PREFACE

Coevolution is a hot topic. Over the past decade the number of papers on coevolution has increased by an order of magnitude. Research on coevolution is diverse, ranging from mathematical modeling, to experimental evolution studies, to cophylogenetic reconstruction. In this book we provide an introduction to coevolution in both microevolutionary (ecological) and macroevolutionary (historical) time. We emphasize the integration of cophylogenetic, comparative, and experimental approaches in testing coevolutionary hypotheses. The overriding question is "how do ecological interactions influence patterns of codiversification?"

The book is limited to the coevolution of interacting species. The term coevolution is sometimes used to describe antagonistic evolution between sexes *within* species, or the evolution of molecular interactions, such as those between RNA codons and anticodons. There is even a body of literature devoted to the coevolution of genes and culture. We address none of these. Rather, we restrict our attention to the coevolution of interactions between species, particularly those involving external parasites that live on hosts (rather than in them).

External parasites are a diverse assemblage of organisms, ranging from herbivorous insects on plants, to monogenean worms on fish, to mites on insects, to feather lice on birds. Ectoparasites are great models for studies of coevolution. They are relatively easy to observe, mark, and count. They can be eliminated to generate "clean" hosts for experiments, and they can be transferred between host individuals, populations, and species. Some forms of host defense, such as grooming behavior, can be experimentally manipulated to test the consequences of suboptimal defense on host fitness. Members of ectoparasite communities can be added to hosts in different combinations to study competitive interactions between parasites that share hosts.

Recent work in coevolutionary biology has been successful in demonstrating coadaptation between species in response to reciprocal selection. In contrast, few studies have tested the influence of coadaptation on diversification of interacting taxa. Short of inventing time travel, unraveling the role of different ecological factors in long-term macroevolutionary patterns is a serious challenge. However, we review attempts to do just this, some of which have met with moderate success. Many of our examples involve parasitic lice of birds and mammals, which represent unusually tractable systems for studies seeking to integrate ecology and history.

Lice are "permanent" parasites that pass all stages of their life cycle on the body of the host. They are closely associated with hosts in both micro- and macroevolutionary time. Some lice cospeciate with hosts, yielding congruent host-parasite phylogenies. Other lice do not cospeciate with hosts, and there is little or no concordance between their phylogenies. This variation in cophylogenetic history within a single order of insects is useful; it allows the exploration of ecological factors underlying very different macroevolutionary patterns without having to compare apples and oranges. By themselves, congruent phylogenies are not evidence for coadaptation; however, they are powerful frameworks for studies of coadaptation, as we illustrate in this book.

Although we frequently turn to lice, we also cover studies of plants, butterflies, moths, beetles, ants, fungi, wasps, bacteria, and other groups of coevolving organisms. In addition to coadaptive processes and cophylogenetic patterns, we consider factors that influence parasite dispersal and population structure, which are lynchpins between micro- and macroevolution. Rates of dispersal are central to evolutionary processes such as gene flow and random genetic drift. Dispersal arranges individuals and species into new interactions, altering selective regimes and the fitness landscape, as summarized by the geographic mosaic theory of coevolution. The *absence* of dispersal can reinforce interactions, even over long periods of time. Acting together, selection and dispersal provide much of the ecological context for host-parasite codiversification.

Studies of coevolution are often restricted to a single group of parasites, even though parasites seldom live in isolation. Indeed, many hosts support very diverse communities of parasites. Competitive interactions between these parasites can lead to character displacement and other forms of coadaptation between parasites. We show how interspecific competition in lice has fundamental effects on host use and diversification. We also show that broader community interactions, such as the phoretic dispersal of specialist parasites on generalist parasites, influence patterns of codiversification.

A major goal of this book is to illustrate how cophylogenetic, comparative, and experimental approaches can be integrated to demonstrate the influence of complex selective interactions on diversification. Reciprocal selection and coadaptation influence the codiversification of parasites and hosts, and the coadaptive radiation of parasites on hosts. Unfortunately, coevolutionary biology has a good deal of arcane terminology—enough to frighten even the most seasoned evolutionary biologist. We have therefore taken care to define the terminology we use, and to prepare figures illustrating relationships among different coevolutionary concepts and processes.

The book begins with an overview of the basic principles of coevolutionary biology, including both micro- and macroevolutionary approaches (chapter 1). In chapter 2 we provide an overview of the biology of lice, and in chapter 3 we survey the effects of lice on their hosts. Chapters 4–6 focus on coadaptive interactions in microevolutionary time. Chapter 4 reviews adaptations that mammals and birds have evolved to resist lice and other ectoparasites. Chapter 5 outlines counter-adaptations that lice have evolved to circumvent these host defenses. Chapter 6 reviews parasite competition, and the role of competition in the coadaptation of different species of lice that share hosts. Chapters 7 and 8 concern dispersal and population structure, initiating a transition from micro- to macroevolutionary time.

In chapters 9–12 we review patterns of codiversification between ectoparasites and their hosts, and the influence of different ecological parameters on these patterns. Chapter 9 explores the influence of cospeciation, host switching, and other processes on macroevolutionary patterns of association. In chapter 10 we consider the role of ecological factors, such as host resistance and parasite competition, in the dissimilar cophylogenetic histories of different groups of lice and their hosts. In chapter 11 we review the influence of coadaptation on the diversification of lice within single host species, and across multiple host species. Finally, in chapter 12 we explore the relationship of coadaptation to codiversification across a wider range of coevolving systems. We emphasize the need for more studies that integrate coadaptation and codiversification.

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