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Another look at the richness of helminth communities in tropical freshwater fish

Robert Poulin *Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand*

Abstract

Aim Recently, Choudhury & Dick (2000) argued that helminth parasite communities in tropical freshwater fish are not richer than those in temperate fish. Here their data is re-examined in an analysis that takes into account important confounding variables, and their conclusions are revisited.

Location The data set covers fish species from many tropical areas and from the north temperate area of the nearctic zone.

Methods Multivariate analyses are used to control the influence of sampling effort and host body size, two factors that may confound the comparison between tropical and temperate helminth communities. In addition, phylogenetically independent contrasts are derived from the fish taxa included in the data set and used to remove the potential effect of shared phylogenetic history on the richness of helminth communities.

Results Both host body size and the number of hosts examined correlated positively with the number of species found in a helminth community, and fish body size also correlated with measures of richness corresponding to the mean number of helminth species per fish individual. After controlling for the effects of these two confounding variables, temperate helminth communities still had higher richness scores than those from the tropics. The analysis using independent contrasts removed the remaining potential confounding factor, i.e. host phylogeny, and it again showed that helminth communities of temperate fish taxa are richer than those of related fish taxa from the tropics. This last result, however, applies only to the number of helminth species found in a helminth community, and not to the mean number of helminth species per individual fish host.

Main conclusions The general conclusion of the present study is similar to that of Choudhury & Dick (2000). However, the new analysis has ruled out some confounding factors as potential explanations for the patterns, and has served as an indirect test of a version of the area hypothesis (i.e. helminth diversity is explained by host size). The reason why this latitudinal gradient in richness runs counter to those usually observed in other plant and animal assemblages remains to be found.

Keywords
Parasites, diversity, latitudinal gradient, host body size, sampling effort, phylogeny.

INTRODUCTION

Latitudinal gradients in species richness and diversity are one of the clearest and most universal patterns in nature (Rosenzweig, 1995; Maurer, 1999; Gaston & Blackburn, 2000). The trend also appears to hold for some parasitic organisms, with the richness of monogenean parasite communities on marine fishes generally increasing with decreasing latitude (Poulin & Rohde, 1997; Rohde & Heap, 1998). Recently, Choudhury & Dick (2000) surveyed published studies to test the general prediction that helminth parasite communities of freshwater fishes are richer and more diverse in the tropics than in temperate regions. Their analysis did not lend support to this prediction. Instead,

Correspondence: Robert Poulin, Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand.
E-mail: robert.poulin@stonebow.otago.ac.nz

Choudhury & Dick (2000) concluded that host diet was a major determinant of helminth community richness, and that, if anything, helminth communities of fishes from the north temperate region tended to be richer than those of tropical fishes. The study of Choudhury & Dick (2000) was the first to confront an expectation widely held by parasite ecologists with actual empirical evidence. However, their analysis did not control for three important and well-documented confounding variables. Their results and conclusions may be valid, but they and the various possible underlying processes can only be evaluated properly once corrections are made with respect to the three confounding factors.

First, variation in sampling effort among host species can either generate spurious patterns or it can mask existing ones (Gregory, 1990; Poulin, 1995; Walther *et al.*, 1995). Simulated sampling of hypothetical or real host populations have clearly demonstrated that the probability of detecting rare parasite species increases with sample size (Poulin, 1998a; Walther & Morand, 1998). The duration of sampling, i.e. sampling over one or many months, can also influence estimates of species richness, but is usually not as easily available from many studies as sample size itself. Choudhury & Dick (2000) found that the number of hosts examined explained 21% of the variation in total helminth richness, and 12% of the variation in enteric helminth richness, across the tropical fish species surveyed. Host sample size is thus clearly an important confounding variable.

Secondly, and more important, Choudhury & Dick (2000) did not consider the potential influence of host body size. Because of the greater area or volume of all their organs, their higher rate of food consumption, and their longer life span, larger-bodied hosts are likely to be exposed to higher colonization rates by parasites (on both ecological and evolutionary time-scales) and to offer parasites more niches than small-bodied hosts. Hosts are often compared with islands in parallel with the island biogeography theory, and their size is therefore seen as a determinant of parasite richness (Kuris *et al.*, 1980). Indeed, in comparative studies across related host species, host body size generally emerges as a good predictor of helminth parasite richness (see Poulin, 1995, 1997, 1998b; Morand, 2000). In addition, differences in available land or ocean surface area between tropical and temperate regions provide the simplest explanation for latitudinal gradients in the richness and diversity of free-living organisms (the so-called area hypothesis: Rosenzweig, 1995; Rosenzweig & Sandlin, 1997; Rohde, 1998a; Gaston & Blackburn, 2000). As host body size is the equivalent measure of available habitat size for parasites, it seems only fitting to include it in an analysis comparing tropical and temperate hosts.

Thirdly, and most important, it is inappropriate to compare helminth communities among fish species from different geographical regions without also taking into account their phylogenetic relatedness. Fish species from the same family are likely to have inherited certain parasite lineages from their common ancestor, and their parasite communities will tend to show similarities whether or not they now inhabit the same geographical area. This point has been made before, and numerous ways to deal with phylogenetic influences have been proposed (Poulin, 1995, 1998b; Gregory *et al.*, 1996; Sasal *et al.*, 1997). Choudhury & Dick (2000) pooled species data within geographical regions, with their unit of comparison being the region; this would not account for phylogenetic influences, if any. Furthermore, they not only treated different host species as statistically independent observations regardless of their phylogenetic affinities, they also included data from more than one populations for certain fish species. This may exacerbate the problem of pseudo-replication, with certain host species being counted more than once. The only level of analysis at which truly independent observations can be obtained is the one where comparisons are made only between a temperate fish taxon and either its tropical sister taxon, or a closely related taxon from the tropics. The influence of phylogeny can only be eliminated by focusing on independent events of evolutionary divergence between pairs of related taxa that moved to different latitudes.

These issues have been discussed in detail elsewhere (Poulin, 1995, 1997, 1998b; Morand, 2000; Poulin & Morand, 2000), and here I will not discuss them further. Instead, I will re-examine the data of Choudhury & Dick (2000) in new analyses that will eliminate the three confounding factors mentioned above. By ruling out the possibility that the results are merely artefacts of one kind or another, the present study provides a more rigorous test of existing differences in richness between helminth communities from tropical and temperate fishes.

METHODS

The data set used is exactly the same as that of Choudhury & Dick's (2000) analysis (listed in their Table 1 and Appendix 2); details on how it was assembled can be found in their paper. It consists of data on 159 helminth communities from 118 species of tropical freshwater fish, and 130 helminth communities from 47 species of north temperate freshwater fish. For each helminth community, the variables considered were: the total number of fish examined (N), the total number of helminth species observed (n), the number of enteric, or gut, helminth species observed (n_g), the mean species richness considering all helminths (S_n), and the mean species richness considering only enteric helminths (S_{ng}). Mean species richness was computed according to Bell & Burt (1991); prevalence of each helminth species is used to calculate this measure, and it corresponds to the mean number of helminth species per individual host fish. In addition, I obtained information on fish size from *FishBase Online* (www.fishbase.org). As body size data of the fish specimens examined for parasites in individual studies were not available, I instead recorded the maximum known body length of each fish species. This life history parameter covaries with average adult body length, age at maturity and life span, and thus serves as a good comparative estimate of host body size. I also adopted the taxonomic classification used in *FishBase*.

Table 1 Summary of multiple regression analyses assessing the effect of two independent variables (host body size and number of hosts examined) on four different measures of helminth species richness, computed either using helminth communities or host species as independent observations. The influence of the two predictor variables is indicated by their standardized regression coefficient and its significance

Richness measure	No. communities or species	r^2	Host body size	No. hosts examined
Across helminth communities				
n	240	0.17	0.252***	0.303***
n_g	254	0.17	0.336***	0.194***
S_n	211	0.10	0.289***	0.089
S_{ng}	222	0.24	0.493***	−0.026
Across host fish species				
n	136	0.21	0.219*	0.375***
n_g	146	0.17	0.251**	0.289***
S_n	118	0.10	0.242*	0.176
S_{ng}	122	0.22	0.467***	0.006

*$P < 0.01$; **$P < 0.005$; ***$P < 0.001$.

Three analyses were performed on these data (Note: data were not always available on all the above variables for certain helminth communities, and sample sizes vary among analyses). First, as in Choudhury & Dick (2000), I treated each helminth community as an independent observation. All six continuous variables (N, n, n_g, S_n, S_{ng} and host body length) were log-transformed to meet the assumptions of parametric tests. In separate multiple regressions, each of the four measure of helminth species richness was regressed against the number of hosts examined (N) and host body length, to assess the independent influence of these two confounding variables. The residuals from these regressions were then used as measures of richness corrected for both host body size and sampling effort. The residuals may appear as mathematical abstractions, but they are easy to interpret biologically: positive values indicate that the observed richness was greater than expected based on host size and the number of hosts examined, whereas negative values indicate that the observed richness was lower than expected. Two-tailed t-tests were used to compare these residual values between tropical and temperate helminth communities.

Secondly, I treated each fish species as an independent observation. Therefore only one helminth community per fish species was included in this analysis. To choose among the many host populations available for certain fish species, I used total helminth richness as the main criterion. When more than one helminth communities were listed from the same fish host species, I used only the one with the highest value of n, provided that its host sample size (N) was given; in case of ties, I picked the one with the largest N-value. All analyses performed on this subset of the larger data set were exactly as described above, following log-transformations.

Finally, the third analysis took into account the potential influence of host phylogeny and was performed on phylogenetically independent contrasts (Harvey & Pagel, 1991). Using the proposed fish phylogeny of Lauder & Liem (1983) and Nelson (1994), I derived ten independent contrasts between pairs of closely related taxa, i.e. one taxon in each pair was from the tropics, the other was its closest available relative from the north temperate zone. Once used in a contrast, taxa were excluded from the calculation of other contrasts, ensuring that paths through the phylogeny linking taxa in each contrast do not cross and therefore that contrasts between pairs of related taxa are independent (Burt, 1989). When contrasts were made between higher taxa, mean values for higher taxa were computed following the standard taxonomic hierarchy, i.e. values from congeneric fish species were first averaged, then values from the different genera within a family were averaged, etc. As before, all analyses were performed on log-transformed data; two-tailed paired t-tests were used to compare helminth richness values between the paired tropical and temperate taxa across all ten independent contrasts.

RESULTS

Using each helminth community as an independent observation, there was no difference in the average number of hosts examined per community between tropical and temperate communities ($t = 0.623$, d.f. $= 275$, $P = 0.5336$). However, there was a difference in host body size ($t = 4.695$, d.f. $= 263$, $P = 0.0001$), with temperate hosts being on average longer than tropical ones (mean ± SE: temperate, 75.8 ± 4.1 cm; tropical, 51.1 ± 3.6 cm). There is thus a need to control for this potentially confounding variable. In the regression analyses, host body length correlated positively and highly significantly with all four measures of helminth parasite richness (Table 1). The number of hosts examined correlated positively with the total number of helminth species (n) and the number of enteric helminth species (n_g), but not with either of the two mean richness measures (Table 1). Combined, host size and number of hosts examined explained between 10 and 24% of the variation in helminth richness, depending on the measure used. Still, using the residuals from these regressions, all comparisons between the richness of helminth communities in temperate and tropical fish were significant (n, $t = 7.002$, d.f. $= 238$, $P = 0.0001$, n_g, $t = 7.348$, d.f. $= 252$, $P = 0.0001$, S_n, $t = 3.898$, d.f. $= 209$, $P = 0.0001$, S_{ng}, $t = 4.703$, d.f. $= 220$, $P = 0.0001$). Whatever the richness measure used, helminth communities in temperate fish were richer than expected based on host size and number of hosts examined, whereas those of tropical fish were always poorer than expected (Fig. 1).

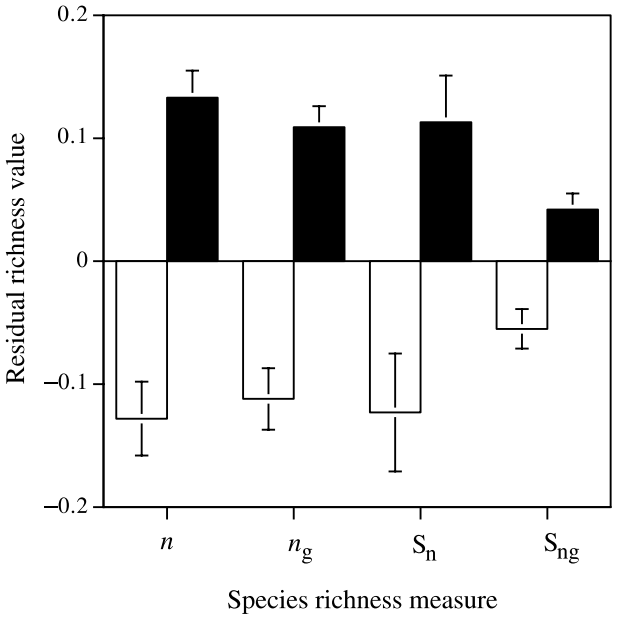

Figure 1 (Mean ± SE) species richness of helminth communities from tropical (open bars) and temperate (black bars) freshwater fish, in which some fish species are represented more than once. The four different measures of helminth richness shown are described in the text. The values are residuals from multiple regressions, and are in fact corrected for host body size and sampling effort. The number of helminth communities included ranges from 96 to 125 tropical communities, and 110–129 temperate communities, depending on the measure of richness.

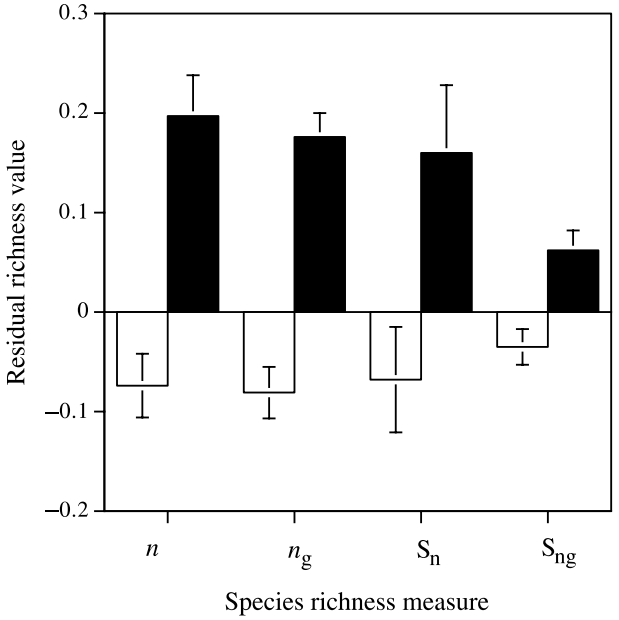

Figure 2 (Mean ± SE) species richness of helminth communities from tropical (open bars) and temperate (black bars) freshwater fish, in which all fish species are represented only once. The four different measures of helminth richness shown are described in the text. The values are residuals from multiple regressions, and are in fact corrected for host body size and sampling effort. The number of fish species included ranges from 78 to 100 tropical fish, and 35 to 46 temperate fish, depending on the measure of richness.

Using each fish species as an independent observation, there was no difference between tropical and temperate fish species in either the average number of hosts examined per species ($t = 0.627$, d.f. $= 162$, $P = 0.5313$) or in host body size ($t = 1.002$, d.f. $= 148$, $P = 0.3181$). In the regression analyses, host body length again correlated positively and significantly with all four measures of helminth parasite richness (Table 1). As before, the number of hosts examined correlated positively with the total number of helminth species (n) and the number of enteric helminth species (n_g), but not with either of the two mean richness measures (Table 1). Combined, host size and number of hosts examined explained between 10 and 22% of the variation in helminth richness, depending on the measure used. As in analyses using communities as independent points, when using the residuals from the regressions all comparisons of richness between helminth communities in temperate and tropical fish were significant (n, $t = 4.637$, d.f. $= 134$, $P = 0.0001$, n_g, $t = 6.15$, d.f. $= 144$, $P = 0.0001$, S_n, $t = 2.463$, d.f. $= 116$, $P = 0.0153$, S_{ng}, $t = 3.487$, d.f. $= 120$, $P = 0.0007$). Helminth communities in temperate fish were richer than expected based on host size and the number of hosts examined, whereas those of tropical fish were always poorer than expected (Fig. 2).

Finally, using phylogenetically independent contrasts as independent observations, some entries in the data set of Choudhury & Dick (2000) could not be included in any contrasts and were left out. In the end, though, most fish species (98% of those available in the data set) were included in one of the 10 independent contrasts (see Table 2). There were no differences between tropical fish taxa and their temperate relatives in either host body size (paired test: $t = 0.414$, d.f. $= 9$, $P = 0.6889$) or number of hosts examined ($t = 0.914$, d.f. $= 9$, $P = 0.3844$). There were, however, differences in both the total helminth richness or n ($t = 2.69$, d.f. $= 9$, $P = 0.0248$) and the enteric helminth richness or n_g ($t = 3.924$; d.f. $= 9$; $P = 0.0035$) between tropical fish and their temperate relatives. As suggested by the earlier analyses that ignored phylogenetic influences, temperate fish clearly tended to have richer helminth communities than their close relatives from tropical regions (Fig. 3). The outstanding exception to this trend comes from the contrast between the two eels, *Anguilla rostrata* from the north temperate region and *A. reinhardtii* from the tropics, in which the tropical species has a richer helminth community than its temperate relative. The pattern found with the richness measures n and n_g did not apply to the two mean richness measures, S_n and S_{ng} (both $P \geqslant 0.30$). After controlling for both host size and the number of hosts examined, i.e. using the residuals from regressions, essentially the same results were obtained: temperate fish taxa had higher values of n ($t = 2.852$, d.f. $= 9$, $P = 0.019$) and n_g ($t = 4.512$, d.f. $= 9$, $P = 0.0015$)

Table 2 Details of the ten pairs of related taxa that could be derived from the species used by Choudhury & Dick (2000) and the fish phylogeny proposed by Lauder & Liem (1983) and Nelson (1994). Each contrast includes a taxon from the tropics and its closest available relative from the temperate zone

Contrast no.	Tropical fish taxa	North temperate fish taxa
1	Family Polypteridae (3 spp.)	Family Acipenseridae (1 spp.)
2	Two Osteoglossiform families (5 spp.)	Family Hiodontidae (1 spp.)
3	Family Anguillidae (1 spp.)	Family Anguillidae (1 spp.)
4	Family Cyprinidae (24 spp.)	Family Cyprinidae (13 spp.)
5	Five Characiform families (19 spp.)	Family Catostomidae (5 spp.)
6	Family Ictaluridae (1 spp.)	Family Ictaluridae (2 spp.)
7	Nine Siluriform families (38 spp.)	Fam. Salmonidae (8 spp.) and Esocidae (1 spp.)
8	Three Atherinomorph families (6 spp.)	Family Gasterosteidae (2 spp.)
9	Family Tetraodontidae (1 spp.)	Family Cottidae (3 spp.)
10	Seven Perciform families (21 spp.)	Fam. Percidae (4 spp.) and Centrarchidae (4 spp.)

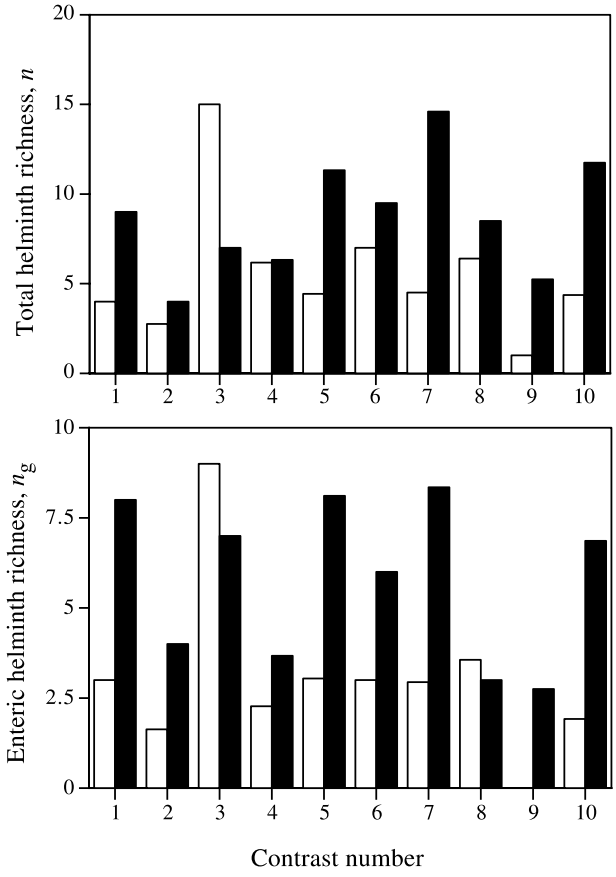

Figure 3 Total helminth richness and richness of enteric helminths for each taxon in 10 pairs of related taxa representing phylogenetically independent contrasts. For each pair, richness of the tropical taxon is shown by the open bar, and that of the temperate taxon by the black bar. Contrast numbers correspond to those in Table 2. Values are raw values not corrected for either host body size of sampling effort.

than their tropical relatives, but the pairs of related taxa did not differ with respect to S_n and S_{ng} (both $P \geqslant 0.17$).

DISCUSSION

In their paper, Choudhury & Dick (2000) concluded that the expectation that helminth communities from tropical freshwater fish would be richer and more diverse than those of temperate fish was not supported by the data. Here, I have used the dame data set to address the same question. In the end, I arrive at a similar general conclusion, but with some major improvements on Choudhury & Dick's (2000) analysis for at least two reasons.

First, the results presented here are statistically more robust. I have used a sequence of statistical analyses to progressively remove the influence of confounding variables. First the effects of sampling effort and host body size were controlled, then the threat of pseudo-replication was removed by taking the analysis to the host species level, and finally to the level of independent evolutionary events. In the process, I have generated relative measures of helminth species richness, i.e. richness per unit of host body length and per unit of sampling effort, whereas Choudhury & Dick (2000) relied on absolute measures of richness, not corrected for any potentially influential variables. True effects of latitude on species richness can only be evaluated once confounding variables are eliminated as sources of variation.

The second reason why the present results are useful is that they allow at least one popular explanation for latitudinal gradients in species richness to be tested. The simplest hypothesis to account for the high species diversity of terrestrial organisms in the tropics is that the geographical area (i.e. land area) of the tropics is much greater than that of temperate regions (the area hypothesis: Rosenzweig, 1995; Rosenzweig & Sandlin, 1997). A larger surface area usually means a lower risk of extinction and higher speciation rates. In the case of helminth parasites of freshwater fish, this does not seem to be the case. Temperate fish species harbour richer helminth communities than tropical fish; as temperate fish tend to be larger-bodied than tropical ones, a version of the area hypothesis might be at work. As shown here, however, host body size (the equivalent to land area for terrestrial organisms) is not enough to

account for richness patterns: even after controlling for differences in host body lengths, helminth communities in temperate fish are still clearly richer than those of tropical fish. One or more of the many other hypotheses invoked to explain latitudinal gradients in richness (Rohde, 1992, 1998a; Gaston & Blackburn, 2000) may be responsible for the observed pattern.

Another important result to come out of the present analyses is that once phylogenetic influences are removed from the pattern, the differences in helminth richness between temperate and tropical fish apply only to actual numbers of species found in a fish population (n or n_g), and not to the mean species richness scores (S_n and S_{ng}). This result is based on few independent contrasts and must be interpreted cautiously. Nevertheless, it suggests that the number of helminth species exploiting a fish population tends to be greater at higher latitudes, but not the mean number of helminth species per individual fish. The evidence suggesting that individual fish can become saturated with helminth species is far from overwhelming (Poulin, 1998b; Rohde, 1998b). It is still possible, however, that the number of niches available to parasites on a single fish is rather limited (Kennedy & Guégan, 1996), and one may need to consider all fish in a sample to obtain a true estimate of local helminth richness. Choudhury & Dick (2000) suggest that using mean helminth richness, S_n and S_{ng}, may be preferable in comparative studies; on the contrary, I suggest these measures can be misleading.

The latitudinal gradient reported here and by Choudhury & Dick (2000) is the opposite of the one found almost universally in other taxa, i.e. an increase in richness at low latitudes (Rosenzweig, 1995; Gaston & Blackburn, 2000). Many factors not considered here can also influence helminth richness in fish communities and may explain why temperate fish species tend to harbour richer helminth assemblages than tropical fish. These factors are reviewed elsewhere (e.g. Poulin, 1997; Morand, 2000), and they include diet, a factor shown by Choudhury & Dick (2000) to be important. As these authors suggest, however, an essential step towards understanding patterns in the diversity of parasites will involve elucidating why certain parasite lineages radiate. In other words, the emphasis must shift from identifying host features associated with high parasite diversity, to studies of parasite speciation and diversification. Recent developments in this area include analyses of the occurrence of congeneric helminths in different host species (Poulin, 1999) and phylogenetic analyses of the radiation of certain helminth lineages in hosts from specific habitats (e.g. Bray *et al*., 1999). Advances of this kind are needed to link the phylogenetic history of parasites with their biogeographical patterns of diversity.

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BIOSKETCH

Robert Poulin is an Associate Professor in the Department of Zoology, University of Otago. His research interests include all ecological and evolutionary aspects of host–parasite interactions. In particular, his recent work has focused on the patterns of parasite biodiversity and the underlying processes behind them, and the impact of parasitism on host ecology and on the functioning of ecosystems.