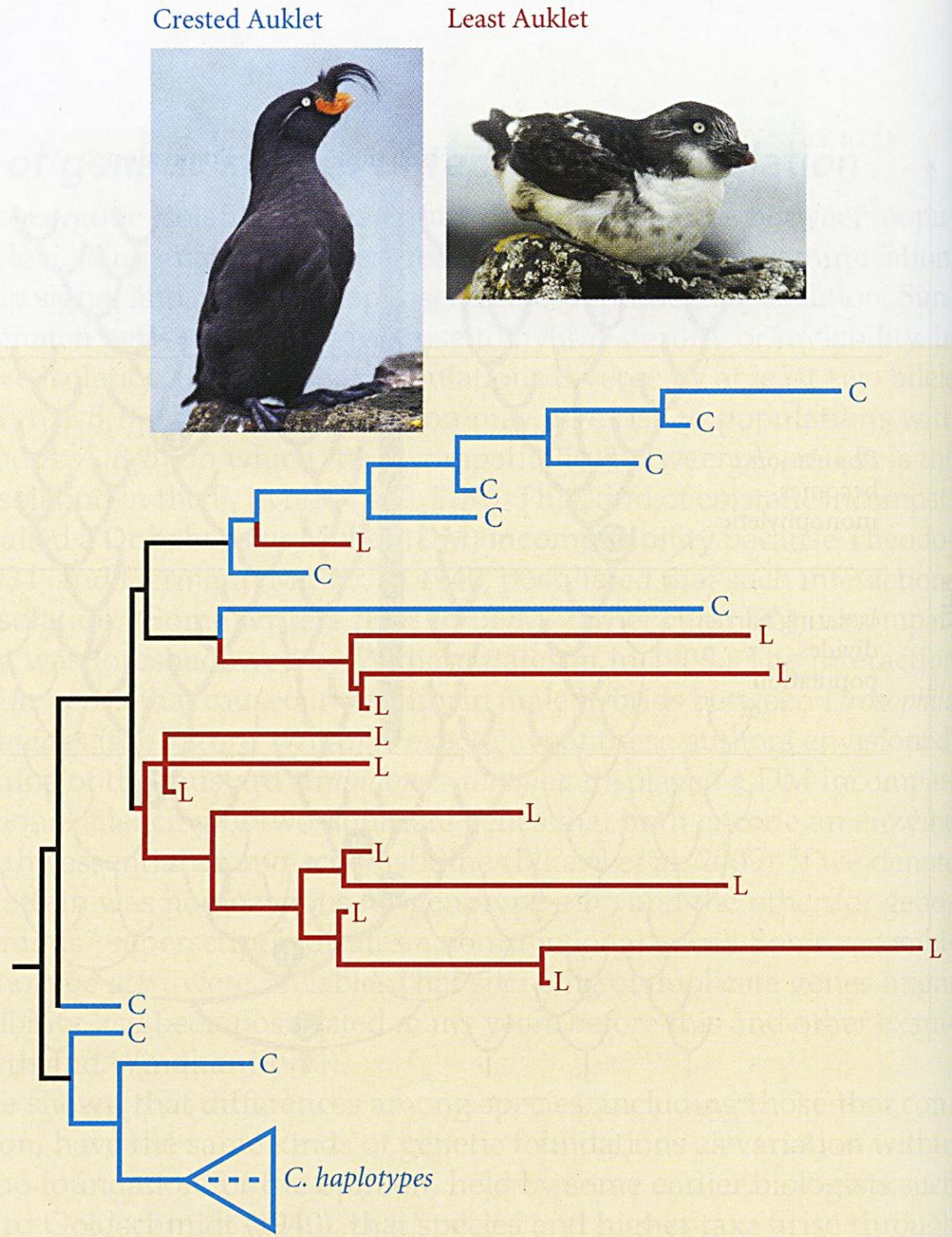
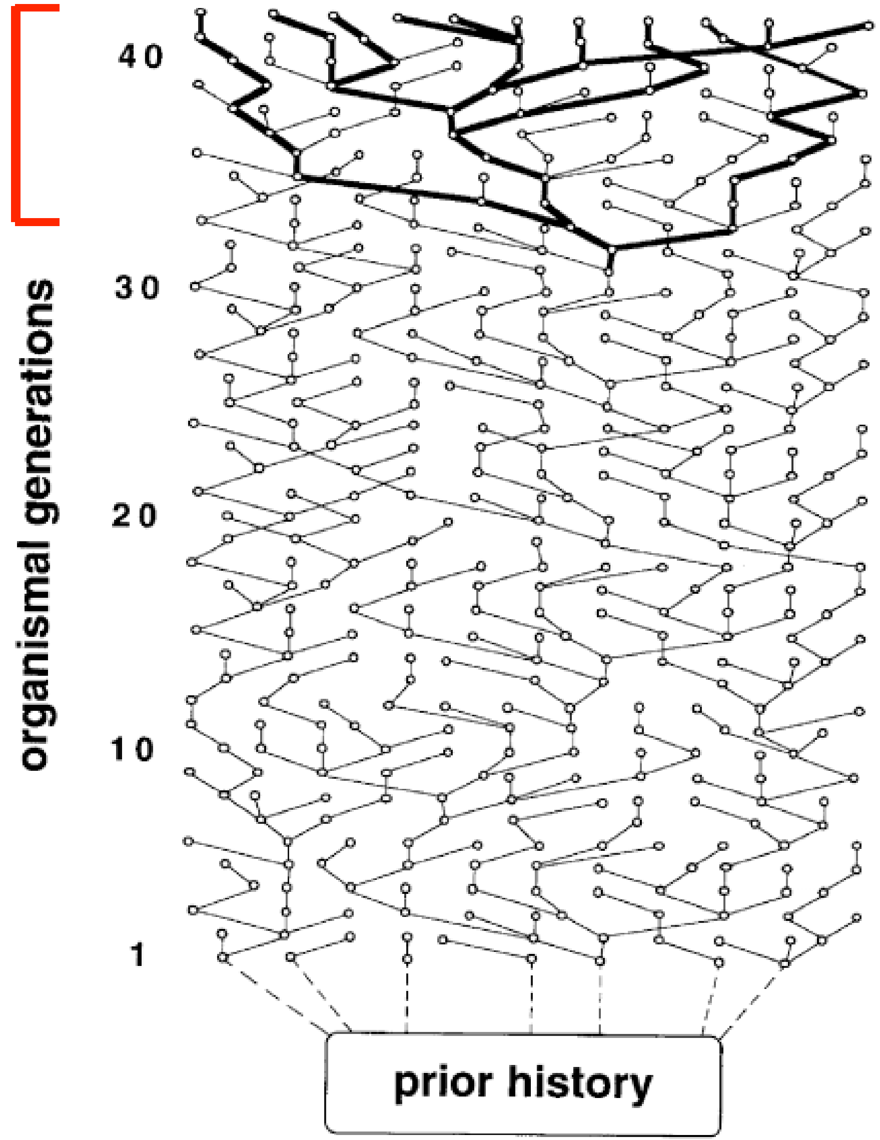


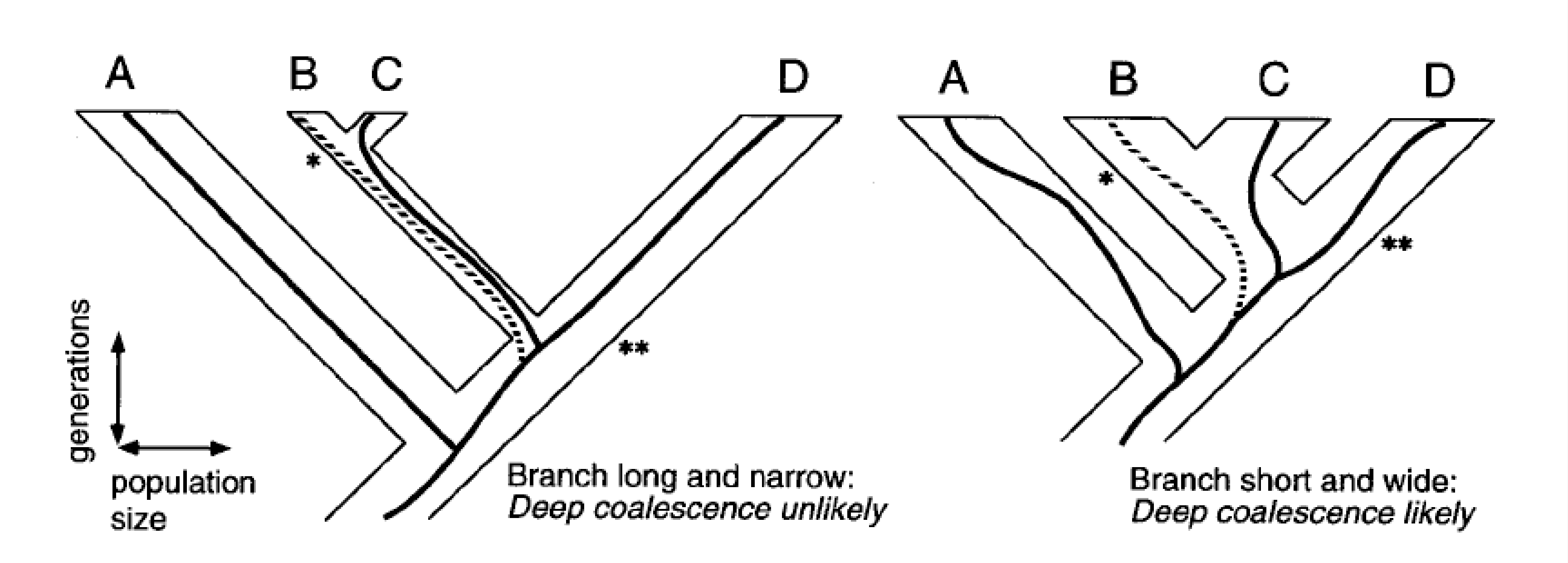
FIGURE 17.16 Incomplete lineage sorting results in a polyphyletic gene tree for the α-enolase locus in two closely related seabird species. Blue (C) and red (L) branches mark haplotype lineages found in the crested auklet (*Aethia cristatella*) and the least auklet (*A. pusilla*), respectively. (After Walsh et al. 2005; *A. cristatella* photo courtesy of Art Sowls, U.S. Fish and Wildlife Service.)

Time to monophyly



Time to monophyly depends on the population size and the number of generations, and is ~Ne generations

From Brad Shaffer Po: http://bodegaphylo.wikispot.org/2009_Workshop



* Gene tree/species tree conflict (aka deep coalescence , lineage sorting, etc.) less likely when branches long, narrow, and well spaced
* Gene tree/species tree conflict likely when branches short, thick, approximate

Figures from Maddison. (1997). Sys. Biol. 46: 523-536

Expected time to monophyly for neutral mitochondrial and nuclear genes (with times given in N_e generations)

Number and location of loci	Probability reciprocal monophyly			Probability monophyly		
	0.05	0.50	0.95	0.05	0.50	0.95
1 mitochondrial	0.38	0.94	2.20	0.29	0.71	1.80
1 nuclear	1.50	3.80	8.70	1.20	2.80	7.30
5 nuclear	4.00	6.70	11.80	3.00	5.50	10.50
15 nuclear	6.00	8.90	14.10	4.80	7.60	12.80
25 nuclear	7.00	9.90	15.20	5.70	8.60	13.90
11,500 nuclear	19.10	22.1	—	17.90	20.80	26.30

Source: Hudson and Coyne, 2002

* mitochondrial genes coalesce 4x more quickly because only female gametes carry mitochondrial and only a single haplotype is represented in gametes

Selection is both the primary cohesive and disruptive force in evolution, and that the selective regime itself determines what influence gene flow (or isolation) will be is presented for this.

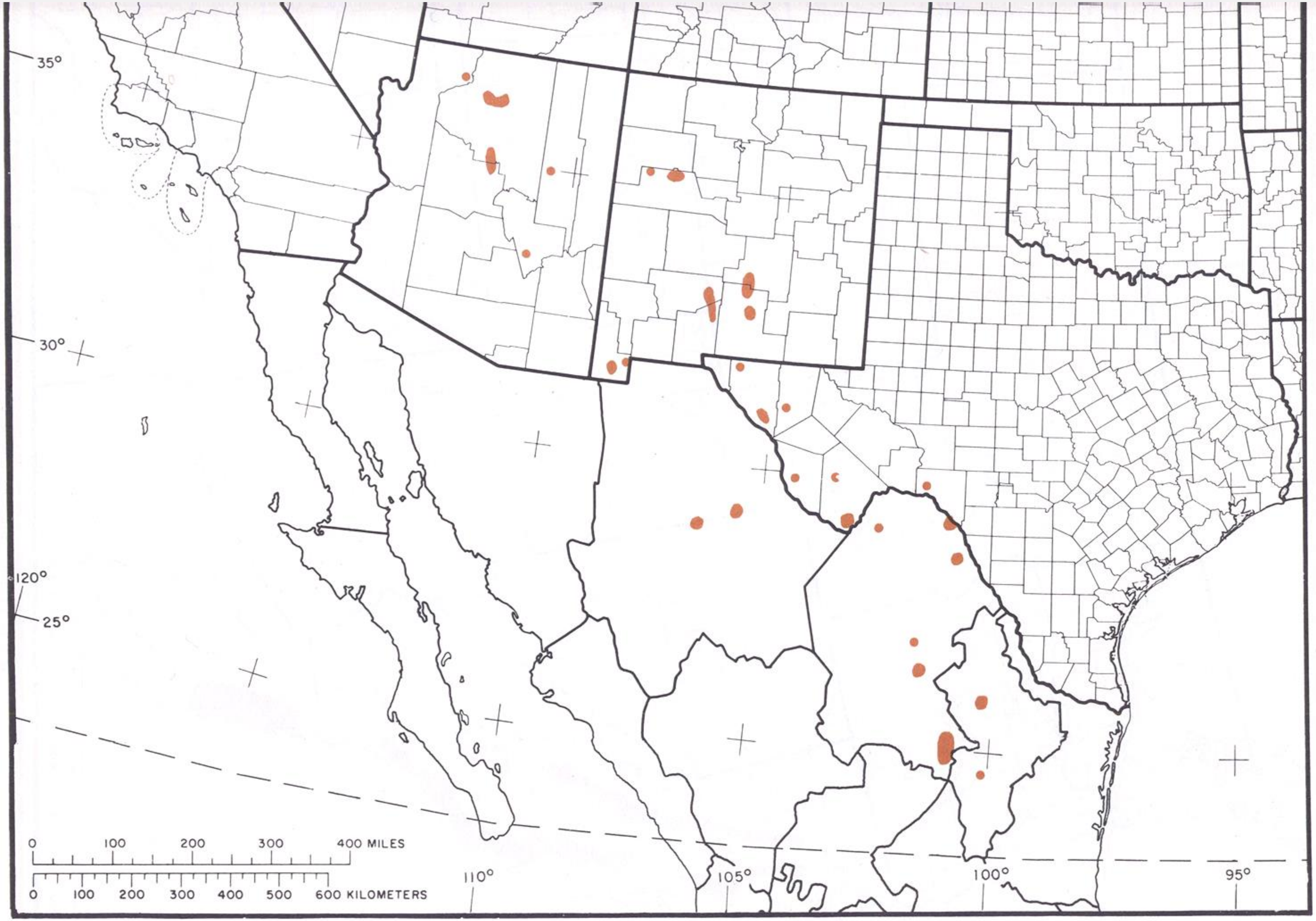
1. Gene flow in nature is much more restricted than commonly thought
2. Populations that have been completely isolated for long periods often show little differentiation
3. Populations freely exchanging genes but under different selective regimes may show marked differentiation

Ehrlich and Raven (1969)

Ehrlich and Raven (1969) conclude by pitting gene flow and against natural selection:

“The most basic forces involved in the differentiation of populations may be antagonistic selective strategies, one for close “tracking” of the environment and one for maintaining “coadapted” genetic combinations—combinations which have high average fitness in environments which are inevitably variable through time.”

“Selection itself is both the primary cohesive and disruptive force in evolution; the selective regime determines what influence gene flow has on observed patterns of differentiation. Populations will differentiate if they are subjected to different selective forces and will tend to remain similar if they are not.”



Map 77. *Fraxinus cuspidata* Torr., fragrant ash.