
Linking Evolutionary Pattern and Process

The Relevance of Species Concepts for the Study of Speciation

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Species are fundamental units of natural diversity—of obvious interest to systematists, evolutionary biologists, ecologists, and conservation biologists. However, both within and among these disciplines, there is considerable disagreement about the way in which species should be defined. As a result, the last two decades have witnessed a proliferation of new species concepts and a rapidly expanding literature, in which the merits of the various definitions are vigorously debated. Much of the debate has been carried out within the community of systematic biologists, who see the definition of species as the province of their discipline. The emergence of phylogenetic systematics resulted in profound unhappiness with the Biological Species Concept (BSC), which until recently remained the default framework for thinking about species and speciation. One faction among the phylogenetic systematists has argued for the primacy of pattern over process in defining species. Wheeler and Nixon (1990) articulated the views of such pattern cladists: “The appropriately militant view that systematists need to embrace is that the responsibility for species concepts lies *solely* with systematists. If we continue to bow to the study of process over pattern, then our endeavors to elucidate pattern become irrelevant” (p. 79).

Speciation is the process by which new species arise, and evolutionary biologists who study this process should be concerned with how species are defined. However, with only a few exceptions, students of speciation have not engaged systematists in a debate about species concepts. Unlike phylogenetic systematists, many evolutionary geneticists appear quite satisfied with the BSC of Mayr and Dobzhansky, which focuses attention on reproductive isolation or barriers to gene exchange. They see no need for any change. Coyne (1994) summarized this point of view: “It is a testament to the power of the BSC that virtually everyone studying the origin of species concentrates on reproductive isolating mechanisms” (p. 22). Despite accusations that the BSC is both concep-

tually and operationally inadequate, Coyne (1994) wrote that he has “no idea why the BSC . . . seems to ignite so much controversy” (p. 22).

A second reason that evolutionary geneticists have generally absented themselves from debates about species concepts is that many are willing to acknowledge that there cannot be a single concept that serves the needs of both evolutionary geneticists and systematists. The two groups have very different perspectives on evolutionary pattern and process. Systematists are primarily interested in fixed character state differences between species (or higher taxa) and inferences about phylogenetic relationships among defined terminal taxa (nonreticulating lineages). In contrast, population biologists study variation within “species,” patterns of reticulation (mating), and the processes (mechanisms) by which one lineage splits into two. The interface between these two disciplines has only recently emerged as a subject of intensive research, a transition catalyzed by the increasing availability of DNA sequence data and the recognition that there is a direct connection between ancestor–descendant relationships within populations (genealogy) and phylogeny (Avice et al. 1987; Harrison 1991; Templeton 1994; Hey 1994). Analysis of gene genealogies using coalescent theory (e.g., Hudson 1990) has focused attention on that connection.

Finally, discussions of the nature of species seem to arouse passion and self-righteousness not found in most “scientific” debates. Each side tends to caricature the logic of its opponents, emphasizing the obvious weaknesses and not mentioning the strengths. Furthermore, some of the issues appear to be philosophical, not scientific. For these reasons, it is hardly surprising that the response of many evolutionary geneticists has been to ignore (if not disparage) these discussions. Again, Coyne (1992) expresses what may be a common response among population geneticists and process-oriented evolutionary biologists: “It is clear that the 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" (p. 290).

I am not so pessimistic. Recent contributions to the literature on species concepts offer a variety of new and useful perspectives, although no single concept has emerged that will satisfy all parties. Defining relationships among these concepts will help to integrate the disciplines of systematic and evolutionary biology. My goal in this chapter is simple: to discuss a sample of species concepts or definitions and to consider how they might provide a context for research on speciation. I do not propose any new concepts—but rather, try to explicate, critique, and organize those already in the literature. I suggest that each species (or lineage; see de Queiroz, this volume) has a distinctive life history, which includes a series of stages that correspond to some of the named species concepts discussed below.

Species Concepts

Table 2.1 summarizes seven different species concepts or definitions, using quotations taken directly from the literature. The list is by no means comprehensive, and a number of frequently cited alternatives (e.g., the phenetic species concept of Sokal and Crovello [1970], the ecological species concept of Van Valen [1976], and Simpson's [1961] original version of the evolutionary species concept) are not included.

Taxonomy of Species Concepts

It is useful to start by attempting a taxonomy of species concepts. A number of potential contrasts have been proposed as organizing principles for characterizing species concepts. For example, definitions of species may be motivated by an interest in pattern alone or by attempts to understand the speciation process. Concepts may be retrospective or prospective (O'Hara 1993), mechanistic or historical (Luckow 1995), character based or history based (Baum and Donoghue 1995). Unfortunately, none of these contrasts allows unambiguous characterization of all species concepts. Moreover, many species concepts do not easily satisfy one or more of the established dichotomies; that is, the dichotomous categories are not necessarily mutually exclusive alternatives. Nonetheless, it is useful to consider how they might apply to the species definitions listed in table 2.1.

Prospective species concepts explicitly invoke criteria (e.g., genetic cohesion or isolation) that have implications for the future status of populations. In contrast, retrospective concepts view species as "end-products" of evolution (Luckow 1995), as units that have evolved rather than lineages that are evolving (Frost and Hillis 1990). O'Hara (1993) suggests that "our judgement as to what individuals belong to a particular population or

reproductive community will always depend to some extent upon our expectation of the future behavior of those individuals and their descendants" (p. 242). Therefore, he argues that all species concepts "depend to some extent upon prospective narration" (p. 242).

According to Luckow (1995), mechanistic species concepts "begin with a theory of how speciation (evolution) works" (p. 590). They rely on knowledge of the genetics and ecology of natural populations and use that knowledge in defining species, which are viewed as "participants" in the evolutionary process. In contrast, historical species concepts focus exclusively on the outcome of evolution. In Luckow's (1995) terminology, both the "character-based" and "history-based" concepts of Baum and Donoghue (1995) are historical species concepts.

The contrast between character-based and history-based species concepts reflects a fundamental division within phylogenetic systematics. Proponents of these two sorts of phylogenetic species concepts have engaged in a lengthy debate in the systematic biology literature (e.g., de Queiroz and Donoghue 1988, 1990; Wheeler and Nixon 1990; Nixon and Wheeler 1990; Baum 1992; Baum and Donoghue 1995; Luckow 1995). The essence of the disagreement is whether species definitions should rely simply on characters (with no necessary prior inference of historical relationships) or whether species should be defined using the inferred historical relationships (genealogy) among component organisms. In the rest of this chapter, I refer to the character-based definition (Cracraft 1983; Nixon and Wheeler 1990) as the phylogenetic species concept and use the genealogical species concept (Baum and Shaw 1995) as an example of the historical approach. In fact, both sorts of definitions are phylogenetic (see de Queiroz [this volume] for a clear discussion of this issue).

The several dichotomies useful for characterizing species concepts are not necessarily independent. Historical concepts are, of course, retrospective and tend to focus on patterns of variation; mechanistic concepts are prospective and usually derive from a fundamental interest in the evolutionary process. Furthermore, patterns of variation are used to infer past processes and thereby shed light on how speciation has occurred.

The first three concepts in table 2.1 (BSC, recognition, cohesion) are clearly motivated by an interest in the process of speciation. They are prospective, in the sense that isolation and cohesion are viewed as important because they allow us to predict future patterns of variation (e.g., whether an advantageous mutation will spread, whether two distinct entities can persist in sympatry, whether a lineage will become an exclusive group). These concepts would be termed mechanistic by the pattern cladists, although I will argue below that this characterization is inaccurate. Contrary to the claims of their critics, prospective species concepts do not necessarily imply the action of particular evolutionary mechanisms in species formation.

Table 2.1. Seven species concepts or definitions from the systematic biology and evolutionary biology literature.

1. Biological Species Concept (Isolation Concept) (BSC)

“[G]roups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr 1963, p. 19).

“[S]ystems of populations, the gene exchange between these systems is limited or prevented in nature by a reproductive isolating mechanism or by a combination of such mechanisms” (Dobzhansky 1970, p. 357).
2. Recognition Species Concept

“[T]he most inclusive population of individual biparental organisms which share a common fertilization system [specific mate recognition system]” (Paterson 1985, p. 15).
3. Cohesion Species Concept

“[T]he most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms [genetic and/or demographic exchangeability]” (Templeton 1989, p. 12).
4. Phylogenetic Species Concept (Character-Based)

“[A]n irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent” (Cracraft 1989, p. 34).

“[T]he smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals” (Nixon and Wheeler 1990, p. 218).
5. Genealogical Species Concept

“‘[E]xclusive’ groups of organisms, where an exclusive group is one whose members are all more closely related to each other than to any organisms outside the group. . . . [B]asal taxa . . . , that is taxa that contain no included taxa” (Baum and Shaw 1995, p. 290).
6. Evolutionary Species Concept

“[A] single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley 1978, p. 18).
7. Genotypic Species Cluster Definition

“[D]istinguishable groups of individuals that have few or no intermediates when in contact. . . .

“ . . . [C]lusters are recognized by a deficit of intermediates, both at single loci (heterozygote deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters)” (Mallet 1995, p. 296).

The phylogenetic species concept and genealogical species concept are clearly retrospective and emphasize pattern rather than process (although consideration of process is not excluded). The phylogenetic species concept and the genotypic clusters definition are explicitly character based, in contrast to the genealogical species concept, which is history based (in the sense of Baum and Donoghue 1995).

Criteria for Recognizing and Defining Species

De Queiroz (this volume) clearly distinguishes between species concepts and species criteria. The distinction is an important one because different species concepts may share a common criterion for species delimitation. The seven species concepts or definitions in table 2.1 suggest

a number of possible criteria for evaluating whether groups of individuals are distinct species: (1) species are characterized by genetic isolation or the absence of cohesion (i.e., there are intrinsic barriers to gene exchange); (2) species are demographically nonexchangeable (ecologically distinct); (3) species are diagnosable (characterized by fixed character state differences); (4) species are exclusive groups; (5) species have a separate identity and independent evolutionary tendencies; (6) species are recognized as distinct genotypic clusters.

All species delimitations (even those based on isolation or cohesion concepts) ultimately depend on inferences from patterns of variation and character state distributions. The need to infer process from pattern argues that the pattern/process dichotomy discussed in the previous section will often break down. For similar reasons,

implementing isolation or cohesion concepts (which I have termed prospective) may require an explicitly retrospective approach (e.g., see Templeton 1994; see also Templeton, this volume).

The criteria of diagnosability and separate genotypic clusters would appear to have the advantage of being operational, because species are defined directly in terms of the distribution of character states rather than in terms of descent relationships or interbreeding inferred from such distributions. The genotypic clusters definition, however, can only be applied directly to entities that are sympatric or parapatric. Furthermore, patterns revealed by character-state distributions are not always easy to interpret and often require either knowledge of or assumptions about current evolutionary process or mechanism (see critique by Baum and Donoghue 1995). For example, if two distinct morphs co-occur at a single site, do we conclude that this pattern is evidence of a single polymorphic population or of two sympatric species? Clearly, additional information about patterns of genetic exchange is needed.

Populations are diagnosable (in theory and practice) when they exhibit one or more fixed character-state differences. If taxa are exclusive groups only when all gene genealogies become concordant, with coalescence of genes within each group occurring more recently than any coalescence of genes between groups, then exclusivity is a far more stringent requirement for species status. For example, humans and chimpanzees are not exclusive groups for all parts of the genome, because some human major histocompatibility complex (MHC) alleles are more closely related to chimp alleles than to other alleles in humans. Baum and Shaw (1995) do not say that all gene genealogies must be concordant if two populations are to be considered genealogical species, but the threshold beyond which lineages become genealogical species remains obscure. How to apply the criterion of separate identities and independent evolutionary tendencies is also not clear, especially since Wiley (1981) explicitly requires that species be lineages in the sense of sharing a common history (being monophyletic or exclusive).

Isolation and Cohesion as Criteria for Defining Species

Both cohesion and isolation are clearly important components of the BSC. Mayr characterizes species as groups of interbreeding populations, and Dobzhansky describes species as "systems of populations," emphasizing that single species are cohesive. At the same time, both versions of the BSC view reproductive isolation or "isolating mechanisms" as defining the boundaries between species in the natural world. Thus, Mayr (1963) wrote: "The mechanisms that isolate one species reproductively from others are perhaps the most important set of attributes a species has, because they are, by definition, the species criteria" (p. 89).

In contrast, the recognition and cohesion concepts attempt to be "nonrelational" and to define species as inclusive groups. Genetic cohesion is at the heart of the recognition concept. Paterson (1985) describes a species as a common "field for recombination"—or as a group of organisms sharing a common fertilization system. However, he is inconsistent in application of the first criterion, since postzygotic barriers are not viewed as reason to recognize two entities as different species (despite the fact that such entities no longer constitute a single field for recombination). Templeton (1989) recognizes the importance of genetic exchangeability (gene flow) in defining species boundaries, but argues that it is not the only sort of cohesion mechanism that needs to be considered. He views the isolation and recognition concepts as "exclusively concerned with genetic relatedness promoted through the exchange of genes via sexual reproduction" (p. 14).

In addition to genetic cohesion, Templeton (1989, this volume) adds the criterion of demographic exchangeability to emphasize ecological (rather than genetic) interactions. Groups of organisms that are demographically exchangeable are ecologically equivalent, occupying the same niche. This criterion for determining species status is particularly useful when applied to sympatric, asexual lineages, which are considered conspecific (even in the absence of gene exchange) when they are demographically exchangeable. At the other extreme, hybridizing populations may be considered distinct species (despite some gene flow) if they are demographically nonexchangeable.

The notion that a nonrelational species concept (e.g., the recognition concept) is superior has been argued by Paterson and his supporters (Paterson 1985; Masters et al. 1987; Lambert et al. 1987). However, description of a mate recognition system or of an array of cohesion mechanisms that operate within a single species or lineage will not directly provide insights into how new species arise. Relational concepts may be a more appropriate framework for studying speciation; it is essential to obtain comparative data from sister species or sister populations and to infer the changes (apomorphies) that have resulted in (or at least co-occurred with) fission. Species may be held together by multiple cohesion mechanisms, but the breakdown of only one of those may lead to lineage splitting and speciation (figure 2.1). Only by comparing sister taxa will it become evident which cohesion mechanisms are labile (hence likely to be important in speciation events) and which are conservative.

Decisions as to species status depend on information about patterns of genetic exchange, regardless of whether one attempts to delineate species in terms of the boundaries between them ("intrinsic barriers to gene flow") or the limits of common cohesion mechanisms or common fertilization systems. Thus, the distinction between dichotomous states in the taxonomy of species concepts (in

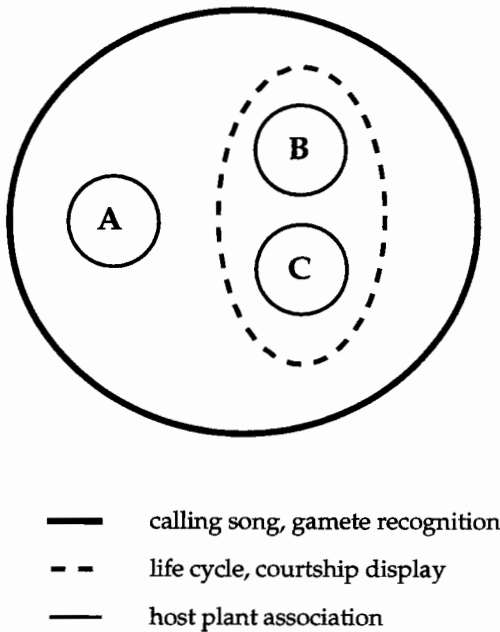


Figure 2.1. Example of three species of insects (A–C) with overlapping arrays of “cohesion mechanisms.” The cohesion mechanisms operating in these imaginary insects are host plant association, life cycle (phenology), calling song, courtship display, and gamete recognition. Lines enclose groups of individuals that share one or more cohesion mechanisms. Differences in any one of these may result in descendant lineages becoming separate “fields for recombination.” Characterizing the array of possible cohesion mechanisms is only a first step in the study of speciation. Understanding what makes A, B, and C distinct species involves identifying which cohesion mechanisms have changed over time. In the example shown here, host association differs among all three species, life cycle and courtship display distinguish A from B+C, but calling song and gamete recognition are cohesion mechanisms still shared by all three species.

this case, relational versus nonrelational) again becomes fuzzy when different concepts are used to generate criteria that actually delimit species.

Proponents of historical and character-based species concepts also recognize the importance of interbreeding, reproductive isolation, or barriers to genetic exchange, although these are not the criteria on which they determine species status.

Species must be reproductively isolated from each other to the extent that this is required for maintaining their separate identities, tendencies and fates. (Wiley 1981, p. 27)

Interbreeding is relevant not only for population biologists, but also to phylogenetic systematists. (de Queiroz and Donoghue 1990, p. 89)

[P]hylogenetic species are the least inclusive populations or set of populations among which there is character-based evidence in the form of fixed differences that gene exchange does not occur. (Davis and Nixon 1992, p. 428)

Wiley (1981) and Davis and Nixon (1992) presumably invoke absence of genetic exchange because diagnosable differences (separate identities) between populations most often arise and persist in that context. However, boundaries between populations can be semipermeable (Harrison 1986, 1990); that is, the extent of introgression can vary across the genome. As a consequence, fixed allelic differences can be maintained at some loci, whereas gene exchange leads to homogenization of allele frequencies at other loci. Therefore, it is possible for populations to be diagnosably distinct or maintain separate identities without being completely genetically or reproductively isolated. Mallet’s (1995) genotypic cluster definition seems consistent with this view, because it allows some gene exchange to occur as long as the distribution of multilocus genotypes or phenotypes remains bimodal where the distinct entities come into contact. The genealogical species concept is potentially far more stringent, if a group must exhibit exclusivity at a large proportion of loci in order to be considered a genealogical species.

The role of isolation or barriers to gene exchange, however, is fundamentally different in historical or character-based species concepts than in the BSC. For purposes of species definition, proponents of the BSC are clearly interested only in intrinsic barriers to gene exchange (those that are due to biological differences between species and not simply due to geography). In contrast, the phylogenetic, evolutionary, and genealogical species concepts do not discriminate between intrinsic and extrinsic barriers. Thus, Davis and Nixon (1992) argue that intrinsic barriers hold “no special position [in defining species] except in suggesting stability of the observed situation” (p. 429). But extrinsic barriers are ephemeral, whereas distinct cohesion mechanisms or intrinsic barriers to gene exchange often represent permanent genetic changes in the evolutionary fabric that can be used as predictors of future patterns of evolution. It is these sorts of changes that have traditionally attracted the attention of students of the speciation process.

Do Species Concepts Constrain or Bias Our Views about How Speciation Occurs?

“What is a species? This fundamental question must be answered before the process of species formation can be investigated” (Templeton 1989, p. 3). Most systematists

and evolutionary biologists would agree with Templeton that without a clear definition of species, we cannot begin to study the process of speciation. However, some propose that we first define speciation (usually as the reduction and eventual elimination of gene flow) and then ask what will be the properties of the "species" that result (Bush 1994). Whichever path we follow, an obvious danger is that our definition of species or speciation will make assumptions that constrain our views about evolutionary process.

Speciation from the Perspective of the Phylogenetic and Genealogical Species Concepts

If species are simply diagnosably distinct populations, then a new species can appear as the result of the fixation of a single new mutation within a local population or from random sorting of an ancestral polymorphism. With this perspective there is no longer a clear distinction between the genetics of speciation and the genetics of species differences (Templeton 1981), because all fixed differences are cause for recognizing distinct species. Speciation and divergence become synonymous and the study of speciation becomes the study of the relative importance of migration, genetic drift, and natural selection in the evolution of fixed differences between local populations. This is an important problem in population genetics, but it is certainly not what most evolutionary biologists have traditionally viewed as the speciation process!

The genealogical species concept is concerned with the evolution of exclusive groups. Like the phylogenetic species concept, it assigns no special status to the origin of intrinsic barriers to genetic exchange (although such barriers obviously promote the evolution of exclusivity). Baum and Shaw (1995) focus attention "on mechanisms by which divergent (phylogenetic) patterns of relationship emerge out of reticulating patterns" (p. 301). Because coalescent times vary among genes (due to history, chance, and differences in selection), diverging lineages gradually become exclusive groups for an increasing fraction of the genome, and species necessarily have "fuzzy boundaries." Maddison (1995) articulates the same view of species boundaries, suggesting that a species phylogeny is not a "single, simple entity, but rather appears more like a statistical distribution" (p. 285).

Implications of "Isolating Mechanisms" and "Cohesion Mechanisms"

The BSC defines speciation in terms of the origin of barriers to gene exchange or of reproductive isolation. However, both Dobzhansky and Mayr used the term "isolating mechanisms," which implies that biological differences that limit or prevent gene exchange are indeed mechanisms to isolate, that they arose for that pur-

pose, that isolation is a function rather than an effect (in the sense of Williams 1966). Dobzhansky was convinced of the importance of the process of reinforcement, in which prezygotic barriers arise as a result of selection against hybridization in areas of secondary contact. In this scenario intrinsic barriers to gene exchange are indeed isolating mechanisms. Mayr was not a strong supporter of the reinforcement model and more often viewed barriers to gene exchange as incidental by-products of divergence in allopatry. Nonetheless, his language was not always consistent with that view: "It is a function of the isolating mechanisms to prevent such a [hybrid] breakdown and to protect the integrity of the genetic system of species" (Mayr 1963, p. 109). Advocates of the recognition concept (Paterson 1985; Masters et al. 1987; Lambert et al. 1987) have vigorously campaigned against use of the term "isolating mechanism," principally because they deny the possibility of reinforcement as a mechanism for speciation. However, others (Templeton 1989; Mallet 1995) have also been quite critical.

I agree that the term "isolating mechanism" is misleading and that use of the term should generally be avoided. Without sacrificing clarity it is possible to substitute more neutral language (e.g., "barriers to gene exchange") that does not imply a particular origin (process). Only when differences between species have evolved as a result of selection against hybrids (=reinforcement) should the term "isolating mechanism" be used. Because recent reviews do not suggest that reinforcement is a common mode of speciation (Butlin 1989; Howard 1993; but see Coyne and Orr 1989), it is certainly important to avoid the implication that all prezygotic barriers have arisen in this way.

Mallet (1995) also criticizes use of the term "isolating mechanisms" because it includes "under a single label" an incredible diversity of possible biological differences between taxa (e.g., from chromosomal differences to behavioral differences to presence/absence of reproductive parasites). One could easily extend the argument to reject terms like reproductive isolation or barriers to gene exchange. But it is the common effect of all these differences (limiting or preventing gene exchange) that provides the rationale for grouping them. I see no reason not to adopt a single term (e.g., "barriers to gene exchange") to refer to the set of differences that have this very important effect.

The terms "fertilization mechanisms" (used by Paterson 1985) and "cohesion mechanisms" (used by Templeton 1989), although appropriate in some contexts, may be as misleading as the term "isolating mechanisms." Many (perhaps most) biological properties of organisms that confer "cohesion" did not arise for that purpose. They are also effects not functions! Thus, life cycles that result in adults appearing at the same season, or habitat/resource associations which lead to aggregation of individuals in particular places, facilitate fertilization or lead to genetic and/or demographic cohesion. But in most

cases, life cycles and habitat associations have not been molded by selection for the purpose of "cohesion." Gamete recognition systems and behavioral components of mate recognition systems are more likely candidates for true cohesion mechanisms.

Pattern, Process, and Mechanism in Species Concepts

Proponents of the phylogenetic species concept are adamant that pattern not process should form the basis of any species definition. According to Cracraft (1983), "a species concept is best formulated from the perspective of the results of evolution rather than from one emphasizing the processes thought to produce those results" (p. 169). I think that most evolutionary biologists would agree. But Cracraft (1983) and other proponents of the phylogenetic species concept (e.g., Luckow 1995) go one step further and imply that the BSC defines species in terms of particular processes or mechanisms. For example, Luckow (1995) states that the BSC "recognizes the inability to interbreed as being the most important causal factor (mechanism) in speciation" (p. 590). Mallet (1995) also suggests that mechanism should be excluded from species definitions. His argument is that "since theories of speciation involve a reduction in ability or tendency to interbreed, species cannot themselves be defined by interbreeding without confusing cause and effect" (p. 295).

These arguments represent a misinterpretation of the BSC. Reproductive isolation (or a barrier to gene exchange) is a result, not a process (as is a new cohesion mechanism). The inability to interbreed is not the "cause" or "mechanism" of speciation; it is the signal that speciation is complete. I see no confusion of cause and effect if species are defined in terms of barriers to gene exchange. The "cause" of speciation is divergence of populations due to drift or selection (with or without the presence of *extrinsic* barriers to gene exchange) and the "effect" of the resulting differences is the appearance of *intrinsic* barriers to gene exchange. These barriers may be either pre- or postzygotic, thereby including factors that determine the probability of hybrid zygote formation and factors that affect the relative fitnesses of zygotes of mixed ancestry. The BSC (stripped of the term "isolating mechanism") does not, by itself, prejudice us with respect to mechanisms of speciation (or its geographic context). It is essential that we distinguish the implications of particular concepts and the arguments/biases of those who invoke them. I am afraid that many critics of the BSC are guilty of this confusion.

Cracraft (1983, 1989) touts the phylogenetic species concept as the most appropriate framework for what he calls "speciation analysis" (which might be thought to be the study of speciation). But speciation analysis focuses primarily on the description of historical patterns (e.g., areas of endemism, scenarios for vicariance). There seems

to be little concern for what an evolutionary geneticist would call mechanism, no apparent interest in knowing what evolutionary forces have acted. A phylogenetic species concept may be an appropriate framework for systematists and biogeographers, but a quite different outlook will be necessary if we hope to unravel what goes on at the boundary between genealogy and phylogeny.

Must Species Be Consistent with "Recovered Evolutionary History"?

The logic of phylogenetic systematics leads to complete rejection of the BSC and cohesion species concepts, because interbreeding or other mechanisms for cohesion almost always represent a shared ancestral condition (plesiomorphy) and thus cannot provide reason for grouping. De Queiroz and Donoghue (1988) identified interbreeding and common descent as the two "processes" through which organisms are related. They clearly characterized the tension between these two processes in providing a basis for species definition. If species are defined solely on the basis of current interbreeding or cohesion, they frequently will represent "paraphyletic assemblages of populations" (Mishler and Donoghue 1982; see also Bremer and Wanntorp 1979); that is, they will include some but not all descendants of a common ancestor (figure 2.2).

Fear of Paraphyly

Such paraphyletic assemblages are anathema to those phylogenetic systematists who argue that species should be monophyletic or exclusive groups. If species B is paraphyletic with respect to species A, then some members of species B will be more closely related to members of species A than they are to other conspecifics (figure 2.2). Obviously, if recency of common ancestry is to

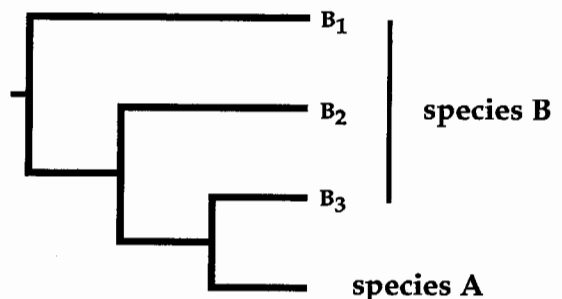


Figure 2.2. Example of a species (B) that appears to be a paraphyletic assemblage of populations. In this gene genealogy, B₁, B₂, and B₃ represent distinct genotypes within species B (perhaps derived from three discrete localities).

provide the criterion for species definition, then such “paraphyletic species” are not allowed. Indeed, many phylogenetic systematists view them as positively misleading. Thus, Frost and Hillis (1990) not only suggest that species concepts must be consistent with “recovered evolutionary history,” they also suggest that the BSC “often hinders attempts to recover the history of evolution” (p. 88). Similarly, Cracraft (1989) argues that “non-monophyletic species imply that history has been misrepresented” (p. 39). These claims are exaggerated. If we accept that species are defined by isolation and/or cohesion and do not start with the assumptions that they must be exclusive groups and the units of phylogeny, then including paraphyletic assemblages as species does not misrepresent history.

There is no doubt that a robust phylogeny is a prerequisite for studying speciation, because inferences about change over time depend upon knowing the relationships of the populations or species being compared. The observation that one species comprises a paraphyletic assemblage of lineages and a second species is a lineage embedded within that assemblage can provide valuable information about the history of divergence/speciation. In the example shown in figure 2.2, we would want to know whether, in a set of independent gene genealogies, genotypes of species A consistently appear as sister to genotypes from the same population (e.g., B₃) or whether the tree topology depends on which gene we choose. In the former case, we might conclude that speciation has involved local divergence, either in sympatry or as a result of a local vicariance or founder event. In the latter case, gene genealogies may simply represent random lineage sorting from a polymorphic ancestor.

Both isolation and cohesion species are often paraphyletic. If A and B (e.g., figure 2.2) are reproductively isolated (due to changes along the branch leading to A), then they are isolation species. But they are not comparable entities in terms of evolutionary history, because A is a monophyletic group and B is the paraphyletic assemblage of lineages remaining after divergence of A. In order to distinguish these two distinct entities, alternative names have been proposed for such paraphyletic assemblages of populations (“metaspecies” [Baum and Shaw 1995], a modification of the original definition of that term by Donoghue [1985]; or “ferespecies” [Graybeal 1995]).

Molecular phylogenies of groups of closely related species have revealed a number of clear examples of currently recognized species that appear to be paraphyletic assemblages of populations. Figure 2.3 shows two examples within the prodoxid moth genus *Greya*, in which a mitochondrial DNA (mtDNA) phylogeny indicates that a widely distributed species is paraphyletic with respect to a close relative that has a limited geographic range and has shifted to a new host plant (see Brown et al. 1994). In one case, the mtDNA haplotype found in the narrowly distributed species shares a most recent common ancestor

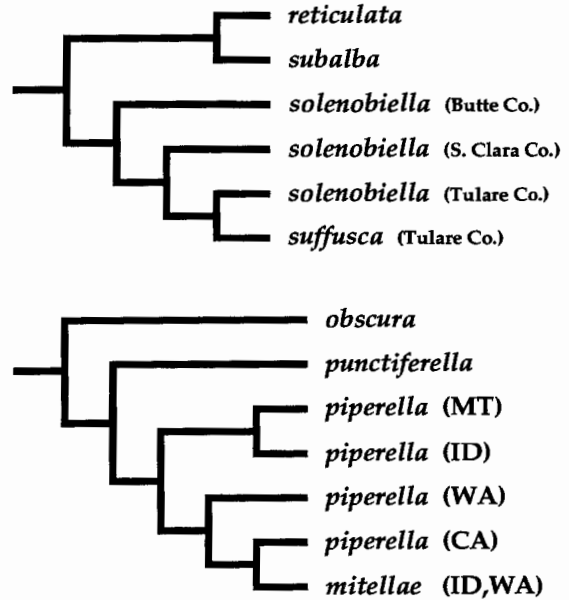


Figure 2.3. Two species of moths in the genus *Greya* (Prodoxidae) appear as paraphyletic assemblages of populations in mtDNA phylogenies. (a) The *Greya solenobiella* group. *Greya solenobiella* is a widespread species in California and Oregon found on *Yabea microcarpa* (Apiaceae). *G. suffusca* is restricted to Tulare Co., California, and is found on *Osmorhiza brachypoda* (Apiaceae). (b) The *Greya punctiferella* group. *Greya piperella* is widespread throughout the western United States and Canada, feeding on plants in the genus *Heuchera* (Saxifragaceae). *Greya mitellae* is found only in northern Idaho and southeastern Washington on *Mitellae stauropetala* (Saxifragaceae). The mitochondrial DNA data are from Brown et al. (1994).

with a haplotype of the widespread “paraphyletic” species from the only locality where the two species occur together. A plausible model for divergence involves a host shift “within” one region (either sympatrically or through divergence of a small isolated population), giving rise to a narrowly distributed daughter species on a new host plant. Funk et al. (1995) provide additional examples of insect host shifts resulting in two daughter species, one paraphyletic with respect to the other. In fact, divergence of peripheral isolates or island populations may commonly lead to the same sort of pattern, with a widespread “ancestral” species giving rise to local derivatives (figure 2.4). Data from mice (Avice et al. 1983), pocket gophers (Patton and Smith 1994), macaques (Melnick et al. 1993), and *Drosophila* (Powell 1991; Hey and Kliman 1993) provide likely examples of such situations. Rieseberg and Brouillet (1994) argue that paraphyletic species will be common in plants, given the prevalence of “local speciation” (Levin 1993).

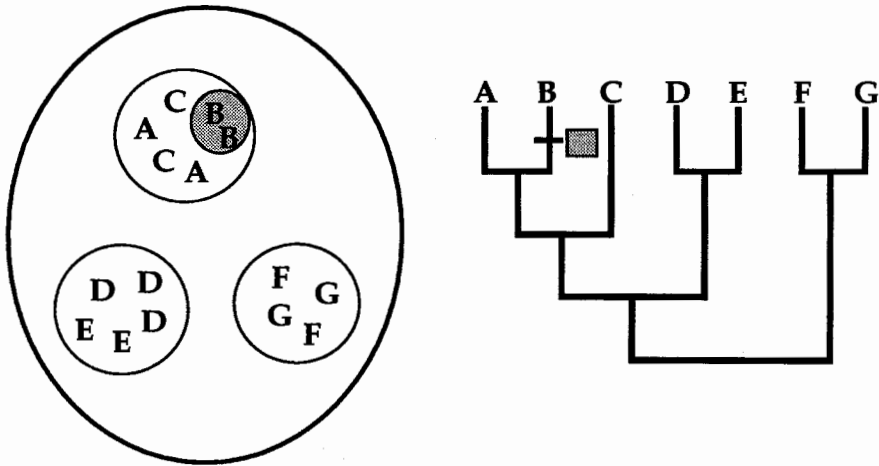


Figure 2.4. Origin of a new species “within” one of several populations of a widely distributed ancestral species. Regardless of the local geography of speciation, the resulting gene genealogy shows that the widely distributed daughter species is paraphyletic with respect to the locally derived species. A–G are distinct genotypes (DNA sequences). Only genotype B is found in the narrowly distributed daughter species. In the example shown here, the three populations of the widely distributed species exhibit fixed differences and would be considered three distinct phylogenetic species according to the criteria of Nixon and Wheeler (1990).

Gene Genealogies, Species, and Speciation

Analyses of gene genealogies in recently subdivided populations suggest that paraphyly (and perhaps polyphyly) will be common and that the phylogenetic status of populations changes over time (Tajima 1983; Neigel and Avise 1986; Hey 1994). Consider a single panmictic population that is subdivided into two daughter populations with complete interruption of gene flow at time t (figure 2.5). The daughter populations each contain N diploid individuals, and selection and recombination are assumed not to occur. If two gene copies are sampled from each of the daughter populations, relationships must conform to one of four possible tree topologies (figure 2.5). These four gene genealogies correspond to situations in which the daughter populations are polyphyletic, one is paraphyletic with respect to the other, or the two populations are both monophyletic. Tajima (1983) calculated the probabilities of each genealogy as a function of the time since interruption of gene flow (table 2.2). With this sampling scheme, the most likely gene genealogy immediately after divergence is that both populations appear polyphyletic, but the probability of polyphyly declines quickly and is less than 10% after $2N$ generations. The probability of paraphyly increases to nearly 40% after N generations and then gradually declines. The initial probability of reciprocal monophyly is small, but this probability continues to increase over time. However, even $4N$ generations after interruption of gene flow, only about 83% of gene genealogies will show this pattern.

Using computer simulations, Neigel and Avise (1986) reached very similar conclusions, arguing for a progression from polyphyly through paraphyly to reciprocal monophyly. They extended the analysis by examining the influence of “mode of speciation”—varying the way in which the original population was partitioned and the subsequent demography of the daughter populations. Probabilities of initial polyphyly, paraphyly or monophyly depend on the numbers of founders and whether

Table 2.2. Probabilities of tree topologies (a)–(d) in figure 2.5, as a function of the number of generations since interruption of gene flow between populations A and B.

Generations	Topology			
	(a)	(b)	(c)	(d)
$N/10$	0.134	0.263	0.201	0.402
$N/2$	0.231	0.364	0.135	0.270
N	0.354	0.400	0.082	0.164
$2N$	0.570	0.340	0.030	0.060
$4N$	0.828	0.160	0.004	0.008

Data were calculated using the formulae given by Tajima (1983). Topology (a) corresponds to reciprocal monophyly, topology (b) to paraphyly, and topologies (c) and (d) to polyphyly. N is the size of the two populations (assumed to be constant).

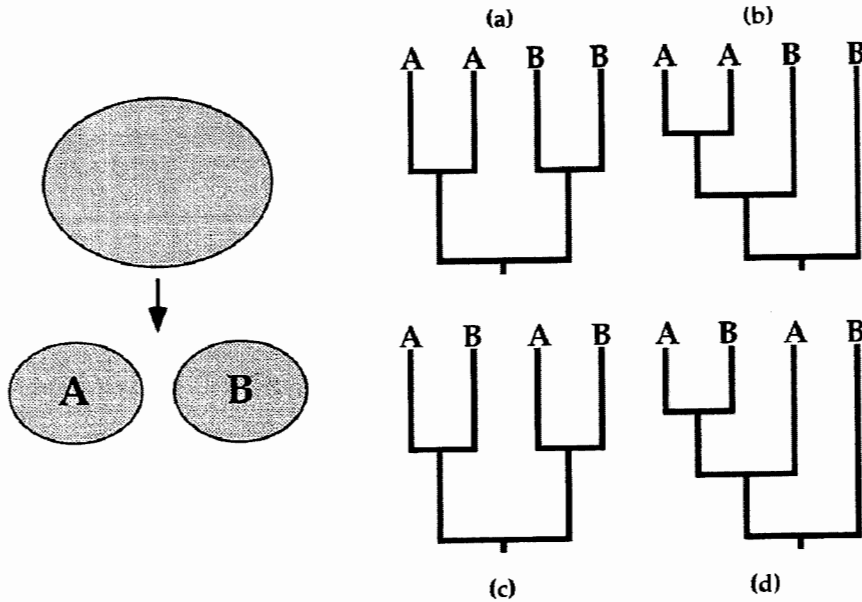


Figure 2.5. Model (based on Tajima 1983) in which a single ancestral population is subdivided into daughter populations A and B. Gene genealogies (a)–(d) represent the four possible tree topologies if two gene copies are sampled from each of populations A and B at some time after interruption of gene flow.

these individuals are chosen at random or from a restricted portion of the ancestral population. When one of the daughter populations derives from a small number of founders, the initial probability of paraphyly is very high. Hey (1994) showed that the probability of one or both daughter populations forming exclusive groups depends on the number of genes sampled from the daughter populations, decreasing as the sample size of genes increases.

Obviously, time to reciprocal monophyly (both daughter populations exclusive groups) depends on the effective population size (Tajima 1983; Neigel and Avise 1986). The time also depends on the nature of natural selection (assumed to be absent in all of the above models). Divergent selection (different alleles favored in the two daughter populations) will speed the approach to exclusivity. In contrast, balancing selection will slow it down (and can, in some cases like human and chimp MHC, prevent populations that have diverged for a very long time from becoming exclusive groups). Finally, all of the above models invoke complete interruption of gene flow. In a stepping-stone or isolation-by-distance model, probabilities of the alternative tree topologies depend on migration rate and geographic distance (Barton and Wilson 1995).

Life History of a Species

I propose that species (in a very broad sense) have a life history (figure 2.6). The details of the life history will

depend on the geography of speciation, demographic events during and after population subdivision, the impact of natural selection, and constraints on the evolution of cohesion (isolation). First, consider the case when speciation is allopatric. In this case, populations pass through a series of life stages following interruption of gene flow. The trajectory displayed in figure 2.6a is probably a common one—especially in organisms like many insects that have labile mate recognition systems, life cycles, and host associations. Soon after gene flow interruption, daughter populations A and B become phylogenetic species. This stage is completed either when (1) detectable mutations occur and are fixed in a single population or (2) random sorting of ancestral polymorphism results in fixed character state differences between populations. The consequence of either sort of event is a pair of populations that are diagnosably distinct. The probability of observing fixed character state differences depends on the effort expended in looking for such differences. Therefore, the timing of this initial “speciation” event will be a function of the level of resolution achieved in defining character state differences. It will obviously also depend on effective population sizes (small size promotes sorting of ancestral polymorphisms) and selection regimes (divergent selection will more likely lead to alternative fixation).

The second stage in the trajectory shown in figure 2.6a is the evolution of barriers to gene exchange or new cohesion mechanisms. These events are not apparent from

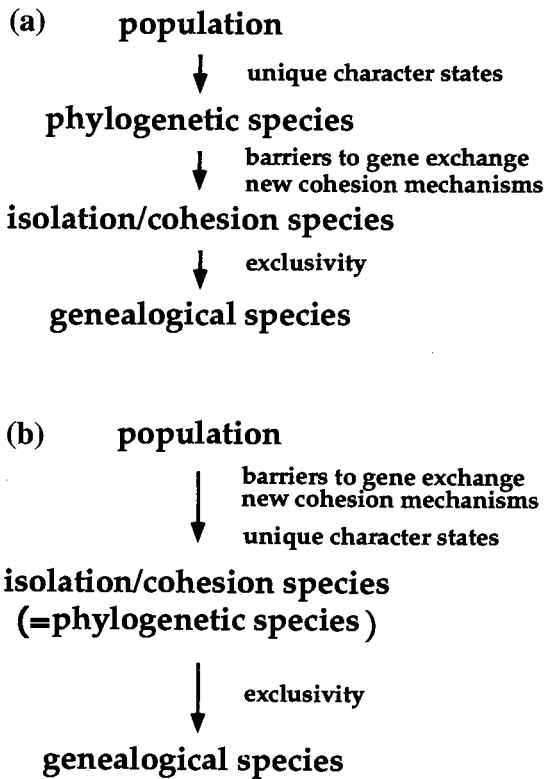


Figure 2.6. Species' "life histories" that trace change over time in the status of a pair of populations. In (a) speciation occurs in allopatry and the populations first become phylogenetic species, then isolation/cohesion species, and finally genealogical species. In (b) speciation is sympatric and populations become isolation/cohesion species at the same time as they become phylogenetic species.

a gene genealogy and are, to some degree, unpredictable. In many cases they may simply occur as a result of further divergence between populations (i.e., as a by-product of divergence in allopatry). The rate at which this stage is completed is no doubt taxon dependent; in some groups mate recognition systems and habitat/resource associations change quickly, whereas in others they are likely to be very conservative.

To be genealogical species, the two daughter populations must be exclusive groups. This third stage takes a very long time, unless N is small or we relax the requirement that exclusivity apply to all segments of the genome. Avise and Ball (1990) suggested "genealogical concordance" as a criterion for recognizing taxa (subspecies). This is a somewhat arbitrary criterion, representing the stage in the ontogeny of a species in which some but not all gene genealogies show concordant patterns of reciprocal monophyly.

In some circumstances, diverging populations may become genealogical species before they become isolation/cohesion species. This will be most likely when a polymorphic ancestral population becomes subdivided and sustained population bottlenecks result in pairs of exclusive groups in the absence of the evolution of any intrinsic barriers to gene exchange. Graybeal (1995) suggests that "exclusivity marks the point where the connections [between populations] can be considered lost" (p. 249). I agree that exclusivity can be viewed as a genealogical endpoint—but it is not one that is by any means irreversible (e.g., exclusive taxa may be able to hybridize, and introgression will destroy exclusivity).

When speciation is sympatric, populations often become isolation/cohesion species at the same time as they become phylogenetic species (figure 2.6b), because fixed character state differences first arise at the strongly selected loci that are responsible for the elimination of gene flow. With parapatric divergence, models of isolation by distance apply and fixed differences are also more likely to be due to selection.

Evolutionary geneticists have generally regarded the transition to isolation/cohesion species as the essence of the speciation process. Systematists have clearly been more concerned with the evolution of diagnosable and exclusive groups. Both of these views are legitimate. The origin of isolation and cohesion is of particular interest not because the underlying evolutionary processes are unique but because of the nature of the changes that occur (defined by their subsequent effect). As evolutionary biologists interested not only in what has been but also in what will be, most students of the speciation process remain convinced that it is the evolution of new barriers to gene exchange or new cohesion mechanisms (i.e., the "second stage" in figure 2.6a or the "first stage" in figure 2.6b) that should be the focus of attention for those who claim to be studying speciation. For organizing the diversity of life and naming taxa, other stages in the life history of species may prove more useful.

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