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Natural Hybridization and Evolution

Michael L. Arnold

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Natural Hybridization and Evolution

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To Frances, Brian, and Jenny for your patience
and support throughout this process

Preface

This book is an exploration of the evolutionary process of natural hybridization. My motivation for writing this book comes from the view that crosses between genetically divergent individuals have a major influence on the evolution of some plant and animal species complexes. In particular, I want to examine the role that natural hybridization has as a creative force in organismal evolution. I realize that my emphasis on the "creative" aspect of natural hybridization could lead some to conclude that I believe that this is the only possible outcome from hybridization and gene exchange. To obviate this conclusion, I present the following quote: "Natural hybridization and introgression . . . may lead to . . . the merging of the hybridizing forms . . . the reinforcement of reproductive barriers through selection for assortative (conspecific) mating . . . the production of more or less fit introgressed genotypes . . . a 'hybrid sink' to which pest species are preferentially attracted . . . [or] to the formation of hybrid species" (Arnold, 1992). However, the hypothesis addressed in this book is that natural hybridization affects the evolutionary history of the groups in which it occurs primarily through the production of novel genotypes that in turn lead to adaptive evolution and/or the production of new lineages. This hypothesis is not new (e.g., see Anderson, 1949; Stebbins, 1959); however, it seems to have fallen on hard times over the past several decades (e.g., see Mayr, 1963; Wagner, 1970). Thus, most recent studies of natural hybridization have, at best, viewed this process as a tool for defining barriers to gene exchange to infer how speciation (i.e., within the framework of the Biological Species Concept) might occur. In contrast, I will examine these same barriers to facilitate predictions concerning what hybrid genotypes may be produced, because an array of hybrid genotypes represents material for evolution.

Another common theme of this book is an analysis of the viewpoints that underlie most studies of natural hybridization. For example, I will address the dogma that is the explicit or implicit framework used by a large proportion of evolutionary biologists, regardless of their organism of interest, to study this process—that the process of natural hybridization is "bad" because it represents a violation of divergent evolution. Two statements from Templeton (1989) illustrate this framework: " 'Good species' are generally regarded as geographically cohesive taxa that can coexist for long periods of time without any breakdown in genetic integrity. . . . Speciation is generally a process, not an event. . . . While the process is still occurring, the tendency is to have 'bad species' " (e.g., species that exchange genes with other species).

There is a second dogma that has also been used to argue against any evolutionary importance for natural hybridization. Natural hybridization is an evolutionary dead end because crosses between genetically divergent individuals may only infrequently result in viable or fertile offspring. The problem with this conclusion is that the importance of rare events is negated (Arnold and Hodges, 1995a). Descent with modification relies on unlikely events (Futuyma, 1986). Could not the rare production of partially fertile hybrid individuals be such an event? I will stress that there is an alternative to the relatively negative viewpoint reflected by the above dogmas. This alternate approach assumes that natural hybridization may, in and of itself, profoundly affect the pattern of organismal evolution.

Chapter 1 introduces the definitions used in the remainder of the text, and gives a brief history of analyses of natural hybridization. The main emphasis in this historical treatment will be the exploration of one question: Was the motivation behind specific investigations a desire to understand the process of natural hybridization per se or to decipher other evolutionary processes? I will argue that the majority of analyses were designed to test for processes underlying divergent evolution (i.e., speciation) or to decipher species relationships. In Chapter 2, I address the topic of species concepts and the study of natural hybridization. The discussion will focus on how these concepts have treated the occurrence of natural hybridization. In Chapter 3 the frequency and taxonomic distribution of reticulate events in plant and animal taxa is discussed. Chapter 4 is a review of components concerning the reproductive biology of plants and animals (e.g., pollen/style interactions) that affect the potential for hybridization to occur and the hybrid genotypes produced. Chapter 5 is an examination of the conceptual frameworks and theoretical models designed to explain the role of various microevolutionary processes (e.g., natural selection) in the outcome of natural hybridization. I address how these concepts and models influence the types of studies undertaken and the conclusions reached. I also examine numerous cases of hybridization to determine if the biological characteristics of hybrid populations match what is expected under specific models. Chapter 5 includes a discussion of expectations that should be met if natural hybridization leads to new genotypes that are more or less fit relative to their progenitors. Finally, I propose a "new" conceptual framework for determining the evolutionary importance of natural hybridization. Chapter 6 is a review of various outcomes of natural hybridization, including the impact of this process on rare and endangered plants and animals. Chapter 7 is a brief summary of the overall patterns described in the previous text. I also suggest areas of investigation that are of particular importance for a deeper understanding of this fascinating process.

Numerous colleagues have aided and abetted in the formation of this book. Among these are Mark Bulger, John Burke, Shanna Carney, Simon Emms, David Geiser, Matt Hare, Scott Hodges, and Joe Williams. I want to particularly thank my colleagues from the Department of Genetics who freed me from many duties during the period of writing: Wyatt Anderson, Jonathan Arnold, Marjorie Asmussen, John Avise, Jim Hamrick, and John McDonald. The Louisiana iris research discussed throughout this book has been supported by various grants from the National Science Foundation and the American Iris Society Foundation. The Society for Louisiana Irises awarded a grant to aid in the production of this book. J. Williams, B. Boecklen, D. Howard, H. Wang, E. McArthur, S. Sanderson, J. Graham, and C. Freeman allowed me access to unpublished results. Special thanks go to my three "outside" reviewers, Dan Howard, Loren Rieseberg, and Pam Soltis, and the series editors, Paul Harvey and Bob May, all of whom spent enormous amounts of their limited time to improve the manuscript. Of course, mistakes and oversights are my responsibility.

I have dedicated this book to my family—my wife Frances and my children Brian and Jenny. Finally, to quote Bach, *Soli Deo Gloria.*

Athens, Georgia M.L.A.
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Natural Hybridization and Evolution

1

Natural hybridization: Definitions and history

The role of hybridization in evolution has been one of the most controversial topics in the whole field of evolutionary study. (Stebbins, 1963)

1.1 Natural hybridization: Definitions

Several terms used in this book need clear definitions. These include hybridization, hybrid, and hybrid zone. Harrison (1993) has discussed the various definitions of the term hybridization that have been used in scientific literature. Each of these relates to levels of divergence between the individuals that undergo reproduction. The extremes of these definitions are crosses between genetically distinct individuals, and between individuals from different species (Harrison, 1993). The former is frequently used by plant and animal breeders and the latter by evolutionary biologists. Harrison's (1990) definition includes crosses between "individuals from two populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters." I have adopted this definition with the following modifications. First, *natural* hybridization involves matings that occur in a natural setting—this excludes cases of experimental hybridizations. Second, I will consider those crosses that are successful in producing some viable F_1 progeny that possess some level of fertility. This latter restriction reflects my desire to focus on the potential ongoing evolutionary effects from hybrid generations past the initial F_1. However, it is important to point out that almost all cases of natural hybridization result in at least a few viable individuals with some measure of fertility (e.g., Grant, 1963). Thus, when an author states that inviable or infertile offspring are produced, it is usually meant that the offspring are fewer in number or are less fertile relative to progeny from crosses between genetically more similar individuals. The reduction in levels of viability and fertility has led most authors to discount natural hybridization as an evolutionarily important process. This conclusion ignores the importance of rare events in evolution and is contradicted by actual cases where unlikely hybrid events have led to diversification (Arnold and Hodges, 1995a). The validity of the arguments presented in this book do not depend on hybrids being relatively common in nature. However, it is also apparent that natural hybridization does not usually lead to 100% inviability or infertility.

With the above modifications in mind, *natural hybridization involves successful matings in nature between individuals from two populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters.* This process thus includes cases involving crosses between individuals considered to be conspecific, but not crosses between individuals from the same gene pool that happen to possess alternate states of a polymorphic character. Following from this definition, *a natural hybrid individual derives from crosses in nature between individuals from two populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters.* In this book, I will use the terms *natural hybridization, reticulate evolution, reticulate events,* and *reticulation* interchangeably. This reflects the viewpoint that hybridization between divergent individuals usually results in a genetic, ecological, behavioral, or other change in the hybridizing populations (e.g., incorporation of genetic variability from one taxon into another allowing a habitat expansion). Such change is thus "evolutionary" even though in some cases it is relatively transient.

Harrison (1993) outlined three advantages for his definition of hybridization; (i) its application does not depend on the acceptance of any particular species concept; (ii) the populations from which the hybridizing individuals derive do not need to be assigned to particular taxonomic categories; and (iii) it is unnecessary to know the relative fitness of hybrids or the adaptive norms (Stebbins, 1959) of parental types. A fourth advantage is that this definition rests on straightforward empirical analyses. It is thus relatively easy to test whether individuals involved in the putative hybridization event are drawn from populations that are "diagnosably different" (Harrison, 1993) in at least one heritable character. Finally, as mentioned above, it is important to examine the evolutionary consequences of recombination between divergent genomes, whether they reside in certain taxonomic units or not. For example, some hybrid genotypes from crosses between species and subspecies often demonstrate equivalent levels of fitness relative to their parents (Arnold and Hodges, 1995a,b). This suggests that these hybrids are equally likely to persist for long periods of time, invade novel habitats, or found new evolutionary lineages. In this book, the nonreliance on a particular species concept allows the examination of numerous evolutionary processes (rather than one or a few) that may affect the outcome of natural hybridization.

The above definition can also be extended to define the term *hybrid zone.* As with the terms *hybrid* and *hybridization,* hybrid zone has been used to describe various phenomena, for example, instances of either primary or secondary intergradation (Endler, 1977). Also, the persistence of hybrid zones has alternatively been ascribed to either (i) selection against hybrid individuals and dispersal of the parental forms into the zone of contact (Barton and Hewitt, 1985), or (ii) selection for certain hybrid genotypes in the zone of contact (Endler, 1977; Moore, 1977). I will use the term *hybrid zone* to indicate those instances in nature where *two populations of individuals that are distinguishable on the basis of one or more heritable characters overlap spatially and temporally and cross to form viable and at least partially fertile offspring.*

1.2 Natural hybridization: History of investigations

I have suggested elsewhere (Arnold, 1992) that investigations of natural hybridization have had one of three emphases. First, investigators desired to understand the systematics of a particular group of organisms (Fig. 1.1). In these cases, the occurrence and extent of natural hybridization between the taxa of interest have been used as one data set for inferring evolutionary relationships (e.g., Wiegand, 1935; Clausen et al., 1939; Lenz, 1958; Gillett, 1966; Heiser et al., 1969). A second emphasis has been to use this process to decipher mechanisms that limit gene flow, with the inference that the development of barriers to gene flow is equivalent to the process of speciation (e.g., Ball and Jameson, 1966; Hopper and Burbidge, 1978; Shaw and Wilkinson, 1980; Howard, 1986; Lamb and Avise, 1986; Rand and Harrison, 1989; Baker and Baker, 1990; Howard and Waring, 1991). The third approach has been to assume that natural hybridization has the potential to be evolutionarily important in its own right (Fig. 1.2). Such studies have tested the role of natural hybridization in generating novel genotypes that may lead to adaptive evolution and/or in founding

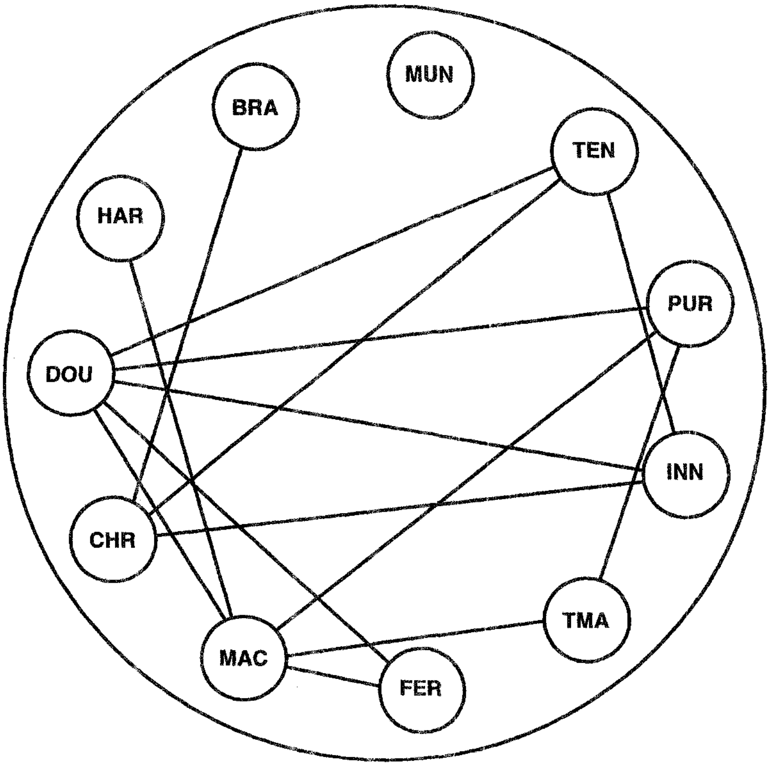

Fig. 1.1. Naturally occurring hybrid combinations in the *Iris* series *Californicae* (from Lenz, 1959).

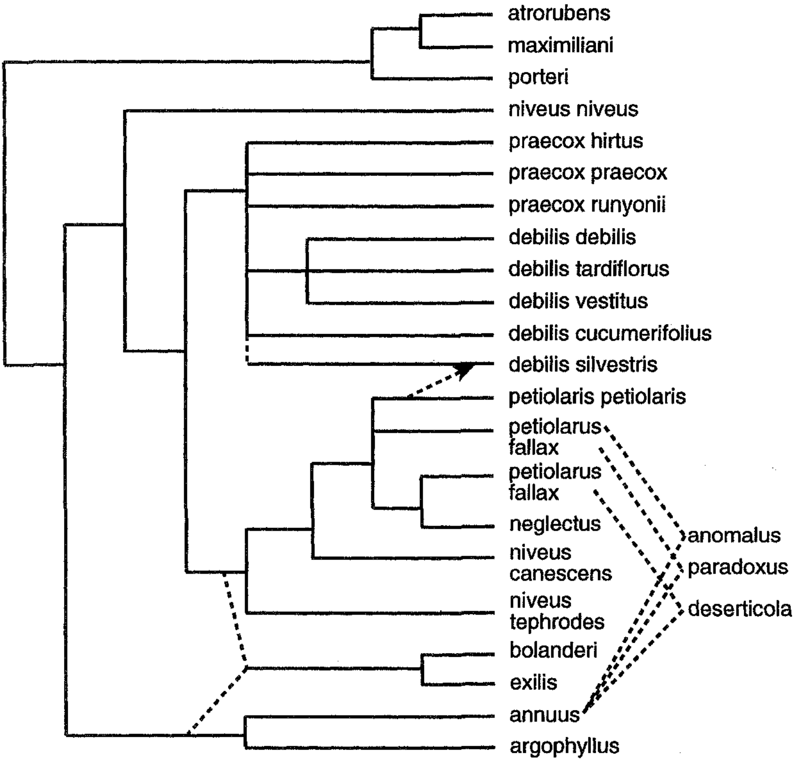

Fig. 1.2. Phylogeny for *Helianthus* (sect. *Helianthus*) species based on rDNA and cpDNA restriction site and length data. The phylogeny was constructed by Wagner parsimony using PAUP (Phylogenetic Analysis Using Parsimony). All internodes had bootstrap values of 50% or greater. Reticulate events are indicated by dashed lines (from Rieseberg, 1991a).

new evolutionary lineages (e.g., Anderson and Hubricht, 1938; Anderson, 1949; Anderson and Stebbins, 1954; Lewontin and Birch, 1966; Kaneshiro, 1990; Arnold et al., 1991; Ehrlich and Wilson, 1991; Grant and Grant, 1992; Dowling and DeMarais, 1993; Rieseberg and Wendel, 1993; Arnold, 1994; Arnold and Hodges, 1995a).

The history of scientific investigations into aspects of natural hybridization can be traced at least to Linnaeus. The Linnean species concept and system of classification (Linné, 1753) were based on the assumption that species were reproductively isolated. However, his ability to cross recognized species successfully led Linnaeus to propose a model of speciation by hybridization (Linné, 1774). Darwin (1859) also used experimental data to infer the outcome of matings in nature between divergent individuals. In contrast to Linnaeus, Darwin observed that heterospecific crosses were difficult to form and that the offspring from such crosses were generally sterile. Darwin (1859) thus concluded that naturally occurring varieties would show more difficulty in forming fertile hybrids than those that had been domesticated. Another historical benchmark is the work of Lotsy (1916, 1931), who argued that natural hybridization was the primary mechanism for evolutionary change. Specifically, he stated that the origin of new taxa was due to the interbreeding of individuals from different *syngameons* ("an habitually interbreeding community"; Lotsy, 1931). His underlying assumption appears to have been that heterospecific matings were the foundation for evolutionary diversification.

Shortly after Lotsy's (1931) publication, and coincidental with the formulation of the Modern Synthesis, was a period of intense conceptualization and research associated with the process of natural hybridization. The literature beginning in the late 1930s reveals two parallel approaches. The first, based on similar assumptions to those of Lotsy, accepted natural hybridization as a pervasive and important evolutionary process. Botanists, in particular such workers as Anderson, Stebbins, Heiser, and Grant (Anderson and Hubricht, 1938; Anderson, 1949; Heiser, 1949; Grant, 1953; Anderson and Stebbins, 1954), were the primary advocates of this viewpoint. They provided evidence suggesting (i) the widespread occurrence of this process in many plant groups and (ii) significant evolutionary effects through the production of new hybrid species and novel adaptations. The second approach, pursued mainly by evolutionary biologists studying animal taxa, viewed natural hybridization as an important mechanism for completing the process of speciation or as a tool for understanding the process of speciation (Dobzhansky, 1937, 1940; Mayr, 1942).

The divergence between botanical and zoological workers has both scientific and historical explanations. For example, Dobzhansky and Mayr were the primary architects and expositors of the Biological Species Concept and were interested in determining how speciation (i.e., the development of reproductive barriers) occurred (Dobzhansky, 1937; Mayr, 1942). Because of this they emphasized the observation that natural hybridization was maladaptive for the individuals that took part in the matings. This emphasis led to the formulation of a model in which hybridization was viewed as a process that could lead to the final development of barriers to reproduction through "reinforcement"—Blair (1955) coined this term for the process described by Dobzhansky. Thus, Dobzhansky (1940) proposed a model of speciation that depended on the process of secondary intergradation to finalize the development of premating isolation. Zoologists have also considered cases of natural hybridization to be a useful tool for understanding processes other than reinforcement that lead to reproductive isolation (Mayr, 1942). This interest reflects the desire to understand the process of speciation as defined by the Biological Species Concept. Thus, two aspects of hybridization have been deemed important by those investigators examining animal species complexes. The importance ascribed to natural hybridization in these studies is inherent not in the process itself, but in its contributions toward understanding speciation. The period marked by the Modern Synthesis laid the foundation for subsequent evolutionary research. It appears that most contemporary zoologists perceive natural hybridization to be of little long-term evolutionary importance based on the ideas established during the 1930s and 1940s.

A very positive outcome of the framework established by the Modern Synthesis is reflected in the current multiplicity of studies that examine microevolutionary processes (i.e., process-oriented analyses) in animal hybrid zones (Barton and Hewitt, 1985; Harrison, 1990). This large number of elegantly described cases of animal hybridization (e.g., *Allonemobius,* Howard et al., 1993; *Caledia,* Shaw et al., 1993; *Geomys,* Baker et al., 1989; *Gryllus,* Harrison, 1986; *Mus,* Vanlerberghe et al., 1986; *Podisma,* Hewitt, et al., 1989; *Sceloporus,* Sites et al., 1995; *Sorex,* Hatfield et al., 1992) reflect the emphasis placed by evolutionary biologists such as Mayr and Dobzhansky on the role of natural hybridization in understanding the process of speciation. Although numerous now, such studies are a relatively recent phenomenon, with analyses of animal hybrid zones having increased greatly over the past two to three decades (see Arnold, 1992, for references). This increase is due both to a resurgence of interest in studying speciation phenomena and to the availability of molecular techniques (Hubby and Lewontin, 1966; Botstein et al., 1980; Saiki et al., 1985, 1988). The technical developments have led to detailed genetic analyses that have allowed inferences into the effects of natural selection and migration on the outcome of hybridization episodes (Barton and Hewitt, 1985).

In contrast to the case of animals, relatively few studies have examined population-level phenomena involving plant hybridization (Harrison, 1990; Arnold, 1992). This is surprising because plants are, in general, much more amenable to this type of study and manipulation. However, few researchers (but see Anderson, 1949; Heiser, 1949; Grant, 1963; Stebbins, 1959, 1963) have carried out detailed, population-level examinations of a particular plant species group until very recently (e.g., *Carduus,* Warwick and Thompson, 1989; Warwick et al., 1989, 1990, 1992; *Iris,* Arnold et al., 1990a,b; Bennett and Grace, 1990; Arnold et al., 1991, 1993; Cruzan and Arnold, 1993, 1994; Carney et al., 1994; *Helianthus,* Rieseberg et al., 1988, 1990a,b, 1995a,b; Rieseberg, 1991a; Dorado et al., 1992).

I have suggested that the numerous analyses of animal hybrid zones reflect interests in the process of speciation (i.e., speciation is equivalent to the formation of barriers to reproduction). A number of factors may have reduced the frequency of hybrid zone analyses in plants. First, botanists have placed a greater emphasis on the systematic implications of natural hybridization (e.g., Heiser et al., 1969). Cases of hybridization were viewed as opportunities not necessarily to observe incipient speciation, but rather to infer systematic relationships. A second reason may relate to the fact that allopolyploidy has been viewed as the major outcome of hybridization (Stebbins, 1963). Studies of hybridization in plants have thus emphasized testing for polyploidy, rather than examining introgressive hybridization.

At the present, studies of natural hybridization between animal taxa continue to be process-oriented, with few analyses (Fig. 1.3) incorporating historical (i.e., phylogenctic) information (e.g., Solignac and Monnerot, 1986). Interestingly, this is an aspect of the study of natural hybridization in which plant biologists have taken the lead (Fig. 1.2); numerous studies have used a phylogenetic approach to test for reticulate evolution between plant species (e.g.,