

### 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.

## SPECIATION

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*To Anne and Lynne*

Chapter 10 deals with reinforcement, the enhancement of prezygotic isolation by natural selection in response to maladaptive hybridization. This topic has been controversial, its popularity rising and falling over the years. We conclude that recent theory shows that reinforcement is formally possible and that recent empirical work reveals evolutionary patterns consistent with the process. But because other processes can also produce these patterns, we cannot conclude with confidence that reinforcement is common in nature. In the end, we suggest a new way to distinguish between reinforcement and these alternative possibilities.

We then take up a controversy that we believe is now settled: the relative roles of selection versus drift in speciation. While Chapters 5–8 deal in passing with the evolutionary origin of reproductive isolation, Chapter 11 summarizes and evaluates this scattered evidence. We conclude that, despite the perennial popularity of models based on genetic drift, there is little evidence that drift plays an important role in speciation. There is, in contrast, a growing body of evidence for the importance of natural and sexual selection.

Finally, Chapter 12 addresses several macroevolutionary problems connected with speciation. The first involves calculating speciation rates, a problem as difficult to frame as to solve. The second involves identifying which, if any, biological factors affect speciation rates. The development of comparative methods now allow us to infer those organismal traits that have increased or decreased biodiversity, an enterprise that may tell us which isolating barriers were important in speciation. This leads naturally to a consideration of “species selection”—the differential proliferation of traits due to their association with higher or lower speciation rates. While species selection is a controversial topic, we argue that comparative studies strongly support its action in nature.

In summary, we have tried to survey, analyze, and synthesize what is known about speciation, offering not only a critique of the field but some new (and hopefully fruitful) ideas for research. Although our attempt surely suffers from the problems afflicting any broad survey—too little detail about some issues, and an occasional factual error—we hope that it at least imposes some order on, and draws some nontrivial conclusions from, a vast literature. More important, we hope that this book will stimulate younger scientists to pursue their own work on speciation.

## 1

## Species: Reality and Concepts

When on board the H.M.S. ‘Beagle,’ as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species—that mystery of mysteries, as it has been called by one of our greatest philosophers (Darwin 1859).

So begins *The Origin of Species*, whose title and first paragraph imply that Darwin will have much to say about speciation. Yet his magnum opus remains largely silent on the “mystery of mysteries,” and the little it does say about this mystery is seen by most modern evolutionists as muddled or wrong. The study of speciation is thus one of the few areas of evolutionary biology not overshadowed by Darwin’s immense achievements. For years after publication of *The Origin*, biologists struggled, and failed, to reconcile the continuous process of evolution with the discrete entities, namely species, that it produces. Now, 120 years after Darwin’s death, a reconciliation has been achieved: we have a reasonably complete picture of what species are and how they arise.

But we must start at the beginning—with the question of whether biological nature really is discontinuous. Do species exist as discrete, objective entities, or are they, as Darwin believed, purely arbitrary constructs? If species are not real, then the problem of speciation is moot and we need go no further.

Most biologists certainly *act* as if species are real: naturalists label their specimens, systematists reconstruct the history of life from species-specific traits, population geneticists measure DNA variation within species, and ecologists calculate species diversity. Yet a vocal group of biologists, including many botanists, dissent, claiming that species are subjective divisions of nature made for human convenience. This view is common enough to merit serious examination.

If species *are* real, a second question immediately arises: How do we define them? That is, how do we encapsulate in words the discrete groups that we see in nature? There have been endless arguments about the “right” species concept, and it is clear that one’s favorite answer depends on what one wants to understand—how one views the “species problem.” Systematists, whose task is unraveling the history of life, often prefer species concepts different from those used by evolutionists more interested in evolutionary processes. Accordingly, deriving a species concept is important because it frames one’s entire research program on the origin of species.

Finally, if one assumes that species are real, one can ask a related question: *Why* do they exist? This query does not involve describing species, but rather determining what properties of organisms and their environments cause nature to be divided into discrete groups.

In this chapter, we consider three fundamental questions: Are species real? If so, what are they? Finally, why do they exist? We contend that species are in fact real, and that the species concept most useful for understanding their origin is a modified version of Ernst Mayr’s “biological species concept.” At the end, we offer some approaches to the question of why species exist—a badly neglected problem.

## The Reality of Species

As Mayr (1982, p. 285) noted, “The so-called species problem can be reduced to a simple choice between two alternatives: Are species realities of nature or are they simply theoretical constructs of the human mind?”

Thus, when one inquires about the reality of species, one asks whether assemblages of individuals—populations—are partitioned into discrete units that are objective, not subjective. Determining whether such groups exist is best accomplished by studying organisms that live in the same area—in *sympatry*. Because entities widely considered to be species show geographical variation in traits (e.g., *Homo sapiens*), one can easily demonstrate morphological or genetic “gaps” between populations from different regions. If hybridization occurs, however, such gaps would often disappear were the populations to inhabit the same area. Such is the case in modern humans.

In *The Origin*, Darwin apparently felt that species were not real:

From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms (Darwin 1859, p. 52).

In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the

undiscovered and undiscoverable essence of the term species (Darwin 1859, p. 485).

For Darwin, the origin of species was identical to the origin of adaptations within species—the production of different varieties. He therefore conflated the problem of change within a lineage with the problem of the origin of new lineages. Surprisingly, however, in his unpublished notebooks and post-*Origin* publications, Darwin sometimes took a different stance, tacitly accepting the idea of organic discontinuity and even suggesting (in the first quote given below) that this discontinuity might result from reproductive barriers:

My definition [in wild] of species, has nothing to do with hybridity, is simply, an instinctive impulse to keep separate, which no doubt be overcome, but until it is the animals are distinct species (Notebook C, entry 616, Barrett et al. 1987; see also Kottler 1978).

Independently of blending from intercrossing, the complete absence, in a well-investigated region, of varieties linking together any two closely-allied forms, is probably the most important of all the criterions of their specific distinctness. . . (Darwin 1871, p. 215).

It is unclear why these views did not find their way into *The Origin*.

A number of biologists have agreed with Darwin’s published view that species are arbitrary constructs. Surprisingly, this group includes the evolutionist J. B. S. Haldane, who observed that “the concept of a species is a concession to our linguistic habits and neurological mechanisms. . . a dispute as to the validity of a specific distinction is primarily a linguistic rather than a biological dispute” (1956, p. 96). Raven (1976), Mishler and Donoghue (1982), and Nelson (1989) have made similar arguments. Still others consider the gradual nature of speciation as evidence against the distinctness of its products: “Today, an essential species ‘reality’ strongly conflicts with our understanding of gradual speciation, and is no longer accepted at all generally. . .” (Mallet 2001, p. 887). We contend, however, that the process of speciation is likely to be short relative to the duration of well-demarcated species, and that brief transitions between long lasting and discrete entities do not make those entities unreal. The existence of puberty, for example, does not mean that one cannot distinguish between children and adults.

A different view, common among botanists, is that while *some* species are real, other groups are less discrete owing to extensive hybridization or the presence of uniparental reproduction (e.g., selfing or clonal reproduction). We find it puzzling, if not contradictory, that many evolutionists who doubt the reality of species nevertheless act as if species were real when doing their own research, using Linnaean names and treating members of one species as equivalents.

Because of the continuing debate about the reality of species, we will describe methods that can help determine whether species are subjective or objective, and will show the outcome when these methods are applied to

real organisms. We treat sexually and asexually reproducing taxa separately, for a group's mode of reproduction may affect its propensity to form discrete taxa. We will conclude that species are indeed discrete in sexually reproducing organisms, probably discrete in asexually reproducing organisms, but often *not* discrete in organisms that reproduce both sexually and asexually.

### ***Sexually reproducing eukaryotic taxa***

Biologists have used three methods to determine whether species are real in sexually reproducing groups. We discuss these methods in order of increasing rigor, weighing their pros and cons.

1. *Arguments from common sense.* This method settles the question by fiat: species are real because everyone recognizes that they are real. This was the argument Dobzhansky used in *Genetics and the Origin of Species*: "Discrete groups are encountered among animals as well as plants, in those that are structurally simple as well as in those that are very complex. Formation of discrete groups is so nearly universal that it must be regarded as a fundamental characteristic of organic diversity" (Dobzhansky 1937a, p. 5).

Indeed, clusters in a given locality are often discrete to even the casual and nonscientific observer. This is especially true in well-studied groups such as birds: nobody, for example, claims that there is a continuum between eagles and crows. The value of field guides is proportional to the discreteness of the taxa they cover, and of course, many such guides are useful.

While we find these arguments intuitively convincing, they are not hard evidence. We must confront, for example, the argument that humans have a propensity to divide a continuous array of organisms into discrete units, just as we separate the rainbow's continuous spectrum of light into seven discrete colors. To investigate this claim, we can compare the way that people from very different cultures divide up the organisms living in one area.

2. *Concordance between "folk" and "scientific" species.* Scientific facts ultimately derive from the agreement of independent observers. One can apply this principle to the problem of species reality by determining whether different observers—particularly those not sharing obvious biases—see the same divisions in nature. Biologists and anthropologists alike have conducted these studies. Typically, they survey a region's indigenous people, who lack formal biological training, and ask them to list the types of animals or plants in their habitat. These groupings of organisms into "folk species" can then be compared to the "Linnaean species" recognized by modern taxonomists.

Such comparisons can yield three possible results. First, there can be a one-to-one correspondence between Linnaean and folk species, which is strong evidence that nature is partitioned into units consistently recognized by people of different backgrounds. Second, a folk species can be *underdifferentiated*, mean-

ing that it includes two or more Linnaean species. Such a result might be considered evidence for the reality of species if the Linnaean species are very similar to each other, differing in traits cryptic to nonscientists. Finally, folk species can be *overdifferentiated*, with a Linnaean species in one area being described as two or more folk species. Consistent overdifferentiation would constitute evidence against the reality of species.

The results of these studies are consistent: there is a remarkable coincidence between folk species and Linnaean species. Moreover, of the exceptions that do exist, most involve under- rather than overdifferentiation. The first compelling evidence was Mayr's (1963) observation that tribesmen of the Arfak Mountains of New Guinea had 136 vernacular names for the 137 Linnaean species of birds they encountered. In a more thorough analysis, Diamond (1966) studied bird names used by the Fore people of New Guinea. Their habitat contained 120 Linnaean species, with roughly 80% of these showing a one-to-one correspondence with Fore names. Diamond notes (1966, p. 1103):

To a zoologist, the ability of the Fore to distinguish between closely similar species is impressive. . . [In two species of warblers] the differences are sufficiently subtle that I was often in doubt about the identity of the species held in the hand. Nevertheless the Fore not only had different names for the two birds. . . but also could identify them correctly in the field at moderate distances without binoculars. In this case small differences in behavior and call-note had probably alerted them to the fact that more than one kind of bird was present.

Diamond also took a group of Fore to lower elevations and asked them to give names to bird species they had never encountered. Ninety percent of the 103 Linnaean species were recognized as distinct folk species. Diamond argues, "That the elements in these two dissimilar classificatory systems nevertheless usually show a one-to-one correspondence strikingly illustrates the objective reality of the species" (1966, p. 1104).

Majnep and Bulmer (1977) obtained similar results studying animals encountered by the Kalam people of New Guinea. Of 176 bird species recognized by Western zoologists, 123 had a one-to-one correspondence with the folk designation, while there were 24 cases of underdifferentiation. This yields a 70–80% correspondence between names. The concordance between Kalam and Linnaean species is about 80% for frogs and 95% for reptiles (Bulmer and Tyler 1968; Bulmer et al. 1975).

In view of the common claim that species are less "real" in plants than in animals, one might expect to find less correspondence between Linnaean and folk species of plants. However, the work of Berlin et al. (1974) among the Tzeltal of southern Mexico shows that this expectation is incorrect. The Tzeltal have 471 folk names for plants growing in their area; of these, 66% are identical to Linnaean species. (Some of the plants surveyed are not sympatric, and geographic variation within Linnaean species may have reduced this correspondence.)

Regardless of the group surveyed, then, there is a very strong, although not perfect, correspondence between folk and Linnaean species—a correspondence of around 70%. Given the subtle traits used to designate Linnaean species (which can cause underdifferentiation of folk names) and the geographic variation of some species, there can be no reasonable expectation of perfect correspondence. Strikingly, one sees few cases of overdifferentiation. These results strongly support the view that people of different backgrounds recognize similar units of natural diversity. This buttresses the claim that species are real.

It must be admitted that not everyone finds this evidence convincing. Ridley (1996, p. 421) notes, “[T]he fact that independently observing humans see much the same species in nature does not show that species are real rather than nominal categories. The most it shows is that all human brains are wired up with a similar perceptual cluster statistic.” (See also Mishler and Donoghue 1982, p. 493.)

These views can be interpreted in two ways. The weaker claim is that humans have an evolved tendency to subdivide and categorize, even when presented with a continuum. Yet this hypothesis does not explain why, if species are not discrete, people of widely diverse backgrounds—geographical, cultural, and scientific—tend to recognize the same groups. Proponents of the view that species are illusory must then make the stronger claim that human neurological wiring somehow constrains us to divide continua *at the same boundaries*. They might argue, for instance, that the three types of cones in the human eye—with differential sensitivities to blue, red, and green light—cause all humans to divide the continuous spectrum of light into a largely identical set of colors. Indeed, as different societies incorporate colors into their vocabulary, the six “primary constituent colors” are added in a nearly identical sequence (Durham 1991).

However, while the “neurological wiring” argument might conceivably explain congruent divisions of *single* traits, the claim loses force when dealing with *groups* of traits. We must remember that the congruence of species names between folk and Western taxonomy reflects the assessment of multiple traits. And there is no reason why our neurological wiring for recognizing, say, size, would divide up a biological continuum into the same groups as would our wiring for shape, for color, and so on. Moreover, using one set of traits yields clusters identical to those recognized using a different set of traits. It is well known, for example, that morphological discontinuities almost always coincide with genetic discontinuities in DNA sequences. This consistent carving of nature at the same joints is a powerful argument for the reality of species.

One can make a related argument based not on humans but on other species. In animals, individuals recognize conspecifics but not heterospecifics during the breeding season—the same differences recognized by humans. A male robin courts only female robins, not birds that humans consider members of other species. Pollinator-specific insects also discriminate between plant species recognized as different by humans. Likewise, many host-specific herbivores and parasites are good “taxonomists,” recognizing the same species as do biolo-

gists. Even if one accepts that all human brains are wired with the same “perceptual cluster statistic,” it hardly seems reasonable to assume that this statistic is identical in other animals.

3. *Statistical identification of clusters.* Folk taxonomy is a form of cluster analysis, but one can use more sophisticated statistical tools to look for clustering. When we apply these advanced tools to various traits—morphological, behavioral, reproductive, and molecular—do we still see sympatric individuals falling into distinct clusters? While such methods are designed to determine whether clusters exist or to choose the characters that best discriminate groups designated a priori, it is important to realize that these methods cannot identify such groups if they do not exist.

Given persistent arguments about the reality of species, it is curious that these statistical studies are rare. Aiming to distinguish rare hybrids from parental species, Neff and Smith (1978), for example, used discriminant-function analysis of morphology in the sunfish *Lepomis macrochirus* vs. *L. cyanellus* and in the shiners *Notropis spliapterus* vs. *N. whippeli*. In both cases, sympatric species were well separated and hybrids morphologically intermediate. Humphries et al. (1981) used combinations of traits to discriminate sympatric species of the pupfish *Cyprinodon*, sympatric species of minnows (*Richardsonius* and *Rhinichthys*), and allopatric populations of ciscoes (*Coregonus*) that had been considered two species based on size and shape. While the sunfish and pupfish were completely distinguished, the populations of ciscoes could not be separated unambiguously. The authors conclude that the cisco “species” are probably only morphologically differentiated populations. This underscores the difficulty of distinguishing discrete taxa when samples are taken from different places.

Avise (2000) notes that there is usually a strong concordance between vertebrate species differentiated by morphological criteria and by mitochondrial DNA (mtDNA) sequence. He concludes (p. 309) that “this compatibility of outcomes probably reflects an underlying historical reality to many of the biotic discontinuities traditionally recognized as species.” Especially well-studied groups, such as birds and *Drosophila*, show almost no cases of indistinct sympatric taxa except for rare, morphologically intermediate hybrids (Gupta et al. 1980; Grant and Grant 1992). The question remains, however, whether birds and *Drosophila* form more discrete clusters than do other groups, such as plants.

Mayr (1992) conducted a comprehensive study of discontinuities in vascular plants using the flora of Concord Woods, Massachusetts. While this represented Mayr’s attempt to show that his “biological species concept” (based on interbreeding and reproductive isolation) applied to plants, he examined discontinuities not of reproductive compatibility but of morphology and chromosome number (Whittemore 1993). His investigation is thus a better test of the reality of species than of the usefulness of his species concept.

According to Mayr, of 838 plant species in this area recognized by previous workers, 616 fell into easily recognized morphological groups. Fifty-three

others were either allopolyploids, autopolyploids, or sibling species, recognizable on genetic or chromosomal grounds. Thus, 669 taxa—80% of the total named species—were easily distinguished. Fifty previously named “species” were found to be only aberrant individuals, possibly chromosomal aneuploids or nongenetic, developmental variants. Only 72 of the 838 groups were truly problematic, including possible hybrid swarms, offspring of polyploids that had mated with their ancestors, clones, and variable entities that were not well studied. Overall, about 9% of named species did not correspond to locally well-demarcated groups. (See Whittemore 1993 for a critique of this study.)

The presence of hybrids does not necessarily refute the distinctness of species, for hybrids can be rare or sterile. Indeed, some studies suggest that the “fuzziness” of plant species boundaries caused by hybridization may be overstated. Ellstrand et al. (1996) estimated the frequency of plant hybrids in five regions: the British Isles, Scandinavia, the Great Plains and Great Basin of the United States, and the Hawaiian Islands. They found a low rate of hybridization: between only 6 and 16% of genera within an area contained one or more reported hybrids. Given the likelihood that some hybrids have not been observed, this is almost certainly an underestimate of the frequency of hybrid-producing genera. On the other hand, not every species in a genus forms hybrids, so the frequency of hybridizing *species* is certainly much lower than 6%.

Nevertheless, it is likely that some taxa in plants are less distinct than those in animals, for plants have a greater diversity of mating systems, including selfing and apomixis, that can blur species boundaries. Animals generally lack the “difficult” complexes, such as dandelions, that plague plant systematists (see below). We know of no systematic data supporting the claims of some botanists that plant species are not real or hybridize promiscuously (Stebbins 1950; Raven 1976). Diamond (1992) concludes that such claims derive from “anecdotal horror stories” of botanists who concentrate on difficult groups or hybridizing taxa.

It appears, then, that most sexually reproducing organisms (which form a sizeable majority of plants and animals) fall into discrete groups in sympatry, confirming the intuition of most biologists that species are real. Of course, most taxa have not been examined carefully, and it would be useful to do more cluster analyses of groups like angiosperms or insects living in one area. In light of existing evidence, however, it seems fair to ask those who deny the existence of species to support their claim with systematic surveys instead of anecdotes.

**ARE “HIGHER” TAXA REAL?** Most biologists agree that species are real in a way that supraspecific taxa—including ranks like genera and families—are not. Higher-level groups often share a common ancestor (i.e., are *monophyletic*), and can even be distinguished as large morphological clusters. Yet because evolutionary trees can branch at any level, higher-level groupings are necessarily somewhat arbitrary. Indeed, systematists such as Griffiths (1976) have even suggested doing away with formal taxonomic ranks altogether.

We can demonstrate the difference between the reality of species and of higher taxa by examining the three species *Drosophila pseudoobscura*, *D. persimilis*, and *D. miranda*. All occur sympatrically in northwestern North America and can be clearly distinguished by breeding relationships, chromosome configuration, and morphology (Dobzhansky and Powell 1975). The first two are sister species, with *D. miranda* the outgroup. All are, in turn, more closely related to each other than to species in the European *D. obscura* group. What are the “real” higher taxa here? *D. pseudoobscura* + *D. persimilis* is one, but the combination of these species with *D. miranda* is another. Both of these two higher groups are monophyletic and thus share at least one derived trait that distinguishes them from other such groups. But there are many such groups, which overlap in a nested fashion. The “reality” of such groups thus consists only of their common ancestry and the traits that allow us to recognize it. Unlike species, such groups do not evolve as a unit nor are they homogenized by interbreeding. Nevertheless, their common ancestry—reflected in the possession of shared derived traits—might sometimes channel their fate in a collective fashion, leading to broad patterns of speciation and extinction (Chapter 12).

The fact that the “reality” of higher-level groupings reflects only ancestry means that these groups are less distinct to laymen than to professional systematists. This is shown by the breakdown of the correspondence between folk and Linnaean taxonomy when one goes above the species level. “Higher” folk taxa are often based on superficial morphological traits such as body size. Considering the Tzeltal’s higher-level classification of plants, Berlin (1992, p. 167) notes that “life-form groupings do not generally represent biologically natural categories in the same sense that taxa of intermediate or generic rank do, in that they often cross-cut biologically natural groupings.” The Tzeltal divide plants, for example, into “trees,” “vines,” “grasses,” and “broad-leaved herbs,” reflecting evolutionary convergences among distantly related groups. Some species, like bamboo and agave, are not included in *any* higher group. The Rofaifo of New Guinea have five higher groupings of animals (Berlin 1973), including *Hefa* (eels, cassowaries, large marsupials, and rodents), *Huneme* (small marsupials and rodents), *Nema* (bats, and all birds except cassowaries), *Hoiifa* (lizards, snakes, fish, molluscs, worms, and centipedes), and *Hera* (frogs other than those of three genera). Such groupings do not seem to reflect functional or economic considerations, such as our distinction between farm animals and wild animals.

### **Groups with little or no sexual reproduction**

While species may be real in sexually reproducing groups, species are often said to be either absent or much harder to distinguish in partly or fully asexual groups. In sexual groups, interbreeding among individuals can enforce genetic and phenotypic homogeneity. As interbreeding diminishes, however, individuals can diverge more extensively, effacing genetic and morphologi-

cal gaps between clusters. This leads to a simple prediction for sympatric organisms: as sexual reproduction becomes less important, one should see less differentiation between species and greater differentiation among individuals within species. This tendency will make species less distinguishable in groups having limited sexual reproduction. Does this prediction hold? As we shall see, the answer depends on how much sex there is.

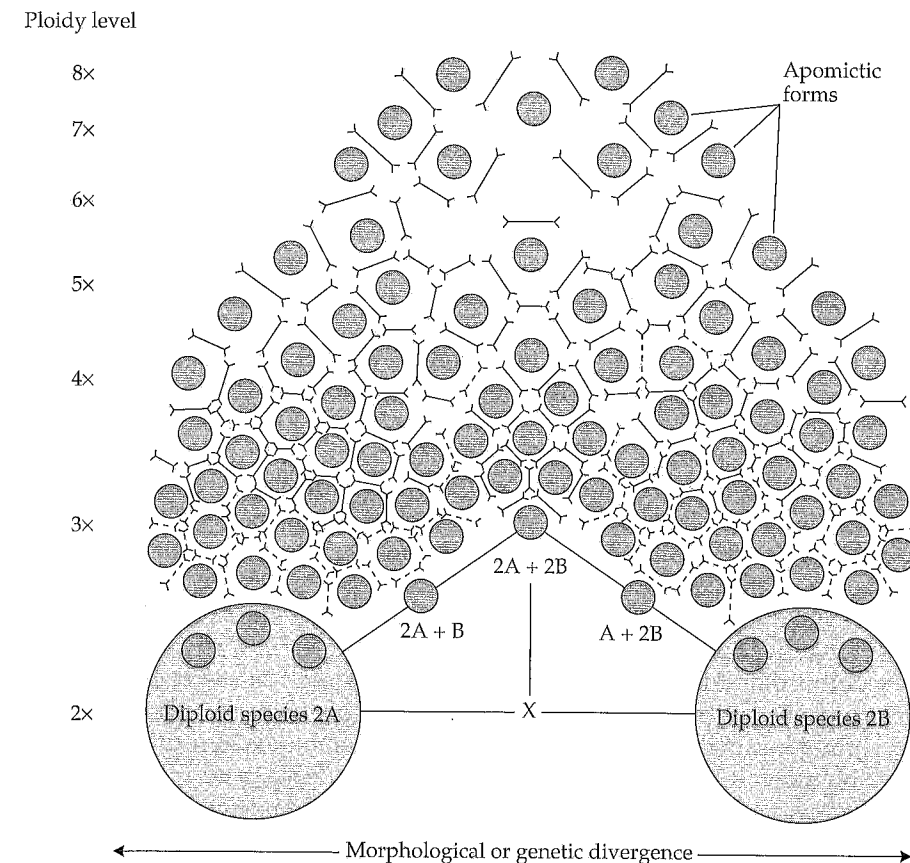
**UNIPARENTALLY REPRODUCING EUKARYOTIC TAXA.** Eukaryotes have several forms of uniparental reproduction, including vegetative reproduction, self-fertilization, and the production of seeds or fertile eggs without sexual reproduction (apomixis or agamospermy). Although such modes of reproduction are more common in plants than in animals, there is nonetheless a surprisingly large number of unisexually reproducing vertebrates (Vrijenhoek et al. 1989). Strictly uniparental groups are expected to form clones, which in theory could be recognized as distinct entities whose members are genetically identical to each other and distinct from other groups. If one is willing to regard *completely* asexual clones as distinct units, then one can indeed define and group them into "species." However, as more complete DNA sequences become available, such species will break down, for one must then delimit species based on differences at single nucleotide sites. Such a practice makes each individual, with its own unique mutations, a distinct species.

Complete uniparental reproduction is, however, quite rare. For example, most selfing plant species engage in at least some form of outcrossing. Recent work on some species thought to be completely asexual suggests that they might occasionally engage in covert sex (Walliker et al. 1987; Hurst et al. 1992; Pernin et al. 1992). Only among the bdelloid rotifers is there evidence for nearly complete asexuality over very long periods of time (Welch and Meselson 2000).

Reviewing the origin and evolutionary fate of unisexual species in vertebrates, Vrijenhoek et al. (1989) and Avise et al. (1992) show that nearly all of the 70-odd uniparental "species" are generated by hybridization of sexual species, with the hybrids reproducing via parthenogenesis. These "species" are well demarcated phenotypically, but can be *polyphyletic* (i.e., having multiple independent origins from repeated hybridizations between parental species). These hybridizations produce multiple clones, which, as in the hybrid fish *Poeciliopsis monacha-lucida*, can be ecologically diverse. The question then becomes whether to recognize as a cluster the entire group of hybrids, an ecologically similar group of clones, or a single genetically distinguishable clone. If one adopts the first solution, different unisexual vertebrates cluster simply because they are hybrids between distinct pairs of sexually reproducing species. That is, asexual taxa are distinct because their sexual ancestors are distinct. This may also be true for many uniparental plant "species" that are repeatedly derived from sexual ancestors.

Some plants form important but taxonomically confusing "agamic complexes" that harbor a core of diploid species with obligate sexual reproduction. The sexual species hybridize to form polyploids that may themselves repro-

duce sexually, but more often reproduce through agamospermy. Repeated bouts of interspecific hybridization, polyploid formation, and occasional sexual reproduction of the agamospermous forms can produce a continuum of variation between the sexual forms (Figure 1.1). The dandelion genus, *Taraxacum*, for example, contains 26 diploid sexual core species, all of which can be crossed in the greenhouse, producing polyploids that can be either obligately or facultatively apomictic (Grant 1981). The polyploids and their derivatives constitute the nearly 2000 described "microspecies" of *Taraxacum* (Richards 1973). Similar agamic complexes include *Alchemilla* (lady's-mantle), *Crataegus*



**Figure 1.1** The structure of an agamic complex such as *Taraxacum* (dandelions). The complex includes core diploid sexual species (2A and 2B), whose  $F_1$  hybridization can produce triploids ( $2A + B$ ;  $A + 2B$ ) and allotetraploids ( $2A + 2B$ ). Individuals occupy all levels of ploidy from diploid (2X) to octaploid (8X), yielding a variety of apomictic forms that, as shown by the barriers, are largely reproductively isolated from each other (dashed lines between nondiploid taxa indicate some possibility of gene exchange). (From Grant 1981, after Babcock and Stebbins 1938.)



(hawthorn), *Hieracium* (hawkweed), and *Rubus* (Grant 1981; Richards 1997; Sepp and Paal 1998).

One might expect groups with such diverse modes of reproduction to form clusters less distinct than those seen in sexual groups. Unconstrained by the cohesion of sexual reproduction, uniparental taxa are free to fill up the genetic, ecological, and morphological gaps that exist between sexual species. One might also expect a similar lack of distinctness in selfing groups. Yet even experienced botanists disagree about whether agamic groups comprise distinct clusters:

When examined closely, species in these predominantly asexual genera [*Taraxacum*, *Hieracium*, and *Rubus*] are every bit as distinct (morphologically, geographically, and ecologically) as species in large, complex, exclusively sexual genera such as *Carex* or *Senecio* (Mishler 1990, p. 95).

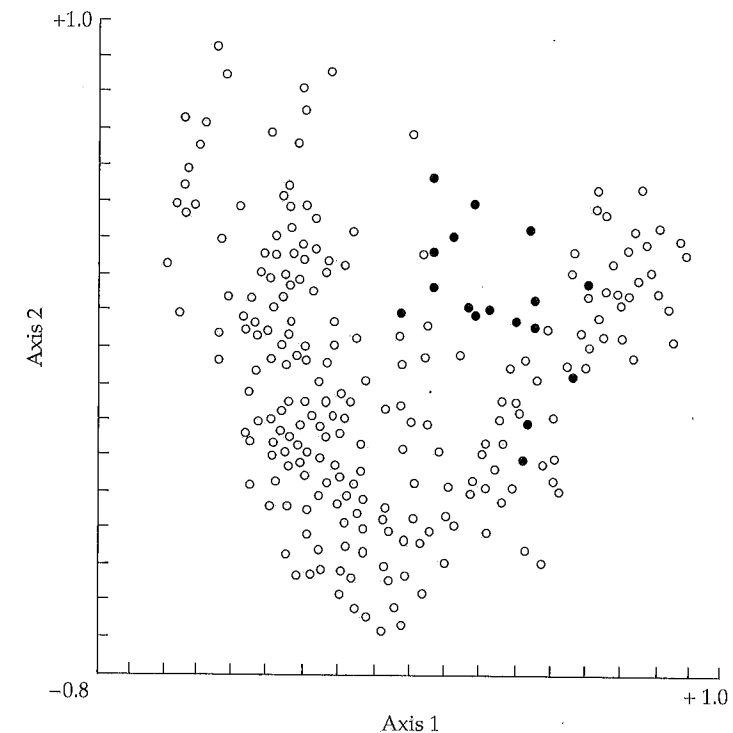
Versus:

The delineation of morphologically-based species [in obligate apomicts] becomes an arbitrary matter (Baker 1959, p. 188).

The genera *Rubus*, *Crataegus*, *Taraxacum*, and *Hieracium* have each been divided into hundreds or thousands of "microspecies" or "agamospecies" based on minute morphological differences, many of which might reflect only developmental plasticity in different habitats. There is little agreement among systematists on how many groups should be recognized. Camp (1951) recounts how three botanists, working independently, divided North American *Rubus* into 24, 205, and 494 species, respectively. Even single bushes have been designated as species (Asker and Jerling 1992).

The heavily studied group *Taraxacum* best exemplifies this confusion. Richards (1972) lists 132 dandelion species in the British Isles, and notes (p. 2) that he "became increasingly convinced that the microspecies obeyed all the dictates of 'good' species, being well-defined by constantly correlated characters, each microspecies with its own diagnostic geographical, ecological and genetic behavior." Yet Richards adds that when he gave his key to other botanists, they correctly identified only 40% of all species. Even a cursory survey of this literature validates Stebbins's (1950, p. 409) assessment of agamic groups: systematists "have not been able to agree on the boundaries of species. . . . [I]n attempting to set up species like those found in sexual entities, they are looking for entities which in the biological sense are not there."

The best way to test whether such groups form discrete taxa is to perform cluster analysis on many sympatric individuals. Unfortunately, only one such study exists: that of Sepp and Paal (1998) on *Alchemilla*. This genus has been divided into more than 1000 microspecies, with some biologists claiming that species are discrete and easily recognized (Walters 1986). Sepp and Paal analyzed 23 named species from Estonia, scoring herbarium specimens for 43 morphological traits. A principal component analysis (Figure 1.2) showed that the specimens largely formed a morphological continuum containing almost no distinct clusters. They conclude that only three species (one of them represented by the filled dots in Figure 1.2) constitute discrete entities in morphospace, and that the



**Figure 1.2** Principal coordinates analysis of 373 individuals (dots) in 23 named "species" of the agamic complex *Alchemilla*. Only the first two axes are shown. Filled dots represent individuals of one of the three species that the authors consider truly distinct (*A. plicata*). (From Sepp and Paal 1998.)

remaining 20 species form a continuum. They further note (p. 531) that "most of the species cannot be clearly distinguished, and surprisingly some pairs of species that are considered by several authors to be quite different (i.e. belonging to different series or sections), cannot be distinguished from a statistical point of view." In light of these results, one should be cautious about claims that agamic species are discrete when these assertions lack statistical support.

Although some researchers (e.g., Grant 1981; Dickinson 1998) have proposed ways to designate species in agamic complexes, most of these methods are more or less arbitrary, serving, as Mayr notes (1992, p. 411), "simply as a means of bringing some type of order to a situation which from the biological point of view is incapable of resolution."

Turning to plants that are largely selfing (autogamous), we are unable to judge from the literature whether they usually include distinct taxa. Some outcrossing species in genera such as *Linanthus* and *Mimulus* can repeatedly produce derivatives that are largely selfing (e.g., Macnair and Gardner 1998; Goodwillie 1999). These selfers may form small allopatric populations adapted to restricted ecological conditions. Because of their homozygosity and allopatry, such selfers are indeed distinct.



**CLUSTERING IN UNIPARENTAL VERSUS SEXUALLY REPRODUCING EUKARYOTES.** There have been only a few tests of the relative distinctness of groups in sexual versus asexual taxa, none of which is completely satisfactory. Holman (1987) compared bdelloid rotifers (which include roughly 370 named species that appear to have reproduced without sex for at least 40 million years) with monogonont rotifers (consisting of about 1450 named species capable of sexual reproduction). Using three taxonomic monographs to estimate the stability of nomenclature in these groups, Holman quantified stability by first counting the number of "synonymous" genus and species names, and then calculating the ratio of synonymous species names to synonymous genus names. ("Synonymy" is a sign of taxonomic uncertainty, with greater synonymy reflecting greater difficulty in classifying individuals.)

Noting that the ratio was actually *higher* for monogononts than for bdelloids, Holman concluded that "bdelloid species are more consistently recognized than monogonont species" (1987, p. 384). If true—and this is not entirely clear given the use of synonymous genera in the statistic—this difference in recognizability seems to show that, contrary to expectation, sexually reproducing rotifers are *less* distinct than those that breed asexually. But it is questionable whether the distinctness of taxa can be judged from the stability of nomenclature. In fact, systematists have paid far more attention to monogononts than to bdelloids (C. Ricci, pers. comm.), resulting in more taxonomic revisions of the former than of the latter. As all systematists know, the number of synonyms increases with the number of revisions. Holman's results may thus be an artifact of different amounts of taxonomic work in different groups.

Deploying a different strategy, Baker (1953) compared morphological variation among populations of an obligatorily outcrossing and a partially selfing subspecies of the plant *Armeria maritima*. The homogenizing effect of gene flow leads one to expect less variation among populations of sexual than of asexual species. In fact, Baker observed just the opposite. He concludes that, when taking into account geographic variation, sexually reproducing species are not more discrete than those that breed asexually. But this conclusion is questionable. The proper test for species distinctness is not the relative amount of geographic variation, but the recognizability of taxa *in a single location*. If, for example, asexual taxa form clones that are widely distributed, one may see less spatial variation among asexual than among sexual taxa.

None of these studies answers the question of whether clusters are as distinct in asexual as in sexual taxa. Arriving at an answer requires measuring a wide variety of traits and/or genotypes in many individuals from a single locality, regardless of species, and subjecting these data to multivariate analysis. One can then compare the discreteness of sexual versus asexual clusters in morphospace or "genospace." Such studies are badly needed.

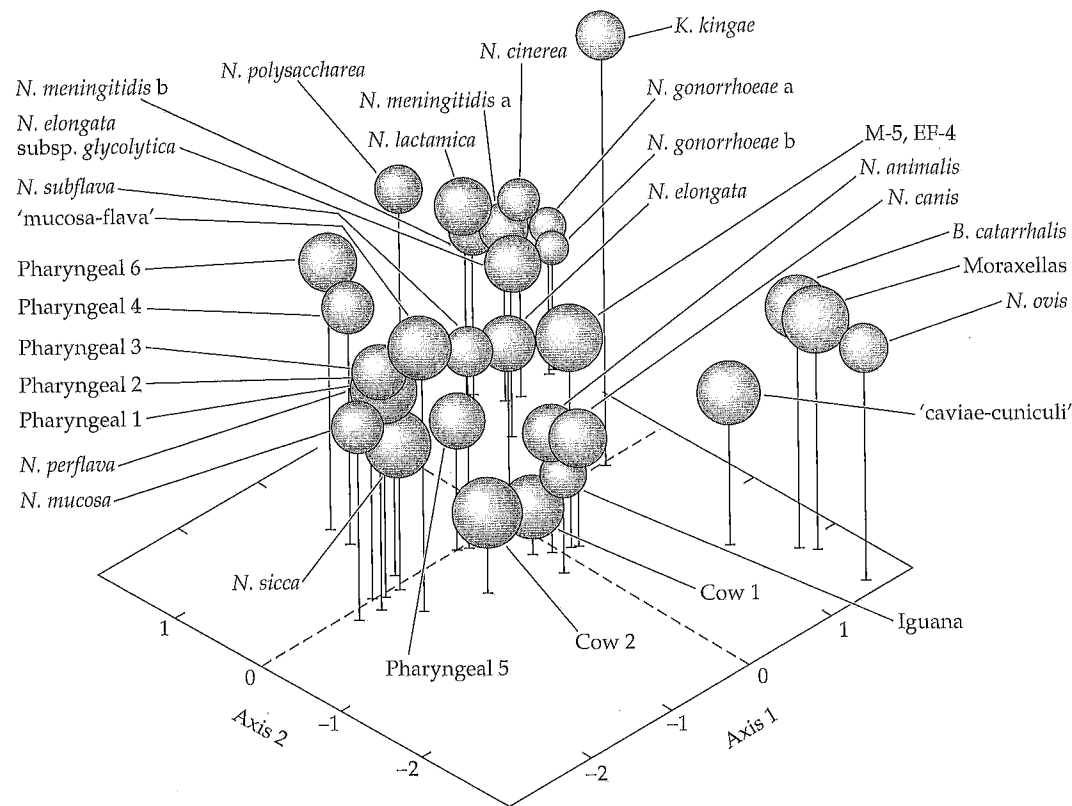
**PROKARYOTES.** It is a mistake to regard prokaryotes—or at least Eubacteria—as asexual. Transduction, transformation, and conjugation can cause rare gene

transfer and recombination ("homologous exchange") between individuals of the same taxon, or between different taxa that are not too distantly related. In fact, bacteria even show a form of reproductive isolation: homologous recombination rates decay exponentially with increasing sequence divergence between taxa. It is difficult to recombine genomes between strains whose DNA sequences differ by more than 20% (Vulic et al. 1997; Majewski and Cohan 1998). However, genes can also be acquired from more distant relatives by "horizontal transfer," probably involving the uptake of naked DNA from the environment. This process can have important effects on bacterial genomes. For example, about 18% of the loci in *Escherichia coli* were acquired by horizontal transfer from different lineages over a period of nearly 200 million years, with many of these genes coding for ecological adaptations, antibiotic resistance, and pathogenicity (Lawrence and Ochman 1998).

Given that bacteria can exchange genes with both close and distant relatives, and that they are largely asexual, one might expect them to resemble agamic complexes of plants, in which clusters are difficult to discern. Cohan (2001 p. 515) notes, "One could imagine that an asexual or rarely sexual species might have no cap on its divergence, such that a closely related group of bacteria would grow indefinitely in its diversity of sequences and phenotypes." However, most microbiologists (e.g., Barrett and Sneath 1994; Roberts and Cohan 1995; Ochman et al. 2000; Cohan 2001, 2002 and references therein) agree that many bacteria do form discrete clusters, a view supported by evidence from bacterial phenotypes and DNA sequences. Although most studies involve bacteria taken from different hosts or localities (multiple samples of bacteria are rarely taken in sympatry), distinct taxa of *Bacillus* have been found in soil samples retrieved from a single location (Roberts and Cohan 1995; Roberts et al. 1996). In addition, analysis of multiple genes has revealed discrete clonal complexes within the named species *Neisseria meningitidis* and *Streptococcus pneumoniae* (Feil et al. 1999, 2000).

The most thorough study included 315 strains of the endoparasitic bacterial genus *Neisseria*, involving analysis of 155 phenotypic traits (Barrett and Sneath 1994). Although infecting many species, *Neisseria* has been especially well studied in humans because some "species" cause gonorrhea and meningitis. While some strains could not be placed in distinct groups, cluster analysis distinguished 31 fairly discrete groups in phenotypic space ("phenons") (Figure 1.3). Surprisingly, some clusters included strains from hosts as diverse as guinea pigs, fur seals, deer, and rabbits. Distinct clusters were also seen within the same host, but the clusters most difficult to distinguish occurred sympatrically—in the human nasopharynx. These strains, however, generally fell into clusters when DNA sequences were examined (Smith et al. 1999).

Because only a few groups have been examined and many of the strains are from different locations, the general degree of distinctness in bacteria is unclear. Moreover, one might often *expect* pathogenic asexual taxa to cluster by hosts (if transmission to other host species is rare) or for allopatric strains to cluster by location because of episodes of "periodic selection" that purge



**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<sup>a</sup>*

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 (Paterson 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).

<sup>a</sup>The 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 autopolyploid 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), once 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<sub>1</sub> 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 Whittmore 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 (F<sub>1</sub>) 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.

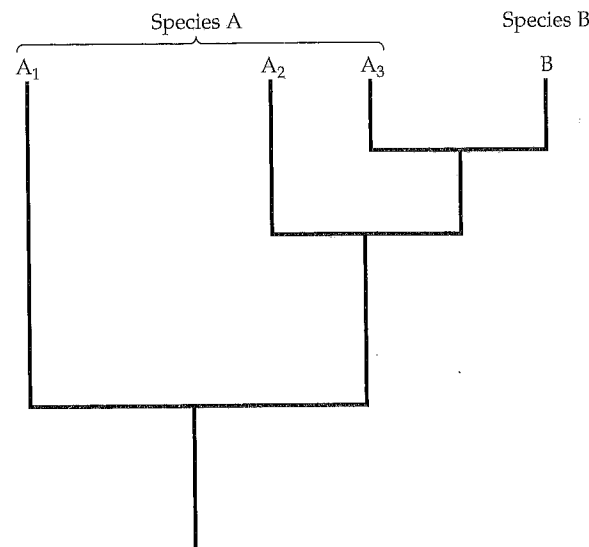
**DELINEATING "SPECIES" IN A SINGLE EVOLVING LINEAGE, OR IN FOSSILS, OR PRESERVED MATERIAL.** Mayr (1963) dealt extensively with the problems these matters pose for the BSC, and we can add little to his arguments. Under every species concept, the division of a continuously evolving lineage into named 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 1.1). 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 1.1, 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.