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Evolutionary perspective

The evolution of taxonomic diversity in helminth assemblages of mammalian hosts

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Abstract. Several studies have searched for the key forces behind the diversification of parasite assemblages over evolutionary time. All of these studies have used parasite species richness as their measure of diversity, thus ignoring the relatedness among parasite species and the taxonomic structure of the assemblages. This information is essential, however, if we want to elucidate which processes have caused an assemblage of parasites to acquire new species. Here, we performed a comparative analysis across 110 species of mammalian hosts in which we evaluated the effects of four host traits (body mass, population density, geographic range, and basal metabolic rate) on the diversity of their assemblages of helminth endoparasites. As measures of diversity, we used parasite species richness, as well as the average taxonomic distinctness of the assemblage and its variance; the latter measures are based on the taxonomic distance between two parasite species, computed across all possible species pairs in an assemblage. Unlike parasite species richness, both the average taxonomic distinctness and its variance were unaffected by the number of hosts examined. These two measures of parasite diversity also proved highly repeatable among host populations of the same mammalian species; in contrast, parasite species richness was unreliable as a species character, as it varied as much within a host species than among different host species. Using phylogenetically independent contrasts, and correcting for potential confounding variables, we found that host population density correlated positively with parasite species richness. There were, however, no other relationships between any of the four host traits investigated and either of our measures of parasite diversity. The processes facilitating the taxonomic diversification of parasite assemblages thus remain unclear, but their elucidation will be necessary if we are to fully understand parasite evolution.

Key words: geographical range, helminths, host body size, phylogeny, population density, species richness, taxonomic distinctness

Introduction

As scientists strive to understand how current patterns in biodiversity have developed over evolutionary time (Huston, 1992; Rosenzweig, 1995; Tokeshi, 1999; Enquist *et al.*, 2002), studies of the diversity of parasite assemblages are playing an increasingly important role (Poulin and Morand, 2000). Because the evolutionary history of the parasites' habitats can be reconstructed in the form

of host phylogenies, and because the events leading to new species joining parasite assemblages are relatively well understood, it is possible to search for the key factors that have caused certain parasite assemblages to diversify more than others over time (Poulin, 1998; Page, 2003). Parasite assemblages thus represent excellent models for studies of biodiversity.

Two different theoretical frameworks have served to generate predictions about the factors that may promote the diversification of parasite assemblages. First, based on island biogeographical theory (MacArthur and Wilson, 1967; Kuris *et al.*, 1980), host features that promote high rates of parasite speciation or colonization by new parasite species should be associated with high parasite diversity. For instance, hosts with broad geographical ranges should overlap with the distributions of several other host species, from which they can acquire new parasite species (Gregory, 1990). Host species with high metabolic rates should have higher food intake, and thus a greater likelihood of acquiring most of the food-borne parasites in a particular habitat, than hosts with lower metabolic rates (Gregory *et al.*, 1996). As with larger islands, larger-bodied host species should be able to accommodate more parasite species than small ones, as they represent greater and more permanent resources for parasites. Across host species, relationships between the richness of parasite assemblages and either host body mass, host geographical range or host metabolic rate have been reported for a range of host and parasite taxa, but they are far from universal (Gregory, 1990; Bell and Burt, 1991; Gregory *et al.*, 1991, 1996; Poulin, 1995, 1997, 1998; Morand and Poulin, 1998; Morand, 2000; Morand and Harvey, 2000).

The second theoretical source of hypothesis regarding parasite diversity has been epidemiological modelling (Dobson and Roberts, 1994; Roberts *et al.*, 2002). It is possible to derive from epidemiological models the conditions necessary for a parasite species to invade and persist in a host population. A key factor facilitating the establishment of a parasite is host population density, which determines the contact rate between infective stages and hosts: below a given threshold host density, a parasite species cannot persist in a host population. In comparisons among different host species, we can predict that those occurring at higher population density should harbour more species of parasites, because they exceed the persistence threshold of more parasite species than hosts with low population density. Some comparative studies on mammals have found empirical support for this prediction (Morand and Poulin, 1998; Arneberg, 2002).

To date, all previous studies have used species richness (usually corrected for sampling effort) as their sole measure of the diversity of parasite assemblages. Richness is a convenient measure, but it does not capture all facets of diversity (Purvis and Hector, 2000). Recent advances in phylogenetics are now complementing studies of the community ecology of free-living organisms, allowing

one to take into account the evolutionary relationships among species coexisting in an assemblage (see Shimatani, 2001; Webb *et al*., 2002). Applied to parasite assemblages, measures of diversity that incorporate information about the relationships among parasite species could shed light on the actual processes of diversification. There are two main ways in which new species can join a parasite assemblage (Poulin, 1998; Page, 2003). First, they can originate from within the assemblage, when one parasite species undergoes speciation without the host also speciating. Such intra-host speciation by parasites may appear unlikely, but there is evidence that it does happen (Paterson and Gray, 1997). The large numbers of congeneric parasite species occurring in certain assemblages, forming true species flocks, also indicate that parasite lineages can radiate within single host species over time (Schad, 1963; Kennedy and Bush, 1992; Beveridge *et al*., 2002). Second, new parasite species can come from outside the assemblage, when a parasite from a sympatric host species colonizes the assemblage by switching hosts (Paterson and Gray, 1997). Studies of parasite diversity that focus on species richness cannot distinguish between intra-host speciation and host-switching, and thus cannot determine which of these two processes has been the main source of diversity. If intra-host speciation has been rampant in a parasite assemblage, we would expect most of its species to be closely related, belonging to the same genera or families. If, in contrast, host-switching has been the main cause of parasite diversification in an assemblage, we would not expect the parasite species to be too closely related, since they are the product of independent colonization events. We need a measure of diversity that goes beyond mere species richness, a measure that takes into account the relationships between parasite species in an assemblage if we are to unravel their evolution.

Host features known or expected to influence parasite species richness may do so by facilitating either intra-host speciation or the acquisition of new parasites via host-switching. Specifically, we predict that host geographical range and host metabolic rate should be associated with the acquisition of new parasites by host-switching, because they determine the exposure of a host to novel parasites. Hosts with broad geographical ranges inhabit a wider variety of habitats and are in contact with more other host species than those with restricted ranges, and hosts with high metabolic rate consume more food and are open for colonization by more food-borne parasites than those with lower metabolic rates. Host body size and host population density, in contrast, should facilitate both intra-host speciation and acquisition of parasites by host switching, because they influence mainly the number of parasite species that can be supported in an assemblage, and not necessarily their origins.

In the present study, we examine the relationship between four features of host species (body mass, geographical range, population density, and basal metabolic rate) and the diversity of helminth parasite assemblages across

species of mammal hosts. We use two measures of diversity, parasite species richness and the taxonomic distinctness of species within an assemblage. The latter measure is based on the average taxonomic distances between species in an assemblage, ranging from a minimum value when all species belong to the same genus, and a maximum value when they all belong to different phyla (Clarke and Warwick, 1998, 1999; Warwick and Clarke, 2001). Ours is the first study of the determinants of parasite diversity that also attempts to distinguish between the possible evolutionary origins of this diversity.

Methods

Data collection

We revisited the data base assembled by Poulin (1995) from published sources to construct our data set, with additional information from other surveys published more recently (the data used and the original literature sources are in an Appendix available from http://www.otago.ac.nz/zoology/downloads/poulin/MammalHelminthData.xls or from RP upon request). The surveys chosen all provided data on the helminth endoparasites (trematodes, cestodes, nematodes and acanthocephalans) found in populations of mammal hosts. We focused on gastrointestinal helminths. Given the ambiguous information presented in some of the surveys, some helminths from other organs may have been included occasionally by mistake; however, given the size of the data set, such small errors are unlikely to obscure existing patterns. We only included host populations in which at least two helminth species have been found, because the taxonomic distinctness of a parasite assemblage cannot be computed for single-species assemblages (see below). For each host population, the total number of hosts examined for parasites and the total number of parasite species (i.e. parasite species richness) found were recorded. The number of hosts examined, or sampling effort, is often a key determinant of the number of parasites found in a survey (Walther *et al.*, 1995), and must therefore be included as a potential confounding variable. For the computations of taxonomic distinctness (see below), we used the proposed taxonomies of Gibson *et al.* (2002) for trematodes, Khalil *et al.* (1994) for cestodes, Anderson (2000) for nematodes, and Amin (1985) for acanthocephalans. The original authors' identification of parasite species was taken as valid, with synonymous names checked using the preceding taxonomic references.

Data on body masses of all mammalian host species were obtained from Damuth (1987) or Grzimek (1990). Data on host population density (number of individuals per km^2) were obtained for a subset of host species from Damuth (1987). Data on host basal metabolic rate (cm^3 O_2/g h) were obtained from a

different subset of host species, mainly from McNab (1988), but also from Elgar and Harvey (1987) and McNab (1992). Data on geographic range size (number of 500 km wide squares covering the species' range when its distribution is plotted on a cylindrical equal-area projection map) were obtained for a small subset of host species from Diniz-Filho and Torres (2002).

Taxonomic distinctness of parasite assemblages

For each mammal population, we computed the average taxonomic distinctness (Δ^+) and the variance in taxonomic distinctness (Λ^+) of the parasite species present. When parasite species are placed within a taxonomic hierarchy, based on the Linnean classification into kingdom, phyla, classes, orders, families, genera and species, the average taxonomic distinctness, Δ^+, is simply the mean number of steps up the hierarchy that must be taken to reach a taxon common to two parasite species, computed across all possible pairs of parasite species in an assemblage (Clarke and Warwick, 1998, 1999; Warwick and Clarke, 2001). Thus, if two species are congeners, one step (species-to-genus) is necessary to reach a common node in the taxonomic tree; if the two species belong to different genera but the same family, two steps will be necessary (species-to-genus, and genus-to-family); and so on, with these numbers of steps averaged across all species pairs. For any given species pair, the number of steps corresponds to half the path length connecting two species in the taxonomic tree, with equal step lengths being postulated between each level in the taxonomic hierarchy. Step lengths are standardized so that the distinctness of two species connected at the highest taxonomic level is set equal to 100 (Clarke and Warwick, 1999); with six levels above the species in the taxonomy we used, each step length was thus equal to 16.67. The greater the taxonomic distinctness between parasite species, the higher the number of steps needed, and the higher the value of Δ^+. A high value means that on average the parasites in a host population are not closely related. Formally, Δ^+ is computed as follows (see Clarke and Warwick, 1998):

$$\Delta^+ = 2\frac{\sum\sum_{i<j}\omega_{ij}}{s(s-1)}$$

where s is the number of parasite species, the double summation is over the set $\{i = 1,\ldots,s;\ j = 1,\ldots,s,$ such that $i < j\}$, and ω_{ij} is the taxonomic distinctness between parasite species i and j, or the number of taxonomic steps required to reach a node common to both.

The index Δ^+ measures the average taxonomic distinctness between species, and does not capture all of the taxonomic structure of a set of parasite species. It is possible to have two host populations, each harbouring the same number of parasite species and each characterised by an identical value of Δ^+, but with

one host population clearly supporting a broader taxonomic range of parasites. Asymmetries in the taxonomic distribution of species across higher taxa can sometimes be missed by Δ^+, which is only the average taxonomic distinctness; in these situations complementary information can be obtained by examining the variance in taxonomic distinctness (see Clarke and Warwick, 2001; Warwick and Clarke, 2001):

$$\Lambda^+ = \frac{\sum\sum_{i\neq j}(\omega_{ij} - \varpi)^2}{s(s-1)}$$

where ϖ is simply the average taxonomic distinctness, or Δ^+. The variance Λ^+ conveys separate information of how much taxonomic heterogeneity there is among a group of parasite species. Note, however, that Λ^+ can only be computed when at least three parasite species are found in a host population (it always equals zero with two species). To calculate Δ^+ and Λ^+, a computer program was developed using borland C++ Builder 5.0 (it can be downloaded from http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2).

Statistical analyses

To determine whether parasite species richness, average taxonomic distinctness, Δ^+, and the variance in taxonomic distinctness, Λ^+, are true host species characters, i.e., features that vary less among populations of the same host species than among host species, we performed a repeatability analysis following that of Arneberg *et al.* (1997). Using host species for which at least two samples were available, we analysed the variation in helminth species richness, Δ^+ and Λ^+ using an ANOVA in which host species was the only factor. A significant effect of host species would indicate that the measures are repeatable within host species, i.e., that they are more similar to each other than to values from other host species. We estimated the proportion of the total variance originating from differences among host species, as opposed to within species, following Sokal and Rohlf (1995, p. 214).

The analyses were first carried out using all host samples in the data set. They were then repeated using only host samples in which at least 20 host individuals have been examined for helminths, to reduce the potential effect of sampling error on our findings. We report in detail the results of the first set of analyses, and only present information from the more conservative analyses where relevant.

Closely related host species are likely to harbour similar number of parasite species, and possibly taxonomically related parasite species, because these were inherited from a recent common ancestor; this means that they do not represent independent statistical observations. We must therefore control for phylogenetic influences when evaluating the effects of host body mass,

geographical range, basal metabolic rate or population density on the diversity of parasite assemblages. To achieve this, we used the phylogenetically independent contrasts method (Felsenstein, 1985; Harvey and Pagel, 1991), implemented with the CAIC version 2.0 program (Purvis and Rambaut, 1994). Contrasts were derived from a host tree constructed from published studies on mammalian phylogenetic relationships (McKenna *et al.*, 1997; Bininda-Emonds *et al.*, 1999; DeBry and Sagel, 2001; Matthee *et al.*, 2001; Murphy *et al.*, 2001; Jones *et al.*, 2002). For host species represented in the data set by more than one population, we obtained species values by averaging population values. Contrasts were computed on log-transformed data and all regression analyses were forced through the origin (Garland *et al.*, 1992). We obtained contrasts corrected for the influence of one or more confounding variables (e.g., sampling effort) by taking the residuals of regressions of a selected variable against the potential confounding variables. Because the subsets of host species for which we had data on population density, basal metabolic rate or geographical range were different and in one case rather small, the influence of each of these variables on parasite species richness and taxonomic diversity was assessed in separate analyses, all controlling for the confounding effect of host body mass.

Results

In total, data from 188 mammalian populations, representing 110 host species (across 18 orders), were obtained from 128 published surveys (see electronic Appendix available from http://www.otago.ac.nz/zoology/downloads/poulin/MammalHelminthData.xls or from RP). These data were derived from the examination of 17,378 individual mammals, for an average of 92.4 hosts per sample (range 5–1142). Only 94 of the 110 host species included populations from which a sample of at least 20 individuals had been taken. Although data on host body mass were obtained for all 110 mammalian species, data on other variables were only available for a subset of these species: population density for 59 species (7 orders), basal metabolic rate for 64 species (8 orders), and geographic range size for 18 species (order Carnivora only).

Across all samples, the number of hosts examined per sample correlated positively with parasite species richness ($r = 0.382$, $n = 188$, $p = 0.0001$), but not with either Δ^+ ($r = 0.083$, $n = 188$, $p = 0.2584$) or Λ^+ ($r = 0.0003$, $n = 179$, $p = 0.997$). Measures of taxonomic distinctness are thus independent of sampling effort, as shown in earlier studies (Rogers *et al.*, 1999). However, parasite species richness correlated negatively with Δ^+ ($r = -0.352$, $n = 188$, $p = 0.0001$) and positively with Λ^+ ($r = 0.237$, $n = 179$, $p = 0.0014$), indicating that measures of taxonomic distinctness are influenced by the number of parasite species

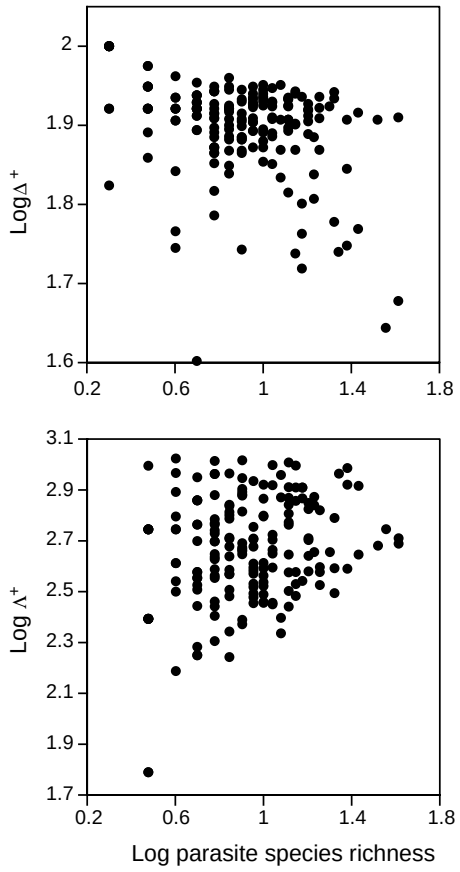

Figure 1. Relationships between helminth parasite species richness and both their average taxonomic distinctness, Δ^+, and its variance, Λ^+, across 188 mammalian populations.

in a sample (Fig. 1). Also, Δ^+ and Λ^+ covaried negatively ($r = -0.357$, $n = 179$, $p = 0.0001$), such that an increase in average taxonomic diversity is associated with a decrease in its variance. Essentially the same relationships were found when we used host species values rather than values from individual host populations, and whether host samples with fewer than 20 individual hosts were included or not. Thus, in the comparative analyses below using phylogenetic contrasts, parasite species richness is always corrected for sampling effort, and Δ^+ and Λ^+ are always corrected for parasite species richness.

Using only the 35 mammalian host species for which data were available from at least two populations, the repeatability analyses indicated that helminth taxonomic distinctness, measured as either Δ^+ and Λ^+, can be treated as a host species character, but that helminth species richness is a little too variable within species to be reliably taken as a host species characteristic (Fig. 2).

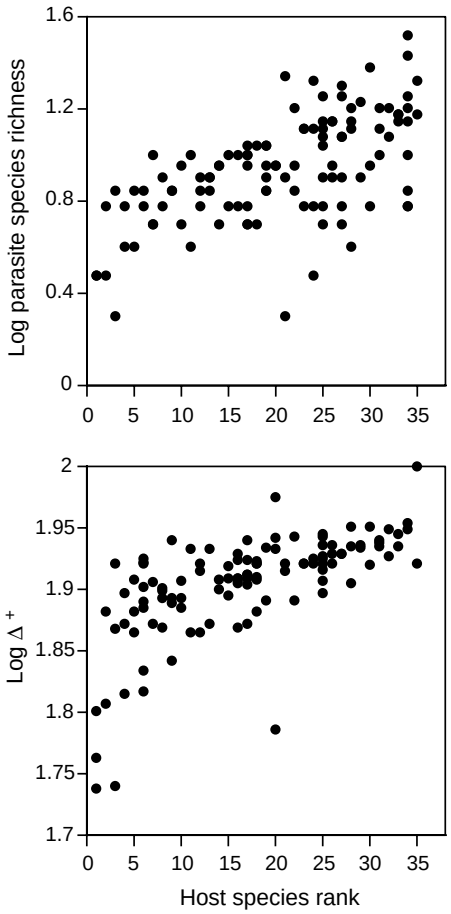

Figure 2. Rank plots of helminth species richness and average taxonomic distinctness, Δ^+. The 35 mammalian host species for which more than one populations were sampled are ranked according to their mean log-transformed values of either parasite species richness or Δ^+, with rank 1 given to the species with the lowest mean value; all sample estimates are plotted for each species. If variation is small within compared to between host species, we expect a relatively narrow band of points from the lower left to the upper right corner, with few or no points in either the upper left or lower right corner.

Estimates of helminth species richness from different populations of the same host species tend to be more similar to each other than to those of other species, but this trend is not quite significant ($F_{34,78} = 1.526$, $p = 0.0639$). Only 14.5% of the variation in helminth species richness among host samples is associated with differences between host species, rather than with differences among populations within species. In contrast, estimates of average helminth taxonomic distinctness, Δ^+, from the same host species are more similar to each other than expected by chance ($F_{34,78} = 3.146$, $p = 0.0001$), with 48% of the

variation among samples accounted by differences between host species. Thus, estimates of helminth Δ^+ are repeatable within the same mammalian host species, whereas those of helminth species richness are much more variable (Fig. 2). Similarly, estimates of Λ^+ are also more similar within than among host species ($F_{33,76} = 2.552$, $p = 0.0004$), with 39% of the variation among samples accounted by differences between host species.

Using independent phylogenetic contrasts, we found that host body mass correlated negatively with both host population density ($r = -0.320$, $n = 47$, $p = 0.0282$) and host basal metabolic rate ($r = -0.813$, $n = 51$, $p = 0.0001$), and positively with host geographic range ($r = 0.552$, $n = 16$, $p = 0.0265$). The latter three variables were therefore corrected for host body mass in the following analyses.

Across phylogenetic contrasts, there were only two significant relationships between a host variable and any of the three measures of parasite diversity we used (Table 1). First, parasite species richness covaried positively with host population density ($r = 0.404$, $n = 47$, $p = 0.0052$; Fig. 3). This remained true when we included only host species with sample sizes of at least 20 individuals ($r = 0.350$, $n = 41$, $p = 0.0248$). Second, the variance in parasite taxonomic distinctness, Λ^+, correlated positively with host basal metabolic rate ($r = 0.334$, $n = 48$, $p = 0.0204$; Fig. 4). This relationship, however, was greatly influenced by an outlier in the bottom left corner of the plot in Figure 4; if this point is removed from the analysis, the relationship disappears ($p = 0.2166$). When including only the 94 host species with sample sizes of at least 20 individuals, the same positive relationship was also found ($r = 0.347$, $n = 45$, $p = 0.0196$), again breaking down when the same outlier is removed.

Table 1. Summary of the correlations between host traits and three measures of helminth parasite diversity among mammal hosts, using phylogenetically independent contrasts

Host trait	Parasite species richness	Δ^+	Λ^+
Host body mass	0.115 (85)	−0.010 (85)	−0.122 (80)
Host population density	0.404* (47)	−0.009 (47)	0.077 (45)
Host geographic range	0.146 (16)	−0.157 (16)	0.051 (16)
Host basal metabolic rate	0.193 (51)	−0.138 (51)	0.334** (48)

Host population density, geographic range and basal metabolic rate are corrected for host body mass, parasite species richness is corrected for sampling effort, and the average (Δ^+) and variance (Λ^+) in parasite taxonomic distinctness are corrected for parasite species richness; numbers of pairs of contrasts in each analysis are given in parentheses.
* $p < 0.01$; ** $p < 0.05$.

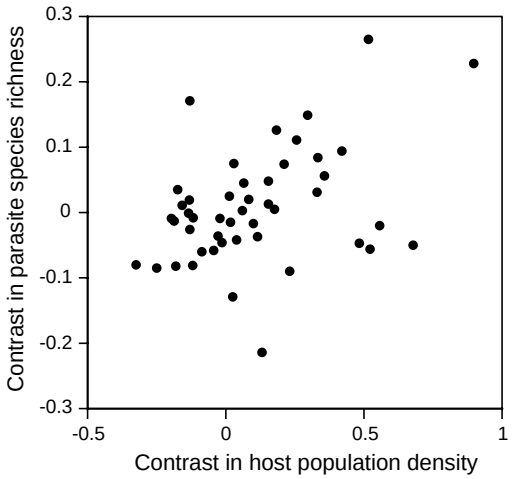

Figure 3. Helminth parasite species richness (corrected for sampling effort) as a function of host population density (corrected for host body mass) in mammalian host species, based on 47 phylogenetically independent contrasts.

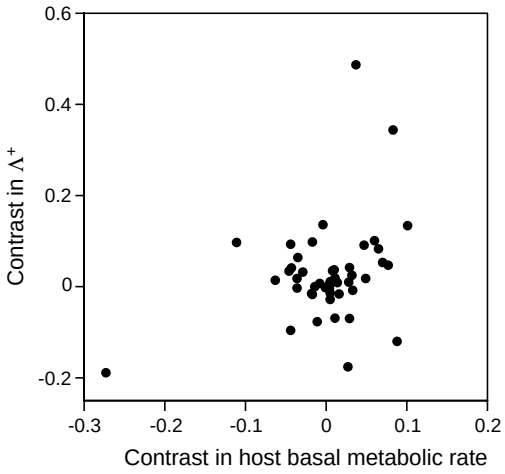

Figure 4. Variance in helminth taxonomic distinctness, Λ^+ (corrected for parasite species richness) as a function of host basal metabolic rate (corrected for host body mass) in mammalian host species, based on 48 phylogenetically independent contrasts.

Discussion

Although several relationships between host features and the number of parasite species they harbour have been documented (Poulin, 1997, 1998; Morand, 2000), these have provided little information on the likely processes that have

led to the diversification of parasite assemblages. Here, we attempted to shed light on whether certain host features, if any, might influence which process of diversification, intra-host speciation or host colonization, has been predominant in a parasite assemblage. We focused on the taxonomic distinctness of the species in endoparasite assemblages, rather than their mere numbers. Our results show that the taxonomic distinctness of a host's helminth assemblage is similar enough across conspecific host populations to be considered a host species trait, whereas helminth parasite species richness is too variable. However, none of the four host features we investigated (body mass, population density, geographic range, and basal metabolic rate) correlated with the taxonomic distinctness of helminth parasite assemblages.

We did find a positive relationship between host population density and helminth species richness. This association has been reported before for both helminth endoparasites (Poulin and Morand, 1998; Arneberg, 2002) and arthropod ectoparasites (Stanko *et al*., 2002) of mammals. It highlights the importance of epidemiological processes in determining how many parasite species can coexist in a host population. However, neither host population density nor any of the other three host characteristics examined here had any influence on the taxonomic distinctness of parasite assemblages. In particular, we expected host geographical range and host metabolic rate to affect the acquisition of new parasites by host-switching, because both should influence the exposure of a host to novel parasites. Hosts with broad geographical ranges come into contact with more other host species than those with restricted ranges (Gregory, 1990), and hosts with high metabolic rates consume more food and are accessible for colonization by more food-borne parasites than those with lower metabolic rates (Gregory *et al*., 1996). The latter is true because basal metabolic rate correlates strongly with rates of energy expenditure by active animals, at least in mammals (Koteja, 1991), such that basal metabolism is a good estimator of an animal's overall activity levels and food requirements. After excluding the effect of a single outlier (see Fig. 4), there was no evidence that either host geographic range or metabolism correlates with the taxonomic diversity of helminth parasite assemblages.

Mammals are a suitable host group for a study like the present one. Among species of vertebrate hosts, the number of genera represented in parasite assemblages increases as a power function of the number of species (Mouillot and Poulin, 2004). In groups such as birds or fish, the exponent of the power function is almost one, suggesting that almost all parasite species belong to different genera. Such a pattern would be consistent with a history dominated by independent host colonization events (Mouillot and Poulin, 2004). In contrast, in mammals, the exponent is significantly lower, suggesting that a mixture of host colonization and intra-host speciation is probably responsible for the observed diversity of parasite assemblages in mammals (Mouillot and

Poulin, 2004). At one extreme, there are mammal species dominated by a very few well-represented genera or families. These congeneric parasites are sometimes so numerous that they appear to form true species flocks; examples include strongyloid nematodes in horses and other ungulates, cloacinid nematodes in kangaroos, and lecithodendriid trematodes in bats (Schad, 1963; Kennedy and Bush, 1992; Beveridge *et al.*, 2002). And at the other extreme, there are mammal species harbouring no more than one parasite species per genus. The reasons for this variation are unclear. At first glance, large host body size appears to be associated with a higher probability of harbouring many congeneric parasite species, but this relationship is not very robust (Poulin, 1999). As the results of the present study indicate, the causes of the taxonomic diversity of parasite assemblages remain to be found.

It may even be futile to search for host characteristics that shape the taxonomic diversity of parasite assemblages. Recently, Enquist *et al.* (2002) suggested that the processes which structure the taxonomic diversity of woody plant communities operate in a regular manner over millions of years and across broad geographical gradients. Diversity might be more strongly regulated by local ecological and evolutionary rules, and only weakly influenced by environmental or historical factors such as dispersal barriers or speciation (Gotelli, 2002). The lack of explanation coming from host body mass, population density, geographic range or basal metabolic rate for taxonomic diversity patterns in parasite assemblages substantiates this hypothesis, i.e., such external factors may have less influence on diversity patterns than general processes ruling species coexistence at the within-host scale. Alternatively, historical events may be responsible for much of the parasite diversity observed in extant host species, but without any link to gross attributes such as body mass or basal metabolic rate. These host features have probably varied considerably over millions of years of host evolution, and their current state may be a poor predictor of the past diversification of parasite assemblages.

One of the most interesting results of the present study is the finding that helminth species richness is too variable, i.e., not repeatable enough, across populations of the same host species to be considered as a true host species trait. Several examples from our data set can be used to illustrate this. For instance, in three populations of the raccoon, *Procyon lotor*, in the United States of America, helminth species richness was 7, 14 and 33 (Jordan and Hayes, 1959; Snyder and Fitzgerald, 1985; Harkema and Miller, 1964). Host sample sizes were large in all cases (100, 245 and 209, respectively), and cannot explain the considerable variation in the number of helminths found in these populations. In contrast, the values of average taxonomic distinctness, Δ^+, of these assemblages were, respectively, 88.1, 87.7 and 80.7: these were clearly much less variable. Across all nine populations of *P. lotor* included in our data set, the coefficient of variation (standard deviation $\times$ 100/mean) of species

richness values was 62.73, whereas that for Δ^+ was 3.68. The same pattern is true for other mammal species that are well represented in our data. For example, among our eight populations of muskrat, *Ondatra zibethica*, where helminth species richness ranges from 5 to 18, the coefficient of variation in species richness was 40.06, whereas that for Δ^+ was only 9.15. This suggests that although some host populations do not accumulate as many helminth species as others, they all sample across the same taxonomic breadth of parasites. This has huge implications for the many earlier comparative studies of parasite diversity (see reviews in Poulin, 1997, 1998; Morand, 2000) that have all used parasite species richness as a measure of diversity. These studies are all using a measure that is too variable within host species to be informative, or even reliable.

The use of diversity measures other than species richness can cast a different light on certain aspects of biodiversity. Recently, introduced salmonid fish populations were shown to acquire parasite assemblages just as taxonomically diverse as those found in their native range (Poulin and Mouillot, 2003); in contrast, earlier findings, based on species richness, had suggested instead that introduced fish populations invariably have depauperate parasite assemblages (Kennedy and Bush, 1994). Although in this study we could not find an ecological feature of mammalian hosts that was associated with the taxonomic distinctness of their helminth parasite assemblages, we showed that the measures Δ^+ and Λ^+ can be viewed as host species traits whereas parasite species richness is just too variable. The use of these new measures of diversity will undoubtedly bring us closer to understanding how parasite biodiversity evolves.

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References

Amin, O.M. (1985) Classification. In D.W.T. Crompton and B.B. Nickol (eds) *Biology of the Acanthocephala*. Cambridge University Press, Cambridge, pp. 27–72.

Anderson, R.C. (2000) *Nematodes Parasites of Vertebrates*. 2nd edn. CABI Publishing, Wallingford, UK.

Arneberg, P. (2002) Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**, 88–94.

Arneberg, P., Skorping, A. and Read, A.F. (1997) Is population density a species character? Comparative analyses of the nematode parasites of mammals. *Oikos* **80**, 289–300.

Bell, G. and Burt, A. (1991) The comparative biology of parasite species diversity: internal helminths of freshwater fish. *J. Anim. Ecol.* **60**, 1047–1064.

Beveridge, I., Chilton, N.B. and Spratt, D.M. (2002) The occurrence of species flocks in the nematode genus *Cloacina* (Strongyloidea: Cloacininae), parasitic in the stomachs of kangaroos and wallabies. *Aust. J. Zool.* **50**, 597–620.

Bininda-Emonds, O.R.P., Gittleman, J.L. and Purvis, A. (1999) Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biol. Rev.* **74**, 143–175.

Clarke, K.R. and Warwick, R.M. (1998) A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* **35**, 523–531.

Clarke, K.R. and Warwick, R.M. (1999) The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Mar. Ecol. Prog. Ser.* **184**, 21–29.

Clarke, K.R. and Warwick, R.M. (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.* **216**, 265–278.

Damuth, J. (1987) Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linn. Soc.* **31**, 193–246.

DeBry, R.W. and Sagel, R.M. (2001) Phylogeny of Rodentia (Mammalia) inferred from the nuclear-encoded gene IRBP. *Mol. Phyl. Evol.* **19**, 290–301.

Diniz-Filho, J.A.F. and Torres, N.M. (2002) Phylogenetic comparative methods and the geographic range size – body size relationship in new world terrestrial Carnivora. *Evol. Ecol.* **16**, 351–367.

Dobson, A.P. and Roberts, M. (1994) The population dynamics of parasitic helminth communities. *Parasitology* **109**, S97–S108.

Elgar, M.A. and Harvey, P.H. (1987) Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Funct. Ecol.* **1**, 25–36.

Enquist, B.J., Haskell, J.P. and Tiffney, B.H. (2002) General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. *Nature* **419**, 610–613.

Felsenstein, J. (1985) Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Garland, T. Jr., Harvey, P.H. and Ives, A.R. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.

Gibson, D.I., Jones, A. and Bray, R.A. (2002) *Keys to the Trematoda*, Vol 1. CABI Publishing, Wallingford, UK.

Gotelli, N.J. (2002) Biodiversity in the scales. *Nature* **419**, 575–576.

Gregory, R.D. (1990) Parasites and host geographic range as illustrated by waterfowl. *Funct. Ecol.* **4**, 645–654.

Gregory, R.D., Keymer, A.E. and Harvey, P.H. (1991) Life history, ecology and parasite community structure in Soviet birds. *Biol. J. Linn. Soc.* **43**, 249–262.

Gregory, R.D., Keymer, A.E. and Harvey, P.H. (1996) Helminth parasite richness among vertebrates. *Biodiv. Conserv.* **5**, 985–997.

Grzimek, B. (1990) *Encyclopedia of Mammals*, five volumes. McGraw-Hill, New York.

Harkema, R. and Miller, G.C. (1964) Helminth parasites of the raccoon, *Procyon lotor*, in the Southeastern United States. *J. Parasitol.* **50**, 60–66.

Harvey, P.H. and Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.

Huston, M.A. (1992) *Biological Diversity*: *The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.

Jones, K.E., Purvis, A., MacLarnon, A., Bininda-Emonds, O.R.P. and Simmons, N.B. (2002) A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biol. Rev.* **77**, 223–259.

Jordan, H.E. and Hayes, F.A. (1959) Gastrointestinal helminths of raccoons (*Procyon lotor*) from Ossabaw Island, Georgia. *J. Parasitol.* **45**, 249–252.

Kennedy, C.R. and Bush, A.O. (1992) Species richness in helminth communities: the importance of multiple congeners. *Parasitology* **104**, 189–197.

Kennedy, C.R. and Bush, A.O. (1994) The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* **109**, 187–196.

Khalil, L.F., Jones, A. and Bray, R.A. (1994) *Keys to the Cestode Parasites of Vertebrates*. CABI International, Wallingford, UK.

Koteja, P. (1991) On the relation between basal and field metabolic rates in birds and mammals. *Funct. Ecol.* **5**, 56–64.

Kuris, A.M., Blaustein, A.R. and Alió, J.J. (1980) Hosts as islands. *Am. Nat.* **116**, 570–586.

MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Matthee, C.A., Burzlaff, J.D., Taylor, J.F. and Davis, S.K. (2001) Mining the mammalian genome for artiodactyl systematics. *Syst. Biol.* **50**, 367–390.

McKenna, M.C., Bell, S.K. and Simpson, G.G. (1997) *Classification of Mammals Above the Species Level*. Columbia University Press, New York.

McNab, B.K. (1988) Complications inherent in scaling the basal rate of metabolism in mammals. *Q. Rev. Biol.* **63**, 25–54.

McNab, B.K. (1992) The comparative energetics of rigid endothermy: the Arvicolidae. *J. Zool.* **227**, 585–606.

Morand, S. (2000) Wormy world: comparative tests of theoretical hypotheses on parasite species richness. In R. Poulin, S. Morand and A. Skorping (eds) *Evolutionary Biology of Host-Parasite Relationships*: *Theory Meets Reality*, Elsevier Science, Amsterdam, pp. 63–79.

Morand, S. and Harvey, P.H. (2000) Mammalian metabolism, longevity and parasite species richness. *Proc. Roy. Soc. London B* **267**, 1999–2003.

Morand, S. and Poulin, R. (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evol. Ecol.* **12**, 717–727.

Mouillot, D. and Poulin, R. (2004) Taxonomic partitioning shedding light on the diversification of parasite communities. *Oikos* **104**, 205–207.

Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang, Y.P., Ryder, O.A. and O'Brien, S.J. (2001) Molecular phylogenetics and the origins of placental mammals. *Nature* **409**, 614–618.

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

Paterson, A.M. and Gray, R.D. (1997) Host-parasite cospeciation, host switching, and missing the boat. In D.H. Clayton and J. Moore (eds) *Host-Parasite Evolution*: *General Principles and Avian Models*. Oxford University Press, Oxford, pp. 236–250.

Poulin, R. (1995) Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecol. Monogr.* **65**, 283–302.

Poulin, R. (1997) Species richness of parasite assemblages: evolution and patterns. *Annu. Rev. Ecol. Syst.* **28**, 341–358.

Poulin, R. (1998) *Evolutionary Ecology of Parasites*: *From Individuals to Communities*. Chapman & Hall, London.

Poulin, R. (1999) Speciation and diversification of parasite lineages: an analysis of congeneric parasite species in vertebrates. *Evol. Ecol.* **13**, 455–467.

Poulin, R. and Morand, S. (2000) The diversity of parasites. *Q. Rev. Biol.* **75**, 277–293.

Poulin, R. and Mouillot, D. (2003) Host introductions and the geography of parasite taxonomic diversity. *J. Biogeogr.* **30**, 837–845.

Purvis, A. and Hector, A. (2000) Getting the measure of biodiversity. *Nature* **405**, 212–219.

Purvis, A. and Rambaut, A. (1994) *Comparative Analysis by Independent Contrasts*, *CAIC version 2.0*. Oxford University, Oxford.

Roberts, M.G., Dobson, A.P., Arneberg, P., de Leo, G.A., Krecek, R.C., Manfredi, M.T., Lanfranchi, P. and Zaffaroni, E. (2002) Parasite community ecology and biodiversity. In P.J. Hudson, A. Rizzoli, B.T. Grenfell, H. Heesterbeek and A.P. Dobson (eds) *The Ecology of Wildlife Diseases*. Oxford University Press, Oxford, pp. 63–82.

Rogers, S.I., Clarke, K.R. and Reynolds, J.D. (1999) The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. *J. Anim. Ecol.* **68**, 769–782.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Schad, G.A. (1963) Niche diversification in a parasite species flock. *Nature* **198**, 404–406.

Shimatani, K. (2001) On the measurement of species diversity incorporating species differences. *Oikos* **93**, 135–147.

Snyder, D.E. and Fitzgerald, P.R. (1985) Helminth parasites from Illinois raccoons (*Procyon lotor*). *J. Parasitol.* **71**, 274–278.

Sokal, R.R. and Rohlf, F.J. (1995) *Biometry*, 3rd edn. W. H. Freeman and Co., New York.

Stanko, M., Miklisova, D., Goüy de Bellocq, J. and Morand, S. (2002) Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia* **131**, 289–295.

Tokeshi, M. (1999) *Species Coexistence*: *Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.

Walther, B.A., Cotgreave, P., Price, R.D., Gregory, R.D. and Clayton, D.H. (1995) Sampling effort and parasite species richness. *Parasitol. Today* **11**, 306–310.

Warwick, R.M. and Clarke, K.R. (2001) Practical measures of marine biodiversity based on relatedness of species. *Oceanogr. Mar. Biol. Annu. Rev.* **39**, 207–231.

Webb, C.O., Ackerly, D.D., McPeek, M.A. and Donoghue, M.J. (2002) Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* **33**, 475–505.