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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Taxonomic partitioning shedding light on the diversification of parasite communities

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Power relations were used for 297 parasite communities of fish, bird and mammal hosts between the number of genera (G) and the number of species (S) per community to test for the relative importance of different processes in their diversification. For the bird hosts the relation was $G \propto S^{0.92}$, and for fish hosts it was $G \propto S^{0.97}$, but for mammal hosts, the number of parasite genera increases more slowly as a function of species richness ($G \propto S^{0.83}$), suggesting, among other possibilities, a higher rate of within-host parasite speciation in mammals than in other vertebrates.

In a recent study, Enquist et al. (2002) introduced a new theoretical perspective on the processes that regulate species coexistence and diversity over millions of years and across broad geographical gradients. They report that the number of higher taxa (genera or family) is a simple power function of species richness in assemblages of woody plants, with exponents being statistically invariant across and within biogeographical areas, types of plant physiognomy, and geological time. The exponents are also less than 1, suggesting that increasing species richness leads to an increasing proportion of congeneric species and confamilial genera. Thus, the surprising regularity observed in taxonomic diversity is certainly influenced more by local processes such as species interactions than by historical and environmental factors such as dispersal barriers (Gotelli 2002). These fruitful advances must be followed by exploration of biological, ecological or evolutionary hypotheses explaining these invariant patterns. Here, we investigate the relationship between numbers of genera and species in parasite communities of fish, mammal and bird hosts to test hypotheses about their diversification.

The diversification of parasite assemblages over evolutionary time is the result of several processes. Associations between parasites and their hosts are generally inherited from ancestors: though they may co-speciate with their hosts, parasite lineages often track host lineages through time with great fidelity (Page 2003). Diversification (i.e. increases in parasite species richness) of the parasite fauna of a host lineage, however, can occur in two ways (Poulin 1998, Page 2003). First, certain parasite species can speciate without host speciation, giving rise to several closely-related species, sometimes forming true species flocks (Inglis 1971, Kennedy and Bush 1992). Second, completely new parasite lineages may be acquired by transfers from other host taxa, a phenomenon referred to as host-switching.

If the number of higher taxa in parasite assemblages is a simple power function of species richness, as shown by Enquist et al. (2002) for plant communities, we can gain some insight into which of the above two processes has been most important in the diversification of parasite communities. If we find an exponent of one for the relationship between the number of, say, parasite genera and the number of parasite species across several comparable parasite assemblages, then host-switching has been the main cause of diversification, because each species present in a community is taxonomically-independent of the other species, and must therefore have had a separate origin. If, on the other hand, the exponent is much less than one, then several species belong to the same genus or genera, suggesting that they have a common ancestor and that they may have radiated following a host-switch by that ancestor. In the first scenario, the number of host-switches in the past is approximately equal to the current number of species, whereas in the second scenario there are currently much more species than there were host-switches, the difference being the result of within-host parasite speciation.

We compared the relationship between the number of genera (G) and the number of species (S) in communities of Helminth endoparasites (cestodes, trematodes, acanthocephalans and nematodes) in fish, birds and mammals (Fig. 1). Among communities in 107 species of fish hosts, the relationship was almost one for one ($G \propto S^{0.97}$). It is a little weaker among communities of 76 bird species ($G \propto S^{0.92}$), although the exponents for parasite communities in both fish and birds are not significantly different from the 0.94 found by Enquist et al. (2002) for plant communities ($p > 0.05$ for a slope test in a log-log regression). However, among the parasite communities of 114 species of mammal hosts, the number of parasite genera increases more slowly as a function of species richness ($G \propto S^{0.83}$, Fig. 1). This exponent is significantly lower than the two previous exponents for fish and birds ($p < 0.05$ for a slope test in a log-log regression).

Multiple congeneric species of parasites, especially nematodes, are common in the parasite faunas of several mammals. Examples include strongyloid nematodes in horses and other ungulates, cloacinid nematodes in kangaroos, and lecithodendriid trematodes in bats (Inglis 1971, Kennedy and Bush 1992, Beveridge et al. 2002). Our results suggest that in mammals in general, the slower increase in the number of parasite genera as a function of increasing species richness may be due to greater rates of within-host parasite speciation relative to rates of parasite acquisition via host-switching than in other vertebrates. This pattern is difficult to explain at present, but could result from a combination of features in certain mammals that may facilitate within-host speciation. These features may include the large body size and restricted diet of some large herbivores, which could provide many niches for similar parasite species while limiting opportunities for the acquisition of new food-borne Helminths via host-switching. Indeed, if we separate the 114 mammal species in our data set into strict herbivores (61 species) and species that include animal material in their diet (53 species), we find that the power relationship between the number of genera (G) and the number of species (S) in their Helminth communities is clearly weaker for herbivores ($G \propto S^{0.77}$) than for other mammals ($G \propto S^{0.90}$).

A central aim of ecology is to find global rules or general process to explain patterns of diversity; when a pattern such as the one we report here is observed, we must be careful about interpretations and consider spurious effects. For example, although Helminth communities in fish, bird and mammal hosts are comprised of the same four large taxa (cestodes, trematodes, acanthocephalans and nematodes), there are small differences in the relative contributions of these taxa to the Helminth faunas of different groups of vertebrates. Indeed, trematodes are often the dominant group in fishes but rare in most of mammals, whereas nematodes and cestodes are very species-poor in most fishes. We could not test the relationship between numbers of species and genera separately for each of the four large taxa, because taken individually they are very often represented by only 1 or 2 species, or not present at all, in a vertebrate host species. Nevertheless, we do not think that the weaker relationship in mammals is due to some differences in taxonomic classification. On the other hand, one could argue that our result is an artefact of statistical sampling; in mammal species, being larger in body size than birds or fishes, each individual host may sample a larger proportion of the available parasite fauna leading to a lower exponent in the power function; however, host body size appears

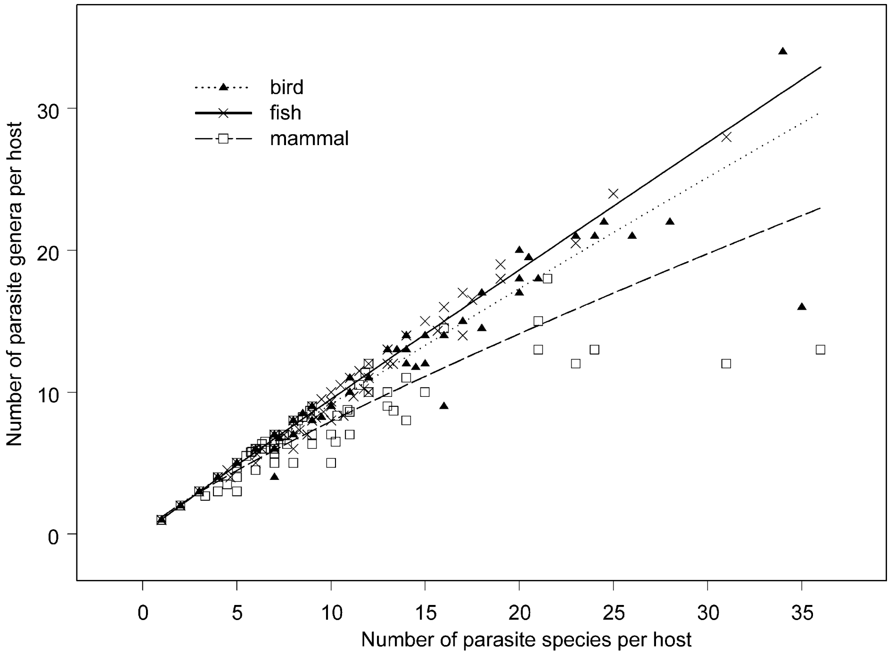

Fig. 1. Relationship between the number of parasite species and parasite genera per host across 76 birds, 107 fishes and 114 mammals. With S and G being the numbers of parasite species and genera, for birds the power relation is $G = 1.098\ S^{0.92}$ ($R^2 = 0.97$), for fishes we have $G = 1.018\ S^{0.97}$ ($R^2 = 0.99$) and for mammals we obtain $G = 1.173\ S^{0.83}$ ($R^2 = 0.92$). For some host species, data were available for more than one population; these were averaged to obtain species values.

not to influence parasite species richness in vertebrates in general, and mammals in particular (Poulin 1995, Watve and Sukumar 1995, Gregory et al. 1996). Another confounding factor could be the difference in the number of studies on the taxonomy or systematics of parasite species between groups of vertebrates. For example, more intense research on the parasites of mammals could lead to finer taxonomic distinctions among the parasite species of mammals, which in turn could lead to the lower exponent we found for the power function of mammals. In a search of the ISI Web of Science, using taxonomy or classification and parasite as key words, we found 90 articles on mammals, 255 on fishes and 82 on birds published since the year 1975 (oldest reference found). Thus we cannot use this last argument to explain our findings. Some questions which cannot be resolved here remain about these results. For instance, is the selection of host species in our data set truly representative, i.e. do the mammals with diverse parasite communities belong to the same groups as those with less diverse faunas? How do host shifts within a genus of parasite affect our conclusions? Are mammals parasitised by as many genera of parasites as the other vertebrate groups? These effects could influence the relationships between numbers of genera and species in parasite communities of fish, mammal and bird hosts, and need further investigation. For the moment, our speculations about the processes generating diversity in parasite communities can serve to stimulate both theoretical and empirical studies.

Since the pioneering study of West et al. (1997) on scaling laws in biology, general rules or models for patterns of biomass or taxonomic partitioning in natural communities have been proposed (Enquist and Niklas 2002). These suggest that despite the apparent complexity of biological organisms and communities, some fundamental invariant scaling relationships can help scientists identify underlying processes and mechanisms. Our results, based on simple scaling relationships, indicate that there may be fundamental differences in the modes of diversification of parasite communities among different groups of vertebrate hosts.

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