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Evolutionary Ecology Meets Phylogenetics
Edited by Serge Morand , Boris R. Krasnov , D. Timothy J. Littlewood
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Introduction

Serge Morand, Boris R. Krasnov and D. Timothy J. Littlewood

The development of molecular tools and phylogenetic methods have contributed to the explosion of taxonomic and phylogenetic investigations on parasites (both micro- and macroparasites, i.e. from viruses, bacteria, protists to arthropods and helminths), increasing our knowledge of considerable, and often cryptic, parasitic diversity. Concomitantly, the studies of host–parasite interactions and parasitism have influenced many scientific disciplines from biogeography to evolutionary ecology by using various comparative methods based on phylogenetic information to unravel shared evolutionary histories.

The idea behind this book is indebted to the influential contributions of Roderic Page and Dan Brooks. Rod Page, in his edited book *Tangled Trees* (Page, 2003), has shown the importance of history, depicted by phylogenetics, for understanding the processes that may explain the macroevolutionary patterns of host–parasite co-diversification. Daniel Brooks and Deborah McLennan, in their book *Nature of Diversity* (Brooks & McLennan, 2002), have shown the importance of history, using also phylogenetics, as a background that is necessary for understanding processes and contingencies explaining the co-diversification of hosts and their parasites.

The main objective of this book is to join two active fields of research activities – phylogenetics and evolutionary ecology – in order to better explore the diversification processes that may reveal and explain the patterns of parasite diversity, and concomitantly the diversification of their hosts.

The two important aims of this book are, first, to provide an overview of recent advances in the evolutionary diversification of several major groups of micro- and macroparasites, and, second, to present an insight into established and emerging tools that can help test mechanisms and hypotheses that underlie the diversification and adaptation of these parasites. The present book is organized in three parts, namely (1) evolutionary ecology of parasite diversity, (2) evolutionary history of parasite diversity and (3) combining ecology and phylogenetics.

The first part of this book starts with a chapter on quantifying parasite diversity, where Robert Poulin presents an overview of the ways in which parasite diversity can be measured. Several indices that quantify different facets of diversity, and that can be

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implemented with free software packages, are presented. This culminates in a brief discussion of how the simultaneous measurement of two or more of these facets of diversity can be achieved with a single index. This chapter provides a toolkit for the quantification of parasite diversity, and guidelines for their use.

In the second chapter, Boris Krasnov and Robert Poulin investigate the relationships between parasite diversity and host diversity, using both compositional (species richness) and phylogenetic components of parasite and host diversity across distinct geographical areas or regions. They examine how these relationships may vary across continental and global spatial scales.

Tommy Leung, Camilo Mora and Klaus Rohde, in the third chapter, discuss what is known about the diversity of aquatic invertebrates themselves, the gaps in the knowledge of the diversity of parasites in aquatic invertebrates, and some biogeographical studies which have addressed the macroecological and biogeographical patterns of parasite communities found in aquatic invertebrates.

In Chapter 4, Lajos Rózsa, Piotr Tryjanowski and Zoltán Vas consider the relationship between host range shifts and parasite diversification. They recall that several authors have repeatedly emphasized that the ongoing loss of non-parasite diversity decreases parasite diversity and the periods of expansions of hosts' geographical ranges promote host-switches. But they outline a scenario that adds the characteristic processes of the leading edge versus the rear edge of the moving margins of the host's range, the relatively low parasite richness of an invasive host population and the role of sexual selection in parasite speciation in relation to their geographic position.

The last chapter (Chapter 5) of this first part reviews the impacts of parasite diversity on wild vertebrates. Frédéric Bordes and Serge Morand emphasize the limited knowledge on the impacts of multiple infections despite their commonness in nature. They illustrate how parasite diversity may potentially impact hosts.

The second part of this book, rather than starting by the actual ecology, puts the emphasis on the evolutionary history of the parasite diversity (i.e. the parasite diversification). Several chapters illustrate the historical diversification of the major groups of parasite organisms. In Chapter 6, Aurélie Chambouvet, Thomas Richards, David Bass and Sigrid Neuhauser introduce the most widely used molecular techniques for studying natural microbial diversity. They provide examples of newly described parasites in aquatic environments, and discuss the implications and limitations of these methodologies.

Ahidjo Ayouba and Martine Peeters describe in Chapter 7 the spatio-temporal distribution and evolution of simian retroviruses (SIV, STLV and SFV) and the relationship with their human progeny and their prosimian precursors, if known.

Lucy Weinert describes in Chapter 8 the diversity and phylogeny of the genus *Rickettsia*. She explores the range of known transmission strategies, with the existing data on *Rickettsia* incidence and prevalence across host groups, in the light of Rickettsial phylogeny.

Chapter 9 concerns a small, but peculiar, group of parasites, the acanthocephalans. Martín García-Varela and Gerardo Pérez-Ponce de León review the research on the phylogenetic relationships among the major classes of acanthocephalans, which help understand the evolution of their morphology and ecological traits (life-cycle and transmission patterns).

David Reed, Julie Allen, Melissa Toups, Bret Boyd and Marina Ascunce outline in Chapter 10 how the evolutionary history of lice can shed light on not only the evolutionary history of their primate and human hosts, but also on the ecology of those hosts. They illustrate how lice were used to determine when humans first began wearing clothing, how host-switching in lice three million years ago is suggestive of early hominids living in close proximity to gorilla ancestors, and finally how the use of lice may help to study the patterns of human migration around the world.

Lajos Rózsa and Zoltán Vas review the diversification of avian lice in Chapter 11. While the global fauna is relatively well explored at higher taxonomic levels, a large proportion of known louse species has only been collected from one (or a few closely related) host species, while few others appear to occur across a wide range of host species, genera and even families. Results of several studies indicate that speciation of lice is sometimes, though by far not always, synchronized with speciation of their hosts more than expected by chance.

Katharina Dittmar, Qiyun Zhu, Michael Hastriter and Michael Whiting give an overview of the evolutionary history of fleas in Chapter 12, using data from fossils, phylogeny and ecology. They show that compared to the diversity in other clades of Hexapoda, fleas (Siphonaptera) encompass a relatively small group, the majority of which is adapted to rodents.

In Chapter 13, Katharina Dittmar, Solon Morse, Carl Dick and Bruce Patterson present the bat fly, a parasitic group of Diptera. They review the studies on the evolution of these flies, currently encompassing around 500 described species.

Ashley Dowling argues that mite diversity has not been as well documented as insect diversity, but shows that mites have successfully exploited both invertebrates and vertebrates, principally as ectoparasites but also as endoparasites. In Chapter 14 he provides a basic overview of mite biology and discusses the evolution of parasitism and the diversity of parasitic mites.

Serge Morand, Steve Nadler and Arne Skorping explore the diversity of nematode life-traits in the light of their phylogenetic diversification (Chapter 15). The nematodes are a highly diverse group with a stunning variability in lifestyles, with repeated evolution of parasitism throughout the phylum, making this group a fascinating model for comparative studies of speciation and life history evolution of parasitism.

Tim Littlewood, Rod Bray and Andrea Waeschenbach (Chapter 16) consider the advances in resolving the phylogenies of trematodes and cestodes using molecular data and how improved resolution from a growing database highlights major transitions in the evolution of complex life-cycles, but gaps also in our knowledge of these helminths.

Bryan Falk and Susan Perkins, in the last chapter (Chapter 17) of this second part, review the diversity of parasites reported from Caribbean *Anolis* lizards, and discuss more specifically the diversification in their malaria and nematode parasites.

The last part of this book includes contributions on how to combine ecology and phylogenetics with illustrations on several important topics in the study of host–parasite

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interactions. In the first chapter (Chapter 18) of this last part, Yves Desdevises, Serge Morand, Boris Krasnov and Julien Claude illustrate the recent developments in comparative analysis techniques. Current approaches are reviewed, with applications to investigate putative adaptations to parasites' lifestyle.

In Chapter 19, Boris Krasnov, Serge Morand and Robert Poulin consider how phylogenetic signal acts on two ecological traits of parasites, namely abundance and host specificity. They also consider geographic variation and scale-dependence of phylogenetic signal in these traits. Using fleas parasitic on small mammals as an example, they demonstrate that the search for phylogenetic signal in various ecological traits of parasites may lead to better understanding of parasite evolution.

Andrea Šimková and Serge Morand, in Chapter 20, revise the mechanisms leading to niche segregation and restriction in parasites. They focus on two important aspects of the parasite niche: host specificity and host microhabitat selection. Using the example of congeneric monogeneans from a group of fish species, they illustrate using phylogenetic reconstructions how parasite morphology and niche segregation facilitate the coexistence of congeneric monogenean species.

Evolution of parasite virulence is questioned by Hadas Hawlena and Frida Ben-Ami in Chapter 21. Beginning with a brief review of the 'trade-off' hypothesis, they consider communities of parasites – two or more parasite strains or species infecting the same host – and argue that multiple parasites introduce additional trade-offs that should be considered in future studies on the evolution of virulence. Moving to communities of hosts – two or more host groups, strains or species – they demonstrate that while host heterogeneity makes model-based prediction more complicated, such heterogeneity generates more realistic insights into virulence evolution.

In Chapter 22, Maarten Vanhove and Tine Huyse investigate the evolution of host specificity and the role of species jumps in fish–parasite systems. They show that although host specificity is a key factor governing the distribution and introduction of parasite species, it is also an important aspect of parasite species diversity and diversification.

Timothée Poisot reviews in Chapter 23 empirical and theoretical studies in order to clarify when co-phylogeny provides evidence of coevolution. Challenging the idea that detecting a co-phylogenetic structure alone is required to demonstrate coevolution, he shows that coevolution is neither necessary (co-phylogenetic structure can emerge outside of coevolving interactions) nor sufficient (coevolution can lead to non-matching phylogenies) to establish a co-phylogenetic structure.

Tania Jenkins and Philippe Christe attempt to bring together phylogenies and behaviour in the study of host–parasite interactions (Chapter 24). They discuss the conceptual background uniting the links between specialization, cospeciation and behaviour and provide case studies illustrating how host and parasite behaviour affect the patterns of parasite specialization and host–parasite cospeciation.

In the last chapter (Chapter 25), Peter Markov, Rebecca Gray, James Iles and Oliver Pybus show the recent advances in gene sequence analysis, phylogenetics methods for inferring evolutionary history and processes and statistical approaches that employ phylogenetic, molecular clock, and population genetic models. These methods are

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contributing to the measurement and understanding of the genetic diversity of a wide variety of micro-organisms, including many important human pathogens such as the hepatitis C virus.

The conclusion and opening perspectives are given by Armand Kuris.

We hope this book will be stimulating and that students and researchers in the fields of ecology and evolution of parasitism, animal and human health will find in it examples and encouragement to integrate phylogenetics when investigating parasitism in evolutionary ecology, health ecology, medicine and conservation.

References

Brooks D. R. & McLennan, D. A. (2002). *The Nature of Diversity*. Chicago, IL: University of Chicago Press.

Page, R. D. M. (2003). *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. Chicago, IL: University of Chicago Press.

Part I

Evolutionary ecology of parasite diversity

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1 Quantifying parasite diversity

Robert Poulin

1.1 Introduction

It has become almost customary for parasitologists to state that parasites represent a large proportion of the living species on Earth when arguing that parasitism is a driving force in ecology and evolution (Windsor, 1998; Poulin & Morand, 2000, 2004; Dobson *et al.*, 2008). On smaller scales, parasite diversity is considered an important selective force acting on local populations and shaping communities and ecosystems. But how exactly does one measure the diversity of parasites? There is a lot more to it than merely counting the number of parasite species infecting a host species or occurring in a given area. The same question has plagued ecologists, who have been trying to quantify biodiversity in all its forms for over a century. In this respect, there is nothing unique or special about parasites, and the huge progress made by ecologists in the measurement of organismal diversity (see Magurran & McGill, 2011) therefore also applies to the measurement of parasite diversity.

The number of ways in which diversity is interpreted has increased over time, as has the number of different indices measuring one or other of its many aspects. Far from being a disadvantage, the proliferation of metrics of diversity has expanded and deepened our understanding of the origins of diversity and of its maintenance in the face of environmental changes. Modern ecologists embrace the multifaceted view of diversity and the more nuanced interpretations it allows (Magurran & McGill, 2011). Parasitologists have lagged a little behind in adopting this broader view of diversity, but they are rapidly catching up.

Here, I present an overview of the ways in which parasite diversity can be measured. I begin with a discussion of how the set of parasite species whose diversity is to be measured must first be defined clearly, how it should be sampled, and why it may be necessary to exclude certain species from all calculations. Then, I proceed to define several aspects of diversity in a stepwise manner, from the simplest to the more complex. In each case, I present indices that quantify these different facets of diversity and that can be implemented with free software packages. This culminates in a brief discussion of how the simultaneous measurement of two or more of these facets of

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diversity can be achieved with a single index. Overall, the goal of this chapter is to provide parasite ecologists with a toolkit for the quantification of parasite diversity, and guidelines for the use of these tools.

1.2 Parasite assemblages as study units

As with any ecological investigation, analyses of parasite diversity require that the basic unit of study be clearly specified from the outset. An estimate of diversity only makes sense within a comparative framework; high or low diversity only has meaning when two or more values can be compared to each other. Therefore, the unit of study must be a type of parasite assemblage that either occurs as several independent replicates, or allows repeated measurements over time. Here, *parasite assemblage* means a set of parasite species that occur within given spatial and temporal limits, regardless of whether these species interact or not.

Depending on the biological question driving the research, these spatial and temporal limits can vary widely. In ecological parasitology, the traditional approach has been to use the parasites' hosts to establish the spatial boundaries of assemblages. Thus, using the terminology of Bush *et al.* (1997), a parasite assemblage may consist of an infracommunity, i.e. all the parasite species found in an individual host, a component community, i.e. all the parasite species exploiting a host population (or all free-living stages of the different parasite species found in a given habitat), or a supracommunity (or compound community), i.e. all the parasite species in all the hosts in a given habitat. The boundaries are not always discrete; for instance, where does one host population end and another begin? Unless one is working with well-defined habitats, such as lakes or islands, the boundaries of parasite component communities are often arbitrary. Further limits can be imposed to restrict parasite assemblages to subsets of the above. For example, one can define an assemblage with respect to parasite taxonomy (nematodes versus trematodes), site of infection on the host (ecto- versus endoparasites) or parasite developmental stage (larval versus adult endohelminths). At the other end of the scale, it is also possible to define parasite assemblages above the supracommunity scale – for instance, by specifying geographical areas (biogeographical regions, latitudinal bands, countries, continents, etc.) as the spatial limits of assemblages.

The various parasite assemblages form a hierarchy of scales, with each assemblage representing a subset of a higher-level one; an infracommunity is a subset of a component community, and so on (Bush *et al.*, 1997; Poulin, 2007). The choice of a particular level, i.e. infracommunity versus component community, should be motivated entirely by the biological question being addressed. The lower levels are generally more suited to questions about individual differences in host susceptibility, whereas the higher ones are more appropriate for studies of the evolutionary or environmental factors promoting the diversification of parasite faunas. It is the task of researchers to choose and then clearly define the parasite assemblages on which they take diversity measurements to facilitate the interpretation of their results.

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1.3 Sampling for parasite diversity

The purpose of sampling is to obtain the best representation possible of the parasite assemblage by minimizing sampling bias and sampling error. This can be achieved by a sampling design guided by clear, explicit objectives and based on an appropriate sampling unit.

In studies of parasite diversity at most scales, the sampling unit will consist of an individual host. Thus, to quantify the diversity of a parasite component community, say, that of helminths in a lake fish population, one would need to sample several individual fish hosts and recover all the helminths they harbour. Sampling bias occurs when the individual hosts sampled are not truly representative of the host population (Southwood & Henderson, 2000), such that all parasite species do not have a probability of being included determined solely by their relative abundance in the component community. In the case of the helminth component community in a lake fish population, avoiding sampling bias would mean randomly sampling fish while taking into account the spatial and age structure of the population to obtain fish of all sizes and ages, from all microhabitats, etc. This is easier said than done, and any potential bias in diversity estimation resulting from sampling constraints should be acknowledged upfront.

Sampling error is easily measured and should always be reported in association with any estimate of diversity. It is generally quantified as the variability around the estimate, and expressed as standard error or confidence intervals. Thus, with individual hosts as sampling units, sampling error is simply the variability of the mean diversity per host computed across all hosts sampled. Sampling error depends not only on heterogeneity among hosts, but also on the number of hosts sampled. The more hosts are sampled, the greater the probability of collecting rare species (see Section 1.5), but also the narrower the confidence intervals around the estimate of mean diversity.

1.4 Inclusion and exclusion of species

Even in well-defined parasite assemblages, there may be reasons to exclude certain species from the calculation of diversity indices. Consider, for example, what parasitologists have referred to as ‘stragglers’ – parasite species which occur at very low prevalence in what appear to be rare cases of accidental infection of the ‘wrong’ host. In studies of free-living communities, when modelling ranked abundance distributions to estimate species richness (see Section 1.5), the excess of rare species resulting from the inclusion of accidentals creates a mismatch between observed patterns and those predicted by theoretical models like the lognormal (Magurran & Henderson, 2003). This argues strongly in favour of their exclusion from all diversity analyses.

Should straggling parasites be excluded from the calculation of diversity indices on the parasite assemblage of a host they are not meant to infect? Probably, although this may depend on the specific objectives of the study. There is no easy way of identifying straggling parasite species. Low prevalence is not a sufficient criterion, since there may well be rare parasite species that are genuine members of a host’s parasite assemblage.

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Failure of the parasite to develop properly in the host, for instance stunted growth or lack of sexual maturation, could be a sign that this host species is not in the parasite's normal repertoire. In the end, expert opinion may be required to identify stragglers, and the decision to either include or exclude them should be based on the study's objectives.

Another type of parasite may also be considered for exclusion. Published surveys of parasite diversity often include one or a few parasite taxa not identified to species level, but only down to genus or family level. For instance, for helminth assemblages of vertebrates, two-thirds of published surveys present lists of parasite 'species' in which fewer than 90% of taxa are actually identified to the species level (Poulin & Leung, 2010). If what is listed in a given survey as a family has actually been confirmed, either through detailed morphological examination of specimens or using molecular markers, as consisting of a single species, then the fact that it is unnamed may not matter. However, in the absence of such confirmation, a parasite taxon listed only by its family name may consist of several species. Many large-scale studies of parasite diversity use databases compiled from published surveys, and the low taxonomic resolution for many parasites in these surveys is a real issue. There is no simple rule regarding the inclusion or exclusion of such 'species' from diversity studies. Again, the specific objectives of the study should guide any decision.

1.5 Parasite species richness

Species richness, or the number of species in an assemblage, is the simplest and most intuitive measure of diversity, and by far the one most widely used in past research on parasite biodiversity (Poulin, 1995; Gregory *et al*., 1996; Morand, 2000; Poulin & Morand, 2004; Poulin *et al*., 2011a). However, quantifying species richness accurately involves a lot more than merely counting the different parasite species from a series of samples. Because many parasite species occur at low prevalence (i.e. in a small percentage of individuals in a host population), there are rare species likely to be missed by any sampling design other than the most exhaustive. As a consequence, the observed number of parasite species in an assemblage is almost invariably an underestimate of the true species richness of the assemblage.

Among others, Gotelli and Colwell (2011) provide a good summary of existing methods to estimate true species richness. Three general approaches can be used (see Longino *et al*., 2002). First, if data on the abundance, i.e. the total number of individual parasites in the assemblage, for each parasite species are available, a statistical distribution can be fitted to rank abundance data. Abundance models such as the lognormal, the log-series, the geometric series, the Zipf–Mandelbrot and the brocken-stick, can be fitted to parasite abundance data to estimate the total number of species in an assemblage (Chao *et al*., 2009). This approach may not always work with parasite assemblages, however, as the generally low richness of many parasite assemblages limits the statistical power of this method (Poulin *et al*., 2008).

The second approach consists of extrapolating a species accumulation curve to its asymptote. Again, let us consider the parasite component community in a lake fish