1 Introduction

Ecology is the scientific study of interactions between organisms of the same or different species, and between organisms and their nonliving environment. One of the main goals of ecologists is to explain the abundance and distribution of organisms over space and time. The scope of ecology includes all sorts of interactions, from the most intimate, permanent associations to the briefest of encounters. Although parasitism qualifies as the sort of interaction of interest to ecologists, it has somehow become the focus for another branch of science, parasitology, which uses a multidisciplinary approach to investigate host-parasite interactions. Because of the intimate and intricate nature of the association between host and parasite, a broadly trained parasitologist using techniques ranging from molecular biology all the way to ecology seemed the most appropriate investigator. The problem with this takeover of parasitism by parasitologists, however, is that parasites have been ignored by ecologists for a long time. Sections on parasitism have only recently begun to appear in ecology textbooks (for instance, Begon et al. 2005 and earlier editions), and these bear mainly on the ecological impacts of parasites on free-living organisms. Studies on the population or community ecology of parasites themselves are practically absent from the ecology literature; they are almost exclusively restricted to parasitology journals, and often devoid of any references to important ecological studies on free-living animals.

Similarly, parasite evolution has until recently been studied by parasitologists rather than by evolutionary biologists. As with ecological studies, evolutionary investigations of host-parasite interactions undertaken by nonparasitologists are relatively recent (Poulin 1995a), but rapidly growing in number. While the quality of studies on the ecology or evolution of parasitism performed by parasitologists is not in doubt, it is unfortunate that for many years there have been few exchanges of ideas between parasitology and either ecology or evolutionary biology. Researchers in these disciplines attend different meetings and read different journals. Ecologists and parasitologists have even developed their own jargon; although they use similar terms, they assign different meanings to the same words, which hinders effective communication between the two disciplines (Bush et al.

1997). More importantly, the separation between parasitology, ecology, and evolutionary biology has lead to philosophical differences between these branches of biology, some of which are important. For instance, parasitologists have long known that parasites can affect host population dynamics, but ecologists took some time to realize this. Similarly, ecological parasitology developed as a discipline, in the mid- to late twentieth century, with strong doses of natural history and field biology; this period is beautifully captured, with a hint of nostalgia, by Esch's (2004) historical essays. During that time, however, most theoretical advances in ecology and evolutionary biology were ignored by parasitologists; those that were eventually adopted by parasitologists were only applied to parasites years after their introduction in other fields. For example, until recently and in part because of the influence of medical science on parasitology, many parasitologists accepted that evolution led to a decrease in parasite virulence, whereas modern evolutionary theory would have predicted a greater range of outcomes (Anderson and May 1982, 1991; Ewald 1994). These disagreements could have been avoided had there been a better integration of ecology, evolution, and knowledge of parasite biology by students of parasitism.

My purpose in this book is generally the same as in the first edition: to present an evolutionary ecologist's view of the biology of parasites. I want to discuss various aspects of the biology of parasites using an approach compatible with current theory in evolutionary biology and ecology. Many studies of parasite ecology or evolution published in the past fifty years were thorough descriptive investigations but failed to test the general hypotheses put forward by ecologists and evolutionary biologists; here I will try to rectify this by emphasizing the link with theory. In this book I approach parasites as an evolutionary ecologist would approach any other group of organisms, while recognizing the special attributes of parasites. The book focuses on parasites themselves rather than on the interaction with hosts. Instead, hosts are seen as a key part of the parasite's environment and as a major source of selective pressures. The influence of parasites on host biology has been dealt with extensively in recent reviews; it will only be covered here if it relates to the ecology or evolution of parasites.

My other objective is to suggest a research agenda for the next several years. Where relevant, I point out the gaps in our knowledge, and try to suggest ways of filling these gaps. With this book, I want to capture the present state of parasite ecology and evolution, and propose directions for its future growth.

1.1 The Evolutionary Ecology Approach

Organisms interact with one another and with the nonliving environment on an ecological time scale, measured in days, months, or years. These interactions, however, are the product of natural selection acting over evolutionary time, over thousands and millions of years, to produce organisms well suited to their environment. Evolutionary ecology is the study of the selective pressures imposed by the environment, and the evolutionary responses to these pressures. Natural selection has shaped not only the traits of individual organisms, but also the properties of populations and species assemblages. The subject matter of evolutionary ecology, therefore, includes topics such as the trade-off between the size and number of offspring produced by individual animals, the proportion of males and females in animal populations, and the composition of animal communities. All these phenomena can be studied on a human time scale but to understand the differences observed among organisms, one must consider the forces and constraints that have acted during their evolutionary history.

The study of evolutionary responses is not always as straightforward as that of phenomena occurring on shorter time scales. A major goal of science is to demonstrate causality; it can be inferred that an event causes a response if the response always follows the event in an experimental situation. For example, exsheathment of many nematode larvae and hatching of many cestode eggs always follow their exposure to the conditions encountered in their host's gut in in vitro experiments, therefore it can safely be inferred that these conditions cause exsheathment or hatching, at least in a proximate sense. In evolutionary ecology, the manipulation of variables in controlled experiments is often impossible. Instead, we must rely heavily on comparisons between species that have been exposed to different selective pressures. If species under a given selective regime have consistently evolved a certain combination of traits, these "natural" experiments can be used to draw conclusions about the effects of certain factors over evolutionary time. Obviously, similarity between species can be the result of inheritance of traits from a common ancestor as much as the product of independent lines of convergent evolution. A careful distinction must be made between phylogenetic influences and the true action of natural selection (Brooks and McLennan 1991; Harvey and Pagel 1991). In the absence of other evidence, comparisons across taxa can help to identify true adaptations, defined here as genetically determined traits that have spread or are spreading through a population because they confer greater fitness on their bearers.

Although only applied recently to parasitological problems, the comparative approach can shed much light on parasite evolution. This approach can do more than identify relationships between species traits. It can also be used to test evolutionary hypotheses even though it does not follow the classical experimental approach consisting of the manipulation of independent variables in controlled conditions (see Brandon 1994). Different parasite lineages leading to extant species can be viewed as different evolutionary experiments, in which the ancestor represents the initial experimental conditions and the current phenotype represents the experimental outcome. Comparing lineages evolving under different selective pressures (e.g., in different types of hosts) is like comparing the responses of subjects exposed to different experimental conditions, or their responses to the manipulation of selected variables. In this context, controlling for phylogenetic influences corresponds to avoiding pseudoreplication.

Proper comparative analyses are powerful tools for hypothesis testing in evolutionary ecology (Harvey and Pagel 1991). They are not, however, a panacea for the study of adaptation. Used in isolation from other kinds of evidence, comparative studies provide limited insights into evolutionary mechanisms and the causal links between biological traits (Doughty 1996). On the other hand, the comparative approach is the most useful to identify general patterns that can guide further research. Although the results of controlled experiments or field observations are used as tests of theory wherever possible throughout the book, much of the evidence presented in this book relies on the explanation of variability among species using a comparative approach.

At the same time as the comparative approach became a major tool for evolutionary biologists, a parallel development provided ecologists with a new way of tackling the complexity of natural systems. Macroecology has emerged as a research program aimed at trying to infer the laws of nature from the statistical patterns among its constituent parts (Brown 1995; Gaston and Blackburn 2000). Macroecology consists of the empirical detection of patterns, the formulation of mechanistic hypotheses to account for these patterns, and the empirical testing of the hypotheses. As a whole, macroecology has been remarkably successful at finding general patterns and likely explanations for these patterns (Brown 1995, 1999; Lawton 1999; Gaston and Blackburn 2000; Blackburn and Gaston 2001). Much of the information on parasite ecology presented in this book borrows strongly from the macroecological approach.

The comparative approach in both evolutionary biology and macroecology focuses on large-scale, general phenomena rather than on detail. As a rule, they provide broad, though sometimes tentative, answers to important questions instead of definitive answers to very specific questions. An effort is made throughout this book to combine evidence from comparative or macroecological studies with that from experimental studies, to provide different perspectives on the same problems.

This book is not an elementary treatise of evolutionary ecology. The reader who wants a more general overview of the theory and mathematical models at the core of modern evolutionary ecology can read any of several recent texts on the subject (e.g., Cockburn 1991; Bulmer 1994; Pianka 1994; Fox et al. 2001). This book applies many ideas from evolutionary ecology specifically to parasites, and aims to foster the use of evolutionary thinking in the study of parasite ecology. Some of the questions that will be addressed include: Why do some parasites have more complex life cycles than others? Why are some parasites more host-specific than others? Why are some parasites much more fecund than others? Why are some parasites much more virulent than others? Why are some parasites more highly aggregated among their hosts than others? Why is there greater gene flow among populations in some parasite species than in others? Why are some parasite communities richer than others? These questions have been addressed before by parasitologists, but usually not in an evolutionary context or not with appropriate comparative methods.

1.2 Scope and Overview

Because of its vague definition, the term *parasite* has been applied to a wide range of plant and animal taxa. One can even argue that parasites *sensu lato* greatly outnumber free-living organisms (Windsor 1998). The most widely accepted definition of a parasite is that it is an organism living in or on another organism, the host—feeding on it, showing some degree of structural adaptation to it, and causing it some harm (when the harm incurred by the host invariably leads to its death, the parasite is often referred to as a parasitoid). Interpretations of this definition vary among authors (see Zelmer 1998). Price (1980) included phytophagous insects as parasites, but excluded blood-sucking flies. Barnard (1990) included behavioral parasites, such as many birds that are not physiologically dependent on their host but exploit it in other ways, for example by stealing food from the host. Combes (1995, 2001) even included strands of DNA among parasitic entities. To avoid confusion, it is therefore necessary to specify the taxonomic scope of this book, which will focus exclusively on protozoan and metazoan parasites of animals. These include several diverse taxa of parasites (table 1.1) that have had several independent evolutionary origins. Because helminths and arthropods have been the subject of the majority of relevant studies, they will provide most examples. The general biology and life cycles of these parasites are described in detail in any basic parasitology text (e.g., Noble et al. 1989; Schmidt and Roberts 1989; Cox 1993; Roberts and Janovy 1996; Kearn 1998; Bush et al. 2001), and it will be assumed that the reader is at least superficially familiar with them. Some of the patterns discussed here and some of the conclusions they suggest may also apply to other groups of parasites, but these are beyond the scope of this book.

The evolutionary ecology of parasites can be studied at several hierarchical levels. The smallest unit of study in ecology is the individual organism, but ecologists also deal with populations of individuals of the same species, and with communities made up of several populations of different species. This book first examines how ecological traits of individual parasites have evolved, and then considers population and community characteristics. Chapter 2 begins with a discussion of how organisms that made a transition to parasitism from a free-living ancestral lifestyle have undergone changes in their biology; it also considers how historical events and selective pressures have shaped complex life cycles, and how these life cycles in turn have influenced the ecology of the parasites adopting them. Chapter 3 explores the reasons why some parasites have evolved the ability to exploit a wide range of hosts whereas others are restricted to a single host species. For organisms often thought to be small, degenerate egg-production machines, parasites also show a tremendous range of life-history traits. Chapter 4 discusses how much of this variation is explained by selective pressures from the host or the physical environment, and how much is due to phylogenetic constraints. The final characteristic of individual parasites that will be considered is their ability to harm or manipulate the host. Far from evolving to become benign commensals, parasites can be selected to become highly virulent exploiters of host resources, or they can evolve the ability to control the physiology and behavior of their host for their own benefit. Chapter 5 explores the conditions under which host exploitation strategies can evolve toward these extremes.

One of the most easily described properties of animal populations is their distribution in space. Parasite populations are typically aggregated among their host individuals, but the degree of aggregation varies greatly over time and among populations and species of parasites. The opening chapter on parasite population ecology will examine the causes of aggregation, and some of its potential evolutionary consequences (chapter 6).

Table 1.1 Diversity of some of the major taxa of metazoan parasites of animals. Estimates of species numbers are meant to be realistic minimum numbers. (Modified from Poulin and Morand 2004)

Parasite taxon	No. of parasitic species	Definitive host[a]	Life cycle[b]	Habitat[c]
Phylum Mesozoa	>80	Endo, I	S	M
Phylum Myxozoa	>1350	Endo, V	C	M, FW
Phylum Cnidaria	1(?)	Endo, V	C(?)	FW
Phylum Platyhelminthes				
Class Trematoda	>15000	Endo, V	C	M, FW, T
Class Monogenea	>20000	Ecto, V	S	M, FW
Class Cestoidea	>5000	Endo, V	C	M, FW, T
Phylum Nemertinea	>10	Ecto, I	S	M
Phylum Acanthocephala	>1200	Endo, V	C	M, FW, T
Phylum Nematomorpha	>350	Endo, I	S & C	FW, T
Phylum Nematoda	>10500	Endo, I & V	S & C	M, FW, T
Phylum Mollusca				
Class Bivalvia	>600	Ecto, V	S	FW
Class Gastropoda	>5000	Ecto, V	S	M
Phylum Annelida				
Class Hirudinea	>400	Ecto, V	S	M, FW
Class Polychaeta	>20	Endo, I	S	M
Phylum Pentastomida	>100	Endo, V	C	FW, T
Phylum Arthropoda				
Subphylum Chelicerata				
Class Arachnida				
Subclass Ixodida	>800	Ecto, V	S & C	T
Subclass Acari	>30000	Ecto, I & V	S	M, FW, T
Subphylum Crustacea				
Class Branchiura	>150	Ecto, V	S	M, FW
Class Copepoda	>4000	Ecto, I & V	S	M, FW
Class Cirripedia				
Subclass Ascothoracida	>100	Endo, I	S	M
Subclass Rhizocephala	>260	Ecto, I	S	M
Class Malacostraca				
Order Isopoda	>600	Ecto, I & V	S	M
Order Amphipoda	>250	Ecto, I & V	S	M
Subphylum Uniramia				
Class Insecta				
Order Diptera	>2300	Ecto, V	S	T
Order Phthiraptera	>4000	Ecto, V	S	T
Order Siphonaptera	>2500	Ecto, V	S	T
Order Strepsiptera	>600	Endo, I	S	T

[a] Parasites are classified as either endoparasitic (Endo) or ectoparasitic (Ecto) on either invertebrate (I) or vertebrate (V) definitive hosts.

[b] Life cycles are simple (S) if a single host is required and complex (C) if two or more hosts are required for the completion of the cycle.

[c] The habitat of parasites and their hosts can be marine (M), freshwater (FW) or terrestrial (T).

Parasite individuals in a population are not distributed evenly in space, and their numbers also fluctuate in time. The basic models of parasite population dynamics are reviewed in chapter 7, along with a discussion of how evolution may have shaped various population processes. This chapter also includes a synthesis of recent developments in parasite population genetics, from which much has been learned about the spatial dispersion of parasites at various scales, within or among populations.

In nature, any parasite population is likely to coexist with populations of other parasite species. The transition to parasite community ecology will be made by examining how populations of different parasite species interact and how parasites have responded to interspecific competition (chapter 8). Parasites of different species occurring in the same host individual form a community, which itself is only a small subset of the larger community comprising all parasite species found in the host population. In turn, this is a subset of the fauna of parasite species known from the combined populations of that host species. At all these levels of organization, assemblages of parasite species may be structured or they may be random, that is, they may be predictable sets of species drawn from the pool of available species, or an assemblage formed by chance events. This and other issues are addressed at all levels of parasite community organization in chapters 9 and 10.

This book is about the biology of individual parasites such as their transmission pattern and life cycle, the biology of parasite populations including their distribution among hosts, and the biology of parasite communities with emphasis on structure and richness. All these themes are linked to one another and set within an evolutionary or phylogenetic framework. The evolutionary ecology of parasites is still a young discipline and many questions remain unanswered. Throughout the text, areas in which further research is required are highlighted. Hopefully, these suggestions will lead to more investigations and a narrowing of the gap between parasite evolutionary ecology and the evolutionary ecology of free-living organisms. In chapter 11, general guidelines are offered for future studies, and the global importance of evolutionary studies of parasites is discussed.