Preface

As the title suggests, this book concerns the evolutionary role played by genetic exchange. In some cases this exchange can be termed natural hybridization; for other examples it is more apropos to refer to the process as lateral or horizontal gene transfer, and yet for other instances the distinction between these processes is blurred. One goal of this work then is to exemplify the similarities—with regard to fundamental evolutionary outcomes—of genetic exchange, whatever its underlying mechanism. I am unaware of another synthesis that has highlighted these similarities.

One reason I have been unable to identify such a synthesis (other than the fact that I might have overlooked it) is that the processes of natural hybridization and lateral gene transfer are seen as non-overlapping in their mechanism and outcome. Undoubtedly some of the avenues for genetic exchange—such as introgression through sexual recombination versus lateral gene transfer mediated by transposable elements—are based on definably different molecular mechanisms. However, even such widely different mechanisms may result in similar effects on adaptations (new or transferred), genome evolution, population genetics, and the evolutionary/ecological trajectory of organisms.

A second reason, somewhat related to the first, is an organism-biased viewpoint among some evolutionary biologists. This viewpoint can be summed up by a quote from a colleague at a recent congress on evolutionary biology—'Lateral gene transfer occurs in microorganisms and has nothing to do with animals. In contrast, natural hybridization affects the latter, but not the former.' I answered this colleague in the following manner. First, I reminded him that genetic exchange *sensu lato* could produce the same, important evolutionary consequences, notwithstanding the underlying mechanism causing the exchange. For example, this is seen in the evolution of novel adaptations—involving lateral gene transfer—leading to the flea-borne, deadly, causative agent of plague from a rarely fatal, orally transmitted, bacterial species. In terms of evolutionary outcomes, this is quite similar to the adaptations accrued from natural hybridization between annual sunflower species resulting in the formation of several new species. Furthermore, I pointed out that natural hybridization *and* lateral gene transfer have impacted both 'higher' and 'lower' organisms. Consider, on the one hand, evidence for introgressive hybridization between the lineages leading to humans and chimpanzees, and the impact of retroviral-like elements on these same lineages, and on the other hand the effect of natural hybridization and lateral gene transfer on species of trypanosomes or yeast.

The chapter structure of this book reflects my goal of presenting the conceptual framework indicated above. This conceptual framework can be summarized with a metaphor. Thus, instead of a simple bifurcating tree of life, I believe that a better metaphor for describing evolutionary diversification is a web of life. I also believe that this is not a novel viewpoint. The recognition of divergence accompanied by ongoing, or at least episodic, genetic exchange was championed in the last century (e.g. see the work of Ledyard Stebbins and Edgar Anderson) and is also reflected in a growing number of contemporary, evolutionary publications. As with Darwin's descent with modification, a number of groups/workers in evolutionary biology have arrived at the same conclusion nearly simultaneously. I cover the work by many of the groups contributing to this paradigm shift, but I will apologize beforehand for inevitable, and totally accidental, oversights.

Chapter 1 includes a brief history of pre-Darwinian, evolutionary studies concerning genetic exchange. I then turn my attention to various organismal systems to exemplify some ways in which post-Modern Synthesis research has been pursued to test the evolutionary role of genetic exchange. I have chosen examples of well-developed evolutionary model systems including plants, animals, bacteria, and viruses. I have chosen these as exemplars because they reflect broadly based, in-depth studies of the possible evolutionary consequences from natural hybridization and/or lateral gene transfer. Some cases (e.g. viral lineages) also afford the opportunity to point to the uncertainty in categorizing them as either natural hybridization or lateral gene transfer. This reflects a tension that I hope to maintain throughout this book. The tension results from the observation that these processes of genetic exchange blend together somewhat in terms of mechanism of occurrence and evolutionary outcome.

Chapter 2 introduces the topic of species concepts and the study of genetic exchange. I will use only four (biological, phylogenetic, cohesion, and prokaryotic) of the many definitions to illustrate how our concept of (i) what a species is and (ii) how it originates influences what evolutionary importance (or lack there of) we ascribe to genetic exchange. I end this chapter by suggesting how we might use species concepts—often the bane of evolutionists interested in gene exchange—to afford a clearer understanding of the importance of natural hybridization and lateral gene transfer.

In Chapter 3, I discuss methodologies to test the hypothesis of genetic exchange. The goal of this chapter is to indicate the diversity of approaches that facilitate such tests. I begin by examining conflicting conclusions, drawn by different investigators, concerning the importance of gene flow in the genus *Quercus*. I use this to indicate the importance of utilizing a comparative approach when investigating possible instances of genetic exchange. I then discuss five methodologies to test for such exchange: (i) trans-generational hybrid zone analyses; (ii) estimates of phylogenetic discordance; (iii) analyses involving gene genealogies and models of speciation; (iv) estimations of intragenomic divergence; and (v) the application of nested clade analysis. I review examples that highlight the specific utility of each of these approaches.

In Chapter 4, I turn my attention to the barriers that limit genetic exchange. The conceptual framework for this chapter assumes that specific barriers are part of a multi-tiered process. In sexually reproducing organisms these barriers can be easily placed into the categories of pre- and postzygotic. However, even for those organisms thought to spend most of their life history reproducing asexually (e.g. bacterial species) limits to genetic exchange can be typified with this concept. Various ecological, behavioral, gametic, viability, and fertility barriers can thus isolate both 'asexual' and 'sexual' species. The model that I adopt in this chapter is one in which multiple, life-history-stage-specific characteristics must be overcome for gene exchange to occur.

Chapter 5 illustrates possibly the most significant fact highlighted in my first book, *Natural Hybridization and Evolution* (1997, Oxford University Press): hybrid genotypes, like any other set of genotypes, demonstrate a range of fitness estimates. In keeping with the subject of this present work, I demonstrate this point with examples involving natural hybridization, viral recombination, and lateral gene transfer. For all classes the conclusion is the same, some hybrid/recombinant genotypes have lower, some the same, and others higher fitness estimates relative to their progenitors.

Chapter 6 reflects a fundamentally important outcome of genetic exchange, that of gene duplication. As throughout this book, I consider instances where the genetic exchange, in this case resulting in genomic duplications, has derived from sexual reproduction as well as other forms of recombination. I consider how genetic-exchange-induced duplications are seen as affecting genome evolution, gene function, adaptations and radiations of entire clades. In keeping with the tenor of the entire book, I emphasize evolutionarily creative outcomes that derive from the duplication of the genomic components of microorganisms, plants, and animals.

Chapter 7 includes examples of the effects of gene exchange on the formation of new evolutionary lineages. In some cases this can be viewed as the origin of new species, in others the organisms formed from genetic exchange are given subspecific classifications. In some instances, the genetic exchange event is seen to be the basal event for entire evolutionary assemblages. Regardless of the evolutionary timing of such events and the taxonomic identity of the products, the importance remains in the outcome: that is, novelty has been produced, both in terms of new organisms and new adaptations. As in other chapters, I will use examples from a wide range of microorganismic and multicellular lineages. Furthermore, I will highlight cases of diversification that can be placed into the categories of polyploid, homoploid, ecological, and recombinational speciation. Yet, as mentioned above, I will not limit my discussion to only those cases that involve the origin of single lineages recognized as 'species'. Rather, I will include an array of exemplars that reflect the diversity of outcomes that include the formation of novel evolutionary lineages and clades.

Topics in Chapter 8 include those associated with positive and negative effects of genetic exchange on the fate of endangered flora and fauna. In particular, I consider the role that such gene flow may have (i) in replenishing populations with limited genetic variability or (ii) in causing genetic assimilation of rare forms by more numerous, related taxa. I will argue that if evolutionary diversification is indeed a web-like process, then we should not give weight to whether members of one evolutionary lineage exchange genes with another when attempting to determine a value for conservation. Instead, we should ask the question of whether genetic exchange can help or hinder the conservation of manageable units (i.e. taxa). I also examine the hypothesis that invasive species sometimes originate through introgressive hybridization.

Chapter 9 reviews findings relating to the effect of genetic exchange on the evolution of the human lineage and lineages of organisms with which we interact (e.g. disease vectors, food sources). I consider fossil and genetic data that suggest gene flow between various archaic taxa, and between archaic taxa and anatomically modern *Homo* (for this section I borrow heavily from Arnold and Meyer 2006). I demonstrate the disastrous effects of natural hybridization and lateral gene transfer in disease and disease-vector evolution. However, I also consider the highly beneficial results from the same processes in producing food products, drugs, and even clothing. Chapter 9 concludes with a discussion demonstrating that *Homo sapiens* has played an active role in producing new strands of the web of life. Our species has accomplished (and continues to accomplish) this through the genetic modification of microorganisms, plants, and animals. In the past, we were limited in this exercise to methods involving crosses between related organisms—through introgressive hybridization. Most recently, however, we have begun a program of lateral gene transfer, through 'genetic modification', to produce hybrids carrying genes from more and more distantly related forms.

In Chapter 10 I begin by reflecting upon the major theme of this book: that genetic exchange is pervasive across all biological lineages. I discuss the implications of this regarding the tree-of-life and web-of-life concepts. I include a discussion of research directions that will benefit our understanding of the role of genetic exchange in evolution. Some of these, including the use of genomic information to discern web processes, are gaining momentum with the appearance of many new data-sets. Others, such as studies that investigate the role of ecological setting on the outcome of genetic exchange, are rare, yet they represent another Golden Fleece because of their potential to yield new insights of major importance. I conclude Chapter 10 with a quote from Darwin that (as is usual for his writings) encapsulates the theme I try to communicate.

There is a glossary of definitions at the back of the book. All terms listed in the Glossary are italicized in the text where they are first used.

Many undergraduate, graduate, and postgraduate scholars, along with evolutionary biologist colleagues at the University of Georgia and elsewhere, have provided crucial data and concepts that form the basis of this book. I owe a huge debt to Ed Larson—my colleague and friend—who spent countless hours with me in discussion and writing sessions that led to our *Wilson Quarterly* article in which we summarized the concept of the web of life. Wyatt Anderson, the late Marjorie Asmussen, John Avise, Jim Hamrick, Jessie Kissinger, Rodney Mauricio, Daniel Promislow, and John Waves from the Department of Genetics, University of Georgia, have given much of their limited and valuable time to discussions of the ideas presented in this book. Over the many years of our friendships, Dan Howard and Loren Rieseberg have given encouragement and guidance in the research paths taken by my group. Much of their guidance has resulted in the ideas and data collected in this book. The following graduate students and postdoctoral associates in the Department of Genetics, University of Georgia, read, and helped revise, portions of this book: Scott Cornman, Eleanor Kuntz, Noland Martin, Monica Poelchau, Jeff Ross-Ibarra, and Scott Small. Paul Harvey and Peter Holland of the University of Oxford graciously expended much time and effort that resulted in my Visiting Research Fellowship at Merton College, Oxford. Ian Sherman, Abbie Headon, Kerstin Demata, and Stefanie Gehrig provided invaluable editorial support at all stages of this project. During the writing of this book, I have been supported financially by a grant from the National Science Foundation (DEB-0345123). Finally, I take full responsibility for any mistakes or omissions in this text.

As with my first book, I must direct most of my thanks and praise to my wife Frances and my children—now adults—Brian and Jenny. Without their continuous love and support, without their understanding and patience, without their encouragement and faith in my ability to do what I thought impossible—that is, to write books—this project would not have even been contemplated. As with *Natural Hybridization and Evolution*, I dedicate this book to them.