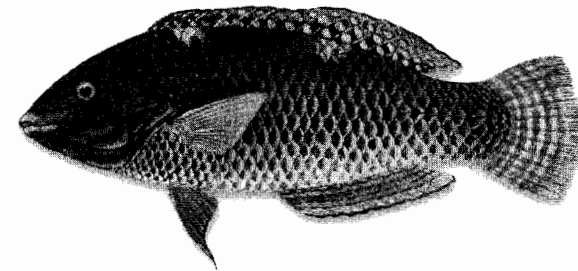
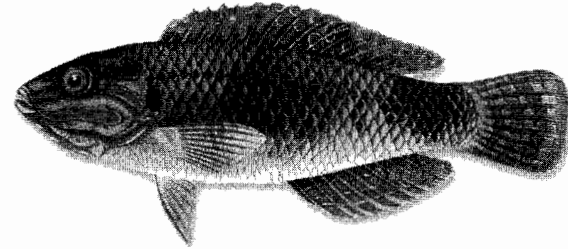
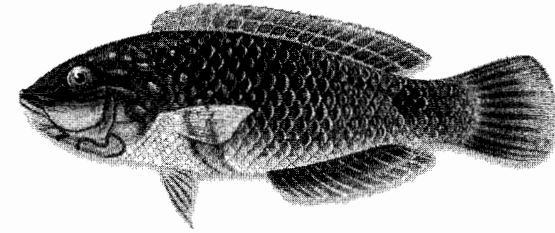


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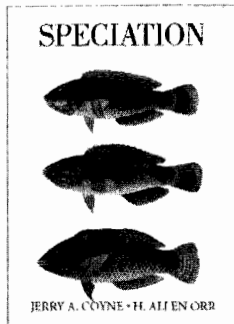


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About the cover

Three congeneric species of Pacific wrasse; from top to bottom, *Halichoeres trimaculatus*, *H. margaritaceus*, and *H. hortulanus*. These paintings, by the Japanese artist Kako Morita, are reproduced from Plates 46 and 47 of *The Fishes of Samoa* by David Starr Jordan and Alvin Seale (1906, Bulletin of the United States Bureau of Fisheries 25:173–456). The illustrations were published with the help of Jordan's friend and fellow naturalist, President Theodore Roosevelt, who interceded when the government's committee on publication deemed the plates too expensive to print.

Jordan (1851–1931) was an influential evolutionist, ichthyologist, and a staunch defender of Darwinism at a time when it was unpopular. A prolific author, his most notable contribution to the study of speciation was his emphasis on the importance of geographic barriers.

To Anne and Lynne

SPECIATION

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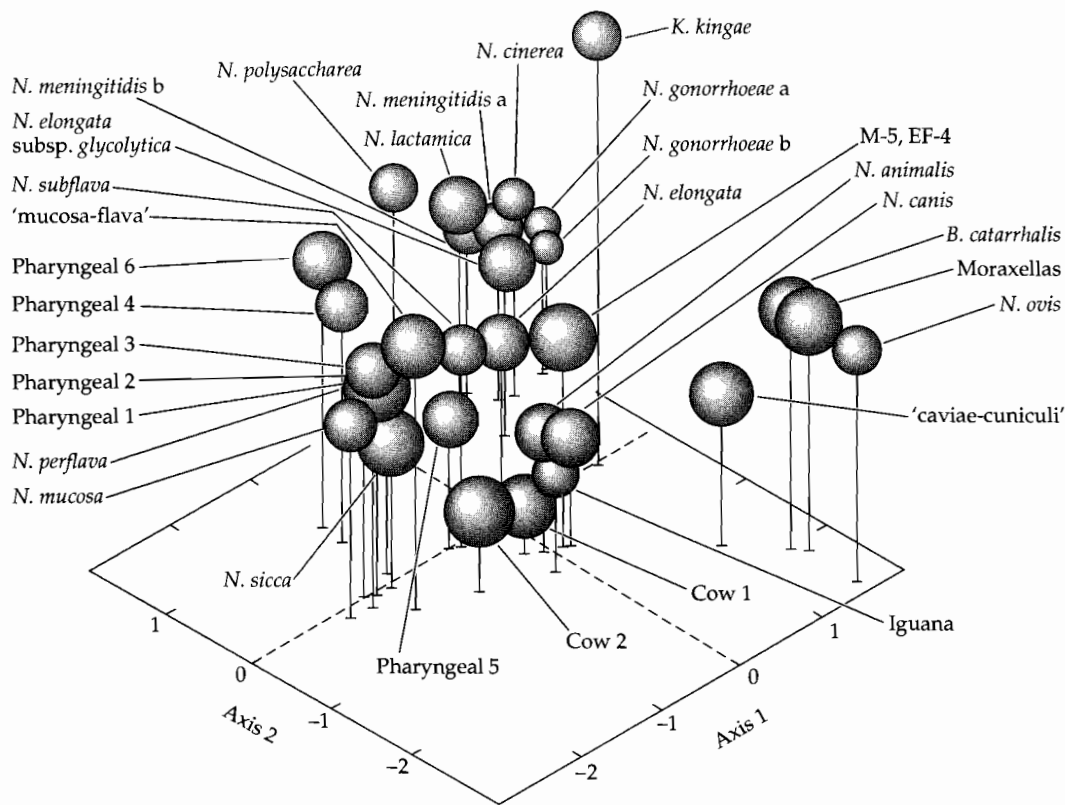


Figure 1.3 Phenotypic clusters of bacterial clones in the genus *Neisseria*. 315 strains were categorized using 155 phenotypic traits. Figure shows the centroids of the 31 named phenotypic clusters (phenons), sorted on the first three axes of a principal coordinate analysis (vertical direction is Axis 3). The degree of overlap between phenons is shown by the proximity of clusters. (After Barrett and Sneath 1994.)

genetic variation within one area. Hence, answering the question of distinctness of *sympatric* bacterial taxa is difficult. Ideally, one should examine samples of many isolates taken from a single substrate (such as soil) in a single area, as did Roberts and Cohan (1995). But most bacteria remain unknown. Although more than 8000 bacterial "species" have been named, there may be as many as a billion ecologically distinct taxa, most impossible to culture and study (Dykhuizen 1998).

Preliminary observations that bacterial taxa appear discrete may seem somewhat surprising. Recent work of Cohan and his colleagues (Majewski and Cohan 1999; Cohan 2001, 2004), however, suggest that episodic natural selection, coupled with a diversity of ecological niches, can produce distinct clusters of bacteria in sympatry. We discuss this process of bacterial "speciation" in greater detail below.

Conclusions

Although most biologists agree that species are real, we lack the rigorous studies needed to convince skeptics that nature is discontinuous. Discrete clusters appear to characterize sympatric, sexually reproducing eukaryotes and perhaps many prokaryotes. However, clusters seem less distinct in groups with mixed mating systems, such as agamic complexes in plants. It may seem odd that taxa appear most distinct in groups that are either completely sexual or nearly completely asexual, and less distinct in groups having both forms of reproduction. Such a result, however, can be understood if one considers how clusters form. We return to this problem at the end of the chapter.

Species Concepts

The essence of the "species problem" is the fact that, while many different authorities have very different ideas of what species are, there is no set of experiments or observations that can be imagined that can resolve which of these views is the right one. This being so, the "species problem" is not a scientific problem at all, merely one about choosing and consistently applying a convention about how we use a word. So, we should settle on our favorite definition, use it, and get on with the science (Brookfield 2002, p. 107).

Most biologists agree that discrete clusters exist among sexually reproducing organisms, and behave in their own research as if these groups were real. However, evolutionists disagree about whether these groups constitute "species," and, if so, how to best define them. As we have seen, the species concept is one of the most hotly debated issues in speciation. While much of the debate seems more philosophical than scientific, the issue is important, for we cannot study how species form until we determine what they are.

Mayr (1942, 1982) reviews the history of species concepts up to about 1980. During the Modern Synthesis, only a few concepts competed for the allegiance of biologists, most prominently Mayr's own "biological species concept" or those based on morphological difference ("typological" concepts). However, in the last twenty years the debate has intensified. New species concepts appear yearly, and there are now entire books devoted to the problem (e.g., Ereshefsky 1992; Claridge et al. 1997; Wilson 1999; Wheeler and Meier 2000; Hey 2001). We count at least 25 concepts, by no means an exhaustive list. It is somewhat depressing that evolutionary biologists continue to spend so much time arguing about what constitutes a species when, as noted by Brookfield (2002), the debate cannot be resolved by normal scientific methods.

There are several reasons why these debates persist. First, there is no concept that, when applied to nature, is free from ambiguities (Hey 2001). Some ambiguities derive from evolution itself: species arise from other species, and

during this process there will be unclear cases, no matter how one defines species. Moreover, any strict concept fails in some situations, and different concepts fail in different situations. If one sees species as groups separated from other groups by reproductive barriers, what does one do upon finding a single fertile hybrid among a million individuals? Or, if one defines species as groups possessing at least one unique, diagnosable trait, does a single nucleotide in the genome suffice? How does one deal with geographically isolated populations that are genetically or morphologically divergent? Further problems arise from the diverse ways in which organisms reproduce. Evolutionists now appreciate that no single species concept can encompass sexual taxa, asexual taxa, and taxa having mixed modes of reproduction. As Kitcher (1984, p. 309) notes: "There is no unique relation which is privileged in that the species taxa it generates will answer to the needs of all biologists and will be applicable to all groups of organisms."

Moreover, biologists want species concepts to be useful for some purpose (i.e., be "operational"), but differ in what that purpose should be. We can think of at least five such goals. Species can be defined in a way that

1. helps us classify them in a systematic manner;
2. corresponds to the discrete entities that we see in nature;
3. helps us understand how discrete entities *arise* in nature;
4. represents the evolutionary history of organisms; and
5. applies to the largest possible number of organisms.

No species concept will accomplish even most of these purposes. We therefore feel that, when deciding on a species concept, one should first identify the nature of one's "species problem," and then choose the concept best at solving that problem.

The biological species concept (BSC)

Our own species concept is one that comes closest to deciphering what we (and many of our predecessors) consider the most important "species problem," namely, why do sympatric, sexually reproducing organisms fall into discrete clusters? This view of the species problem antedates the Modern Synthesis, going back to Bateson (1894). In our opinion, the discontinuities of nature are best encapsulated, and their origin best understood, using a modified version of the biological species concept (BSC; Table 1.1). We do not wish to describe and evaluate here every species concept ever proposed. Table 1.1 also lists eight of the most popular alternatives to the BSC, which we explain and evaluate in the Appendix. Here we describe our version of the BSC and consider its advantages and disadvantages.

To an evolutionary geneticist, the observation of discrete, sexually reproducing groups in sympatry immediately suggests a species concept based on interbreeding and its absence. As Dobzhansky (1937c, p. 281) recognized:

Table 1.1 *The biological species concept and some recently proposed alternatives^a*

Basis of concept	Concept	Definition
1. Interbreeding	Biological Species Concept (BSC)	Species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1995).
2. Genetic or phenotypic cohesion	Genotypic Cluster Species Concept (GCSC)	A species is a [morphologically or genetically] distinguishable group of individuals that has few or no intermediates when in contact with other such clusters (Mallet 1995).
	Recognition Species Concept (RSC)	A species is that most inclusive population of individual biparental organisms which shares a common fertilization system (Patterson 1985).
	Cohesion Species Concept (CSC)	A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms (Templeton 1989).
3. Evolutionary cohesion	Ecological Species Concept (EcSC)	A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen 1976).
	Evolutionary Species Concept (EvSC)	A species is a single lineage of ancestral descendant populations or organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley 1978, modified from Simpson, 1961).
4. Evolutionary history	Phylogenetic Species Concept 1 (PSC1)	A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a paternal pattern of ancestry and descent (Cracraft 1989).
	Phylogenetic Species Concept 2 (PSC2)	A species is the smallest [exclusive] monophyletic group of common ancestry (de Queiroz and Donoghue 1988).
	Phylogenetic Species Concept 3 (PSC3) or Genealogical Species Concept (GSC)	A species is a basal, exclusive group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group, and that contains no exclusive group within it (Baum and Donoghue 1995; Shaw 1998).

^aThe Appendix discusses and evaluates all of these concepts except the BSC.

Any discussion of these problems [of discontinuities in the living world] should have as its logical starting point a consideration of the fact that no discrete groups of organisms differing in more than a single gene can maintain their identity unless they are prevented from inter-

breeding with other groups . . . Hence, the existence of discrete groups of any size constitutes evidence that some mechanisms prevent their interbreeding, and thus isolate them.

Dobzhansky (1935, p. 353) proposed that “a species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of hybrids, or both).” (Among “physiological properties” Dobzhansky also included genetic barriers acting *before* fertilization, such as the unwillingness to mate with dissimilar individuals.) This is close to the definition that we adopt. However, Dobzhansky’s implication that different species must exchange *no* genes seems too extreme, and has promoted both confusion in the field and suggestions that the BSC be rejected.

The BSC is, however, most closely associated with Ernst Mayr, who not only provided its most famous formulation—“Species are groups of actually

Table 1.2 *Classification of reproductive isolating barriers*

-
- I. Premating isolating barriers.** Isolating barriers that impede gene flow before transfer of sperm or pollen to members of other species.
- A. Behavioral isolation** (also called “ethological” or “sexual” isolation). Includes all differences that lead to a lack of cross-attraction between members of different species, preventing them from initiating courtship or copulation.
- B. Ecological isolation.** Isolating barriers based primarily on differences in species’ ecology, i.e., barriers that are direct byproducts of adaptation to the local environment.
- Habitat isolation.** Species have genetic or biological propensities to occupy different habitats when they occur in same general area, thus preventing or limiting gene exchange through spatial separation during the breeding season. This isolation can be caused by differential adaptation, differential preference, competition, or combinations of these factors.
 - Temporal (allochronic) isolation.** Gene flow between sympatric taxa is impeded because they breed at different times.
 - Pollinator isolation.** Gene flow between angiosperm species is reduced by their differential interactions with pollinators. This can occur via pollination by different species, or by pollen transfer involving different body parts of a single pollinator species.
- C. Mechanical isolation.** Inhibition of normal copulation or pollination between two species due to incompatibility of their reproductive structures. This incompatibility can result from lack of mechanical fit between male and female genitalia (structural isolation) or the failure of heterospecific genitalia to provide proper stimulation for mating (tactile isolation).
- D. Mating system “isolation.”** The evolution of partial or complete self-fertilization (autogamy) or the asexual production of offspring (apomixis) that can result in the creation of a new taxon or set of lineages. As noted in Chapter 6, this is not an isolating barrier in the same sense as the others in this list.
-

or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (1942, p. 120)—but also worked out the implications of this definition and defended it against critics (Mayr 1963, 1969).

Dobzhansky’s later contributions to the BSC included compiling a list of various barriers to gene flow, which he called “isolating mechanisms” (1937a, 1951). To some, the word “mechanism” paints a misleading picture of speciation, implying that selection builds reproductive barriers to keep species distinct. But this process occurs only during reinforcement and some types of sympatric speciation, while the rest of the time species are not direct objects of natural selection, but accidental byproducts of evolutionary divergence. When referring to forms of reproductive isolation, we therefore use the less misleading term *isolating barriers*, which we define as *those biological features of organisms that impede the exchange of genes with members of other populations*. These barriers are usually, but not invariably, based on genetic differences between populations; we describe a few exceptions below. Table 1.2 describes and defines the

Table 1.2 *Classification of reproductive isolating barriers (continued)*

-
- II. Postmating, prezygotic isolating barriers.** Isolating barriers that act after sperm or pollen transfer but before fertilization.
- A. Copulatory behavioral isolation.** Behavior of an individual during copulation is insufficient to allow normal fertilization.
- B. Gametic isolation.** Transferred gametes cannot effect fertilization.
- Noncompetitive gametic isolation.** Intrinsic problems with transfer, storage, or fertilization of heterospecific gametes in single fertilizations between members of different species.
 - Competitive gametic isolation.** (conspecific sperm or pollen preference) Heterospecific gametes are not properly transferred, stored, or used in fertilization only when competing with conspecific gametes.
- III. Postzygotic isolating barriers (hybrid sterility and inviability)**
- A. Extrinsic.** Postzygotic isolation depends on the environment, either biotic or abiotic.
- Ecological inviability.** Hybrids develop normally but suffer lower viability because they cannot find an appropriate ecological niche.
 - Behavioral sterility.** Hybrids have normal gametogenesis but are less fertile than parental species because they cannot obtain mates. Most often, hybrids have intermediate phenotypes or courtship behaviors that make them unattractive.
- B. Intrinsic.** Postzygotic isolation reflects a developmental problem in hybrids that is relatively independent of the environment.
- Hybrid inviability.** Hybrids suffer developmental difficulties causing full or partial lethality.
 - Hybrid sterility.**
 - Physiological sterility.** Hybrids suffer problems in the development of the reproductive system or gametes.
 - Behavioral sterility.** Hybrids suffer neurological or physiological lesions that render them incapable of successful courtship.
-

diverse forms of isolating barriers. Our list is indebted to Dozhansky's but is updated in light of recent work.

Because of the difficulty of determining the species status of allopatric taxa, Mayr later struck the word "potentially" from his definition and suggested the following version of the BSC, which we adopt with a few caveats:

Species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1995, p. 5).

Groups of populations thus constitute different species under two conditions: (1) their genetic differences preclude them from living in the same area, or (2) they inhabit the same area but their genetic differences make them unable to produce fertile hybrids.

In our view, distinct species are characterized by *substantial but not necessarily complete reproductive isolation*. We thus depart from the "hard line" BSC by recognizing species that have limited gene exchange with sympatric relatives. But we feel that it is less important to worry about species status than to recognize that the *process* of speciation involves acquiring reproductive barriers, and that this process yields intermediate stages when species status is more or less irresolvable.

The reader may have noticed an apparent discrepancy between the way we recognize species and the way we define them. If we *distinguish* species as discrete morphological and genetic units coexisting in sympatry, why do we not *define* them as such, considering speciation to be the acquisition of diagnostic traits and genes? Indeed, one species concept—the "genotypic cluster species concept" (GCSC)—does exactly that (see Appendix). Schilthuizen (2000, p. 1135) emphasizes this discrepancy between recognition and definition:

In Mayr's writings, two views on species appear. The first is that all individuals of a species share the same well-integrated complex of epistatically and pleiotropically interacting genes. This is the species *concept*, and Mayr [1963] writes that the evolution of two well-integrated gene complexes from a single ancestral one is "the essence of speciation." At the same time, however, the biological species definition makes no mention of gene complexes, but rather of devices for reproductive isolation. Consequently Mayr [1963] can also be found writing that 'speciation is characterized by the acquisition of these devices.'

Schilthuizen's point is clear: If distinctness in sympatry is all that matters, then the BSC is problematic, for he believes that populations can remain distinct in sympatry for reasons other than reproductive isolation. Schilthuizen and others (e.g., Mallet 1995) suggest several ways this can happen.

The first involves disruptive selection in one area. Selection favoring individuals at two extremes of habitat or resource use, for example, can create and maintain groups that differ in genes causing local adaptation. If this selection is strong, it can create groups that remain distinct at several to many loci, although genes not subject to selection will be freely exchanged. Schilthuizen

notes that such groups include "host races," such as the apple and hawthorn races of the apple maggot fly *Rhagoletis pomonella* (Chapter 4). Hybrid zones, in which two forms with contiguous ranges hybridize where they meet but remain distinct, are not uncommon (Barton and Hewitt 1985).

Schilthuizen (2000, p. 1136) argues that these cases show that "the BSC with its reproductive-isolation criterion does not automatically follow from a concept of species as a coadapted gene complex, because the latter can persist in spite of the absence of reproductive barriers." But this contention is incorrect. In sexually reproducing organisms, *the stable coexistence of genetically distinct groups in sympatry requires reproductive barriers between them*. (By "genetically distinct," we mean groups differing at several loci, not discontinuities caused by simple Mendelian polymorphisms.) Without reproductive barriers, the groups would fuse. In many cases, such as strong disruptive selection that causes speciation, the barriers involve *extrinsic hybrid inviability* (see Table 1.2): intermediate forms are ecologically unfit. Such inviability preserves the distinctness of loci affecting the selected traits. Part of the confusion comes from the rather artificial distinction between "selection" and "reproductive isolation." If disruptive selection causes speciation, it does so by creating reproductive isolation. Indeed, much work on the host races of *Rhagoletis pomonella* has involved identifying barriers to gene exchange (Feder et al. 1994, 1997a, b). In many hybrid zones, intermediate forms are unfit, being relatively inviable or sterile (Barton and Hewitt 1985; Howard et al. 1997; Presgraves 2002). We are not claiming that reproductive barriers must exist before selection can create evolutionary divergence. This neoDarwinian view is obviously wrong. Rather, we maintain that disruptive selection and reproductive isolation are two sides of the same coin.

During sympatric speciation and reinforcement, the point at which sympatric taxa should be called "species" is arbitrary. In fact, one could consider speciation as the conversion of "genotypic cluster" species into "biological" species, a process that is continuous, yielding ever-increasing barriers to gene flow. In such situations we prefer to apply our version of the BSC, for under this concept one can view the entire process of speciation as the evolution of reproductive isolation. Arguments about the exact relationship between gene flow and species status have obscured the more important fact that reproductive barriers are essential for producing and maintaining distinct groups in sympatry.

Our view that reproductive barriers are the currency of speciation derives from our belief that understanding how these barriers arise is the solution to the species problem. This does not mean that selection can or should be ignored. Indeed, as we show in Chapter 11, most reproductive barriers probably result from natural selection. Yet before one can understand which forms of selection keep clusters distinct, one must understand which *barriers* keep clusters distinct.

Our version of the BSC differs from the GCSC in two respects. First, we do not consider clusters to be species if they are distinct at only a few loci but freely exchange genes in the rest of the genome. We view such clusters as races or

incipient species. Indeed, even biologists of the "cluster" school appreciate the importance of isolating barriers, and recognize their evolution as a part of speciation (e.g., Mallet et al. 1998). For example, some advocates of the GCSC believe that sympatric speciation is common. However, those who model sympatric speciation consider that it is complete only when isolating barriers reduce gene flow to nearly zero (Rice 1984a; Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999). Second, we consider the BSC better than the GCSC at stimulating research. Defining species simply as clusters offers no insight into how these clusters arise and are maintained.

Finally, we argue that the traits used to *recognize* groups need not be identical to the traits used to define or conceptualize them. This point was best made by Simpson (1961) using the example of identical twins. These twins are recognized by their extreme morphological similarity, but are defined as two individuals derived from a single fertilized egg. The latter concept seems more useful because it accounts for the morphological similarity. Likewise, reproductive isolation accounts for the existence of discrete clusters in sympatry.

In our view, then, reproductive isolation is the proper focus for the study of speciation. In fact, we can hardly imagine writing a substantive book on speciation using any concept other than the BSC. The recent explosion of work on speciation concentrates almost entirely on reproductive isolation.

Our acceptance of isolating barriers as the key to speciation does not mean, of course, that we adhere to every idea espoused by Dobzhansky, Mayr, and other proponents of the BSC. As noted above, for instance, we do not believe that evolutionary divergence in sympatry requires the prior evolution of reproductive isolation.

Moreover, we do not agree that species always form "integrated, coadapted gene complexes." This view was common during the Modern Synthesis, with some holding the almost teleological view that selection erects isolating barriers to protect such complexes:

The division of the total genetic variability of nature into discrete packages, the so-called species, which are separated from each other by reproductive barriers, prevents the production of too great a number of disharmonious incompatible gene combinations. This is the basic biological meaning of species, and this is the reason why there are discontinuities between sympatric species (Mayr 1969, p. 316).

Hence maintenance of life is possible only if the gene patterns whose coherence is tested by natural selection are prevented from disintegration due to unlimited hybridization. It follows that there must exist discrete groups of forms, species, which consist of individuals breeding inter se, but prevented from interbreeding with individuals belonging to other groups of similar nature (Dobzhansky 1937a, p. 405).

Although reproductively isolated groups will eventually acquire sets of harmoniously acting genes—the so-called coadapted complexes—newly formed species need not differ in any traits beyond those causing reproductive isola-

tion. Some species can arise via changes in only one or a few genes, and some cases of speciation may involve no genetic change at all.

To prevent confusion, we deal with several questions that arise about our version of the BSC.

MUST REPRODUCTIVE ISOLATION BE COMPLETE BEFORE TAXA ARE CONSIDERED SPECIES UNDER THE BSC? The BSC is usually seen as requiring absolute barriers to gene flow between taxa. For example, Barton and Hewitt (1985, p. 114) argue that "if two populations are to belong to different biological species, reproductive isolation must be complete: no fertile hybrids can be formed." This strict construction has bothered biologists who consider "good species" to be those that maintain their distinctness in sympatry even if they occasionally hybridize with others. Indeed, molecular studies have shown that hybridization may be far more common than previously suspected.

Historically, one of the most common criticisms of the BSC has been that related species rarely show complete reproductive isolation. Mayr himself wavered about whether the BSC should be modified to deal with this problem. He often took the hard line of "no gene flow permitted," as when asserting that "species level is reached when the process of speciation has become irreversible, even if some of the (component) isolating mechanisms have not yet reached perfection" (Mayr 1963, p. 26). But he argued elsewhere that some hybridization is permissible between biological species so long as they maintain their distinctness. Referring to sympatric taxa of ducks, for example, he noted that "occasional hybrids occur, but at such a low rate that the elimination of the introgressing genes is not too severe a burden on the parental species" (Mayr 1963, p. 552). Considering fish of the genus *Gila*, he observed that "the characters of a few specimens indicated the possibility of introgression, yet there was no blurring of the species border" (1963, p. 116). Such contradictory statements obviously reflect confusion about whether morphological distinctness requires absolute bars to hybridization.

Other contributors to the Modern Synthesis believed that good species could show limited hybridization:

Two or more Mendelian populations can be sympatric, i.e., can coexist indefinitely in the same territory, only if they are reproductively isolated, *at least to the extent that the gene exchange between them can be kept under control by natural selection* (Dobzhansky 1951, p. 264, our italics).

Natural hybridization and gene flow can take place between biological species, even though they are highly intersterile or isolated in other ways, as long as the breeding barriers are less than 100% effective. . . . Some of these results of hybridization do not affect the distinctness of the species involved, and hence do not concern us now (Grant 1971, p. 51).

Even if there is evidence of backcrossing but the intergrading types remain relatively uncommon in comparison with sharply distinct parent types, it may be presumed that there is so much selection against

the hybrids that they do not destroy the integrity of the two species” (Wright 1978, p. 5).

Although Dobzhansky, Grant, and Wright all adhered to the BSC, they obviously did not take a hard line on gene flow.

Our notion of species status, then, involves a sliding scale. We do not consider taxa having substantial gene flow despite morphological distinctness to be species. As reproductive barriers become stronger, taxa become more and more “species-like,” and when reproductive isolation is complete we consider taxa to be “good species.” This view obviously requires some subjective decisions about species status. But this is not unique to the BSC. As we show in the Appendix, *all* species concepts require some subjective judgments.

Some evolutionists have suggested guidelines for gene flow that would allow the BSC to appear more objective. Schemske (2000, p. 1070), for example, proposes that “as a gross yardstick, if the probability of successful hybrid formation is less than the mutation rate, then populations meet the criterion of good biological species.” The rationale appears to be that species status is attained when the variation produced by mutation exceeds that introduced by introgression. Yet even this criterion is arbitrary. “Hybrid formation” is not equivalent to introgression, and most mutations are unconditionally deleterious. Moreover, the criterion is an operational nightmare: to determine species status, one would have to measure mutation and hybridization rates, usually impossible tasks. A further implication of Schemske’s thesis is that, when introgression exceeds mutation, species borders blur. This is almost certainly untrue, as it ignores the fact that selection can eliminate introgressed genes.

Determining BSC status using a sliding scale is of course also difficult in its own right: groups can appear quite distinct while still exchanging many genes. This occurs, for instance, in sympatric morphs of the butterfly *Papilio dardanus* that are Batesian mimics of different species (Clarke and Sheppard 1963). Mimetic forms differ by several genes that are apparently closely linked in clusters of “supergenes,” but appear to interbreed freely. Even taxa with substantial reproductive isolation can show rare gene exchange. Everyone considers *Drosophila pseudoobscura* and *D. persimilis* (two sympatric taxa that are classic subjects of evolutionary genetics) as distinct species. Nevertheless, they hybridize at a low rate: roughly one out of 10,000 females examined is a hybrid (Powell 1983), and hybrid females are fertile. The pattern of molecular variation in these two species also suggests some introgression after evolutionary divergence (Machado et al. 2002).

Adopting a species concept that allows some introgression does not trouble us. Indeed, throughout this book we use the term “species” even when a group exchanges some genes with sympatric relatives. We largely agree with McPhail (1994, p. 400) that “the goal of speciation studies is to understand how coexisting populations come into being, and it is unimportant whether or not systematists consider such divergent populations as species.” However, we also recognize that systematists need a yardstick for delimiting species, and

we are usually happy to recognize the groups that most biologists call species, even though many of these may not conform to our notion of “good” species because they exchange genes with other groups.

Finally, we emphasize that we do not regard our species concept as perfect, and discuss some of its problems later in this chapter.

WHY ISN’T ECOLOGICAL DIFFERENTIATION PART OF THE BSC? We have framed the species problem as the sympatric coexistence of discrete groups, thereby raising issues of ecology. Most ecologists believe that species can coexist only if they show a minimal degree of ecological divergence. Why, then, do we not define species as “reproductively isolated entities having sufficient ecological divergence to permit their coexistence”? Indeed, Mayr (1982, p. 273) amended the BSC to take ecology into account: “A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.” Van Valen’s (1976) ecological species concept also requires that a species occupy a distinct “adaptive zone.” These views are closely connected with Sewall Wright’s idea that species sit atop peaks in the adaptive landscape, with each peak representing a discrete niche (e.g., Wright, 1982).

Not all ecologists, however, agree that extreme ecological similarity prevents the coexistence of species. The “limiting similarity” principle has its own large and controversial literature (e.g., Abrams 1983; Chesson 1991; Hubbell 2001). Coexistence of nearly identical species can be maintained by spatial and temporal fluctuation in resources, or by subtle and virtually undetectable differences in ecology, such as a difference in the shape of the relationship between resource abundance and consumption rate (Armstrong and McGehee 1980). Thus, the hypothesis that species coexistence requires ecological difference seems theoretically plausible but empirically untestable: if one cannot find ecological differences between sympatric species, one may have missed undetectable but important aspects of resource use. Nevertheless, there is much evidence for competition between closely related sympatric species (Schluter 2000), and so we assume that such species usually have some ecological difference.

Nevertheless, we see niche differences as more relevant to the *persistence* of, rather than to the definition of, species, for there is no necessary correlation between reproductive isolation and ecological differentiation. In fact, most biologists implicitly recognize that permanent coexistence is *not* a criterion for species status. This is shown by the number of cases in which one species outcompetes or replaces a close relative in nature. The Chinese parasitoid wasp *Aphytis lingnanensis* has displaced its Mediterranean relative *A. chrysomphali* in Southern California (DeBach and Sundby 1963), but their putative ecological similarity does not affect their acknowledged status as distinct species. Conversely, ecologically differentiated taxa lacking reproductive isolation can fuse in sympatry. Of course, ecological differences are clearly important in speciation. Such differences can themselves constitute barriers to gene flow, as with habitat isolation, or create selective pressures that promote the evolution of

other isolating barriers. In many cases there will be considerable overlap between the factors that prevent gene flow between sympatric species and the factors that allow them to coexist.

This overlap between reproductive isolation and coexistence is especially important in three circumstances. First, divergent natural selection may produce adaptations that simultaneously reduce gene flow *and* allow species to coexist. This is true for habitat isolation (in which adaptation to different niches within one area spatially restricts hybridization), and extrinsic postzygotic isolation (in which two species occupying different niches produce hybrids ecologically inferior to either parent). Second, ecological differences allowing coexistence can promote the evolution of further barriers to gene flow. The ecological inferiority of hybrids, for example, may lead to the evolution of increased mating discrimination, an important part of sympatric speciation and reinforcement. Finally, the creation of a new polyploid plant species must often involve ecological changes that allow it to coexist with its ancestors (see Chapter 9).

MUST REPRODUCTIVE ISOLATION BE GENETIC? Dobzhansky (1937c) initially considered geographic isolation between populations as a form of reproductive isolation, although he later abandoned this view. While geographic barriers impede gene flow and are instrumental in allopatric speciation, we do not consider them isolating barriers, for they neither involve biological differences between taxa nor prevent gene flow between sympatric species.

While nearly all isolating barriers are genetic, there are some exceptions. Nongenetic barriers include “infectious speciation” caused by microorganisms that produce hybrid inviability between their hosts (Chapter 7), “cultural speciation” based on the imprinting of brood-parasitic birds on their hosts (Chapter 6), and “nongenetic allochronic speciation,” as may have occurred in periodical cicadas and pink salmon (Chapters 4 and 5). New autoployploid species are formed by differences in chromosome number, not gene sequence. Because all of these factors prevent gene flow in sympatry and are byproducts of the biology of organisms, we consider them genuine isolating barriers that are distinct from geographic barriers.

CAN ONE DETERMINE WHETHER SYMPATRIC SPECIES ARE REPRODUCTIVELY ISOLATED? Some critics have argued that it is impossible to apply the BSC in nature because one simply cannot perform the many hybridizations needed to determine the number of biological species in one area (Sokal and Crovello 1970). However, in reality this exercise is unnecessary, for reproductive isolation can be *inferred* from morphological, chromosomal, or molecular traits. Thus it is not necessary to identify the barriers to gene exchange to apply our version of the BSC; one need only show that two populations are reproductively isolated. This has traditionally been done (with great success) by analyzing the distribution of several morphological characters, such as bristles and genitalic traits in many insects. Fixed differences in chromosome inversions or molec-

ular markers can serve equally well. Knowlton (1993) enumerates sympatric *sibling species* (related species showing only slight differences in morphology) in marine organisms. In nearly every case, species diagnosis is based not on reproductive isolation but on fixed differences in morphological, ecological, or molecular traits. Finally, one can show that reproductive isolation in the laboratory (such as hybrid sterility or inviability) invariably accompanies morphological or chromosomal differences seen in nature.

DOES THE BSC MAKE SPECIATION “CAPRICIOUS?” In allopatric speciation, reproductive isolation is a byproduct of evolutionary change in isolated populations, and thus can be considered an evolutionary accident. This accidental aspect of speciation violates the notion that species must be the direct object of natural selection—that selection favors isolating barriers *because they cause isolation*. This view of “adaptive speciation” probably derives from Darwin (1859, p. 112), who felt that species arose to pack available niches as fully as possible.

The idea that selection operates to increase isolation was refined by the founders of the Modern Synthesis, who, as we note, saw isolating “mechanisms” as nature’s way of protecting coadapted gene complexes. Dobzhansky (1935, p. 349), for example, seemed reluctant to accept isolating barriers as mere byproducts of evolution:

This diversity of isolating mechanisms is itself remarkable and difficult to explain. It is unclear how such mechanisms can be created at all by natural selection, that is, what use the organism derives directly from their development. We are almost forced to conjecture that the isolating mechanisms are merely by-products of some other differences between the organisms in question, these latter differences having some adaptive value and consequently being subject to natural selection.

This may be why Dobzhansky believed that reinforcement, in which selection acts directly to increase reproductive isolation, is a nearly ubiquitous final step in speciation.

IS SPECIATION REVERSIBLE? The BSC is sometimes described as a “prospective” concept because it characterizes species by their evolutionary potential—their ability to evolve independently without contamination by genes from other species. If reproductive isolation is complete and irreversible, this claim is true. Nevertheless, the BSC is concerned only with isolating barriers operating *at present* and makes no claims about their permanence. Obviously, many barriers can be reversed during speciation, fusing two “good” species back into one. Habitat, temporal, sexual, and extrinsic postzygotic isolation can disappear with a change in environment. The formation of hybrid swarms through human disturbance of the habitat has occurred in *Iris* (Riley 1938; Anderson 1949) and perhaps in Lake Victoria cichlids (Seehausen et al. 1997). Rhymer and Simberloff (1996) describe many other cases of “extinc-

tion through hybridization," all involving either human disturbance or artificial introduction. Many similar fusions must have occurred in the absence of humans.

Intrinsic postzygotic isolation, however, is quite efficient at preventing fusion. As species adapt and diverge, their developmental pathways become less compatible in hybrids, yielding hybrid sterility and inviability. The key point, as we elaborate in the next chapter, is that intrinsic incompatibilities are difficult to undo (Muller 1939). Moreover, the expected number of genetic incompatibilities between two taxa grows at least as fast as the square of the time since they diverged (Orr 1995). Thus, as time passes, the probabilities of reversing all of these incompatibilities quickly approaches zero. At this point speciation *has* become irreversible.

Fusion of species through hybridization contradicts Mayr's view that speciation is not complete until it is irreversible. We cannot predict whether future environmental or genetic changes will undo reproductive isolation that is now "complete." If humans had not disturbed the habitat of *Iris fulva* and *I. hexagona*, we would still consider them good species. The BSC, then, is best viewed as a static and not a prospective species concept.

Advantages of the BSC

In promoting the BSC, Mayr (1942) emphasized what he viewed as its advantages over its competitors. At the time, the strongest competitors were typological species concepts based on morphological difference. In those pre-molecular days, the BSC was superior in diagnosing sibling species showing little or no morphological difference. In the past two decades, however, new species concepts have arisen, many of them similar to the BSC. In fact, most of the concepts listed in Table 1.2 pick out nearly identical sets of sexually reproducing groups occurring in sympatry.

While we concede that our version of the BSC has its own problems (described in the next section), it nonetheless has a major advantage over other concepts: it alone helps solve the species problem—the existence of discontinuities among sexually reproducing organisms living in one area. Other concepts can help recognize and diagnose these entities: a species can be seen as a genotypically distinct cluster, as a group that evolves largely as a unit, or as a group whose genes are more closely related to each other than to genes from other groups. Yet none of these concepts helps us understand why populations fall into discrete groups. "Phylogenetic species," for example, can be recognized as the discrete tips of phylogenies, but phylogenetic species concepts do not tell us *why* the tips are distinct. Likewise, sympatric species can be diagnosed as morphological or genetic clusters, but one cannot understand how these clusters arise and persist without knowing what prevents them from fusing. Of course the BSC does not solve every aspect of the species problem. For instance, it cannot tell us why or how reproductive iso-

lation develops in the first place. But only the BSC leads us to these other problems.

Other concepts, however, can sometimes be more useful in naming species. For example, the BSC cannot resolve the status of completely allopatric populations that produce viable and fertile hybrids. Using one version of the phylogenetic species concept, however, (PSC1, see Table 1.1), one can diagnose such populations as different species if they differ by as little as one trait, even a single nucleotide. Yet is this a substantial advantage? Such a practice enables one to name new species—many more than currently recognized—but forfeits any insight into the origin of distinct sympatric taxa.

Perhaps the most important advantage of the BSC is that it immediately suggests a research program to explain the existence of the entities it defines. Under the BSC, the nebulous problem of "the origin of species" is instantly reduced to the more tractable problem of the evolution of isolating barriers. While some evolutionists argue that the choice of a species concept should not include its pragmatic value, we feel that the best species concepts produce the richest research programs.

Indeed, this very book reflects the increased understanding of nature derived from using the BSC. It is a testament to the BSC that the study of reproductive isolation has become a major enterprise in evolutionary biology. When it comes to actually studying speciation, even severe critics of the BSC concentrate on reproductive isolation, working on barriers such as assortative mating and extrinsic postzygotic isolation. Virtually every recent paper on the origin of species, theoretical or experimental, deals with the origin of isolating barriers. This rich literature stands in vivid contrast to the paucity of research inspired by other species concepts.

Problems with the BSC

Problems with the BSC, including ambiguities of species status and the existence of groups to which the concept cannot be applied, have been extensively discussed by Mayr and others (e.g., Mayr 1963, 1982, 1992; Ereshefsky 1992; Claridge et al. 1997; Wilson 1999; Wheeler and Meier 2000). Rather than retread this familiar ground, we will briefly discuss a few of the most serious concerns.

ALLOPATRIC TAXA. Biological species are best diagnosed in sympatry, and yet some taxa include geographically isolated and morphologically differentiated populations. The European red deer and the North American elk, for example, are both placed in the species *Cervus elaphus*, but are allopatric and differ in traits such as size and color. Such populations are difficult to categorize using the BSC. We do not know whether their differences—assuming they are genetic—would allow them to coexist in sympatry without exchanging genes. In some groups this problem is severe. In the African rift lakes, for example, dozens of allopatric cichlid populations have been diagnosed as species because

of differences in male breeding color (Turner et al. 2001). We cannot be sure whether such differences would prevent hybridization in sympatry. Yet the problem of allopatry is not limited to the BSC: all species concepts, save those based on phylogenetics, have problems with allopatric populations.

Nevertheless, the BSC is not completely powerless in this situation. Many "allopatric" populations are not completely isolated, but exchange migrants. The ability of these migrants to interbreed with local individuals can help resolve their species status. This is why all human populations belong to a single biological species. In addition, some allopatric populations with little or no migration can be unambiguously diagnosed as *different* biological species. This is possible when interpopulation crosses in the greenhouse or laboratory yield hybrids that are completely sterile or inviable due to intrinsic developmental problems. Such problems reflect genomic incompatibilities that would also act in nature. We know of no cases in which hybrids that are intrinsically sterile or inviable in the laboratory are fertile or viable in nature. Allopatric populations can also be considered different species if they show some forms of postmating, prezygotic isolation, such as the failure of pollen to germinate on foreign stigmas.

When experimental studies of allopatric taxa demonstrate that no single isolating barrier is complete, one can only make reasonable guesses about biological species status. These guesses, however, can be informed by measuring reproductive isolation in the laboratory. Coyne and Orr (1989a, 1997) compared estimates of premating and postmating isolation between allopatric *Drosophila* taxa with similar estimates from sympatric species. This comparison allowed judgments about whether allopatric taxa would probably be reproductively isolated if they became sympatric. Similar decisions can be made using morphological or genetic-distance criteria (e.g., Highton 1991), but this is riskier.

Determining whether allopatric populations are biological species is thus a one-way test. Artificial hybridizations can demonstrate that such populations are members of different biological species, but cannot determine whether they belong to the same biological species, since many taxa that produce fertile and viable offspring in the laboratory or greenhouse do not hybridize in nature. The lion (*Panthera leo*) is sympatric with the leopard (*Panthera pardus*) in Africa. Hybrids have not been reported from the wild, but these "leopons" can be produced in zoos, and females are fertile. Obviously, premating barriers break down under the artificial conditions of confinement. Similarly, many orchids that occur sympatrically without hybridization are easily crossed in the greenhouse.

HYBRIDIZATION AND INTROGRESSION. Many critics argue that the BSC fails to deal with gene flow between sympatric taxa. As Grant (1957, p. 75) wrote, "The most important single cause of a species problem in plants is natural hybridization." Indeed, hybridization would be a serious problem for the BSC under two conditions: (1) if one adhered to the strict construction of the BSC in which

no exchange can occur between species, or (2) if gene exchange were *widespread and substantial* between sympatric taxa. Our version of the BSC does not demand complete reproductive isolation, so a low frequency of gene exchange is not a problem. This concept would thus be inapplicable only if nature formed a *syngameon* (a morphological or genetic continuum), so that distinct groups were rarely distinguishable, or if distinct groups seen in sympatry usually differed at only a few loci but exchanged genes freely throughout the rest of the genome. Whether or not recognized sympatric "species" exchange genes promiscuously is a matter for empirical work. In groups like *Drosophila*, in which morphologically distinct taxa have also been thoroughly scrutinized for genetic traits such as chromosome structure and DNA sequence, we find strong concordance between the ability to interbreed and the degree of morphological and genetic similarity. In this genus, pervasive introgression is not a problem. For most groups, however, such information does not exist. Our guess is that morphologically distinct taxa showing rampant gene exchange at many loci will be rare. Syngameons appear to be uncommon except among agamic complexes of plants.

Nevertheless, recent work shows that hybridization and introgression are more frequent than imagined by earlier evolutionists such as Mayr and Dobzhansky. But three recent surveys suggest that such hybridization is not rampant. In birds, 895 out of 9672 described species (9.2%) are known to have produced at least one hybrid with another species in nature (Grant and Grant 1992). Among the roughly 2000 described species of *Drosophila*, there are only 10 examples of naturally formed interspecific hybrids (Gupta et al. 1980; Powell 1983; Lachaise et al. 2000). Some *Drosophila* hybrids have undoubtedly gone undetected, but given the amount of work on this genus it is reasonable to conclude that interspecific hybridization is rare. As noted above, Ellstrand et al. (1996) reviewed the frequency of hybridization in plants, estimating that 6–16% of *genera* contain at least one species that forms hybrids, probably a substantial overestimate of the fraction of species that hybridize. Moreover, in each geographic area hybridization was limited to relatively few groups. Ellstrand et al. conclude (1996; p. 5093) that in plants spontaneous hybridization "is not as ubiquitous as is frequently believed" and is "not universal, but concentrated in a small fraction of families and an even smaller fraction of genera."

Studies of hybridization based on the appearance of morphological or genetic intermediates can either underestimate or overestimate the true amount of gene flow between taxa. Some hybrids, for example, have simply been overlooked. In plants, many hybrids have been collected only once or twice from a single location. In addition, hybrids are usually recognized by morphological intermediacy. This can seriously underestimate the amount of intercrossing if some hybrids, such as individuals from backcrosses, resemble individuals of pure species but still carry foreign genes.

Cryptic introgression can be inferred if phylogenies based on different loci are not concordant (Hey 2001); that is, many or most genes might be highly diverged between taxa, while others are nearly identical. Unfortunately, this

observation cannot always distinguish between gene exchange that occurred in the past (before reproductive isolation was substantial), gene exchange occurring now (Machado et al. 2002), or simply the persistence of ancestral polymorphisms. Yet, one observation can provide indisputable evidence for *current* hybridization: alleles are shared between taxa where they are sympatric but not where they are allopatric. Whittemore and Schaal (1991) describe such a pattern in oaks.

Observing hybrids may also *overestimate* gene exchange because hybridization (the production of individuals from an inter-taxon cross) is not identical to introgression (the infiltration of genes between taxa through the bridge of F_1 hybrids). Among the ten naturally occurring hybridizations in *Drosophila*, three produce completely sterile or inviable offspring, and four produce sterile males. Sterile interspecific hybrids are common in the frogs of the genus *Rana* (Hillis 1988), in Lepidoptera (Presgraves 2002) and in the sedge genus *Carex* (Cayouette and Catling 1992). In the area where the black-capped and Carolina chickadees (*Poecile atricapilla* and *P. carolinensis*) are sympatric, hybridization is pervasive, but introgression is restricted because hybrids show strong intrinsic postzygotic isolation (Sattler and Braun 2000; Bronson et al. 2003). Vollmer and Palumbi (2002) describe a widespread coral “species” composed entirely of hybrids, but these are effectively sterile.

Unfortunately, we lack information about intrinsic and extrinsic postzygotic isolation in nearly all of the bird and plant hybrids described by Grant and Grant (1992) and Ellstrand et al. (1996). The survey of Price and Bouvier (2002) suggests that bird hybrids are unlikely to suffer intrinsic sterility or inviability, but introgression in at least some groups, such as Galápagos finches, is prevented by *extrinsic* hybrid sterility involving differences in ecology or mating behavior (Grant and Grant 1997). The continued persistence of distinct taxa that hybridize surely implies some form of postmating isolation.

Evidence from hybrid zones also suggests that the mere presence of hybrids need not imply massive gene exchange. As we discuss in the next chapter, in many such zones, hybrids are unfit. Estimates of the number of genes involved in this loss of fitness can be large, suggesting that much of the genome cannot move between species because it is linked to divergently selected alleles. This lack of introgression can be seen in clines of allozyme alleles that are diagnostic for hybridizing species. Frequencies of such alleles often go from 0% to 100% as one moves across a hybrid zone, suggesting little introgression outside of the area of contact (e.g., Kocher and Sage 1986; Szymura and Barton 1986).

Several other factors should be considered before concluding that hybrids pose a severe problem for our version of the BSC.

1. Much current hybridization probably results from human disturbance of the habitat—disturbance that is likely to be less common under natural conditions. Cayouette and Catling (1992, pp. 371–372) note that 252 different hybrids have been reported among species in the sedge genus *Carex*, but add that “sedge hybrids vary a great deal in practically all of their characteristics, but the one thing that they almost all have in common is disturbed

site ecology. It is quite possible that sedge hybrids were formerly rare, but have increased dramatically as a consequence of disturbance resulting from human activity.” Rieseberg and Gerber (1995) suggest that some hybrids between Hawaiian plants described in the survey of Ellstrand et al. (1996) may have resulted from human disturbance. This situation may be common in plants given the tendency of some botanists to collect along roadsides.

2. “Hybridization” may be a transient phase of evolution. During sympatric speciation and reinforcement, individuals may appear that are intermediate between two well-demarcated forms, but these intermediates disappear when reproductive isolation becomes complete. Alternatively, hybridizing taxa might be in the process of fusing into a single species.
3. What appear to be hybrids might be only geographic variants for one or a few traits, or nongenetic variants produced by local conditions. This possibility has received little attention despite the ubiquity of developmental plasticity and geographic variation. Plant morphology, for example, can be dramatically altered by environmental differences (Sultan 2000).

OAKS: THE WORST-CASE SCENARIO. The classic example of the supposed failure of the BSC to deal with hybridization is the oak genus *Quercus* in North America and Europe. Oaks thus constitute a good case for testing the validity of the BSC.

Quercus is variously described as either a rampantly hybridizing complex in which distinct taxa cannot be seen, or as a group of fairly well-differentiated entities that sometimes hybridize (Burger 1975; Van Valen 1976). On the other hand, some botanists claim that genuine hybrids are infrequent and that most recognized “hybrids” are actually trivial intraspecific variants (Muller 1952; Jones 1959).

Stebbins (1950, pp. 61–66) reviews the problems in this genus, and Whittemore and Schaal (1991) and Howard et al. (1997) discuss more recent data. There are 16 species of white oaks (subgenus *Quercus*) in eastern North America, distinguished largely by the morphology of leaves and acorns. Fourteen of these are known to hybridize with other species (Hardin 1975). Most botanists who work on *Quercus* describe hybrids as being uncommon, rarely obscuring the morphological boundaries of species (Palmer 1948; Jones 1959), although in some localities hybrid swarms have been described. The situation is complicated by the tendency of some species to hybridize at some locations but not others. Moreover, what are described as “hybrids” may actually be localized genetic ecotypes or even environmental variants having no genetic basis (Jones 1959). Thus, the distinctness of oak species could reflect two possibilities: the species might maintain differences in a few diagnostic traits despite extensive introgression, or they might represent truly distinct gene pools whose hybrids are unfit. Recent molecular work has begun to clarify the situation.

Using both chloroplast DNA (cpDNA) and nuclear DNA, Whittemore and Schaal (1991) studied gene flow among five species of white oaks in the cen-

tral United States. Despite no morphological evidence for hybridization, there was extensive interspecific exchange of cpDNA among sympatric species. In fact, phylogenies based on cpDNA showed that different species living in the same place are genetically more similar than are members of the *same* species inhabiting different places. However, one nuclear marker was species specific, and Whittemore and Schaal note (p. 2543) that "the five species studied here are well differentiated with respect to many morphological characters, allozyme loci (Guttman and Weigt 1989), and probably, judging from their different ecological and geographic range, many physiological traits." In a similar study, Martinesen et al. (2001) describe much more exchange of cpDNA and mtDNA than of nuclear DNA between two species of cottonwood (*Populus*). It is likely that oaks and cottonwoods, like other plant and animal species, show more extensive introgression of organelle DNA than of nuclear DNA (see Appendix). It is thus risky to assume extensive hybridization based on observations of organelle DNA alone.

The situation in *Populus* is mirrored by two species of European oaks, *Quercus robur* and *Q. petraea*, which are sympatric in many places and have been described as hybridizing freely. However, a study of 20 nuclear microsatellite loci from five locations showed that the species were well demarcated from each other, forming two well-separated clusters in all locations (Muir et al. 2000). The authors raise the question of "how the species differences are maintained despite the high levels of interspecific gene flow" (p. 1016). But the observation that the species differ at many loci suggests that gene flow is *not* high.

Likewise, Howard et al. (1997) reported limited introgression between *Quercus gambelii* and *Q. grisea*, whose ranges overlap in the southwestern United States. Although the species are segregated by altitude, in the area of sympatry they form a "mosaic hybrid zone" in which the transition between the species' ranges is not smooth but patchy. Many individuals within this zone appear to be morphologically pure species, but nevertheless carry some foreign genes. However, the extent of introgression drops rapidly outside the area of overlap. Only two kilometers away, one finds few individuals of *Q. gambelii* that carry genes from *Q. grisea*. The authors suggest that "the abrupt genetic and morphological discontinuity between *Q. gambelii* and *Q. grisea*, despite areas of hybridization, indicates that selection acts to maintain coadapted complexes of alleles in the two species" (p. 754).

In California, the genotypes of the few morphological intermediates between *Q. lobata* and *Q. douglasii* show them to be pure-species individuals rather than hybrids (Craft et al. 2002). The authors propose that morphological intermediacy reflects not hybridization but phenotypic plasticity. Nason et al. (1992) found that morphological intermediates between sympatric *Q. kelloggii* and *Q. wislizenii* var. *frutescens* in Southern California were almost all first-generation (F₁) hybrids. They suggest that the absence of backcross or later-generation hybrids reflects their inability to compete with the parental species (i.e., there is extrinsic postzygotic isolation).

The data thus suggest that in many cases nuclear gene flow between oak species is restricted by unknown forms of selection against hybrids. Williams et al. (2001) identified one reproductive barrier between *Q. gambelii* and *Q. grisea*: fruit set was significantly higher in conspecific than in heterospecific pollinations. This reproductive isolation, which reduced gene flow by about 60%, was caused by the inviability of hybrid embryos.

The situation in oaks is complex, and it is clear that named species do not always correspond to good biological species free from introgression. However, genetic studies also show that oak species are not rampantly hybridizing, and are not differentiated by only a few morphological or genetic traits. This implies that, as in *Q. gambelii* and *Q. grisea*, the distinctness of oak species in sympatry reflects disruptive selection causing intrinsic and extrinsic postzygotic isolation.

In summary, the boundaries between oak species may not be as porous as commonly thought. As Howard et al. (1997, p. 754) remark, "Oaks may not represent a greater challenge to traditional concepts of species than many other plant and animal taxa that form hybrid zones with close relatives." Although this group has been considered a problem for the BSC, detailed scrutiny suggests that the difficulties are exaggerated.

The intense interest that botanists have paid to hybridizing species might well overstate the challenge that plants—and other species—pose to our version of the BSC. To determine whether the BSC is *generally* inapplicable, one must extend the work on oaks to random samples of species in a wide variety of taxa.

TAXA WITH WHOLLY OR PARTIALLY UNIPARENTAL REPRODUCTION. The BSC obviously cannot deal with groups in which sexual reproduction is very rare. To the extent that such groups form distinct clusters in sympatry, we recommend using a species concept that addresses the origin and maintenance of such clusters. As described below, recent theories suggest that discrete bacterial groups can arise as a result of natural selection acting on ecologically equivalent clones, coupled with the occurrence of mutations that permit the occupation of new niches. If this is the case, both the cohesion and ecological species concepts (Table 1.2) seem appropriate for dealing with bacterial taxa. There is less evidence that agamic complexes in plants, with their combination of sexual and asexual reproduction, form discrete clusters, and we would be happy to adopt any species concept that helps us understand the evolution of such groups.

DELINEATING "SPECIES" IN A SINGLE EVOLVING LINEAGE, OR IN FOSSILS, OR PRESERVED MATERIAL. Mayr (1963) dealt extensively with the problems these matters pose for the BSC, and we can add little to his arguments. Under every species concept, the division of a continuously evolving lineage into named species is a purely subjective exercise, although one that may be necessary for scientific communication.

Diagnosing species in fossilized or preserved material from a single location is less arbitrary, as one can make reasonable guesses about the likelihood

of reproductive isolation from discontinuities between phenotypes. If one has allopatric samples that show some phenotypic variation, one can search for material from intervening areas to see if the phenotype changes gradually over space (suggesting conspecific status) or if there is an abrupt geographic discontinuity (suggesting two species). If no such material can be found, one can tentatively diagnose allopatric taxa as species if they differ as much or more than bona fide species existing in sympatry. Ward (2001, pp. 591–592) shows how this can be done in ants.

DISTORTING EVOLUTIONARY HISTORY. The BSC has been severely criticized by systematists because species identified using interbreeding and reproductive isolation may distort evolutionary history (Mishler and Donoghue 1982; Cracraft 1989). The most frequent criticism is that populations of a single biological species can be less closely related to each other than populations belonging to different biological species.

Imagine, for example, that species A, consisting of three populations (A_1 , A_2 , and A_3), occupies a continent, and that migrants from population A_3 colonize an isolated island. The descendants of these colonists experience strong selective pressure and rapidly evolve into species B, whose members have isolating barriers strong enough to prevent hybridization with all populations of species A were they to re-invade the continent. In such a situation, genetic analysis might yield the phylogeny depicted in Figure 1.4. Here, individuals of population A_3 appear more closely related to individuals of species B than to those of populations A_1 and A_2 . To use the terminology of modern systematics, species A is *paraphyletic* relative to species B, and the reproductive relationships do not mirror genealogical history. Avoiding use of the BSC because of this possibility has been called “fear of paraphyly” (Harrison 1998).

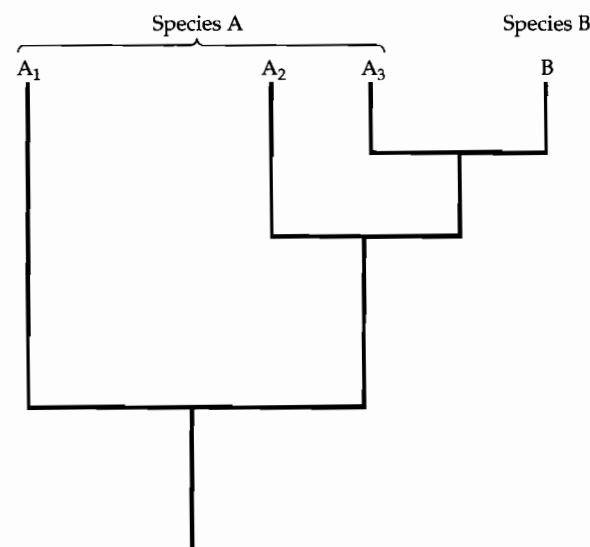


Figure 1.4 The phylogeny of two reproductively isolated species, A and B, in which reproductive relationships do not coincide with ancestry at some genetic locus or loci. Species A consists of three populations (A_1 , A_2 , and A_3), one of which (A_3) gave rise to species B. Phylogenetic analysis might show that individuals in population A_3 are more closely related to individuals in species B than to conspecific individuals in populations A_1 and A_2 . In such cases, species A is considered “paraphyletic” with respect to species B. (After Harrison 1998.)

Our response to this critique is similar to that of Harrison (1998, p. 26): “If we accept that species are defined by isolation and/or cohesion and do not start with the assumption that they must be exclusive groups and the units of phylogeny, then including paraphyletic assemblages as species does not misrepresent history.” Nevertheless, if situations such as that shown in Figure 1.4 are common, we would like to know about them: such a phylogeny might, for example, identify the source of an island endemic.

But is it really possible to reconstruct such histories using genetically based phylogenies? Since populations A_1 , A_2 , and A_3 are conspecific, gene flow will eventually homogenize them, destroying the phylogeny that shows a close relationship between population A_3 and species B. One then obtains a bifurcating phylogeny with species [$A_1 + A_2 + A_3$] as one branch and species B as the other. Since evolutionary history is not seen directly but must be reconstructed, the history given by the latter phylogeny is indeed congruent with the BSC. The genetically distinct populations A_1 , A_2 , and A_3 are transitory entities, and it is not a gross distortion to conclude that species B derives from an indefinable group contained within species A.

Interbreeding among individuals of a biological species thus quickly eliminates our ability to detect paraphyly. This problem is especially serious because interbreeding is likely to erase the history of populations much faster than reproductive isolation can evolve in an isolate. Thus, reconstructing the history of populations is feasible only when these populations are fairly discrete and exchange genes only rarely. If these conditions do not obtain, constructing a bifurcating evolutionary tree will not yield an accurate history of populations. Such a history is complex, and is better represented by a reticulating network than by a tree. An example involves the species *Drosophila sechellia* and *D. mauritiana*, endemic to the Seychelles archipelago and the island of Mauritius, respectively. These species are closely related to *D. simulans*, which is widespread in east Africa. *D. mauritiana* and *D. sechellia* presumably arose after colonization of the islands by a *D. simulans*-like ancestor. Analysis of multiple loci, however, has shown that it is impossible to identify a contemporary population of *D. simulans* that was the source of these colonists (Kliman et al. 2000).

This raises the most serious problem facing those who claim that the BSC often distorts evolutionary history. It is important to recognize that advocates of this view take “evolutionary history” to be the branching sequence of the taxa themselves. (These taxa can be either populations or reproductively isolated species.) The problem, implied above, is that the history of taxa cannot be seen directly, but must be reconstructed from the history of genes. As we show in the Appendix, there are several reasons why these histories can differ. The most important is that each gene has its own evolutionary history that is not necessarily congruent with the history of other genes, or of the populations themselves.

There are thus two causes of a discrepancy between reproductive relationships and gene-based phylogenies. The first is that the reproductive relationships between taxa do indeed distort their true evolutionary history. The second is that phylogenies, while providing an accurate history of some genes, may give an inaccurate history of the taxa containing those genes. In this case

it is the *phylogenies* that distort evolutionary history. It is hard to decide which of these two causes explains an incongruity between phylogeny and reproductive compatibility, especially when species are closely related. In such cases, reconstructing evolutionary history requires *congruent phylogenies of many different genes*, which is difficult to achieve when ancestral polymorphisms persist in descendant taxa, or when gene flow destroys the history of populations. As we note in the Appendix, most cases of “paraphyletic” species have been diagnosed using what is in effect a single gene: mitochondrial DNA. For many reasons, mtDNA behaves differently from nuclear genes, and paraphyly diagnosed using only mtDNA may not reflect the situation in the rest of the genome (Hudson and Coyne 2002; Shaw 2002).

In view of these problems, one can rarely assert with confidence that reproductive relationships distort evolutionary history. We know of only a few such cases, which we discuss in the Appendix. Thus, the seriousness of the “paraphyly problem,” and of other cases in which the BSC seems to conflict with the history of taxa, may well have been exaggerated or misunderstood. Nevertheless, it is likely that some multi-gene phylogenies may show biological species to be truly paraphyletic, and that the relatedness of populations and individuals may not always be concordant with their assignment to biological species. Nevertheless, so long as one keeps these possibilities in mind, we see no compelling reason to abandon the BSC.

Other species concepts

As noted earlier, the Appendix considers the eight most popular rivals of the BSC (see Table 1.2). There we explain why these concepts were proposed as alternatives to the BSC, discuss their advantages and disadvantages, show how they compare to the BSC in dealing with difficult cases, and describe how they define the process of speciation.

These concepts fall into two classes. The first, comprising groups 2 and 3 in Table 1.2, follows the BSC by assuming the species problem to be the origin of organic discontinuities, but considers the BSC an inadequate solution to this problem. Phylogenetic species concepts, on the other hand, take as the species problem the reconstruction of evolutionary history and the assessment of evolutionary relatedness among individuals and groups. These purposes often overlap, for individuals within discrete species must usually share an evolutionary history. Moreover, most species concepts will diagnose the same species in sympatry. Where they differ is how they treat allopatric or hybridizing taxa.

Why Are There Species?

Studying speciation may reveal the origin of discontinuities between sympatric groups, but does not explain why such discontinuities are inevitable. What properties of sexually reproducing organisms and their environments

inevitably lead to the evolution of discrete species? Why are organisms apportioned into clusters separated by gaps? Dawkins (1982) argues that natural selection is an inevitable consequence of any type of life; in fact, he defines “life” as the property that allows its bearers to experience natural selection. Can we also conclude that species are the inevitable results of life—at least life that reproduces sexually?

Dobzhansky (1935, p. 347) found this question intractable: “The manifest tendency of life toward formation of discrete arrays is not deducible from any a priori considerations. It is simply a fact to be reckoned with.” Perhaps we cannot deduce such arrays from a priori considerations, but the inevitability of species might still be understandable a posteriori. Here we consider why discrete clusters might be inevitable in both sexual and uniparental organisms.

In some ways, this topic is more difficult than understanding the origin of species because it is more abstract. Nevertheless, we regard it as one of the most important unanswered questions in evolutionary biology—perhaps *the* most important question about speciation. Yet despite its importance, it has been almost completely neglected: the only extensive discussion is by Maynard Smith and Szathmáry (1995, pp. 163–167). These authors suggest several hypotheses, which we discuss below. An additional explanation is that evolutionary history itself can create clusters: splitting and extinction of lineages will ultimately create groups of genetically and morphologically similar organisms separated by gaps from other clusters—groups such as mammals, fish, and conifers. (See Raup and Gould 1974 for a model of clustering based on random branching and extinction). Nevertheless, while history can create discrete clusters containing *groups* of species, we do not see how it can produce species themselves, at least in sexually reproducing organisms.

Maynard Smith and Szathmáry consider three other explanations:

1. *Species exist because they are discrete “stable states” formed by the self-organizing properties of biological matter.* This view is closely connected with the “structuralist” school of biology, which claims that many adaptations and aspects of development result not from natural selection acting on genes, but from the self-organizing properties of biological molecules (Ho and Saunders 1984). This view of species seems untenable for several reasons. First, it lacks any mechanism that explains the origin of such states. Second, it does not explain the origin of *new* “stable states” (species), which must arise after some unspecified and temporary instability—an “adaptive valley” of molecular organization. Finally, as Maynard Smith and Szathmáry (1995) argue, the pervasive geographic variation of morphological, physiological, and ecological traits within species casts severe doubt on the inherent stability of species.

2. *Species exist because they fill discrete ecological niches.* This explanation sees clusters as resulting from intrinsic discreteness in ways of using resources. For example, the mechanisms by which microorganisms use alternative carbon sources or capture energy might impose distinct phenotypic solutions on the

organism, in the same way that different jaw morphologies are needed to efficiently handle different prey. This effect accumulates as one goes from lower to higher trophic levels, because clusters at lower levels provide discrete niches for organisms at higher levels. This ecological explanation also rests on the inevitability of tradeoffs: being suited for one way of life makes one less suited for another. Such tradeoffs create disruptive selection, with hybrids that fall between niches being unfit. Note that this explanation is not independent of reproductive isolation because it depends on a reproductive barrier: extrinsic postzygotic isolation.

Historically, the ecological explanation is closely wedded to Sewall Wright's view of the adaptive landscape. Dobzhansky (1951, pp. 9–10) emphasized this connection:

The enormous diversity of organisms may be envisaged as correlated with the immense variety of environments and of ecological niches which exist on earth. But the variety of ecological niches is not only immense, it is also discontinuous. . . Hence, the living world is not a formless mass of randomly combining genes and traits, but a great array of families of related gene combinations, which are clustered on a large but finite number of adaptive peaks. Each living species may be thought of as occupying one of the available peaks in the field of gene combinations.

This view does not require that the environment present a discrete array of niches that antedate the evolution of organisms—a difficulty given that organisms create new niches through their own evolution and that the environment itself includes organisms. The ecological explanation merely requires tradeoffs: there is a finite number of ways to make a living in nature, and organisms adopting one way sacrifice their ability to adopt others.

3. *Species exist because reproductive isolation is an inevitable result of evolutionary divergence.* This explanation, which is limited to sexually reproducing groups, relies on the fact that divergent evolution is likely (and given enough time, certain) to yield reproductive isolation. Such isolation allows both the permanent coexistence of taxa in sympatry and future evolutionary divergence without gene flow, factors that both contribute to discreteness. This explanation is also related to the existence of ecological niches, for divergent adaptation to such niches can impede gene flow by producing reproductive isolation as a byproduct. (Plants, for example, can develop reproductive barriers by adapting to different soil types or pollinators.) There are also “developmental niches” that arise because development requires the joint action of many coadapted genes. Sufficiently diverged developmental systems cannot work properly in hybrids, yielding intrinsic hybrid sterility and inviability. Finally, sexual reproduction itself leads to the evolution of anisogamy (disparate sizes of male and female gametes), which in turn creates the possibility of sexual selection. Divergent sexual selection will almost inevitably lead to behavioral or gametic isolation.

The “ecological” and “reproductive-isolation” explanations of species are not mutually exclusive. Indeed, they are intimately connected. Although Dobzhansky leaned more toward the ecological explanation, he also saw a role for reproductive isolation (1951, p. 255):

The patterns with the superior adaptive values [i.e., species] form the “adaptive peak”; the peaks are separated by the “adaptive valleys” which symbolize the gene combinations that are unfit for survival and perpetuation. The reproductive isolating mechanisms, as well as the geographic isolation, interdict promiscuous formation of the gene combinations corresponding to the adaptive valleys, and keep the existing genotypes more or less limited to the adaptive peaks.

In sexually reproducing species, the ecological and reproductive-isolation explanations are intertwined because adaptive valleys between niches imply some reproductive isolation, and isolating barriers may result largely from adaptation to distinct niches. Is it possible to assess the relative importance of these explanations?

One possibility is to see what happens when one leaves niches intact but removes reproductive isolation. If the “ecological” explanation were correct, one would still see distinct clusters in sympatry. This could be addressed by looking at organisms that are almost completely uniparental, thus lacking the possibility of reproductive isolation. As noted above, the jury is out on whether uniparentally reproducing eukaryotes form discrete clusters in sympatry, but there is some evidence for clustering in bacteria.

Recent theory suggests that one can explain the existence of uniparental clusters by considering the invasion of new niches (Cohan 2001, 2004; Barraclough et al. 2003). One might naively expect uniparental organisms to continuously accumulate mutations, producing an infinite variety of clones, each adapted to a slightly different habitat. Cohan (1984, 2001), however, suggested a type of bacterial “speciation” that produces distinct clusters. A lineage of bacteria may indeed accumulate new mutations and begin to fill up ecospace with a panoply of clones. Periodically, however, an individual experiences a new mutation that is generally adaptive. The clone containing this mutation will replace all other clones with which it is ecologically equivalent. The genetic variation within the group of clones then collapses to the genotype of the single mutant clone. These recurrent episodes of “periodic selection” limit the degree to which asexual groups can diverge to form microspecies.

In this theory, a new bacterial “species” arises when a mutation gives an individual the ability to invade a new ecological niche, rendering it and its descendants immune from extinction during episodes of periodic selection. (Such mutations may be relatively common in bacteria because of their ability to incorporate genes from distantly related taxa.) If recombination in bacteria is rare and periodic selection common, the new “species” will form a distinct cluster that could coexist with its ancestor. Such speciation could occur either allopatrically, when a migrant individual lands in a novel habitat, or

sympatrically. In the allopatric case, mutations of large effect are not required, for adaptation to a new niche can be built up gradually. In sympatry, the new bacterial species will persist if the “macromutation” allowing occupation of a new niche has a selective advantage higher than that of subsequent mutations causing periodic selection in the ancestral species.

Bacterial “speciation” thus involves occupying new ecological niches, and a bacterial species can be defined as an “ecological population, [which is] the domain of competitive superiority of an adaptive mutant” (Palys et al. 1997, p. 1145). This is closely related to Templeton’s (1989) cohesion species concept, which incorporates demographic exchangeability as one of the “cohesion mechanisms” that defines species (see Appendix).

The importance of niche differentiation in understanding asexual clustering suggests that ecology might form the basis of an asexual species concept. Just as reproductive isolation suggests why sexual organisms remain discrete, so the occupation of distinct niches by demographically nonexchangeable clones suggests why asexual clusters remain discrete. This idea also yields a research program for bacterial speciation. Sympatric clusters (“species”) of bacteria should always occupy different ecological niches, and should remain distinct when periodic selection occurs in any of them. Moreover, bacteria showing greater gene exchange should form clusters that are less distinct than those seen in more-clonal species. Finally, different sympatric clones within a single bacterial “species” should not be strongly adapted to their local habitat, because such adaptation would prevent periodic selection that homogenizes each cluster. Belotte et al. (2003) support this prediction in a study of *Bacillus mycoides* from a Canadian forest.

More recent theories consider other explanations for clustering besides periodic selection and macromutations. These theories see asexual clusters as simple adaptive responses to resource gradients in either sympatry or parapatry (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2003). However, in both geographic situations, the clustering appears to be either an artifact of the models’ assumptions, or a temporary phenomenon that disappears when resource space eventually becomes filled with a continuum of asexual organisms (Polechova and Barton 2004).

A third explanation for clustering in asexual organisms is that clonal reproduction, coupled with occasional mutations affecting morphology or DNA sequence, will eventually produce clumps as a simple artifact of history. Barraclough et al. (2003) show that this can occur in both sympatric and allopatric populations. But unless this clustering is accompanied by ecological diversification, it will disappear in sympatry—the only place where clusters are truly discernible—through either periodic selection or the relentless accumulation of alleles adapting clones to new microhabitats.

Because we rejected ecological differentiation as part of the BSC in sexually reproducing groups, we obviously endorse the use of different species concepts in different groups. We do not consider this pluralism to be a weakness of the BSC. Because the causes of discreteness may well differ among taxa, so

may the concepts appropriate to addressing the species problem. If groups without sex form distinct clusters, and the explanation for such clusters resembles Cohan’s theory of bacterial speciation, then the answer to “Why are there species?” in such taxa seems to be “Because there are discrete ways of making a living.”

While this may explain species in asexual groups, it will not suffice for sexual groups. For example, in taxa having a mixture of sexual and uniparental reproduction, as in agamic plants, periodic selection cannot eliminate all genetic variation within a group of “demographically exchangeable” individuals: as the new adaptive mutation spreads, recombination will separate it from the genome in which it arose. Moreover, the occurrence of macromutations that create new species by allowing invasion of a new niche must be rare in eukaryotes, which almost never experience the wide gene transfer that causes adaptive leaps in bacteria.

In fact—although this conclusion is tentative—taxa with some sexual reproduction, such as agamic complexes, seem to form clusters that are *less distinct* than those seen in taxa with largely asexual reproduction. If adding a little bit of sex erodes the discreteness of groups, then ecology cannot be the only explanation for discreteness.

When one moves to fully sexual groups, one again finds discrete clusters of genes and traits. This is a clue that sexual reproduction itself must play a role in distinctness. In fact, we suggest that in sexually reproducing groups it is reproduction itself, combined with differential adaptation and the existence of tradeoffs, that ineluctably produces species. This idea derives from understanding how clusters are formed.

Recent theoretical models (Chapter 4) suggest that in sexual groups the ecological explanation is at least partly necessary for the existence of species that arise sympatrically, as the initial steps in sympatric speciation often involve adaptation to discrete resources. Yet, these same models show that clusters will exist only for those traits involved in resource use, and that differentiation of other traits requires the evolution of further isolating barriers such as behavioral isolation. In fact, it is sexual reproduction that allows the coupling of resource use to other isolating barriers, a coupling that is necessary to complete speciation (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999).

However, evidence adduced in Chapter 4 suggests that most speciation is allopatric. Although discrete niches might be necessary to explain the sympatric *coexistence* of allopatrically formed species, such niches are not required for the *formation* of distinct and recognizable species in allopatry. Following geographic isolation, good biological species can arise via nonecological processes (such as sexual selection) that yield behavioral, mechanical, gametic, or intrinsic postzygotic isolation (Chapter 6). Alternatively, when ecology is involved in the allopatric evolution of reproductive barriers, it need not produce a difference in niches. Identical environments, for example, can select for identical traits having different genetic bases, yielding developmental incompatibilities in hybrids.

We suggest, then, that there are different reasons for discreteness in different groups. Clustering in completely asexual or uniparental taxa may rest largely on the ecological explanation, while clustering in sexual taxa rests on a combination of ecology and reproductive isolation. Since there may be different causes for clustering in asexual versus sexual taxa, should one use "species" as the term for asexual clusters and "speciation" for the processes by which they form? We see no problem with this so long as one recognizes that these words mean different things in different taxa.

We predict, then, that statistical analyses of groups having both sexual and asexual reproduction will show that they form clusters less distinct than those seen in either completely sexual or completely asexual groups. Groups with mixed modes of reproduction have too much sex to permit the homogenizing effects of periodic selection, but too little sex to homogenize members of diverging "microspecies." Intermediate levels of sexual reproduction are not conducive to forming discrete taxa.

2

Studying Speciation

It is sometimes argued that speciation is not a distinct field of research. After all, species are largely byproducts of evolution within lineages, a process that has always been the purview of evolutionary genetics. Julian Huxley, for example, declared that

The formation of many geographically isolated and most genetically isolated species is thus without any bearing upon the main processes of evolution. . . . Species-formation constitutes one aspect of evolution; but a large fraction of it is in a sense an accident, a biological luxury, without bearing upon the major and continuing trends of the evolutionary process (Huxley 1942, p. 389).

But while *anagenesis* (evolutionary change within a lineage) is the underpinning of *cladogenesis* (the creation of new lineages by splitting), these two processes are analyzed with different methods. In this chapter we explain why speciation is unique, and suggest ways to study it.

As Mayr has emphasized, a key aspect of species is that they can be defined only relative to other species. Unlike anagenesis, then, speciation involves the joint evolution of two or more groups:

The word species thus became a word expressing relationship, just like the word brother, which does not describe any intrinsic characteristics of an individual but only that of relationship to other individuals; that is, to other offspring of the same parents (Mayr 1992, p. 223).

Critics consider this relativistic aspect of the BSC a weakness. The BSC, however, is not the only relativistic species concept: *every* concept requires comparing different groups of individuals, whether this comparison involves reproductive isolation, morphological distinctness, or phylogenetic relationship.

APPENDIX

A Catalogue and Critique of Species Concepts

Here we describe and evaluate eight species concepts that are considered serious competitors to the biological species concept (BSC) (Table 1.1). We describe the reasons why each concept was proposed (i.e., the “species problem” it was designed to solve), explain why its proponents see it as superior to the BSC, and assess its advantages and disadvantages. We also show how each concept deals with issues that are problematic for the BSC: allopatric populations, gene exchange between taxa that remain distinct, and uniparental organisms. We note how closely each concept coincides with the BSC—that is, whether it identifies the same species in sympatry. Finally, we note what process constitutes “speciation” under each concept. Throughout the discussion, we adhere to our version of the BSC, which allows limited gene exchange, rather than to the strict version that demands complete reproductive isolation between taxa.

We will not deal with strictly typological species concepts—those that define species by specifying an arbitrary degree of morphological or genetic difference. Mayr (1942, 1963) has explained the problems with such concepts. We do, however, discuss two somewhat typological concepts: the “genotypic cluster” species concept and several versions of the phylogenetic species concept.

Genotypic Cluster Species Concept (GCSC)

A species is a [morphologically or genetically] distinguishable group of individuals that has few or no intermediates when in contact with other such clusters (Mallet 1995).

This concept was proposed in response to the observation that, while the BSC *defines* species by the presence or absence of interbreeding, it *recognizes* them as distinguishable clusters in sympatry. (These clusters can be seen in pheno-

typic data as a bimodal distribution of traits, and in genetic data as a deficit of heterozygotes or the presence of linkage disequilibrium among genes.) For advocates of both the BSC and the GCSC, the species problem is identical: understanding the origin of discrete entities in sympatry. Unlike the BSC, however, the GCSC defines species solely by the features used to recognize them. The GCSC does not specify how many traits and/or genes are required to diagnose sympatric clusters as species.

Advocates of the GCSC claim that it has several advantages over the BSC. First, the GCSC is supposedly independent of theories about speciation: it is presented as a way to recognize species rather than understand how they evolved. Defining clusters on the basis of interbreeding is said to lead the BSC into circularity: "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" (Mallet 1995, p. 295; all quotations and page numbers refer to this paper). Mallet feels that the GCSC allows one to consider other causes of clustering besides reproductive isolation: "Gene flow is not the only factor maintaining a cluster; stabilizing selection will also be involved, as well as the historical inertia of the set of populations belonging to the cluster. . . . Clusters can remain distinct under relatively high levels of gene flow provided that there is strong selection against intermediates" (p. 296).

Proponents of the GCSC view the BSC's emphasis on isolating barriers as not only intellectually vacuous, but misleading: "To include such a number of different effects under a single label must be one of the most extraordinary pieces of philosophical trickery ever foisted successfully on a community of intelligent human beings" (pp. 297–298). The BSC is also considered unscientific: "Mayr has repeatedly stressed that the biological concept cannot be refuted by practical difficulties in its application; this means it is untestable" (p. 296). Moreover, the notion of species as reproductively isolated entities is said to impede our understanding of speciation: "Because no gene flow between species is conceptually possible under interbreeding concepts, it is extremely hard to imagine how speciation, which must often involve a gradual cessation of gene flow, can occur" (p. 295). Mallet notes that allopatric speciation is one such mode of speciation, but also argues that the BSC is biased against other modes of cluster formation—such as sympatric and parapatric speciation—that involve gene flow between incipient species. Finally, Mallet echoes the criticism of Sokal and Crovello (1970) that it is impossible to apply the BSC in practice, as this requires making or observing the crosses needed to test the reproductive compatibility of every pair of individuals.

It is important to recognize that, despite its emphasis on species recognition rather than reproductive isolation, the GCSC and our version of the BSC identify nearly the same set of species in sympatry. The real disparity between these concepts is in the amount of genetic difference required for species status. In principle, the GCSC could diagnose sympatric clusters that differ in only one or two genes or traits while exchanging alleles freely throughout the rest of the genome. Such clusters could be maintained by habitat-related selection. For

example, Wilson and Turelli (1986) show that density- and frequency-dependent selection acting on alleles at one or two loci can lead to the stable coexistence of distinct genotypes, even though heterozygotes have the lowest fitness and appear in less-than-expected frequencies. This will produce statistically distinguishable clusters that might be considered species under the GCSC. If one claims, however, that such polymorphisms do not diagnose species because they represent only intraspecific variation, then one is reverting to the BSC. The failure to specify how many loci (or what degree of heterozygote deficit and linkage disequilibrium) are required to diagnose species is a problem for the GCSC. Setting such a threshold would involve an arbitrary decision.

In contrast, the BSC diagnoses species only if there is evidence that gene flow between them is strongly limited. This involves either observing many genetic differences between sympatric taxa—a degree of difference too large to be explained by disruptive selection alone—or observing isolating barriers so strong that gene flow is almost zero. This can also involve an arbitrary decision if there is any introgression between sympatric groups, but clearly genetic differentiation must be higher for recognizing biological than for recognizing genotypic-cluster species.

Another problem for the GCSC involves the *level* of clustering. Because of the hierarchical nature of evolution, genotypic clusters occur at many levels. These clusters can involve intrapopulation polymorphisms, local host races, species, or higher-level groups such as genera. Trying to apply the GCSC to the *Rhagoletis pomonella* complex of tephritid flies, Berlocher (1999, p. 661) observed a "continuum of decreasing degree of cluster overlap as level of genetic divergence increases from host race to distinct species. . . . No species threshold is apparent." Since the GCSC sees no fundamental distinction between species and higher-level groups (p. 296: "Whether species do have a greater 'objective' reality than lower or higher taxa is either wrong or at least debatable; the idea that taxa are qualitatively different from other taxa is therefore best not included within their definition"), the definition of species as "genotypic clusters" must be recast as "clusters that do not include other sub-clusters." But this would lead one to diagnose as species polymorphic forms such as beak morphs in *Pyrenestes* finches (Smith 1987) or Batesian mimicry phenotypes in the butterfly *Papilio memnon* (Clarke and Sheppard 1969). To get around this problem, one must then include a reproductive criterion: such polymorphisms do not diagnose species because their carriers readily interbreed. This, however, defeats the GCSC's goal of avoiding criteria based on reproductive compatibility.

As noted in Chapter 1, the presence of sympatric clusters involving several genes implies the existence of isolating barriers. Thus, disruptive selection that creates and maintains distinct clusters involves a form of reproductive isolation—extrinsic postzygotic isolation. This is recognized in statements such as, "The maintenance of sympatric species is not just due to reproductive traits, but also due to ordinary within-species, stabilizing ecological adaptations that select disruptively against intermediates or hybrids" (Mallet 1995, p. 296). There

is no real difference between positive selection for alternative phenotypes and negative selection against intermediates between those phenotypes.

As for other processes that can create and maintain species, we do not understand how “historical inertia” can play such a role. The maintenance of distinct clusters in sexually reproducing taxa must always involve selection against intermediates (i.e., reproductive isolation). We also fail to see why the BSC is circular. If species are regarded simply as an advanced stage in the evolution of reproductive isolation, then no circularity ensues. We are baffled by the claim that lumping diverse phenomena under the category “isolating mechanisms” involves “philosophical trickery.” As Harrison (1998, p. 24) argues: “[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.”

Moreover, the fact that the BSC is not theory-free—that it immediately suggests a *process* of speciation—seems to us an advantage, not a problem. A theory-free definition of identical twins might be given as “two individuals, born of one mother at the same time, who are exceedingly similar morphologically.” But this definition is surely less useful than one that incorporates process, such as “identical twins are the products of splitting of a single fertilized egg.” The claim that the BSC is untestable holds, as Brookfield (2002) notes, for *all* species concepts: none can be falsified by experiment or observation. A species concept is a tool for research, not a hypothesis subject to refutation.

The claim that under the BSC “it is extremely hard to imagine how speciation, which must often involve a gradual cessation of gene flow, can occur,” seems unfounded. Over the last 60 years, biologists have had no problem imagining how biological speciation can occur. There are well-established genetic and ecological models—both verbal and mathematical—for the origin of isolating barriers in sympatry, allopatry, and parapatry.

Finally, the view that the BSC is not useful because one cannot do breeding tests seems misguided. While breeding tests can be useful for identifying species (e.g., Dobzhansky and Epling 1944), biological species can also be identified by the concordance of many characters and genes that show the existence of isolating barriers, or by the consistent correlation between a group of traits on one hand and reproductive compatibility on the other. Once one has described such a group, even a single trait can then be used to diagnose species. Traditionally, this has been done with great success: genitalia are reliable indicators of biological species status in many organisms (Eberhard 1986), and chromosomal and molecular characters have served equally well.

How does the GCSC differ from the BSC? The most important aspect is how these concepts deal with sympatric taxa showing moderate to substantial gene exchange. Such taxa include sympatric host races of insects such as the apple and hawthorn races of *Rhagoletis pomonella* (Feder et al. 1998), which form GCSC species but would probably not be accorded species status by the BSC. Hybrid zones are another example. If one considers a wide area including the zone of

hybridization, one can recognize two genetic clusters with various intermediate individuals (hybrids) falling between the clusters. The two clusters would be considered species under the GCSC but not the BSC unless there was little gene flow beyond the hybrid zone. However, introgression outside hybrid zones is often limited (Barton and Hewitt 1985), allowing one to diagnose two biological species that are identical to the two genotypic-cluster species.

Both the BSC and the GCSC have difficulty diagnosing *allopatric* taxa that are morphologically distinguishable. (Genotypic clusters are recognizable only in sympatry.) Here, however, the BSC has something of an edge: if allopatric populations form either inviable or sterile hybrids when artificially hybridized, one can say with assurance that they are biological species.

There are arguably two advantages of the GCSC over the BSC. First, the GCSC is less ambiguous at diagnosing species in problematic situations such as taxa that hybridize with limited gene flow. Such cases constitute a gray area for the BSC, but offer no problem to the GCSC if one can observe distinct clusters. But because we are more concerned with process than with diagnosis, we do not consider this a particularly meaningful advantage, especially because GCSC clusters may involve only one or two genetic differences. Second, the GCSC can also be applied to largely or completely asexual taxa, groups where the BSC is impotent. But strict use of the GCSC would diagnose each asexual clone as a different species. For such groups it seems preferable to adopt neither the BSC nor the GCSC, but an ecological species concept (see Chapter 1).

The GCSC is one of the few species concepts that come with an explicit definition of speciation: “Speciation is the formation of a genotypic cluster that can overlap without fusing with its sibling” (Mallet 1995, p. 298). This differs from our own notion of speciation only in that we define “clusters” as “groups between which reproductive barriers are very strong.” However, Mallet adds (p. 298), “To understand speciation, we need to understand when disruptive selection can outweigh gene flow between populations.” This applies only to parapatric and sympatric speciation, because the conflict between selection and gene flow does not exist during allopatric speciation.

The GCSC is the most serious competitor to the BSC because the two concepts share many features. But by concentrating on the identification rather than the origin of species, the GCSC does not yield a particularly fruitful program of research.

Recognition Species Concept (RSC)

Species are the most inclusive population of individual biparental organisms, which share a common fertilization system (Paterson 1985; see also Lambert and Paterson 1984, Lambert et al. 1987, and Masters et al. 1987).

This concept is also motivated by the problem of organic discontinuity. The RSC resembles the GCSC and the cohesion species concept (see below) in that

species are defined by those factors that hold populations together rather than by those that isolate them.

Under the RSC, these cohesive factors constitute their shared "fertilization system": the set of biological features that "contribute to the ultimate function of bringing about fertilization while the organism occupies its normal habitat" (Paterson 1985, p. 24). Important aspects of the fertilization system are included in the Specific-Mate-Recognition-System (SMRS), which includes all features by which organisms "recognize" each other as mates. This recognition can be either active (as in courtship signals and responses), or passive (as in biochemical processes of gamete fusion). Paterson's working definition of a species is a "field for gene recombination" (1985, p. 21). The RSC thus explicitly excludes ecological and temporal isolating barriers, as well as all postzygotic barriers.

Paterson and co-authors claim that the RSC remedies many of the weaknesses they find in the BSC (which they call the "isolation concept") because of the BSC's presumed concentration on species distinctness rather than cohesion. Detailed analysis and criticisms of this theory have been published elsewhere by ourselves and others (Butlin 1987a; Raubenheimer and Crowe 1987; Coyne et al. 1988; Templeton 1989). We refer the reader to these papers and to the counterarguments of Spencer et al. (1987) and Masters and Spencer (1989).

As noted by Coyne et al. (1988), the RSC can be considered a subset of the BSC that involves a limited set of isolating barriers (behavioral, pollinator, and gametic). The RSC excludes other barriers that can create and maintain discrete clusters in sympatry. In Chapter 3, we show that these excluded barriers have clearly played a major role in speciation. In polyploidy, for example, new taxa are created by a combination of intrinsic postzygotic and ecological isolation. We see no advantage, and considerable disadvantage, in concentrating on only the subset of isolating barriers that involve mating and fertilization. Situations that are problematic for the BSC are equally problematic for the RSC. Moreover, the RSC faces additional problems, such as how to deal with cases in which there is some hybridization but no introgression because hybrids are sterile or inviable.

Cohesion Species Concept (CSC)

A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms (Templeton 1989).

The CSC gives a mechanistic underpinning to the GCSC by attempting to include all the factors that *preserve* morphological and genetic clusters in sexual and asexual organisms. It thus takes as its species problem the existence of discrete clusters, but, like the recognition concept, the CSC emphasizes factors keeping members of a cluster together more than those keeping members of different clusters apart.

The CSC is sometimes considered superior to the BSC for two reasons. First, it sees reproductive isolation as a misleading way to think about speciation (Templeton 1989, p. 5; all quotations and page numbers refer to this paper):

For example, under the classic allopatric model of speciation, speciation occurs when populations are totally separated from each other by geographic barriers. The intrinsic isolating mechanisms given in Table 1 are obviously irrelevant as isolating barriers during speciation because they cannot function as isolating mechanisms during allopatry. Hence the evolutionary forces responsible for this allopatric speciation process have nothing to do with 'isolation.'

This is said to cause confusion for adherents to the BSC (p. 6):

This is not to say that [reproductive] isolation is not a product of the speciation process in some cases, but the product (i.e., isolation) should not be confused with the process (i.e., speciation). The isolation concept has been detrimental to studies of speciation precisely because it has fostered that confusion (Paterson 1985).

We do not understand the rationale for separating the process of speciation (the evolution of barriers to gene exchange) from its product (species themselves). Under the BSC, speciation cannot be equated with simple differentiation of populations, because without the evolution of barriers to gene exchange, distinct taxa cannot coexist in sympatry. It is not difficult for us to see species as simply an advanced stage in the evolution of such barriers. And we cannot point to a single case in which research on speciation has been hindered by confusion between process and product.

Second, the CSC is deemed superior to the BSC because it can diagnose species in two difficult cases: asexuality, and hybridization between sympatric groups that nevertheless maintain their distinctness as clusters.

The difference between the GCSC and the CSC is that the latter incorporates explanations for why individuals within clusters remain genetically and phenotypically *similar*. Templeton describes a number of factors, called "cohesion mechanisms," that enforce this similarity. These mechanisms fall into two classes. "Genetic exchangeability" mechanisms include all factors "that define the limits of the spread of new genetic variants through *gene flow*" (p. 13). These include not only the complete list of reproductive isolating barriers characterizing the BSC, but also mechanisms facilitating gene flow *within* clusters, such as a common fertilization system ("the organisms are capable of successfully exchanging gametes") and a common developmental system ("the products of fertilization are capable of giving rise to viable and fertile adults"). But all these mechanisms are simply a different way of describing isolating barriers. A species can be seen as a group of interbreeding populations (i.e., conspecific individuals share "fertilization and developmental systems"), while *different* species can be seen as groups of populations whose fertilization and developmental systems are sufficiently diverged to prevent gene exchange.

The novel aspect of the CSC is the emphasis on cohesion mechanisms that enforce demographic exchangeability. This includes all factors “that define the fundamental niche and the limits of spread of new genetic variants through genetic drift and natural selection” (p. 13). (The fundamental niche is considered “the intrinsic [i.e., genetic] tolerances of the individuals to various environmental factors that determine the range of environments in which the individuals are potentially capable of surviving and reproducing” [pp. 14–15].) Within sexually reproducing populations, of course, selection and genetic drift promote genetic homogeneity of a species. But understanding how these forces operate within a cluster does not explain how *distinct* sympatric clusters arise.

Demographic exchangeability becomes more important when dealing with asexual or uniparental populations, because this factor—and not reproductive isolation—may limit the spread of alleles by natural selection and genetic drift. As noted in Chapter 1, the origin of a new adaptive mutation in a population of bacteria produces a periodic selection event, during which the mutant clone replaces all other clones having similar ecological properties. Such replacement can also occur through the asexual equivalent of genetic drift: random differences in reproductive rates among demographically exchangeable clones. As Templeton notes (p. 15), “Every individual in a demographically exchangeable population is a potential common ancestor to the entire population at some point in the future.”

One might therefore use the CSC to demarcate species or taxa in asexually reproducing groups. It has been so used by Cohan (2001), who connects this species concept to an explicit mechanism for speciation in bacteria. (As we note in Chapter 1, we do not object to applying the words “species” and “speciation” to asexual groups, so long as one recognizes that these words have a different meaning in sexual groups.) We are less convinced that the CSC works better than the BSC in sexually reproducing organisms. Nor do we feel that a species concept is better when it applies to both sexual and asexual groups rather than to sexual groups alone. If the processes of cluster formation differ between these two groups, as we suspect they do, then adopting a single species concept for both groups may impede rather than promote progress.

In many cases, especially those involving sympatric sexual taxa, both the BSC and the CSC identify the same clusters, for the CSC considers isolating barriers to be “cohesion mechanisms.” In other situations, however, the CSC encounters the same difficulties as does the BSC. When forced crosses show that allopatric populations have complete intrinsic postmating isolation, they would presumably be regarded as good species by both the CSC and BSC. But if isolation is not complete, there is no way to diagnose these populations under either concept, for it is impossible to determine the “fundamental niche” of allopatric taxa. Thus, the CSC also faces problems with allopatric populations. Both concepts also have difficulties when dealing with groups, such as host races, that show some gene exchange but that nevertheless remain distinct.

Such hybridizing entities show genetic exchangeability (an adaptive allele can spread between races), but not demographic exchangeability (one group cannot ecologically displace the other).

There are other situations in which the BSC can diagnose species but where the CSC fails because the criteria of genetic and demographic exchangeability conflict. Consider, for example, two sympatric, reproductively isolated species that compete for resources. A new mutation may arise in one species that allows it to outcompete the other, driving it to extinction. In such cases—and in any case in which an invader outcompetes a local species—the two groups are genetically nonexchangeable but demographically exchangeable. Under the BSC they are good species, but under the CSC their status is unclear.

The main problem with the CSC, however, is that it causes confusion, especially through its emphasis on “cohesion mechanisms.” As Harrison (1998 pp. 24–25) notes:

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.”

It is hard to regard forms of natural selection that can create isolating barriers as “cohesion mechanisms.” The fixation of adaptive alleles that cause reproductive isolation as a byproduct do not involve selection for cohesion. Rather, it is the reproductive cohesion of the group that allows such alleles to spread. In such cases the CSC reverses cause and effect. Moreover, not all aspects of sexual reproduction can be regarded as “cohesion mechanisms.” Antagonistic sexual selection, produced by differing reproductive interests of males and females, may be important in speciation (see Chapter 8). But such selection is a manifestly *non-cohesive* evolutionary force.

Under the BSC, it is fairly clear when speciation has occurred—substantial barriers to gene flow exist. Under the CSC, however, speciation is seen as “the process by which new genetic systems of cohesion mechanisms evolve within a population,” or as “the genetic assimilation of altered patterns of genetic and demographic exchangeability into intrinsic cohesion mechanisms” (p. 24). But how can one know whether these processes have caused speciation unless one observes isolating barriers between a population and its relatives?

Finally, the CSC does not seem to lead naturally to a research program that reveals the causes of clustering in sexually reproducing groups. The concept of demographic exchangeability, however, may give insight into the origin of clusters in asexual organisms.

Evolutionary Species Concept (EvSC)

A species is a single lineage of ancestral descendant populations or organisms, which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley 1978, modified from Simpson 1961).

The EvSC differs from the BSC and other concepts discussed above by endowing species with broader evolutionary significance. Under the EvSC, the species problem becomes the recognition of evolutionarily independent entities, and the species is the unit that evolves independently of other species. Wiley asserts that the EvSC is more universally applicable than the BSC because the EvSC deals with both sexual and asexual taxa. Moreover, the EvSC, unlike the BSC, is said to be "capable of dealing with species as spatial, temporal, genetic, epigenetic, ecological, physiological, phenetic, and behavioral entities" (Wiley 1978, p. 18; all quotations and page numbers refer to this paper).

The EvSC differs from the BSC by including no explicit mention of genetic interchange or reproductive isolation. Nevertheless, the arguments in favor of the EvSC show that in most cases it is equivalent to the BSC, at least for diagnosing species in sympatry.

Indeed, this equivalence is recognized by Wiley: "Separate evolutionary lineages (species) must be reproductively isolated from one another to the extent that this is required for maintaining their separate identities, tendencies, and historical fates" (p. 20). But the notion of "separate identities," which implies recognizable genotypic or phenotypic clusters, can conflict with the notion of separate "tendencies" and "historical fates." Two species that hybridize, for instance, may maintain separate identities, but even a small amount of hybridization can allow a generally advantageous mutation to spread from one group to the other, so that their evolutionary fates are connected. The grass *Agrostis tenuis*, for example, has developed local races that can survive high concentrations of lead on mine tailings, while adjacent populations lack the genes for tolerance. Tolerant and non-tolerant populations are often adjacent, and, being wind-pollinated, freely exchange most genes (McNeilly and Antonovics 1968). The populations have diverged in a few traits, but still hybridize pervasively. Are they different evolutionary species? The EvSC gives no clue. With gene flow, taxa may be evolutionarily independent at some loci and not others.

Allopatric populations that are genetically differentiated pose as many problems for the EvSC as for the BSC. While geographic isolation may seem to confer separate evolutionary fates, Wiley (1978, p. 23) notes that "we have no corroboration that this particular geographic event will lead to separate evolutionary paths and thus we have no reason to recognize two evolutionary species." Such recognition becomes possible only when "significant evolutionary divergence" occurs between allopatric populations (p. 23). Wiley, however, gives no idea of what constitutes significant divergence. If "significant"

means "divergence that prevents the populations from exchanging genes were they to become sympatric," then the EvSC becomes the BSC.

Asexually reproducing taxa may be resolvable by the EvSC if significant divergence occurs between them. But the meaning of "significant" is again unclear. Are distinct clusters of many loci necessary to diagnose asexual species, or can they differ at only one or two loci?

The unique aspect of the EvSC is that it can deal with a single lineage evolving through time. According to Wiley, such a lineage is considered to be a single species so long as it does not branch, no matter how much evolutionary change it undergoes. This, of course, may result in some taxonomic confusion, as the same species name will often be used for very different organisms (consider the lineage leading to modern humans). But applying names to stages of a single evolving lineage is always an exercise in subjectivity.

The major problem with the EvSC, then, is that it cannot deal with gene flow between populations of sexually reproducing organisms. Unless one is precise about the meaning of "separate evolutionary tendencies and historical fates," decisions about species status become arbitrary. Clearly, greater evolutionary independence is conferred by stronger barriers to gene flow. In this sense, the EvSC approximates the BSC. Given the choice, we prefer the BSC because it is more useful: in sexually reproducing organisms, this concept explains the evolutionary independence of taxa (whose origin is a mystery under the EvSC) as a byproduct of isolating barriers.

Ecological Species Concept (EcSC)

A species is a lineage (or a closely related set of lineages), which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen 1976).

Van Valen proposed the EcSC to remedy the problem of ecologically differentiated entities that still exchange genes. He specifically mentions hybridizing oaks (see Chapter 1) as "cutting across the frame of reference of the now usual concept of species" (Van Valen 1976, p. 233; all quotations and page numbers refer to this paper). The EcSC resembles the EvSC except that the independently-evolving lineages are also characterized as occupying "minimally different adaptive zones." ("Minimal" is used so that higher taxa are not considered ecological species.) The species problem again seems to be that of explaining discontinuities among sympatric groups.

Requiring that different species occupy different adaptive zones imposes a severe burden on the EcSC. According to Van Valen, adaptive zones are defined a priori, independent of the organisms that inhabit them: "An adaptive zone is some part of the resource space together with whatever predation and parasitism occurs on the group considered. It is a part of the environment, as distinct from the way of life of a taxon that may occupy it, and exists independ-

ently of any inhabitants it might have" (p. 234). Van Valen suggests that occupants of different adaptive zones can be recognized by observing "a difference in the ultimately regulating factor, or factors, of population density" (p. 234).

This definition conflicts with the view that niches cannot be defined independently of their occupants, since many organisms, such as beavers and moles, change the environment to suit their needs (Lewontin 1983). Moreover, some groups can coexist as distinct entities in sympatry without gene flow, even though their adaptive zones are identical or nearly so. This is true, for example, of some temporally isolated species, such as periodical cicadas or the even- and odd-year races of pink salmon described in Chapter 5.

More important, it is often hard to determine whether two sympatric relatives occupy different adaptive zones, much less "minimally different" ones. The haplochromine cichlids of Lake Victoria, for instance, are often considered almost ecologically identical (see Chapter 4). In such cases, Van Valen suggests using a surrogate criterion: the coexistence of species in sympatry *proves* that they occupy minimally different adaptive zones. But this notion makes the EcSC operationally identical to either the GCSC or BSC, depending on the amount of hybridization. It is questionable, however, whether sympatric coexistence always constitutes evidence for "minimally different adaptive zones." As noted in Chapter 1, ecologists have suggested several ways that ecologically identical species can coexist. While we believe that differential resource use is widespread among closely related sympatric species, it may not be necessary.

Further, very different taxa may nonetheless occupy the same adaptive zone, as shown by competitive exclusion. Criticizing ecological species concepts, Wiley (1978, p. 24) notes,

In the case where resources are limiting, one of the species could replace the other through interspecific competition from that portion of the range where they are sympatric, or entirely via extinction. Indeed, if interspecific competition causes at least some extinctions, it can work only where the niches of the competing species are similar enough for competition to occur or where one species' niche completely overlaps the other's . . . one might argue that a species forced to extinction through interspecific competition was not a species at all.

Such situations are common in nature, especially with introduced species. Should the Argentine ant, *Linepithema humile*, be considered conspecific with the unrelated *Pheidole megacephala* because the former outcompeted the latter in Bermuda (Crowell 1968)? It seems better to regard ecological difference as a criterion for species *persistence* than for species status.

Van Valen suggests that it is a matter of taste whether differentiated allopatric populations are considered different species, although it is, in principle, possible to determine whether such populations are regulated by different ecological factors. But he further argues that "reproductive isolation of allopatric populations is of minor evolutionary importance and hence needs

little consideration" (p. 234). Thus, allopatric taxa that yield completely inviable or sterile hybrids in forced crosses might not be considered different ecological species. However, sympatric taxa that exchange genes but maintain phenotypic distinctness, such as oaks, *would* be considered separate species because their different traits imply different niches. Here the EcSC resembles the GSC if there is substantial introgression, but resembles the BSC if introgression is limited.

Finally, Van Valen suggests that the EcSC could be useful for distinguishing species in asexual groups (p. 235): "Species are maintained for the most part ecologically, not reproductively. Completely asexual communities would perhaps be as diverse as sexual ones, with numerous subcontinuities and even discontinuities. This suggests but does not require that the main criterion of species be ecological." We agree that the EcSC (and the CSC) might be more useful than the BSC in dealing with asexual groups, although, as noted by Van Valen, the EcSC encounters difficulties in agamic complexes.

Phylogenetic Species Concepts (PSCs)

PSCs differ markedly from the BSC and the five concepts discussed above, which take as their species problem the origin of discrete groups in nature. In contrast, PSCs are concerned with identifying historically related groups, and their species problem is reconstructing the history of life. Systematists are thus the main proponents of PSCs and the most severe critics of the BSC.

Systematists can be quite caustic when comparing the PSC to the BSC (e.g., Nelson 1989). This acrimony does not derive from their view that reproductive isolation is unimportant—for most of them admit that it is—but from the belief that it is largely irrelevant to reconstructing history. As Baum (1992, p. 1) notes, "The potential for gene exchange is only loosely coupled to historical relatedness—the central consideration of systematics." Wheeler and Nixon (1990, p. 79) state this position forcefully:

The 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.

While most advocates of the BSC recognize that reproductive isolation may sometimes be inconsistent with evolutionary history (see below), they consider historical relationships as largely irrelevant to understanding the discreteness of nature.

Most modern systematists infer phylogenetic relationships using quantitative methods (Felsenstein 2004). One widely used method, cladistics, involves using shared derived characters, or *synapomorphies*. These characters can be either organismal traits or genes. When two or more species share a synapomorphy relative to an outgroup—a taxon known from independent evidence

to be a more distant relative—these species are placed together in a monophyletic group (i.e., a group descended from one ancestral species). Thus, more closely related groups are those sharing more recently evolved synapomorphies.

It is reasonable to suppose that most sympatric species diagnosed by the BSC will be similarly diagnosed as monophyletic groups whose members have synapomorphies. But evolutionary history and reproductive compatibility need not coincide. Perhaps the most common cause of such discordance involves peripatric speciation: colonists originating in only one population of a species invade a new area, and their descendants evolve into a new species. Figure A.1 (A) gives an example of a phylogeny resulting from this scenario. Here, a common ancestor, species A, give rise to three taxa (B_1 , B_2 , and C). Taxa B_2 and C are the most closely related because they share a derived character or charac-

ters, X, that evolved in their own common ancestor and not in the direct ancestor of population B_1 . Taxon C, however, may have invaded a new habitat and evolved traits causing reproductive isolation (RI) from the two taxa B_1 and B_2 , which themselves can interbreed. The BSC would recognize two species, C and $[B_1 + B_2]$, with B_1 and B_2 considered conspecific populations. Most phylogenetic species concepts, however, would recognize a *different* pair of species, B_1 and $[B_2 + C]$. Using cladistics, one would not unite populations B_1 and B_2 based on their reproductive compatibility, for this compatibility is not a shared derived character but a *primitive* character retained from the common ancestor A (a “symplesiomorphy”). In technical terms, biological species $[B_1 + B_2]$ is *paraphyletic* with respect to taxon C. That is, within the group $[B_1 + B_2]$, members of B_2 are more closely related to members of C than to members of B_1 .

In this simple case, taxa B_1 and B_2 , although *capable* of interbreeding, do not. But this situation is unrealistic. After all, populations B_1 and B_2 are members of the same biological species and will exchange genes, erasing their distinctness. When this occurs, *some* genes will show the phylogeny depicted in Figure A.1 (A), while other genes will show B_1 and B_2 to be sister taxa, with C an outgroup. If speciation has occurred recently, different loci or traits will not yield congruent phylogenies, and the true history of populations and the histories of genes within those populations is the biggest problem afflicting phylogenetic species concepts.

Reproductive isolation and evolutionary history can also conflict when two or more reproductively compatible populations arise independently from different evolutionary lineages, a situation known as “parallel speciation.” Limnetic morphs of the threespine stickleback are often cited as an example (see Chapters 4 and 11). Figure A.1 (C) shows a phylogeny resulting from parallel speciation. Here, populations B_1 and B_2 are reproductively compatible, but each has a closer relative, C_1 and C_2 , respectively. The latter two populations have evolved different derived traits (X and Y) but are reproductively compatible with each other and reproductively incompatible with B_1 and B_2 . The BSC would diagnose two species, $[B_1 + B_2]$ and $[C_1 + C_2]$. However, $[C_1 + C_2]$ would not be recognized as a single species by most PSCs because it is *polyphyletic* (i.e., a taxon in which different populations or individuals have different common ancestors that reside outside the group). $[B_1 + B_2]$ also fails to constitute a phylogenetic species because this entity is *paraphyletic*. Despite the reproductive relationships among these groups, most PSCs would recognize only a single species comprising the group $[B_1 + B_2 + C_1 + C_2]$.

Polyphyly might seem to be rare given the implausibility that two independently evolved species would nevertheless be reproductively compatible with each other. But it may be common in one situation: polyploidy. Figure A.1 (D) shows a phylogeny in which hybridization occurs between two biological species, B and C, eventually producing the allopolyploid species D (see Chapter 9). Two independent hybridizations between different individuals or populations of B (B_1 and B_2) and C (C_1 and C_2) can produce two allote-

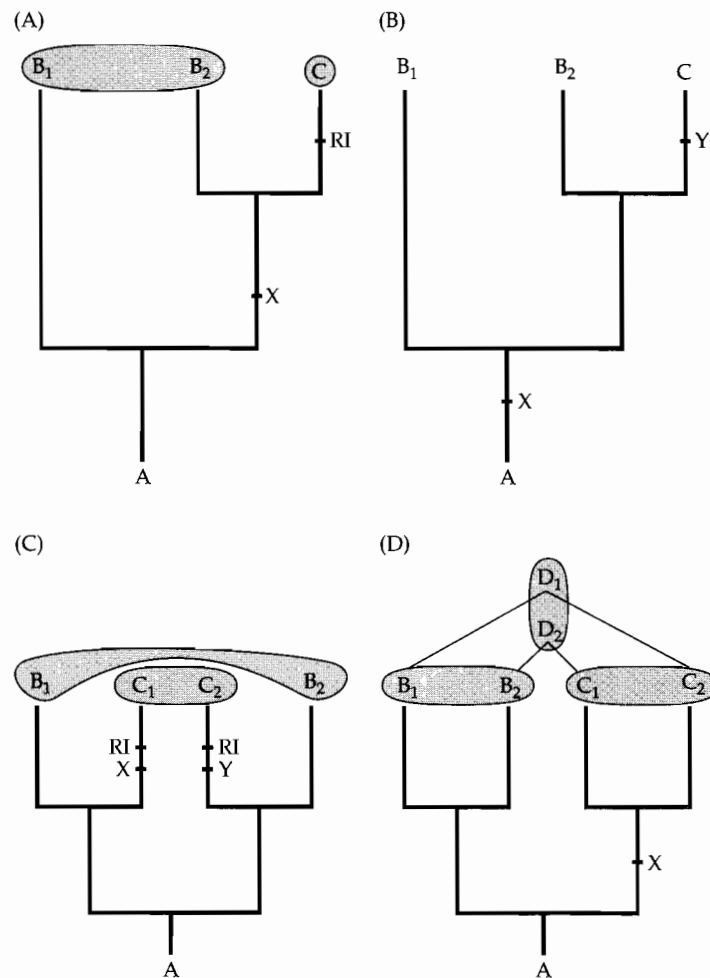


Figure A.1 Phylogenies showing disparities between evolutionary history and reproductive isolation (see text for discussion). (A) Speciation in a peripheral isolate. (B) Species diagnosed by a trait difference using Phylogenetic Species Concept 1 (PSC 1). (C) Parallel speciation yielding a polyphyletic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

traploid populations (D_1 and D_2) that are reproductively compatible with each other but incompatible with species B and C. The reproductive compatibility between individuals of species D conceals the fact that this polyploid species includes two groups with independent historical origins.

But recognizing the polyphyly of populations may be as difficult as recognizing the paraphyly of populations. We are not able to directly witness the history of populations, and so must infer it from gene-based phylogenies. In both cases discussed above (Figures A.1 C, D), interbreeding between populations of a biological species can quickly destroy our ability to reconstruct the history of populations, and thus our ability to show that this history is inconsistent with reproductive relationships.

Finally, some systematists dismiss the BSC because they view reproductive isolation as an *apomorphy*—a trait unique to one species—rather than as a synapomorphy that allows cladistic analysis. But reproductive isolation differs from traditional traits used by cladists, for it is not diagnosable in individuals of one taxon. Rather, reproductive isolation is an *interaction*, or joint property of two taxa. Such interactions cannot be incorporated into cladistic studies, although the traits underlying them can.

There are three main versions of the PSC:

1. *PSC1* A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent (Cracraft 1989; see also Wheeler and Nixon 1990).

PSC1 is essentially a typological species concept that diagnoses species based on fixed differences in traits. (The term “irreducible” means that a species does not contain other diagnostic groups within it, so that large groups sharing diagnostic traits [e.g., mammals] are not deemed a single species. “Parental pattern of ancestry and descent” is included so that species status is not determined by sex differences or segregating polymorphic traits.)

Although advocates of *PSC1* are not explicit on the point, in principle *any* trait can serve to diagnose a new species, even one as trivial as a small difference in color or a single nucleotide difference in DNA sequence. Applying *PSC1* would thus tremendously increase the number of named species. *Homo sapiens*, for example, might be divided into several species based on diagnostic differences in morphology, molecules, or a combination of these features. (For diagnostic purposes, combinations of characters can be considered as single “traits.”) Applying *PSC1* to the birds of paradise, Cracraft (1992) increased the number of named species from about 40 to 90, often diagnosing as a new species an allopatric population having a slight difference in plumage color.

Like all phylogenetic species concepts, *PSC1* cannot help us understand why organisms occur in discrete units, whether those units are defined phylogenetically or morphologically. However, its main difficulty is that its use may distort evolutionary history, the very problem it was meant to solve. Such dis-

ortion can occur because, under *PSC1*, species diagnosis is based not on shared derived traits, but on simple diagnostic traits. Figure A.1 (B) gives an example of such distortion in three taxa whose true evolutionary history is shown by the phylogeny. The common ancestor of three taxa, B_1 , B_2 and C, evolves a trait X. This state is retained in the descendant species B_1 and B_2 . In species C, however, the trait has changed to state Y. Using this trait, the *PSC1* would diagnose two species: [$B_1 + B_2$] and C. This distorts the evolutionary history of the group because B_2 and C are more closely related to each other than either is to B_1 . Similarly, using novel traits may diagnose a polyploid taxon as a phylogenetic species, even if it had a polyphyletic origin. There is no reason to expect that diagnostic traits will always mirror evolutionary history. Other criticisms of *PSC1* are raised by Avise and Ball (1990), Baum (1992), and Baum and Donoghue (1995).

How well does *PSC1* handle situations that are problematic for the BSC? In many cases, these two concepts pick out identical species in sympatry, especially when several traits are used. Coordinated *sets* of diagnostic traits cannot be maintained in sympatry without some form of reproductive isolation. Confronting allopatric populations, *PSC1* considers them different species if they differ in any trait. Likewise, *PSC1* diagnoses each recognizable clone in an asexual group as a different species. Finally, under *PSC1*, speciation consists of the fixation of a diagnostic character in a lineage, making the process identical to divergent evolution. This type of speciation will occur faster than biological speciation: fixation of one new allele is undoubtedly faster than the evolution of reproductive isolation, which usually requires changes at several loci.

2. *PSC2* A species is the smallest (exclusive) monophyletic group of common ancestry (de Queiroz and Donoghue 1988; see also Rosen 1979, Mishler and Brandon 1987, and Baum and Donoghue 1995).

PSC2 goes back to Ronald Fisher, who suggested that all members of a sexually reproducing species should share “the effective identity of . . . remote ancestry” (1930, p. 124). This concept, updated in light of cladistics by de Queiroz and Donoghue (1988) differs from *PSC1* by basing species recognition not on diagnostic characters, but on synapomorphies—shared derived characters that define monophyletic groups.

According to *PSC2*, a taxon is a species if cladistic analysis shows that it is monophyletic, exclusive (i.e., a group whose members are more closely related to each other than to those of any other group), and includes no other exclusive monophyletic groups within it.

When characterized properly, the units diagnosed by *PSC2* will usually be congruent with evolutionary history. The main problem with this concept is operational: how can one *determine* whether a group is monophyletic and exclusive?

The problem arises from population genetics. One wants to know whether populations are exclusive groups sharing a common ancestry, but such a diagnosis can be made only using genes or genetically based traits. Increasingly,

systematists rely on gene sequences to reconstruct this ancestry. DNA-based traits have two advantages over traditionally used morphological traits. First, genetic markers are more likely to be selectively neutral and thus to change in a more time-dependent fashion, making them useful for historical reconstruction. Second, gene sequences offer a nearly infinite number of characters, with each nucleotide potentially yielding information about ancestry.

However, the wealth of genetic data also creates a serious problem for the PSC2, because the ancestry of populations must be inferred from the ancestry of genes, and, as has been emphasized many times, *gene trees need not correspond to species trees*. That is, the historical branching pattern of taxa themselves need not coincide with the historical branching pattern of their genes (Avice and Ball 1990; Hey 1994; Avice and Wollenberg 1997).

This problem is demonstrated in Figure A.2 (A), which shows three taxa of haploid organisms, A, B, and C, derived from a common ancestor. The phylogeny of these taxa is represented by the "fat branches" of the tree. The prob-

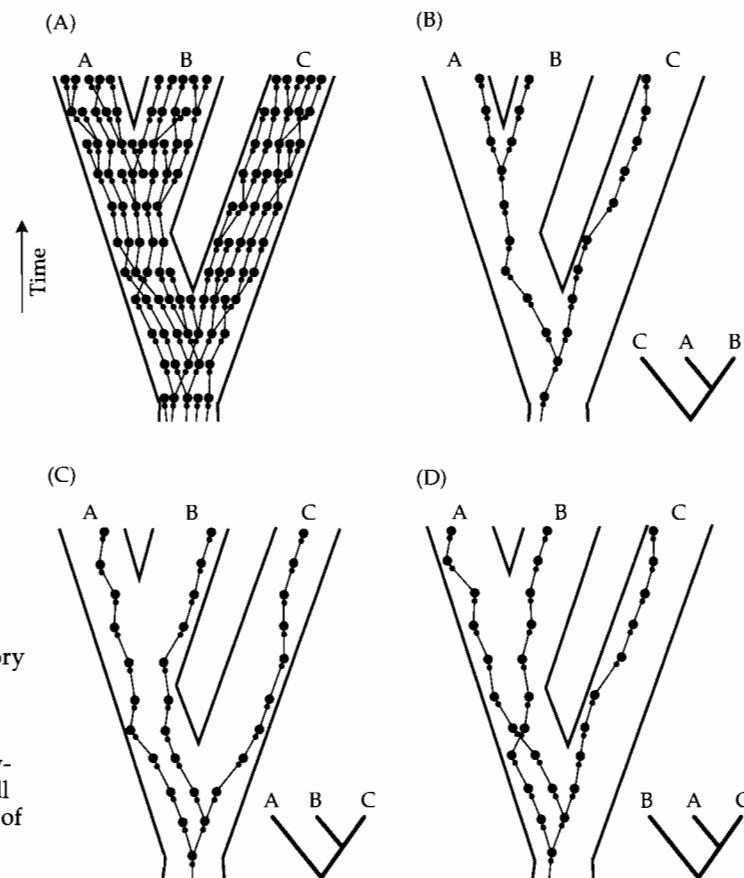


Figure A.2 Gene sorting occurring in a phylogeny whose true population history is shown in (A). Depending on which gene copies are picked for analysis, one can derive all three possible phylogenies, shown by the small diagrams to the lower right of diagrams (B), (C), and (D). (After Hey 1994.)

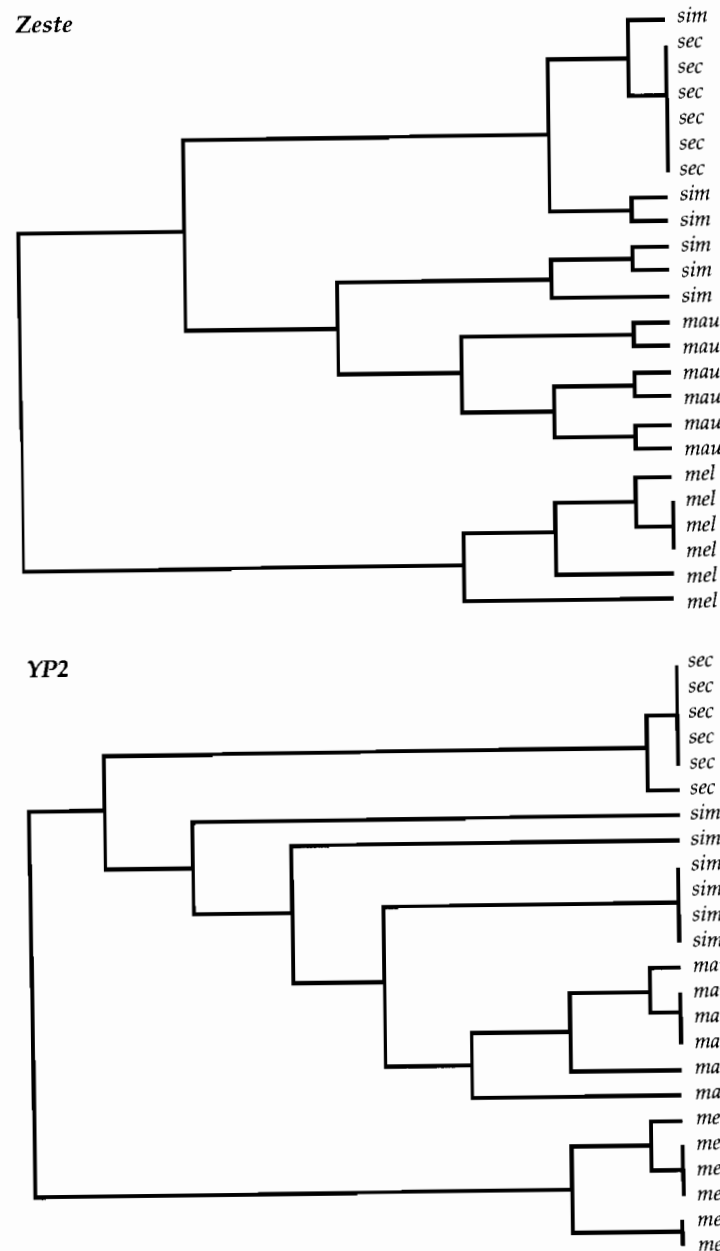
lem is to use the phylogenies of genes to reconstruct the phylogeny of the fat branches—the "true" population history. To illustrate the problems, we consider a single gene, designating each allele present in an individual with a dot. (The different gene copies do not necessarily differ in sequence, but we assume in this diagram that they can be individually identified.)

At the two successive "fat branching" events, gene flow between lineages is instantaneously prevented by geographic isolation or the rapid evolution of reproductive isolation. At each such split, the two descendant branches contain many different copies of each gene. Through the process of "gene sorting" via drift and selection over generations, these gene copies create their own genealogies—"thin branches"—with some copies leaving no descendants, and others copies leaving varying numbers of descendants. ("Splitting" of a gene phylogeny in Figure A.2 (A), reflects passage of a gene copy to more than one descendant, not new mutations or recombination events, which we ignore.) Gene copies present in the common ancestor can persist in descendants, often for long periods after the populations branch. Eventually, selection and drift will cause all gene copies within a lineage to descend from a single ancestral copy occurring within that lineage (that is, a *coalescence* occurs). When this happens, the gene has become monophyletic within the fat branch.

Until coalescence takes place, however, there can be substantial disparity between the true genealogy of the populations (i.e., A and B are sister groups with respect to the outgroup C), and the genealogy inferred from genes. Figure A.2 (B), (C), and (D) show that, using a single gene, one can obtain all three possible phylogenies between populations, only one of which gives the true population history. Although the populations have become evolutionarily independent taxa at the moment of isolation, in the sense that each now contains a nonoverlapping set of ancestors and descendants, one cannot genetically demonstrate that they are monophyletic until considerable time has passed. As noted by Avice and Ball (1990), after two populations become isolated, their genes will go through successive stages of polyphyly and paraphyly before finally becoming *reciprocally monophyletic*—the stage when all gene copies in each population are more closely related to each other than to copies in the other population.

This problem cannot be remedied by using larger samples of alleles or genes, because until reciprocal monophyly is attained, one can obtain conflicting phylogenies using different genes. This can be seen in Figure A.3 for two genes, *zeste* and *YP2*, sampled in four species of *Drosophila* (Hey and Kliman 1993). This group had a common ancestor that existed about 2.5 million years ago. *D. melanogaster* (*mel*) is an outgroup to the three species *D. simulans* (*sim*), *D. sechellia* (*sec*), and *D. mauritiana* (*mau*). All four species are distinguishable morphologically and show either substantial or complete reproductive isolation. Like *D. melanogaster*, *D. simulans* is cosmopolitan, while *D. sechellia* and *D. mauritiana* are endemic to the islands of the Seychelles and Mauritius, respectively. The endemics presumably arose after colonization of the islands by their common ancestor with *D. simulans*.

Figure A.3 Phylogenies based on sequences of copies of two genes (*zeste* and *Yolk protein 2* [YP2]) in four related species of *Drosophila* (*sim* = *D. simulans*, *sec* = *D. sechellia*, *mau* = *D. mauritiana*, and *mel* = *D. melanogaster*). Both sequences show that *D. simulans* is “paraphyletic,” but the paraphyly is almost certainly of these genes and not of the populations themselves. (After Hey and Kliman 1993.)



While the phylogeny of *D. melanogaster*, *D. sechellia*, and *D. mauritiana* is resolved under PSC2 using both genes, some sequences from *D. simulans* are more closely related to sequences found in *D. mauritiana* or *D. sechellia* than to other *D. simulans* sequences. That is, *D. simulans* is a paraphyletic species. Some

systematists suggest that in such cases the paraphyletic taxon should be called a “metaspecies,” so that individuals of *D. simulans* would not be recognized as belonging to *any* species (de Queiroz and Donoghue 1988; Baum and Shaw 1995). A study of 12 additional loci in this group gave similar results, failing to resolve the branching order of the two island colonizations (Kliman et al. 2000).

The most likely explanation for the discordant genealogies among genes is that *D. simulans* is still polymorphic for ancestral alleles that have become monophyletic in its island relatives. If geographic and genetic isolation persists, these species will eventually become monophyletic at all loci, but, as we show in the next section, this may take a very long time. Moreover, if there is any hybridization between the taxa (and there is some evidence for this in the *D. simulans* group), or if balancing selection maintains identical polymorphisms in different species, some genes will *never* become monophyletic within a lineage, and PSC2 status will never be attained.

The PSC2 is thus problematic because it ignores the distinction between monophyly of species and monophyly of genes. The latter is required to diagnose the former, but because of the long period required for different genes to show concordant phylogenies, the PSC2 will fail to diagnose (and resolve the history of) many species that are recognized using other concepts. This is why systematists introduced a third version of the PSC, the *genealogical species concept*.

3. PSC3 (Also called the “genealogical species concept” or GSC.) A species is a basal, exclusive group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group, and that contains no exclusive group within it (Baum and Donoghue 1995; Shaw 1998).

The GSC was proposed as a way to diagnose the phylogenetic status of populations using genes; it is, in fact, an operational definition of PSC2. Avise and Ball (1990) were the first to consider genetically based monophyly as a way to reconstruct the evolutionary history of taxa, but did not deem it a good way to diagnose species.

Like PSC2, the GSC recognizes species as exclusive groups whose members are more closely related to each other than to individuals of other species. The GSC also recognizes species as basal groups that contain no exclusive subgroups within them. The difference between the two concepts is that the GSC explicitly defines the monophyly of taxa as the monophyly of the genes carried by its members. Although diagnosing a group as a genealogical species (GS) should in principle involve many loci—after all, it is individual organisms and not genes that are members of a species—in practice monophyly is determined using a limited sample of genes.

The main task facing the GSC is specifying *how many loci* must be monophyletic to diagnose a group as a genealogical species. The original formulation by Baum and Donoghue (1995) requires *all* loci to be monophyletic. But this demand is too extreme, as balancing selection that preserves two or more

alleles in an ancestral species can keep identical sets of alleles polymorphic in descendants. This is the situation at the MHC locus in humans versus chimps, and in rats versus mice, with both pairs of species having a divergence between 5 and 10 million years (Figueroa et al. 1988; Ayala and Escalante 1996). One also sees ancient polymorphisms of self-incompatibility alleles among species in the genus *Brassica* (Uyenoyama 1995).

Advocates of the GSC recognize the problem with demanding complete monophyly of all genes, but have avoided the question of what proportion of surveyed loci must be monophyletic to allow GS status. Shaw (2001), however, suggests that GS status might be recognized if most loci were monophyletic. Setting this "> 50%" threshold makes judgments about GS status somewhat arbitrary, but no more arbitrary than diagnosing biological species when reproductive isolation is incomplete.

Using coalescent theory, Hudson and Coyne (2002) studied the time to attain GS status when an ancestral species divides into two descendants and the only evolutionary forces operating are mutation and genetic drift. For a single descendant, attaining *complete* monophyly requires a long time, especially if many loci are sampled. To attain a 95% probability of observing monophyly at every sampled gene, where N is the effective size of the population, one requires $1.8 N$ generations to reach GS status for a single mitochondrial or chloroplast gene, $7.3 N$ generations for a single nuclear gene, and $26.3 N$ generations for 11,500 nuclear loci (roughly the number of genealogically independent units within the *Drosophila melanogaster* genome). Attaining *reciprocal* monophyly for both descendant populations takes roughly 10%–30% longer. Directional selection, which speeds the fixation of alleles, will shorten these times; but balancing selection, which retards fixation, will lengthen them. Surprisingly, the number of alleles sampled per gene has little effect on the time required to attain GS status.

Presumably, one uses a sample of loci to infer the GS status of the entire genome. Such a goal requires one to use a large sample of loci and to avoid diagnosing GSs based on single mitochondrial or chloroplast loci. Organelle genes have only one-fourth as many copies as any autosomal locus, and so will become monophyletic well before the rest of the genome. All genes in an organelle are also completely linked, so no additional information about ancestry is gained by using more than one such gene. Nevertheless, genealogical species have been diagnosed on the basis of a single mtDNA haplotype or allozyme locus (e.g., Young and Crother 2001; Leaché and Reeder 2002).

When one relaxes the criteria for GS status, so that only 50% or 95% of sampled loci need be monophyletic, the time to genealogical speciation is reduced. In a sample of 25 nuclear genes, for example, one observes complete reciprocal monophyly with 95% probability after $15.2 N$ generations. This drops to $4.7 N$ generations if only 50% of the loci need be monophyletic, and to $11.3 N$ generations if 95% of the loci need be monophyletic. In the limit, with an infinite sample of loci, one observes complete reciprocal monophyly with 100% prob-

ability after $3.8 N$ generations using the 50% criterion and $8.7 N$ generations using the 95% criterion.

The conclusion is that one should not adopt a GS criterion requiring *complete* reciprocal monophyly for a large number of loci. Under this extreme view, humans and chimps would be considered one species, and rats and mice another. Moreover, attaining genome-wide monophyly takes so long that, before it occurs, taxa will be recognized as species using nearly every other species concept; indeed, many *additional* branching events might have occurred.

What is the relationship between biological and genealogical speciation? While both processes are accelerated by divergent natural selection and geographic isolation, there is no necessary correspondence between the times when species status is attained under the BSC and the GSC. However, biological speciation is almost certain to precede genealogical speciation if GS status requires complete reciprocal monophyly at many loci. *Drosophila simulans*, for example, is not a genealogical species with respect to *D. mauritiana* under even the "50% monophyly" criterion, and these taxa (although allopatric) have diverged in several morphological traits and show substantial reproductive isolation.

While a "relaxed" version of the GSC seems the most reasonable of all phylogenetic species concepts, we favor the BSC over the GSC for several reasons. First, applying the GSC will often involve designating taxa as metasppecies: large groups of individuals, such as *D. simulans*, will not be recognized as belonging to any species. Unlike many doubtful cases in the BSC, the term "metasppecies" describes an *ontological* situation (organisms that are not members of any species) rather than an *epistemological* one (groups that cannot be assigned to recognized species due to a lack of evidence)" (Baum and Shaw 1995, p. 297; our italics). At the moment when an isolated population becomes monophyletic, every individual in every other population instantly loses its status as belonging to any species. It seems odd that, without any change in its own genetic composition, a group can lose species status based on what happens in a remote population. It should be added, however, that systematists disagree on whether the term "metasppecies" should be used, or which entities should be so characterized.

Second, little of biological import occurs at the completion of genealogical speciation. What significance, for example, can one impute to the moment at which the proportion of loci showing exclusivity rises from 50% to 50.1%—the completion of one type of genealogical speciation? In contrast, the completion of biological speciation—the moment when gene flow between sister taxa is no longer possible—corresponds to a biologically meaningful event. It is the moment when taxa become evolutionarily independent (Coyne 1994a). The termination of gene flow also allows genealogies to coalesce without pollution by genes from other taxa. Thus, these reproductive barriers, along with geographical barriers, provide the isolation that *permits* the monophyly required for genealogical speciation. In this sense, reproductive isolation is more fundamental than genetic coalescence.

Finally, genealogical speciation will often be transitory, for the coalescence of genes does not guarantee that geographically isolated populations will remain distinct when they become sympatric. One can envision many small, isolated populations quickly attaining genealogical species status. But range shifts or the disappearance of geographic barriers will quickly eliminate these genealogical species: they will hybridize with other populations and their exclusivity will vanish. In contrast, some forms of reproductive isolation are permanent. It is the permanence of reproductive isolation that guarantees the independence of genealogies among taxa.

The BSC and evolutionary history

Applying the BSC is an exercise not in reconstructing the history of taxa, but in identifying reproductively isolated groups. But implicit in this exercise is the idea that populations of a single biological species are more closely related to each other than to populations of a different species. To justify systematists' assertions that the BSC frequently distorts evolutionary history, one should be able to show many cases in which that history conflicts with reproductive compatibility. The most commonly cited examples are paraphyletic species and polyphyletic species. We have already noted some of the difficulties with using "thin branch" phylogenies of genes to determine whether population phylogenies—"fat branch" phylogenies—are paraphyletic or polyphyletic.

PARAPHYLY. In principle, species with a paraphyletic *origin* should be common. There must be many cases (e.g., peripatric speciation) in which a new biological species, B, originates from only one population of ancestral species A. If species B evolves reproductive isolation from all populations of A, which themselves remain reproductively compatible, then species A is *historically* paraphyletic. That is, if we were present at the moment when the population destined to become species B was geographically isolated, we would see that it derived from only one population of species A.

But we were not present at this moment, and so cannot directly witness the history of taxa. We must rely on the thin branches—the phylogenies of genes—to reconstruct the pattern of fat branches. But gene-based phylogenies can yield false diagnoses of paraphyly for several reasons.

One reason, mentioned above, is that populations of the ancestral species do not remain genetically isolated. Their interbreeding will quickly erase the genetic differences between populations that can be used to diagnose paraphyly. *Recognizable* paraphyly is therefore likely to be a transitory phenomenon. What we expect is that some loci will show paraphyly of alleles in species A relative to those in species B, but that this pattern will not be consistent across all genes. In other words, different traits or loci may yield different patterns of relatedness, with some showing paraphyly and others not. Moreover, as seen in Figure A.2, one expects this discordance even if species A is *not* paraphyletic, for discordance is the expected result when ancestral polymorphisms

are sorted into descendant species. Such paraphyly is an ineluctable part of the speciation process and therefore cannot conflict with the BSC.

How many genes, then, must show concordant phylogenies before we are confident that the taxa themselves are paraphyletic? This crucial issue has been almost completely ignored by systematists. In fact, we do not know of any case in which species paraphyly is demonstrated by concordant genealogies of many (or even several) genes. Claims for species paraphyly are almost always based on one or a few loci, usually on the mitochondria (e.g., Melnick et al. 1993; Patton and Smith 1994; Omland 1997; Omland et al. 2000). Such paraphyly tells us little about the evolutionary history of populations because organelle genes may not accurately mirror the rest of the genome.

Indeed, many studies show that mitochondrial and chloroplast DNA introgress between taxa much more readily than does nuclear DNA (e.g., Ferris et al. 1983; Smith 1992; Bernatchez et al. 1995; Howard et al. 1997; Taylor and McPhail 2000; Martinsen et al. 2001; Shaw 2002). The reasons for this are unclear, but may be due to the nature of mitochondrial genes. Most of these genes are constitutively expressed and perform internal metabolic "house-keeping" or protein-synthetic functions, such as producing tRNA or respiratory enzymes. Such functions may be largely divorced from external selective pressures, making mtDNA less responsive than nuclear genes to local environmental differences. This may also be true for cpDNA, which contains genes for photosynthesis, tRNA, and rRNA. Thus, organelle genes, unlike nuclear genes, may function fairly well in the genetic background of a related species. In addition, the spread of adaptive mutations in organelle DNA is not impeded by their linkage to nuclear genes that are divergently adapted between taxa or cause intrinsic postzygotic isolation in hybrids.

The consequence of introgression and linkage is that organelle DNA may appear paraphyletic even when the species themselves are not. Phylogenies based solely on organelle DNA can also distort history in other ways. For example, Shaw (1996b) showed that a mtDNA-based phylogeny of Hawaiian crickets (*Laupala*) was discordant with traditional phylogenies based on morphology and biogeography. The mtDNA phylogenies showed that the most closely related species were sympatric, implying sympatric speciation. However, later phylogenies based on nuclear DNA were concordant with the traditional ones, supporting allopatric speciation following colonization of new islands (Shaw 2002). The most likely reason for this discordance is the introgression of mitochondria between sympatric taxa, which can hybridize. (One would predict that in species having heterogametic females, such as birds and Lepidoptera, mtDNA would introgress less readily. Because Haldane's rule holds in these groups, F₁ hybrid females, which pass on mtDNA, are often sterile.)

Under the "fat branch" approach, the evolutionary history of populations is usually represented by trees with bifurcating branches. However, the techniques used to reconstruct this history involve genes whose diverse genealogies can yield a complicated set of reticulations instead of a definitive phy-

logeny. Because there is no unitary *genetic* history at the population level, it is almost impossible to recognize true paraphyly among closely related taxa using genetically based phylogenies.

POLYPHYLY. A polyphyletic species includes individuals or populations having independent evolutionary origins from common ancestors residing outside that species. As noted above, polyphyletic species include independently formed polyploid individuals that interbreed with one another, as well as cases of parallel speciation.

There is strong genetic evidence for a polyphyletic origin of some auto- and allopolyploid plant species (see Chapter 9), and of at least one species of terrestrial snail (Ueshima and Asami 2003). These cases indeed show genuine discordance between the evolutionary history of populations and their reproductive relationships. And because hybridization can form new polyploids repeatedly, this discordance may persist for long periods. In some cases, independently derived polyploids co-occur in nature and interbreed, showing that they are indeed members of the same biological species. But phylogenetic species concepts are unable to deal with such polyphyletic species, as they combine the genes of two ancestral species.

Parallel speciation has a similar effect, except that the independent origins of a single species involve convergent evolution rather than repeated hybridization. There are two possible cases of nonhybrid diploid species having multiple evolutionary origins: limnetic morphs of the threespine stickleback, *Gasterosteus aculeatus* (Rundle et al. 2000), and host races of the stick insect *Timema cristinae* (Nosil et al. 2002). However, in both cases there is ongoing gene flow between sympatric taxa. This can yield inaccurate phylogenies, making speciation events appear independent when they are not.

We conclude that while the BSC may occasionally identify species that are not monophyletic, it is not clear that phylogenetic species concepts are better at dealing with this problem.

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