



Macroecological patterns of species richness in parasite assemblages

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Summary

The diversity of parasite species exploiting a host population varies substantially among different host species. This review summarizes the main predictions generated by the two main theoretical frameworks used to study parasite diversity. The first is island biogeography theory, which predicts that host features, such as body size, that are associated with the probability of colonization by new parasite species, should covary with parasite species richness. The second predictive framework derives from epidemiological modelling; it predicts that host species with features that increase parasite transmission success among host individuals, such as high population density, will sustain a greater diversity of parasite species. A survey of comparative studies of parasite diversity among fish and mammalian host species finds support for most of the predictions derived from the above two theoretical perspectives. This empirical support, however, is not universal. It is often qualitative only, because quantitative predictions are lacking. Finally, the amount of variance in parasite diversity explained by host features is generally low. To move forward, the search for the determinants of parasite diversity will need to rely less on theories developed for free-living organisms, and more on its own set of hypotheses incorporating specific host–parasite interactions such as immune responses.

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Zusammenfassung

Die Diversität der Parasitenarten, die eine Wirtspopulation nutzen, variiert erheblich zwischen verschiedenen Wirtsarten. Dieser Review fasst die hauptsächlichen Vorhersagen zusammen, die von den zwei wichtigsten theoretischen Rahmenkonzepten hervorgebracht werden, die für die Untersuchung der Parasiten Diversität genutzt werden. Die erste ist die Inselbiogeografie, die vorhersagt, dass Wirtsmerkmale, die mit der Besiedlungswahrscheinlichkeit durch einen neuen Parasiten verknüpft sind, wie beispielsweise die Körpergröße, mit dem Artenreichtum der Parasiten kovariieren sollten. Das zweite Rahmenkonzept ist aus der epidemiologischen Modellierung

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abgeleitet. Es sagt vorher, dass Wirtsarten mit Merkmalen, die den Übertragungserfolg der Parasiten zwischen den Wirtsindividuen erhöhen, wie beispielsweise hohe Populationsdichten, eine größere Diversität von Parasitenarten erhalten werden. Eine Begutachtung von vergleichenden Untersuchungen über Parasitendiversität bei Fischen und Säugetieren als Wirtsarten unterstützt die meisten der Vorhersagen, die von den oben genannten zwei theoretischen Perspektiven abgeleitet sind. Diese empirische Bestätigung ist jedoch nicht allgemein gültig. Sie ist häufig nur qualitativ, da quantitative Vorhersagen fehlen. Schließlich ist der Anteil der Varianz in der Parasitendiversität, der durch die Wirtsmerkmale erklärt wird, normalerweise gering. Um vorwärts zu kommen muss sich die Suche nach den bestimmenden Faktoren der Parasitendiversität weniger auf Theorien, die für freilebende Organismen entwickelt wurden, und mehr auf ihre eigene Menge von Hypothesen verlassen, die spezifische Wirt-Parasit-Interaktionen, wie beispielsweise Immunreaktionen, mit einbeziehen.

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Introduction

Understanding the determinants of spatial variation in species diversity remains a fundamental problem at the core of modern ecology (Hawkins, 2004). Most ecologists now accept that, at large macroecological scales, patterns in species diversity are caused by a variety of ecological and evolutionary processes, as well as historical and geographical contingencies (Strong, Simberloff, Abele, & Thistle, 1984; Ricklefs & Schluter, 1993; see also Turner, 2004). Untangling the respective influences of these different factors is not always straightforward, however. For instance, to isolate the impact of a given ecological process on patterns of species diversity across different habitats, one would need to remove (in a statistical sense) the influences of biogeographical or historical events that may have affected species diversity in those habitats. This step is sometimes possible, when the geological origins of habitats such as lakes or islands are well known, but often not because of our incomplete knowledge of the deep or recent history of most types of habitats.

This is where the study of patterns in parasite species diversity across different host species can make an important contribution to macroecology. Host species within a taxonomic group are genealogically linked by common descent. With molecular phylogenies now available for a wide range of taxa, it is possible to know the precise relationships between species. For example, for the three species A, B and C, we can determine which of B or C is the most closely related to A, how long ago they diverged from one another, etc. Host species are habitats for parasites; unlike habitats of free-living species, their history and relationships can be elucidated precisely. Resolving the phylogeny of host species provides the historical framework against which hypotheses regarding the role of

ecological processes can be tested (see also Blackburn, 2004). Several comparative methods have been developed that correct for phylogenetic influences (Felsenstein, 1985; Harvey & Pagel, 1991), thus allowing ecological influences to be measured accurately. The physiological and immunological interactions of parasites with their host habitats have no parallel among free-living organisms occupying aquatic or terrestrial habitats; nevertheless, many ecological determinants of species diversity are shared among these different biota, and what we learn about the patterns of parasite diversity can shed light on the patterns of animal diversity in general.

This review will explore patterns in the diversity of parasite assemblages across different host species. The focus will be on the simplest, most intuitive component of diversity, i.e. species richness or the number of species in an assemblage. I will first present some necessary and important background for the study of parasite assemblages. Then, I will present two theoretical approaches to the study of variation in parasite species richness, and the predictions they make about the influence of various ecological factors. Next, I will present empirical evidence from a range of studies on two groups of hosts, fish and mammals. Finally, I draw general conclusions about the current state of our knowledge of the determinants of parasite species richness.

Background in parasite community ecology and evolution

The term *assemblage* is used here to refer to all parasite species found within one microhabitat in or on the host (e.g. the gastrointestinal tract or the external surfaces). I prefer to avoid the related

terms *community* and *guild* because their use often implies that the species within them are interacting, and this may not always be the case in parasite assemblages.

The parasite species exploiting a host species can be studied at several hierarchical levels (see Holmes & Price, 1986; Bush, Lafferty, Lotz, & Shostak, 1997; Poulin, 1998a). These levels are defined by the choice of physical scale for the study of parasite assemblages (Fig. 1). At the lowest level and smallest scale we have the *infracommunity*, comprising all parasites of different species within the same host individual. Infracommunities are short lived, their maximum lifespan being that of the host. During that time, they are in constant turnover because of the recruitment of new parasites from the pool of locally available species, and the death of old ones. Because examination of different host individuals from the same population allows the census of several replicate infracommunities, robust statistical tests of species interactions or deviations from null models of species assembly are possible at this level (e.g. Lotz & Font, 1991; Poulin, 1996; Poulin & Guégan, 2000).

The next level up is that of the *component community*, which consists of all parasite species

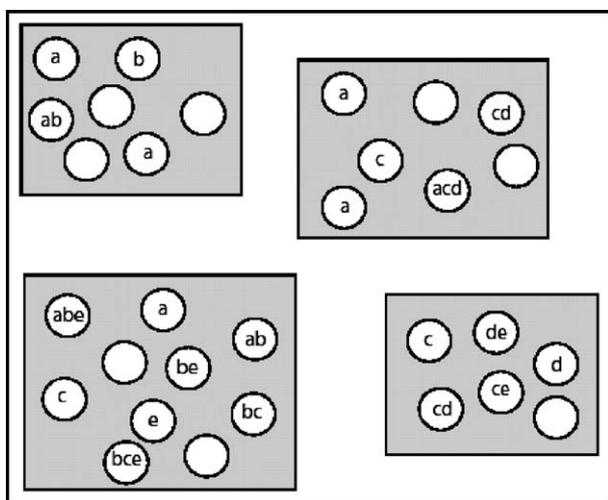


Figure 1. Schematic representation of the hierarchical nature of parasite assemblages. The outer box represents the *parasite fauna* of a host species, which in this case includes five parasite species (a–e); it is the sum of the parasite species found in the various populations (grey boxes) that make up the host species. Each grey box contains a *parasite component community*, which consists of all parasites of all species exploiting the host population; usually, these parasite species are only a subset of those found in the parasite fauna. Within a host population, some host individuals (circles) are uninfected, whereas others each harbour an *infracommunity* of parasites, i.e. the ensemble of all parasites of all species found in an individual host.

exploiting a host population at a given point in time. The component community provides the local pool of parasite species from which infracommunities are formed. It is a longer-lived assemblage; its richness decreases as certain parasite species become locally extinct, and increases as others colonize the host population from other, nearby populations. The similarity in species composition between the component parasite communities of different host populations will depend on their geographical proximity to one another and on the possibilities of parasite exchanges among them (Esch, Kennedy, Bush, & Aho, 1988; Poulin & Morand, 1999). No single host population (i.e. component community) is likely to include all species of parasites known to exploit the host species; instead, each component community is a subset of a larger collection of species referred to as the *parasite fauna* of the host species. Parasite faunas represent the highest hierarchical level of organization of parasite assemblages; they are artificial rather than biological entities, but have nevertheless been the subject of many macroecological studies. In fact, the studies discussed later use data from either the component community level or the parasite fauna level; these are at the relevant scales for macroecological comparisons among host species.

As we will see in later sections, several ecological processes can influence the probabilities of parasite extinction, colonization and even speciation within a given host population (component community) or host species (parasite fauna). From an evolutionary perspective, there are three general explanations for the origins of any parasite species in a parasite fauna (Paterson & Gray, 1997; Vickery & Poulin, 1998; Page, 2003). First, a parasite species may have been inherited by the host species from its ancestor, i.e. parasite species of an ancestral host species are passed down to daughter host species during host speciation (Fig. 2). Such parasite species will be shared with closely related host species (the parasites may have speciated on their own and now be different species, but they are still sibling species inherited from the same ancestor). This is why it is important to control for host phylogenetic influences in comparative analyses of parasite species richness: inherited parasite species are not the product of ecological processes, and can mask patterns of variation resulting from these processes. Second, a parasite species may have colonized the host species, jumping ship from another, sympatric host species (Fig. 2). Host switching is possible provided that the new host species is immunologically and physiologically similar to the original host. Third, a

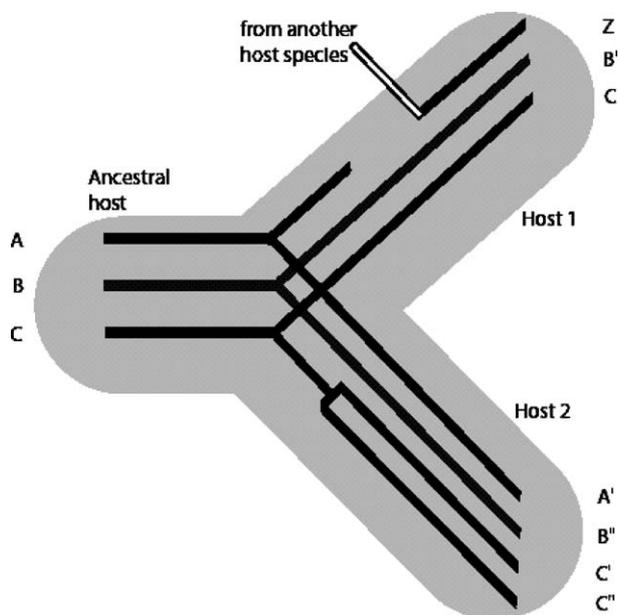


Figure 2. Summary of the evolutionary events accounting for the present richness of different parasite assemblages. Host species 1 and 2 are sister-taxa issued from a common ancestral host species, as indicated by the divergence of the shaded path. They have each inherited certain parasites from their ancestor, such as parasite lineage B (called B' and B'' in the daughter host species because the parasites may have speciated as well). New parasite species may also be acquired via intra-host speciation (e.g. parasite lineage C in host 2) or by colonization from sympatric host species (parasite Z in host 1). Parasite lineages may also go extinct (e.g. parasite A in host 1).

parasite species may be the outcome of an intra-host speciation event, i.e. an ancestral parasite species giving rise to one or more daughter species all within the same host species, without host speciation (Fig. 2). This phenomenon may not be common, but it could account for the presence of many congeneric parasite species in certain host species (Kennedy & Bush, 1992; Poulin, 1999; Beveridge, Chilton, & Spratt, 2002).

There are also two ways in which parasite species may be lost from component communities or parasite faunas (Paterson & Gray, 1997; Vickery & Poulin, 1998; Page, 2003). They may either miss the boat during a host speciation event, such that the founder host population giving rise to a new daughter host species happens to be parasite-free, or go extinct at a later stage (Fig. 2). The likelihood of losing or acquiring parasite species by a parasite fauna over evolutionary time is most probably related to the ecological characteristics of the host species; let us now see how this might work.

Theory and predictions

Two theoretical frameworks have served as the foundation for predictive hypotheses regarding the role of ecological factors in determining parasite species richness in different host species. The first one is the classical theory of island biogeography of MacArthur and Wilson (1967), and the second one is the epidemiological theory that grew out of mathematical models of host–parasite interactions (e.g. Anderson & May, 1985; Dobson, 1989; Roberts et al., 2002).

The theory of island biogeography postulates that the equilibrium number of species on an island reflects the balance between the rate at which new species colonize the island, and the rate at which species go extinct on the island. These rates are influenced by various features of islands, such as their size or their distance from the mainland. Although the analogy shows some weaknesses, hosts can be viewed as islands for parasite colonization (Kuris, Blaustein, & Alió, 1980). In this case, the number of parasite species exploiting a host population (component community level) or a host species (parasite fauna level) should be the product of the rate at which new parasite species colonize the host or arise by intra-host speciation, and the rate at which they go extinct. There is one key difference between hosts and true islands, though: whereas new islands are free of animal and plant species, new host species inherit some parasite species from their ancestors (Fig. 2). Thus, rates of colonization and extinction will cause related host species to have different parasite species richness, but they will most likely have common components in their parasite faunas.

Several ecological features of the host can modulate the rates of parasite acquisition and parasite loss. For instance, host species with large geographical ranges will have a distribution that overlaps with the ranges of several other host species, and they will therefore have greater chances of acquiring new parasite species via colonization. This is similar with islands that are close to the mainland having higher probabilities of being colonized by mainland species. We would thus expect that, all else being equal, there should be a positive, interspecific relationship between parasite species richness and host geographical range (Fig. 3). Several other host characteristics are also likely to affect the rates of parasite colonization (or intra-host speciation) and extinction. The one most often invoked is host body size; larger host species provide more space and other resources for parasites and may be able to support

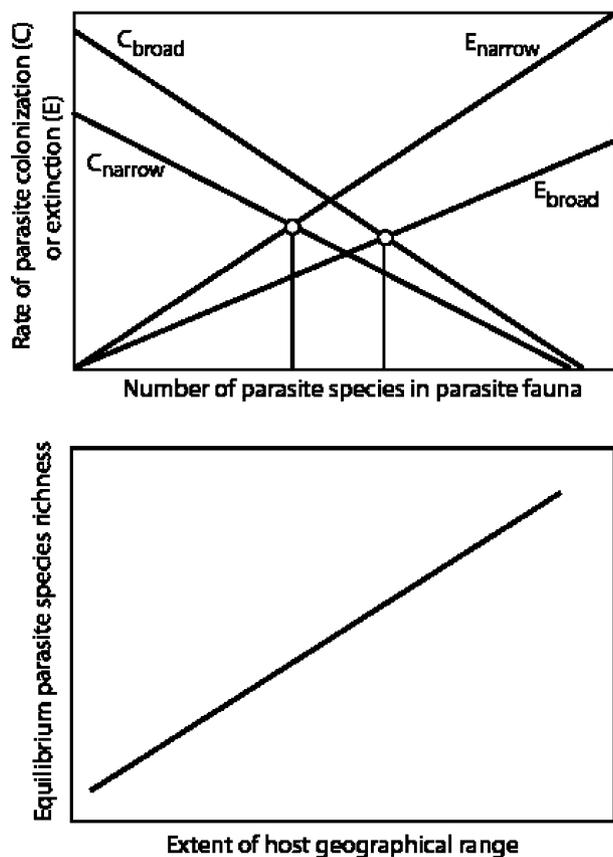


Figure 3. Use of biogeography theory to make predictions regarding parasite species richness. (Top) The equilibrium parasite species richness in a host species reflects the balance between the rates of parasite colonization and extinction (i.e. the intersection between the lines in the figure), as shown here for hosts with either a narrow or a broad geographical range. Colonization rates are assumed to be higher, and extinction rates lower, on host species with broad geographical ranges. (Bottom) Predicted relationship between host geographical range and parasite species richness, from the above figure.

richer faunas. The assumptions on which the link between host body size and parasite species richness is based are basically the same that support species–area relationships in free-living assemblages (see Gaston & Blackburn, 2000). Other important host features include population density, social behaviour, lifespan and diet (Poulin, 1998a; Morand, 2000). They all affect the likelihood that parasite species will colonize and/or persist in new host species, by influencing either the types of parasites that the host will encounter, how easy it will be for them to be transmitted among host individuals, or the permanency of the host as a habitat. One common problem facing anyone attempting to unravel the relationships between these features of hosts and parasite species

richness is the issue of *causality*. It is not straightforward to identify which of these factors matters the most because they are usually highly correlated with one another: for instance, large-bodied hosts are also long-lived and they tend to occur at lower population densities. Even if the main covariate of parasite species richness can be isolated, its association with species richness may be merely coincidental, and not a causal relationship. Nevertheless, several predictions can be made based on an application of island biogeography theory to parasite diversity: parasite species richness should be higher in large-bodied, long-lived host species with dense populations, broad geographical ranges and broad diets. As a rule, these predictions are *qualitative* rather than *quantitative*, i.e. we can predict a general increase in parasite species richness with increasing host body size, but there is no way of predicting how many more parasite species should be expected when host body size is doubled.

The second theoretical framework from which predictions have been derived regarding parasite species richness is an extension of the epidemiological models that were constructed to explain and predict the spread and maintenance of parasitic diseases (Anderson & May, 1985; Dobson, 1989). The use of epidemiological theory for the study of parasite species richness is a relatively recent development (Poulin & Morand, 2000). Epidemiological models allow us to derive a measure of parasite invasiveness, the basic reproductive rate R_0 . It is defined, in the case of metazoan parasites such as helminths and arthropods, as the expected lifetime reproductive success of a single parasite introduced into a population of uninfected hosts. A parasite can invade a host population and persist in it if $R_0 > 1$. The exact mathematical expression for R_0 is obtained from the set of differential equations that describe the host and parasite population dynamics, and thus depends on the type of parasite under consideration (e.g. directly transmitted parasites versus parasites with complex life cycles). In all cases, however, some of the parameters that influence R_0 correspond to intrinsic properties of the host. These include features that will affect parasite transmission, such as host social behaviour or population density. All else being equal, then, we would expect that interspecific variation among hosts in these features should affect the likelihood that various parasite species can achieve threshold R_0 values in these hosts: host species with features favouring high R_0 values should be easier to colonize by new parasite species, and should therefore harbour richer parasite faunas (Roberts et al., 2002). As with predictions issued from an

application of island biogeography theory, the predicted patterns in parasite species richness issued from epidemiological models tend to be qualitative rather than quantitative, i.e. we can predict the direction of a relationship but not its strength or magnitude. For this reason, and because the predictions of island biogeography and epidemiology overlap greatly, it is difficult to distinguish between the two theoretical frameworks in empirical tests. This is not entirely surprising, as the two theoretical approaches are centred on the probability that a species will become established in a new habitat (host); any distinction between them and their predictions may be more artificial than biological.

A third kind of explanation has been used in the context of patterns in parasite species richness. Unlike the two theoretical frameworks presented above, this third explanation is derived from well-known biogeographical patterns of organismal diversity via a simple extension to parasites. Specifically, there are well-documented latitudinal gradients in animal and plant diversity (e.g. Rosenzweig, 1995), and it can be argued that these should also apply to parasites. We may thus expect generally higher parasite diversity in the tropics than in temperate areas. Of course, if parasite diversity and host diversity increase similarly with decreasing latitude, the mean number of parasite species per host species may remain the same. Rohde (1992, 1998) has argued, however, that higher temperatures in the tropics should be associated with shorter generation times and higher rates of mutation, and thus higher evolutionary rates and speciation rates (see also Turner, 2004). He argues that ectoparasites, exposed to external environmental temperatures, should speciate at higher rates in the tropics, and the richness of ectoparasite faunas should therefore be higher on tropical hosts than on related temperate hosts.

When attempting to test these many predictions across host species, one should be wary of two potentially important confounding variables. The first is the phylogenetic history of the host species. As emphasized earlier, many parasitic lineages will be shared by related host species because of common ancestry and not as a result of any parasite diversification processes. If we are to identify the evolutionary or ecological processes responsible for the diversification of parasite faunas, we must distinguish between the inherited component of parasite species richness, and its acquired component, when dealing with different host species or lineages. Several comparative methods are available that do just that (Harvey & Pagel, 1991). The second potential problem in comparative analyses

of parasite species richness is unequal sampling effort among the different host species (Walther, Cotgreave, Price, Gregory, & Clayton, 1995; Poulin, 1998a). As more individuals of a host population or species are examined, the number of known parasite species in the parasite fauna increases asymptotically towards the true richness value (Fig. 4). Approximately one-third of helminth parasite species from bird and mammal hosts occur in fewer than 5% of host individuals (Poulin, 1998b); many of these rare species will be missed in surveys that rely on inadequate sample sizes. This means that a parasite fauna with few known species is either truly species-poor, or some of its component species have been overlooked. There are many ways to deal with unequal sampling effort as a confounding factor in comparative analysis. If detailed data are available, it is possible to use nonparametric estimation methods to extrapolate the likely number of parasite species missed by inadequate sampling, and add those to the number of recorded species for each host species (Poulin, 1998b; Walther & Morand, 1998). Alternatively, one can include sample size as a variable in a multivariate analysis to correct for its effect and get a better idea of the influence of other variables on parasite species richness. The results presented in the following section are based on analyses that have accounted for the potential effects of unequal sampling effort.

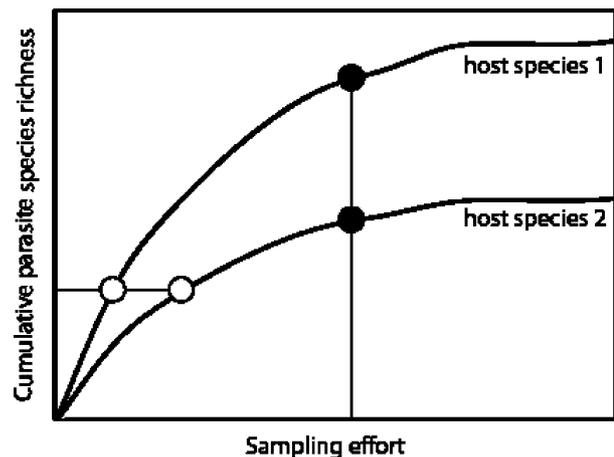


Figure 4. Parasite species accumulation curves for two hypothetical host species. As sampling effort (e.g. the number of host individuals examined) increases, the number of parasite species found approaches the true parasite species richness (the asymptote). For a given sampling effort, more parasite species will be recorded from host species harbouring richer parasite faunas (black circles). However, when identical numbers of parasite species are reported from different host species (open circles), the apparent similarity in parasite species richness may be an artefact of unequal sampling effort.

Empirical evidence

The purpose of this section is not to present a comprehensive review of the empirical studies on patterns of parasite species diversity, but rather to provide an overview of research on two groups of hosts: mammals and their helminth parasites, and fish and their helminth endoparasites and metazoan ectoparasites. Key results will be summarized verbally rather than being described in detail. Other groups of hosts, such as birds (e.g. Gregory, 1990; Gregory, Keymer, & Harvey, 1991; Poulin, 1995), have also been the focus of recent research, but studies on mammalian and fish host will suffice to expose key trends and pitfalls in macroecological analyses of parasite diversity. More exhaustive reviews of all studies of this kind are provided by Poulin (1997) and Morand (2000).

Mammalian hosts

Mammalian body sizes range over several orders of magnitude, from small rodents and insectivores to gigantic elephants and whales. Surely in this group, host body size could be a key determinant of the variability in parasite species richness among host species. The first comparative test of the effect of mammalian body size on parasite species richness included data on the gastrointestinal parasite faunas of 114 species of mammals (Poulin, 1995). The analysis of these data revealed that, across species values not corrected for possible phylogenetic effects, there was a relatively strong positive correlation between host body mass and parasite species richness; following the removal of phylogenetic influences by using the independent contrasts method (Felsenstein, 1985; Harvey & Pagel, 1991), the correlation disappeared. Essentially identical results were obtained in subsequent analyses based on similar or different data sets (Watve & Sukumar, 1995; Gregory, Keymer, & Harvey, 1996; Morand & Poulin, 1998). These findings suggest that, on average, large-bodied mammal species harbour more species of helminth parasites than small-bodied mammals, but that this pattern is explained mainly by inheritance of ancestral parasites and not by more recent processes linked with their body size per se. Similarly, host body size did not influence the rates of diversification (via intra-host speciation) of helminth faunas of mammals, as indicated by the occurrence of congeneric parasite species across mammalian hosts (Poulin, 1999).

If host body size is not important in explaining the interspecific variability among mammals in parasite species richness that is not accounted for

by inheritance of shared parasites from an ancestor, then what factors are? Other comparative analyses have found that, after controlling for phylogenetic effects, factors such as host population density, geographical range, longevity and metabolism all correlate with the richness of the helminth faunas of mammals (Feliu et al., 1997; Morand & Poulin, 1998; Morand & Harvey, 2000; Arneberg, 2002; but see Watve & Sukumar, 1995). Ironically, these mammalian features generally covary with body size, and it is therefore surprising that body size itself does not correlate with helminth species richness. At present, there is no satisfactory or universal explanation for the interspecific variability in parasite species richness among mammals.

Fish hosts

Among vertebrate hosts, fish, both marine and freshwater, have received the most attention from ecologists with respect to the richness of their parasite fauna. It is important to distinguish between endoparasites and ectoparasites for at least three reasons. First, endoparasitic worms living in the gastrointestinal tract all have complex life cycles involving at least two host species, and are acquired by fish hosts via ingestion, whereas ectoparasitic metazoans (copepods and monogeneans, mainly) have direct life cycles and infect fish via free-swimming infective larvae. Second, the diversity of ectoparasites per host species is typically greater than that of endoparasites (e.g. Rohde & Heap, 1998). Monogeneans and copepods living on the external surfaces of fish are exposed to strong water currents that make robust attachment and copulatory organs necessary. These structures can change significantly following single or very few mutations, a phenomenon that could lead to reproductive segregation and hence speciation rates higher than those of endoparasites (Rohde, 2002). Third, endoparasites often occur at much higher abundance than ectoparasites. For these reasons, they will be discussed separately in the first part of this section.

Let us first look at endoparasites. Most of the earliest analyses did not control for potential phylogenetic influences. These studies reported apparent effects of host body size and host geographical range, and in some cases also effects of other variables such as host diet (Price & Clancy, 1983; Gregory, 1990; Bell & Burt, 1991; Chandler & Cabana, 1991; Aho & Bush, 1993; Guégan & Kennedy, 1993). In some of the analyses, controlling for sampling effort tended to decrease the magnitude of the remaining correlation between

any ecological feature of the host and parasite species richness. Later studies included a correction for phylogenetic influences, and produced contrasting results. Some, based on large data sets built from published sources, confirmed a general positive correlation between fish body size and endoparasite species richness (Poulin, 1995; Gregory et al., 1996); others, based on more restricted data sets on marine fish only, did not (Sasal, Morand, & Guégan, 1997; Morand et al., 2000). Other factors emerged as important after phylogenetic influences were removed from the analyses, such as host lifespan (Fig. 5), host density, or host diet. At present, it appears that several predictions from island biogeography theory or epidemiological theory are supported by some studies on fish hosts, but that none receives universal support. Depending on the group of fish studied or their habitat, one or another host feature may have proven important in shaping parasite faunas, but the nature of this feature varies.

The case of ectoparasites is more clear-cut. As a rule, fish body sizes correlates positively, though sometimes not quite significantly, with ectoparasite species richness, even after correction for potential effects of host phylogenetic relationships (Guégan, Lambert, Lévêque, Combes, & Euzet, 1992; Poulin, 1995; Rohde, Hayward, & Heap, 1995; Sasal et al., 1997; Morand, Poulin, Rohde, & Hayward, 1999). Other host characteristics that

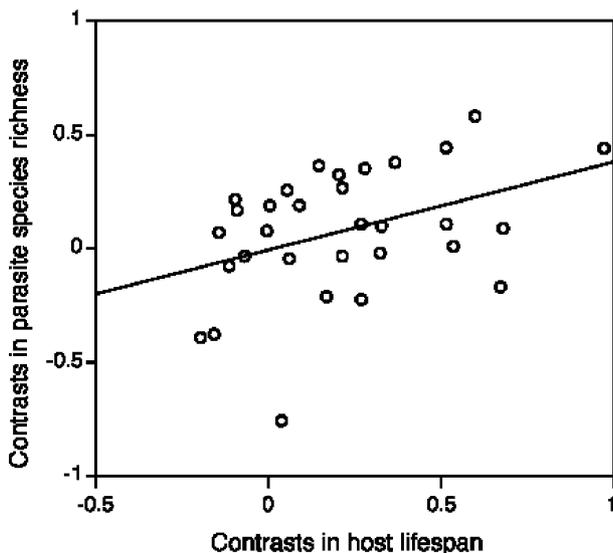


Figure 5. Relationship ($r = 0.465$, $N = 32$, $P = 0.0073$) between the richness of the endoparasitic helminth fauna and the maximum lifespan of the host, across species of North American freshwater fishes. Points are phylogenetically independent contrasts computed on log-transformed variables (adapted from Poulin & Morand, 2000).

covary with host body size can also show associations with ectoparasite richness, though whether this is independent of the effect of body size is not always clear. The other important factor to influence ectoparasite species richness, however, is latitude: ectoparasite species richness tends to be higher in marine fish species from lower latitudes, or warmer waters, than in temperate fish (Poulin & Rohde, 1997; Rohde & Heap, 1998). The higher speciation rates of small organisms living at higher temperatures proposed by Rohde (1992, 1998) may explain this trend. Interestingly, however, this latitudinal gradient does not apply to endoparasites of fish, though they are also exposed to the same external temperatures as ectoparasites, the hosts being ectotherms (Rohde & Heap, 1998; Choudhury & Dick, 2000; Poulin, 2001). In any event, host body size and latitude/temperature appear to be the key determinants of ectoparasite species richness in fish, their relative importance varying from study to study.

A final consideration is necessary. Most published investigations into the determinants of parasite species richness in fish and other hosts have focussed on predictions from theory (island biogeography or epidemiology) or latitudinal gradients. It is also possible that certain hosts features generally ignored in such studies may also affect the likelihood that new parasite species will colonize a host species. Recently, two independent studies have suggested that certain properties of the hosts' genome may be linked with parasite species richness. Guégan and Morand (1996) have shown that, among African freshwater fish, polyploid species harbour more species of ectoparasites than their diploid relatives. Similarly, Poulin, Marshall, and Spencer (2000) found a negative correlation between parasite species richness and host genetic heterogeneity, among North American freshwater fish species. This results suggests that host species or populations with low levels of genetic variability may be more vulnerable to parasite colonization, whereas that of Guégan and Morand (1996) suggests that other genomic anomalies can also affect rates of parasite colonization. These findings emphasize the need to take into account a wide range of factors in our search for the determinants of parasite diversity.

Discussion and conclusions

Several generalizations can be made from the numerous studies available on the determinants of parasite species richness. First, there is no

general rule: a key factor promoting rich parasite faunas highlighted in one study may prove unimportant in another study, even one focussing on a similar group of host species. One reason for this is that several factors act in synergy on rates of parasite colonization and extinction, but their relative contribution depends on other variables. The study of the large-scale determinants of parasite species richness must therefore always take a multivariate approach. Second, even with the substantial evidence presently available, it is not possible to favour either of the two theoretical frameworks, island biogeography and epidemiology, from which the main predictions are derived. To some extent, these two theoretical frameworks present explanations of the same phenomena but seen from different perspectives, so it may be pointless to distinguish between them. It would be useful, though, to obtain more precise, quantitative predictions regarding the expected relationship between various ecological factors and parasite species richness. Good scientific hypotheses are those that are falsifiable; to achieve this standard, we need more than the mere direction (positive or negative) of a predicted relationship, we also need its strength, such as an actual predicted slope value in the bottom graph of Fig. 3. Third, although this was not described in the previous section, the predictive power of the empirical relationships observed between any ecological feature of hosts and parasite species richness is usually pretty low: data points show much scatter and the r^2 value is low (Fig. 5 is a good example). Other macroecological patterns often come out more clearly, in a way that suggests that we have identified a key predictor variable (e.g. Brown, 1995; Maurer, 1999; Gaston & Blackburn, 2000; Storch & Gaston, 2004). Clearly, no single factor can explain much of the variation in parasite species richness, and even combinations of them perform relatively poorly. We have much to learn yet about the evolution of parasite diversity.

This last point needs to be emphasized. Patterns in species richness and the processes that generate them have been intensely studied in free-living organisms (Rosenzweig, 1995; Gaston & Blackburn, 2000; Hawkins, 2004). Several of these have parallels with parasite species richness in host species. Notable among these is the species–area relationship, derived from island biogeography theory, and one of the most robust and general patterns in macroecology (Connor & McCoy, 1979; He & Legendre, 1996; Rosenzweig, 1995; Gaston & Blackburn, 2000). Just as the size of an area, such as a habitat patch, determines the number of species of terrestrial animals found in it, the body

size of a host species should determine the number of parasite species it harbours. The latter relationship indeed exists, but it is much weaker and noisier than that for free-living organisms. Why is this? The main difference between the habitat of terrestrial animals and that of parasites is that hosts are living organisms themselves, and they can fight back against colonization of their body by parasites via immune responses. This fundamental difference may explain why macroecological predictions regarding species richness do not apply as well to parasite assemblages, because the theoretical models on which they are based do not account for the habitat *actively* trying to cause parasite extinctions. The search for the determinants of parasite species richness should perhaps look at the specific biology of the host–parasite interaction, as Hawkins (1994) has attempted with parasitoid insects, rather than rely too much on theoretical frameworks developed for free-living organisms.

A final remark will drive home this point. The habitat of free-living species does not evolve in response to their presence. For instance, an island inhabited by a rich lizard fauna will not ‘evolve’ a volcano or a harsh microclimate to rid itself of those lizards using regular eruptions. Over evolutionary time, however, a host lineage exploited by numerous parasite species will be under strong selection to evolve anti-parasite adaptations. In birds, for example, the spleen plays an important role in immune defence against nematode parasites, and nematode parasite richness correlates positively with spleen mass among bird species, even when controlling for bird body size or avian phylogeny (Morand & Poulin, 2000). Thus, some correlates of parasite species richness may not be determinants of richness, but the responses of hosts to this richness. In other words, some correlates of parasite richness are the *consequence*, and not the *cause*, of rich parasite faunas. This phenomenon makes it even more difficult to explain patterns of variation in parasite species richness among host species, and provides a challenge for future studies.

Looking ahead, the use of diversity measures other than mere species richness may offer glimpses of patterns and processes that have thus far escaped notice (Purvis & Hector, 2000). There are now numerous ways of quantifying taxonomic or functional diversity in an assemblage of species, and applying these methods often reveals patterns in the biodiversity of free-living communities that would not be detectable using only species richness (e.g. Warwick & Clarke, 2001; Petchey & Gaston, 2002). The time has come to do the same for parasite biodiversity. In particular, incorporating

information on the taxonomic or phylogenetic affiliations of parasite species in a host population could shed light on their origins. For instance, several congeneric parasite species coexisting in the same host population may originate from intra-host speciation rather than repeated colonization events. Using more sophisticated measures of parasite diversity will allow more specific hypotheses to be tested, and this may provide us with more satisfying results than the ones available to date.

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