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THE DIVERSITY OF PARASITES

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ABSTRACT

Parasitism is one of the most successful modes of life displayed by living organisms, as measured by how often it evolved and how many parasitic species are presently in existence. Studying the diversity of parasites is particularly relevant because sympatric diversification may be important in some parasite taxa, and because of the opportunity for independent tests of evolutionary hypotheses in the many separate lineages in which parasitism evolved. Our incomplete knowledge of existing parasite species—the result of a range of phenomena that includes inadequate sampling effort or the lumping of different cryptic species under one name—is not always a major obstacle for the study of parasite diversity. Patterns in the diversity of parasites may be associated with either host or parasite characteristics. The distribution of parasite diversity among host taxa does not simply reflect the species diversity of the host taxa themselves; life history and ecological traits of hosts appear to play important roles. These may determine the likelihood that hosts are colonized by parasite species over evolutionary time. It is not yet clear whether some host traits also favor intrahost speciation and diversification of parasites, and the formation of new parasite species. Certain features of parasites may also be associated with speciation and diversification. Only parasite body size has received much attention; the patterns observed are not greatly different from those of free-living species, with small-bodied parasite taxa being more speciose than related large-bodied taxa. Epidemiological parameters such as the basic reproductive rate of parasites, or R_0, *can also generate predictions regarding the distribution or evolution of parasite diversity. For instance, parasite taxa characterized by high* R_0 *values may be more speciose than related taxa with lower values of* R_0*; such predictions remain untested. Large-scale biogeographical patterns of diversity have only been well studied for metazoan parasites of marine fish; for these parasites, latitudinal patterns can be explained by effects of temperature on speciation rates and epidemiological variables, though other causes are possible. The emphasis for future research must shift from pattern description to the elucidation of the processes responsible for the structure and diversity of parasite faunas. A better integration of ecological and historical (or phylogenetic) approaches to the study of parasite diversity should make this objective possible.*

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INTRODUCTION

IF ONE ADOPTS a broad definition of parasitism, such as obligate feeding on a living organism without death to the host, then almost 50% of known animal species can be classified as parasites (Price 1980; Windsor 1998). Stricter definitions, in which an organism must live on or in its host for a significant portion of its life to be considered a parasite, would yield more modest estimates. The number of parasites is still likely to be huge, however, given that probably only 10 to 20% of all existing kinds of organisms are known to science (May 1986; Hammond 1992), and that practically all free-living metazoans harbor at least one parasite species.

Parasites (*sensu stricto*) include representatives from many phyla. Parasitism by metazoans on other metazoans—the focus of this review—has evolved independently at least 60 times in the evolutionary history of animal life on Earth (Table 1). This conservative estimate is based on phylogenetic analyses of metazoan taxa that include parasitic species, and it may increase when better phylogenetic resolution is achieved. We could also add the many transitions to parasitism that produced parasitoid insects (Eggleton and Belshaw 1993; Whitfield 1998), parasitic fungi (Rayner et al. 1987; Pirozynski and Hawksworth 1988), and parasitic protozoans (Siddall et al. 1993)—groups that will not be covered in this review. Parasitism has evolved on at least as many (if not more) occasions than other modes of life, such as predation. Furthermore, several parasite lineages have diversified greatly over evolutionary time, and are now represented by large numbers of distinct species (Table 1). In some instances, parasitic lineages have diversified more than their free-living relatives. In addition, we could also discuss phytophagous insect taxa, which fit in the broad definition of parasitism and are more speciose than related, nonparasitic taxa (Mitter et al. 1988).

Why are there so many parasite species? Questions relating to animal diversity and its causes have long puzzled ecologists (Hutchinson 1959; May 1986; Groombridge 1992). Parasites are particularly important to these diversity issues for at least two reasons. First, the many independent transitions to parasitism allow researchers to study the processes of evolution—as it relates to speciation rates and diversification—in several monophyletic groups with similar lifestyles. This may uncover general evolutionary trends more easily than by studying the free-living animals in which parasites live. There is also much evidence indicating that sympatric speciation may be common in the diversification of parasite lineages (e.g., de Meeûs et al. 1995; Théron and Combes 1995). Parasites may thus be ideal biological models for the study of ecological specialization, speciation mechanisms and diversification (de Meeûs et al. 1998). Second, many parasite species are greatly important to medical and veterinary science, even though little is known about their evolutionary origins. Several human parasites may have switched from wild or domestic animals to colonize mankind (schistosomes: Combes 1990; malaria: Waters et al. 1991). Understanding what biological phenomena facilitate host transfers, and the subsequent speciation and diversification of parasites, is therefore of great relevance.

In this article, we review recent developments in the study of parasite diversity—focusing mainly on parasite species richness—and attempt a synthesis of different approaches to the study of diversity. We limit our coverage to metazoans that are parasitic on other metazoans, for which there is a sufficient amount of information available for a meaningful analysis. The difficulties in quantifying parasite diversity are first summarized. We then discuss, from a phylogenetic perspective, the properties of hosts and parasites that may promote either rates of speciation and diversification, or the accumulation of parasite species in certain hosts. We also recognize that the distribution of parasite diversity and parasite speciation rates are coupled with the ability of parasite species and parasite populations to persist in time and disperse in space, and we present a theoretical framework that links epidemiological models with the distribution of diversity and rates of parasite diversification. Finally, the few documented large-scale biogeographical patterns in parasite diversity are also reviewed and examined. Our aims are not only to clarify which parasite taxa are very speciose, but to explain why they are so, and suggest promising avenues for the study of parasite diversity.

TABLE 1

Minimum numbers of evolutionary transitions to parasitism (sensu stricto) *and numbers of living species in the major groups of metazoan parasites of metazoan hosts*

Parasite taxon	Minimum number of transitions	Minimum number of living species	References
Phylum Mesozoa	1	>80	1
Phylum Platyhelminthes*			
Class Cercomeridea (subclasses Trematoda, Monogenea and Cestoidea)	1	>40000	2,3
Phylum Nemertinea*	1	>10	1
Phylum Acanthocephala	1	>1200	4
Phylum Nematomorpha	1	>350	5
Phylum Nematoda*	4	>10500	6,7
Phylum Mollusca*			
Class Bivalvia*	1	>600	8
Class Gastropoda*	8	>5000	9
Phylum Annelida*			
Class Hirudinea*	3	>400	10
Class Polychaeta*	1	>20	11
Phylum Pentastomida	1	>100	1
Phylum Arthropoda*			
Subphylum Chelicerata*			
Class Arachnida*			
Subclass Ixodida	1	>800	12
Subclass Acari*	2	>30000	13
Subphylum Crustacea*			
Class Branchiura	1	>150	1
Class Copepoda*	9	>4000	14,15
Class Cirripedia*			
Subclass Ascothoracida	1	>100	16
Subclass Rhizocephala	1	>260	17
Class Malacostraca*			
Order Isopoda*	4	>600	18,19
Order Amphipoda*	17	>250	20,21
Subphylum Uniramia*			
Class Insecta*			
Order Diptera*	2	>2300	22
Order Phthiraptera (suborders Ischnocera, Amblycera and Anoplura)	1	>3000	23
Order Siphonaptera	1	>2500	24

*Denotes taxa containing free-living species.

References: 1) Barnes 1998. 2) Brooks and McLennan 1993a. 3) Rohde 1996. 4) Amin 1987. 5) Schmidt-Rhaesa 1997. 6) Blaxter et al. 1998. 7) Anderson 1992. 8) Davis and Fuller 1981. 9) Warén 1984. 10) Siddall and Burreson 1998. 11) Hernández-Alcántara and Solis-Weiss 1998. 12) Klompen et al. 1996. 13) Houck 1994. 14) Poulin 1995a. 15) Humes 1994. 16) Grygier 1987. 17) Høeg 1995. 18) Brusca and Wilson 1991. 19) Poulin 1995b. 20) Kim and Kim 1993. 21) Poulin and Hamilton 1995. 22) Price 1980. 23) Barker 1994. 24) Roberts and Janovy 1996.

Estimating Parasite Diversity

Obtaining a precise count of living parasite species is presently impossible, since we still have not identified all living host species. In the past ten years, several hundred new amphibian species have been described, and this trend shows no sign of slowing down (Glaw and Köhler 1998; Hanken 1999). Clearly, if the list of existing vertebrate species is far from complete, then we are a long way from a comprehensive inventory of all free-living species. This shortfall is more pronounced in parasites for at least two reasons. First, parasites can only be described after their host species have been scientifically identified. Larval helminth parasites are often described before the definitive hosts, in which the adult parasites occur, are identified, but these definitive hosts are previously described species. We know of only one exception to this rule: for unusual reasons, the parasitic copepod *Dinemoleus indeprensus* (Cressey and Boyle 1978) was described years before its host, the deep-sea "megamouth" shark (Taylor et al. 1983; Berra 1997). The typical delay, however, creates an inevitable problem when trying to compile accurate lists of hosts and parasite species. Second, parasite species are obviously smaller than their hosts and therefore more easily overlooked, even when the host species is well known. These problems are unavoidable, and they imply that the numbers in Table 1 are gross underestimates of true diversity. More immediate concerns face those trying to estimate parasite species diversity, however.

The most prominent concern is that, even in detailed surveys, several parasite species go unrecorded because an insufficient number of hosts are examined. Approximately one-third of helminth parasite species from bird and mammal hosts have a prevalence of 5% or less; in other words, they occur in fewer than 5% of the hosts in the population (Poulin 1998). Many rare species will not be identified unless host populations are sampled adequately (Walther et al. 1995). Nonparametric estimators of species richness can serve to extrapolate the number of species missed by inadequate sampling (Poulin 1998; Walther and Morand 1998); they remain, however, poor substitutes for the actual data because they offer no clue regarding the taxonomic affinities of the unidentified species. Nevertheless, the results suggest that, typically, one or two helminth species escape detection in surveys of vertebrate hosts in which fewer than 40 or 50 individual hosts are examined (Poulin 1998).

Even when all parasite species are sampled from all host species in a habitat or region, an accurate tally of parasite species may remain difficult. A parasite species may exploit more than one host species, but show slight morphological differences in accordance with its host species. Considerable host-induced variability in phenotype has been reported in several helminth species (e.g., Kinsella 1971; Amin 1975). This can lead to the incorrect splitting of one species into two or more congeneric species, and an inflated estimate of parasite diversity.

Conversely, several distinct parasite species can be mistakenly lumped into one. The recent use of molecular approaches in systematics has revealed large numbers of morphologically similar "cryptic" species that were previously recognized as a single species (Hillis et al. 1996), and parasite species have been no exceptions (Combes 1995; Thompson and Lymbery 1996). These cryptic species, though highly similar and often sympatric, are completely isolated reproductive entities and would be considered distinct species, regardless of the definition of a species one cares to choose. For instance, some species of cestodes (Euzet et al. 1984; Renaud and Gabrion 1988; Ba et al. 1993) and nematodes (Nascetti et al. 1993), once considered to be capable of parasitizing a few related hosts, have instead often proven to be complexes of related but distinct species, each highly host-specific.

Ironically, we may know more about certain parasite taxa than about their free-living relatives. For instance, our knowledge of the diversity of parasitic nematodes may be more complete than our knowledge of that of free-living nematodes. Nevertheless, we are far from a complete knowledge of parasite diversity. This is likely to be more true for some habitats or host taxa than for others. This may result from the work of one or a few influential and highly productive scientists, who produce remarkably exhaustive inventories of species in certain taxa or areas, as compared to the surveys available for other groups. The unequal knowledge of different parasite groups can also be a consequence of the biological properties of these taxa, such as size or habitat, which determine how easy they are to observe. For instance, we generally know more about the diversity of mammals or vertebrates than about the diversity of invertebrates, just as we know more about temperate terrestrial environments than about deep-sea habitats. Consequently, our knowledge of mammal or vertebrate parasites from temperate terrestrial zones should be better than our knowledge of invertebrate parasites from deep-sea environments. One way to assess our knowledge of parasite diversity is to examine the relationship between the body size of known species and the species' date of description. Recently described species tend to be smaller than previously recognized species, simply because the probability of detection increases with body size (Gaston 1991; Gaston and Blackburn 1994). If no such relationship between body size and date of description is observed in a given taxon, we may infer that it is relatively poorly known. Among trematodes parasitic in mammals, there is a negative correlation between the year in which a species was described and its body size; no such relationship is observed among trematodes parasitic in either birds or fish (Poulin 1996a). Similarly, this negative relationship is found among copepod species parasitic on fish but not among species parasitic on invertebrates (Poulin 1996a).

Clearly, our inventory of some parasite groups is more complete than that of other groups. Nevertheless, despite the many caveats discussed above, it is still possible and informative to investigate patterns in the diversity of parasites as a function of their own biology or that of their hosts.

PARASITE DIVERSITY IN DIFFERENT HOSTS

The rates at which animal lineages diversify over time, and the present-day spatial distribution of diversity, are both determined to some extent by the characteristics of the surrounding habitat (Ricklefs and Schluter 1993; Rosenzweig 1995). In other words, the diversity of species in a given habitat is dependent upon the probabilities of species colonizing the habitat, speciating within it, or going extinct in it. These probabilities depend in part on the properties of the habitat (MacArthur and Wilson 1967; Huston 1994). From the parasite's perspective, the host is the main habitat; it is therefore useful to examine parasite diversity as it relates to the type of host. At the very least, this can explain how the diversity of parasites is distributed among host taxa. By using a phylogenetic approach, however, it may also reveal which historical processes are responsible for observed patterns in parasite diversity.

Most work has focused on the parasites of vertebrates. We will use them to illustrate some concepts regarding parasite diversity and the importance of controlling for phylogeny, keeping in mind that many of these parasites also use invertebrates at some point in their life cycle. Except for pelagic seabirds and a few other hosts with depauperate parasite faunas (Hoberg 1996), aquatic vertebrates generally tend to harbor richer communities of parasitic helminths than their terrestrial counterparts (Figure 1). This pattern may reflect chance factors rather than ecological forces; if phylogenetic influences are removed by contrasting aquatic vertebrate lineages and their terrestrial sister taxa, the effect disappears (Poulin 1995c). Still, although the pattern is perhaps not caused by ecological divergence between aquatic and terrestrial hosts, it reflects the current distribution of helminth parasites among vertebrates.

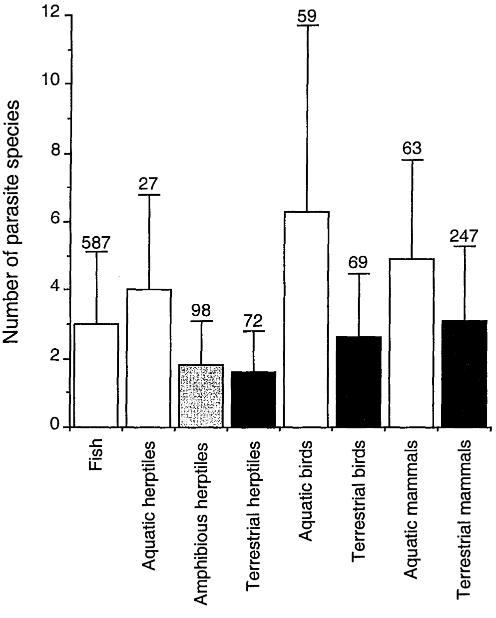

FIGURE 1. HELMINTH PARASITE DIVERSITY IN VERTEBRATES.

Mean (±SD) number of intestinal helminth parasite species per host population in different groups of vertebrates. Numbers above bars indicate the number of studies on which the estimate is based. The data cover 245 species of fish, 112 species of herptiles (amphibians + reptiles), 84 species of birds and 141 species of mammals (data from Bush et al. 1990).

Why do some vertebrate taxa harbor more parasite species than others? The answer may be found by examining the differences in diversity among host taxa themselves. Parasites tend to be very host-specific; they generally only infect one or very few host species. This feature may arise through the coevolution of host and parasite lineages, but it can also result from more immediate ecological phenomena. It was widely accepted some years ago that parasites tend to cospeciate with their hosts so that their phylogenies are, to a large extent, mirror images of one another (see Paterson et al. 1993). According to this scenario, an ancestral host species harboring one parasite species will, after several speciation and cospeciation events, generate *n* host species harboring a total of approximately *n* parasite species. However, recent critical assessments of the available evidence have revealed that cospeciation is not the rule after all (Klassen 1992; Brooks and McLennan 1993b; Hoberg 1997). In host-parasite systems that involve seabirds or pinnipeds and tapeworms, for instance, the transfer of parasites among hosts (i.e., the colonization of new hosts by parasites) has played a major role in the diversification of the parasite faunas (Hoberg 1992, 1995; Hoberg et al. 1997). In other systems, particularly those involving ectoparasitic arthropods and their vertebrate hosts, cospeciation has been extensive (Hafner and Nadler 1988; Paterson et al. 1993). Coevolutionary trajectories therefore vary among host-parasite systems, and one cannot simply assume that cospeciation or host colonization has been predominant.

It is still possible to test certain predictions based on the assumption that certain coevolutionary pathways have been followed more frequently than others. For instance, had cospeciation been the rule in a given host-parasite system, we might expect that the most speciose host taxa should harbor more parasite species than their less speciose sister taxa. The distribution of trematode species among the major vertebrate groups, however, suggests that other processes act on rates of diversification in these parasites (Figure 2). Mammals account for only a small proportion of known vertebrate species, but they host a relatively large share of known trematode species; amphibians and reptiles, on the other hand, represent a quarter of known vertebrates but are hosts to less than 10% of known trematodes.

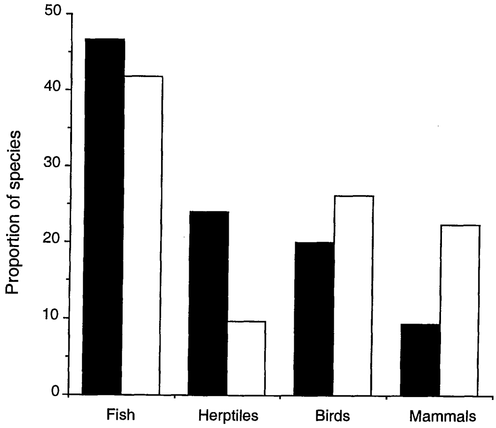

FIGURE 2. RELATIVE TREMATODE DIVERSITY IN VERTEBRATES.

Proportion of the total number of known vertebrate species belonging to four main taxonomic groups (black bars), and proportion of known trematode species parasitizing each of the groups (open bars). Vertebrate data are from Barnes (1998), and trematode data are from Gibson and Bray (1994).

Certain ecological traits of vertebrate hosts could facilitate parasite colonization or within-host speciation, creating differences in parasite species richness among host taxa and obscuring the influence of cospeciation (if it occurs). These features are more easily identified in analyses that involve related species within a taxon, rather than those that involve broad host taxa, because the number of biological differences between hosts is more refined. Comparative analyses of parasite species richness in vertebrates have flourished in recent years (reviewed by Poulin 1997). The most prevalent trend to emerge from these studies is that parasite species richness is positively correlated with various measures of the habitat size, as provided by the host species, such as host body size, population density or geographical range (e.g., Price and Clancy 1983; Gregory 1990; Bell and Burt 1991; Guégan et al. 1992; Krasnov et al. 1997; Sasal et al. 1997; Morand and Poulin 1998). These ecological parameters determine to some extent the likelihood that hosts encounter and are colonized by new parasite species, as well as the diversity of niches available to parasites. Some of these patterns disappear when corrections are made for phylogenetic effects, however, such as the positive correlation between avian body mass and the richness of helminth parasites (Poulin 1995c). Thus, observed patterns may sometimes be caused by the inheritance of ancestral parasites rather than by other evolutionary processes.

The patterns above reflect the distribution of parasite diversity among host species with respect to host features, not necessarily the rates of parasite diversification within these different hosts. In other words, the observed diversity of parasite communities in extant hosts may be the result of cospeciation and colonization events, without any speciation of parasite lineages within a host lineage (Vickery and Poulin 1998). Only the latter phenomenon could cause the proliferation of new species, but different approaches are necessary to distinguish its action. One would need, for example, to look for the occurrence of congeneric parasite species within the same host species to infer which host features facilitate parasite diversification. Multiple congeneric parasite species are commonly encountered within the same vertebrate host species (Schad 1963; Kennedy and Bush 1992). In communities of gastrointestinal parasites of vertebrates, genera represented by a single species are always more frequent than genera represented by two or more species (Kennedy and Bush 1992). Multiple congeners are not rare, however, and are more common in bird and mammal hosts than in fish or herptile hosts (Figure 3). By comparing Figures 1, 2 and 3, we might suggest that parasite speciation within a host lineage is more common in endotherms (birds and mammals) than in ectotherms, accounting for the relatively greater diversity of helminth parasites in birds and mammals. Multiple congeners are also more common in certain host-parasite associations, such as cestodes in aquatic birds, nematodes in certain herbivorous mammals, and monogeneans on freshwater fishes (Schad 1963; Inglis 1971; Kennedy and Bush 1992). Groups of coexisting, monophyletic species are often referred to as species flocks, and viewed as examples of high local rates of speciation and radiation (Mayr 1984). Whether multiple congeneric parasite species are species flocks or not is unclear, but an investigation into which host features are associated with the occurrence of multiple congeners might provide some clues regarding the determinants of parasite diversification.

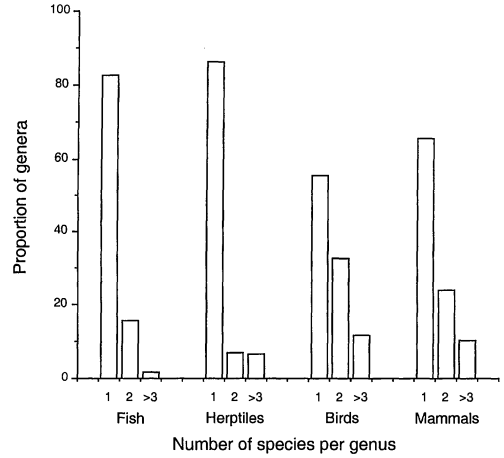

FIGURE 3. CONGENERS AND HELMINTH DIVERSITY.

Frequency of genera of intestinal helminth parasites represented by one, two or more species within a host population for the four main vertebrate taxonomic groups. Numbers of studies from which the data are derived are as in Figure 1 (data from Kennedy and Bush 1992).

DIVERSITY IN RELATION TO PARASITE TRAITS

Intrinsic properties of parasites could influence rates of diversification and create differences in diversity among parasite taxa, independent of the specific ecological characteristics of their hosts, but such effects are hard to isolate.

A relationship between body size and rates of diversification has been proposed for free-living organisms. Habitat heterogeneity is a function of scale, and is likely to be greater for small-bodied organisms. Hence, extinction and speciation rates may be size-dependent and favor the diversification of small-bodied organisms relative to large-bodied ones (Dial and Marzluff 1988; Maurer et al. 1992; Fenchel

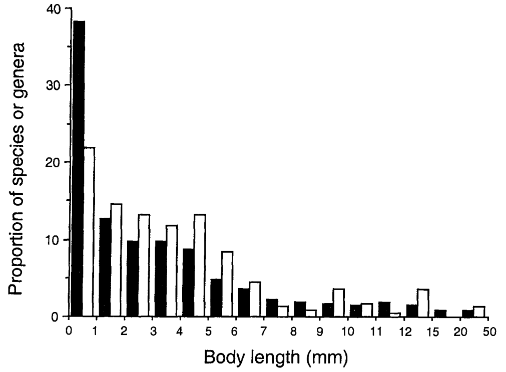

FIGURE 4. MONOGENEAN BODY SIZES.
Frequency distribution of body sizes among 613 monogenean species (black bars) and 228 genera (open bars) that are ectoparasitic on fish. Note the contraction of the scale on the right-hand side of the figure (data from Poulin 1996b).

1993). There is support for this hypothesis based on observations that compare the frequencies of different body sizes among animals. In most free-living animal taxa, body size distributions tend to be right-skewed, even on a logarithmic scale (Blackburn and Gaston 1994). In other words, smaller size classes are more speciose than larger size classes. Does this pattern also apply to parasitic taxa? It depends on the parasite group being investigated. For endoparasitic helminths, log body size distributions are usually right-skewed, whereas they are more likely to be symmetric among ectoparasitic helminths and arthropods (Poulin and Morand 1997). Body size may be more severely constrained among endoparasites—for which living space can be very limited—than among ectoparasites. It must be pointed out, however, that although body size distributions of ectoparasites are symmetric on a log scale, small-bodied species are still more numerous than large-bodied ones. This results from small-bodied genera being more speciose than large-bodied ones, as illustrated by monogeneans that are parasitic on fish (Figure 4).

Perhaps the greatest constraint on parasite evolution, from the perspective of diversification, is the complexity of parasite life cycles. Many helminth parasite lineages have evolved complex cycles that require passage through a specific sequence of host species for successful development and maturation. The complexity of the life cycle may influence the number of opportunities for speciation and diversification. In nematode parasites of vertebrates, the number of genera per family and the number of species per genus did not differ between taxa with simple life cycles (i.e., a single host) and taxa with complex cycles (Morand 1996a). There is therefore no evidence that the complexity of the life cycle is a moderating factor in nematode diversification.

The situation may be different in platyhelminths. The phylum includes two diverse groups of endoparasites with complex life cycles (the trematodes and the cestodes), a large group of ectoparasites with a simple life cycle (the monogeneans), and a few small groups of free-living, symbiotic or parasitic worms. Brooks and McLennan (1993a,b) compared the species richness in the different groups of platyhelminths from a phylogenetic perspective, and found that the high diversity of trematodes, cestodes and monogeneans was independently derived (i.e., it evolved independently in each taxon). Based on other evidence, however, they concluded that an adaptive radiation had occurred only in monogeneans, and not in the other two groups. The monogenean diversification was attributed to a key evolutionary innovation: the loss of one host species from the life cycle and a reversal to a simple, one-host cycle (Brooks and McLennan 1993a). This result would support the suggestion made earlier that complex life cycles may constrain parasite diversification. The conclusions of Brooks and McLennan (1993a,b), however, depend entirely on their phylogenetic hypothesis regarding the relationships among platyhelminth taxa and the evolution of life cycles. Other hypotheses exist, and lead to completely different interpretations (Rohde 1996). It is thus too early to assess the importance of the life cycle in promoting or limiting parasite speciation and diversification.

EPIDEMIOLOGY AND PARASITE DIVERSITY

The previous two sections summarized various attempts to relate parasite diversity with host or parasite characteristics from an ecological or evolutionary point of view. It is also possible to approach the issue from an epidemiological perspective. Epidemiological modeling has been a growing field of research over the past two decades (Anderson and May 1978; May and Anderson 1978; Dobson 1989; Grenfell 1992; Grenfell and Harwood 1997). Mathematical models of host-parasite relationships have been constructed in order to analyze the regulatory effects of parasites on host population dynamics (Anderson and May 1978; Dobson and Hudson 1992). Many other aspects of host-parasite interactions have been investigated using mathematical modeling, such as the evolution of host manipulation (Dobson 1988), the evolution of complex life cycles in parasites (Dobson and Merenlender 1991; Morand et al. 1995), and the evolution of virulence (van Baalen and Sabelis 1995; Frank 1996).

Mathematical epidemiology allows us to derive a measure of parasite invasiveness—the basic reproductive rate R_0—which is defined as the average number of new cases of infection (or new parasites) that arise from one infectious host (or one individual parasite) if introduced into a population of uninfected hosts (Anderson and May 1985). Although the basic reproductive rate is used mainly in discussions of parasite population biology (Dobson 1989; Morand et al. 1999) and/or for the control of parasitic disease (Anderson and May 1985; Woolhouse 1991), R_0 has received attention in the context of evolutionary epidemiology, such as the evolution of parasite virulence (see Frank 1996).

The basic reproductive rate can also be a useful tool for generating predictions on parasite diversity. For example, a directly transmitted parasite can be modeled by a set of differential equations: one that describes the host population (H) dynamics and one that describes the parasite population (P) dynamics. The basic reproductive rate R_0 is obtained by calculating the growth rate of the parasite population when one parasite is introduced into a population of noninfected hosts (see Anderson and May 1985 for derivation). For a directly transmitted macroparasite, the expression for the basic reproductive rate is:

$$R_0=\frac{\lambda\beta H}{(\mu_w+\beta H)(\mu_p+b+r+\alpha)}$$

where λ is the fecundity of adult parasites, b is the mortality rate of the hosts, β is the transmission rate, r the recovery rate, μ_w and μ_p are the mortality rates of free-living stages and adult stages of the parasites respectively, and α is the virulence (i.e., the parasite-induced host mortality).

In this expression, some parameters are intrinsic properties of the host (H and b), others of the parasite (λ, α, μ_w and μ_p), and β depends on the interaction between host and parasite. Indeed, β synthesizes the simultaneous action of numerous factors, such as host behavior, the active search of hosts by the parasites, or the environmental conditions.

A parasite can invade a host population if $R_0 > 1$. The spread of a parasite into a host population increases with an increase of host density (H) and/or parasite fecundity (λ), or with a decrease in host mortality rate (b). However, the spread of a parasite decreases with an increase in parasite mortality rates (both free-living and adult stages) and/or virulence (α).

The basic reproductive rate also leads to predictions about parasite species diversity (in this simple case of directly transmitted macroparasites), assuming that the conditions for parasite invasiveness apply to all such parasite species. The first series of predictions concern the influence of host life-history traits on parasite diversity. A host living at a high population density and/or having a long life span should harbor a richer fauna of parasite species than a related species living at a low density or with a shorter life span because high host densities and long life spans facilitate the invasion and spread of parasite species. Comparative analysis has shown that the parasite species richness of mammals is positively correlated with their population densities (Morand and Poulin 1998). Another comparative analysis on North American freshwater fishes has shown that their endoparasite species richness is positively correlated with their longevity (Morand 2000; Figure 5). Dobson and Roberts (1994), using a different mathematical approach, similarly concluded that host longevity and the growth rate of the host population determine the diversity of their parasite communities.

The second series of predictions concern the influence of parasite life-history traits on parasite diversity. Ignoring the influence of host traits, a nonvirulent parasite with low

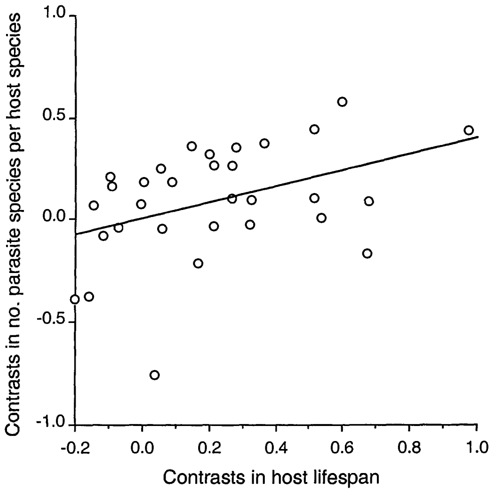

FIGURE 5. HOST LIFE SPAN AND PARASITE DIVERSITY.

Relationship between the number of endoparasitic helminth species per host species and the maximum life span of the host, across species of North American freshwater fishes; the correlation is significant ($r=0.465$, $P=0.0073$). Points are phylogenetically independent contrasts computed on log-transformed variables (data from Morand 2000).

mortality rate and high fecundity would be more easily sustained by the host population than would one with high virulence, high mortality rates and low fecundity. Several theoretical and empirical studies, however, have emphasized that the observed virulence of a parasite is the result of a trade-off between virulence and transmission (β) and may depend on local conditions (Ewald 1994; Frank 1996). Hence, virulence may vary between populations of a given parasite species, and may not be linked with parasite diversity.

We might thus expect that the richness of parasite communities of different host species will reflect some of the epidemiological parameters of both hosts and parasites. However, parasite life-history traits are correlated with each other (Skorping et al. 1991; Morand 1996b). Across nematode species, high fecundity is related to large body size, which positively correlates with adult parasite longevity, whereas high fecundity is negatively correlated with offspring longevity (Morand 1996b). Conversely, the same relationships apply to host life-history traits. Host density is negatively correlated with host body size in many groups, whereas body size can be linked with longevity (Brown 1995). It would thus be necessary to incorporate the above relationships into the basic transmission rate. This new framework could then be used to provide testable predictions that link parasite diversity to life-history traits of both parasites and their hosts. Most of these predictions are similar to the ones derived from ecological theory; they are based on island biogeographic theory and species-area curves (see previous section).

The preceding discussion focuses on the potential of epidemiological models in predicting the actual distribution of parasite diversity among host species. The same approach can also be used to predict the rates of speciation and diversification in different parasite taxa. If parasite species with high R_0 can easily invade, spread and persist in a host population over ecological time, they may also be capable of colonizing and persisting in new host species over evolutionary time. With the subsequent cospeciation of hosts and parasites, the result is a greater likelihood of diversification in taxa with high R_0. One testable prediction would be that parasite taxa—for example, genera—characterized by high R_0 values should be more speciose than related taxa characterized by lower R_0 values. Integrating epidemiological information with studies of parasite diversity is clearly a fruitful avenue for future research.

BIOGEOGRAPHY OF PARASITE DIVERSITY

The geographic component of species diversity is of great interest (Ricklefs and Schluter 1993; Rosenzweig 1995). Are there regions in which we find proportionally more parasite species? Has parasite diversification somehow been facilitated in these regions? Some trends in the biogeography of parasitoid diversity have been demonstrated (Hawkins 1994). Parasites, in the strict sense used in this review, have not received much attention to date, except for some studies on the relationship between local and regional richness in parasite communities (e.g., Kennedy and Guégan 1994), which becomes established on much smaller spatial and time scales than the ones necessary for the evolutionary diversification discussed here. Nevertheless, some biogeographic patterns worth mentioning have emerged.

The main pitfall in biogeographic studies of relatively poorly known organisms such as parasites is the risk that a map of the distribution of diversity among geographic regions merely reflects the variability in research activity among the different parts of the world. Some correction for research effort is therefore necessary when one uses inventories of known species sampled from the literature. Even when such a correction is made, however, the results may be difficult to interpret (see Gibson and Bray 1994). This may be because most null hypotheses assume an even distribution of parasites and their hosts within geographic areas. Thus it is probably more informative to focus on a subset of parasites from a limited number of regions for which reliable information is available.

Biogeographical patterns are best known for the metazoan parasites of marine fish (see Rohde 1993). Only a fraction of the faunas of marine fish and their parasites has been studied, but two main patterns have emerged: the diversity of parasitic helminths is greater in the Indo-Pacific than in the Atlantic Ocean, and the diversity of monogenean parasites (and other groups of ectoparasites, to a lesser degree) increases with decreasing latitude or increasing water temperature (Rohde 1978, 1980, 1993; Rohde and Heap 1998). A simple explanation for these results might be that there are more parasite species in regions inhabited by more host species. If cospeciation were the rule in the evolutionary history of host-parasite associations (Brooks and McLennan 1993b; Paterson et al. 1993; Hoberg et al. 1997), this would be a reasonable null hypothesis in all biogeographical studies of parasite diversity. For example, among different North American rivers, the local diversity of unionid mussel species, whose larvae are parasitic on fish, is strongly correlated with the number of potential host fish species (Watters 1992). This simple explanation, however, is not sufficient to account for the oceanic patterns reported by Rohde (1978, 1980, 1993). Using the number of parasite species per host species examined as a measure of relative diversity, parasite diversity is again greater in the Indo-Pacific or in warm waters than in the Atlantic or in cold seas.

Rohde (1993) proposes that the greater age of the Pacific Ocean could account for the greater diversity of fish parasites. The latitudinal gradient in the diversity of monogeneans and other ectoparasites of marine fish could have several causes, some of which appear unlikely. For instance, the host specificity of monogeneans does not vary with latitude (Rohde 1978), so the greater relative diversity of parasites found in tropical fish is not simply the outcome of these parasites' exploitation of a greater number of host species. Also, the trend is not the product of unequal sampling effort, nor is it a phylogenetic artifact that could have resulted from fish lineages harboring diverse parasite faunas that colonized warm waters long ago; the effect of latitude or water temperature on parasite diversity appears authentic (Poulin and Rohde 1997; Rohde and Heap 1998). Other explanations exist, however, derived from the energy hypothesis, which states that species diversity is a function of the solar energy that enters an ecosystem (e.g., Currie 1991). One of these explanations is that taxa in warm waters have higher rates of diversification because the shorter generation times and higher mutation rates caused by the higher temperatures may lead to evolution itself proceeding at a greater pace (Rohde 1992, 1998). The proposed link with generation times suggests a role for epidemiological parameters, as proposed in the previous section. Thus, according to Rohde (1992), over the same time period, and assuming a nonequilibrium state in which fish do not become saturated with parasite species, higher speciation rates in warm seas would lead to a greater parasite species diversity than in colder waters. This hypothesis cannot account for the different latitudinal gradients in species diversity observed in ectoparasites and endoparasites of marine fish (Figure 6). Intestinal helminths living in ectothermic fish hosts are also exposed to external water temperatures, but they have not diversified at a higher rate in the tropics. Rohde and Heap (1998) propose that other biological differences between internal and external fish parasites can explain the absence of latitudinal diversity gradients in endoparasites.

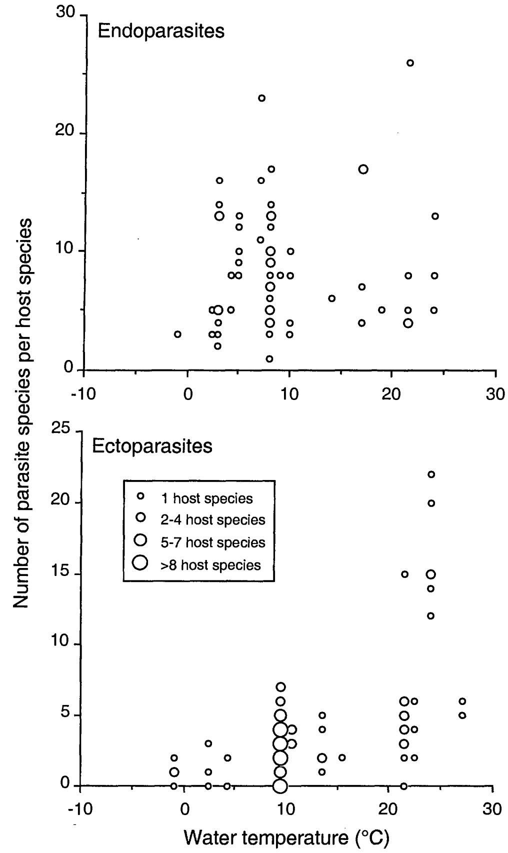

FIGURE 6. WATER TEMPERATURE AND PARASITE DIVERSITY.

Relationship between the number of parasite species per host species and the water temperature at the site of sampling. Results for endoparasitic helminths from 55 marine fish species (62 populations) and for ectoparasitic metazoans from 108 marine fish species (109 populations) are shown separately (data from Rohde and Heap 1998).

Temperature-mediated diversification is an interesting hypothesis that should apply equally well to all organisms, whether parasitic or not (Rohde 1992). It is, however, not the only explanation for the latitudinal gradient in the diversity of ectoparasites of marine fish. Other comparative studies have shown that the body sizes of fish ectoparasites, such as monogeneans, decrease with decreasing latitudes (Poulin 1995a, 1996b). As discussed in the previous section, diversification may generally be greater in small-bodied taxa. Thus the greater diversity of fish ectoparasites in the tropics could result from greater diversification rates caused by both temperature and parasite body sizes; the two explanations are not mutually exclusive.

This example illustrates the sort of challenges waiting for those who attempt investigations into the biogeography of parasite species diversity. In the future, more use should be made of the rapidly accumulating information on host and parasite phylogenies in tests of biogeographical hypotheses. Previous work done at smaller taxonomic and geographical scales (e.g., Brooks and McLennan 1993b; Hoberg 1997) has shown how a phylogeographic perspective could shed new light on the large-scale patterns discussed above.

CONCLUSIONS

We are far from a complete knowledge of all the species sharing the planet with us (Groombridge 1992), and this is even more true for parasite species (Poulin 1996a). From the available information about parasite diversity summarized here, it is clear that we currently know more about the ecology of diversity than about its evolution. In other words, we know more about patterns in the distribution of parasite diversity among host species or geographical areas than we know about the factors that determine rates of speciation, extinction and diversification in different parasite taxa. Part of the remedy resides in the development of robust phylogenies of hosts and parasites, and in their use to test ideas regarding historical biogeography and the processes involved in parasite diversification.

Parasite taxa offer excellent opportunities for the study of evolutionary processes that generate diversity. This is true because of their great specialization, which may have promoted sympatric speciation and diversification (de Meeûs et al. 1998), and because the numerous independent lineages in which parasitism has evolved allow hypotheses to be tested with replication. The marriage between traditional ecological perspectives and epidemiological theory should generate testable predictions regarding the effect of the basic reproductive rate (R_0), and of the various parameters which contribute to R_0, on evolutionary rates of diversification. For many parasitic taxa, there now exist enough data on species richness to allow investigations of the influence of other parasite traits or host features on the diversification of parasite lineages, such as attempted by Brooks and McLennan (1993a) at a broad taxonomic level. Also, there are no meaningful estimates of parasite extinction rates at present (Bush and Kennedy 1994; but see Paterson et al. 1999), although there are enough data for such rates to be quantified with reasonable accuracy in several taxa.

The comparative tools and raw data are available for such investigations, and their time has come. We now have sufficient information on the general patterns of parasite diversity. Future research should specifically attempt to identify the processes responsible for those patterns, in as many parasite taxa as possible and integrating all modern phylogenetic and ecological approaches.

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