Neotrop. Helminthol., 4(2), 2010

ISSN: 2218-6425 impreso / ISSN: 1995-1043 on line

aphia
ASOCIACIÓN PERUANA DE HELMINTOLOGÍA E INVERTEBRADOS AFINES

REVIEW/ ARTÍCULO DE REVISIÓN

LATITUDINAL GRADIENTS IN PARASITE DIVERSITY: BRIDGING THE GAP BETWEEN TEMPERATE AND TROPICAL AREAS

GRADIENTE LATITUDINAL DE DIVERSIDAD PARASITARIA: LLENANDO EL VACÍO ENTRE LAS ÁREAS TEMPLADAS Y TROPICALES

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Suggested citation: Poulin, R. Latitudinal gradients in parasite diversity: bridging the gap between temperate and tropical areas. Neotropical Helminthology, vol. 4, nº 2, pp. 169-177.

Abstract

Although the latitudinal gradient in species richness is one of the clearest global patterns of biodiversity, evidence to date suggests that it either does not apply to parasites, or that if it does then the relationship is weak. In this short review, I use a large database including information from 950 surveys of helminth parasite diversity in vertebrate host populations to show that there is no latitudinal gradient in parasite species richness among bird or mammal hosts, and a weak one among fish hosts going against the general trend: fish from temperate latitudes tend to harbour more helminth species than those from the tropics. However, analyses of that database also show that several disparities between temperate and tropical parasite surveys can underlie the above finding. First, surveys of parasite diversity are accumulating at a much higher rate in temperate areas than in the tropics. Second, the overall level of parasitological knowledge per host species is generally higher for temperate vertebrates than for tropical ones. Third, the taxonomic resolution achieved per survey is also generally higher for temperate vertebrates than for tropical ones. Data from temperate and tropical regions are therefore not truly comparable at present, and it may be premature to attempt any large-scale test of the latitudinal diversity gradient hypothesis, or to accept the conclusions of previous studies attempting such a test.

Key words: biodiversity – helminths – latitude – study effort – taxonomic resolution – tropics.

Resumen

Aunque el gradiente latitudinal de riqueza específica es uno de los patrones globales de biodiversidad más evidentes, sin embargo, hasta la fecha, o bien no se ajusta para el caso de los parásitos, o si ocurre, la relación es débil. En esta breve revisión, utilizo una amplia base de datos con información sobre 950 estudios de diversidad de parásitos helmintos en poblaciones de vertebrados (aves, mamíferos y peces) para demostrar que no existe un gradiente latitudinal de la riqueza específica de parásitos entre aves o mamíferos; y que sí existe una débil relación en el caso de los peces, siendo ésta contraria la tendencia general. Es decir, los peces de latitudes templadas tienden a albergar más especies de helmintos que los de los trópicos. Sin embargo, estos análisis también muestran ciertas discrepancias entre los estudios parasitológicos de zonas templadas y tropicales que subyacen a los resultados obtenidos. En primer lugar, la tasa de elaboración de estudios sobre diversidad parasitaria en áreas templadas es mucho mayor que en áreas tropicales. En segundo lugar, el conocimiento global parasitológico a nivel del hospedador es generalmente mayor para los vertebrados de zonas templadas. Y en tercer lugar, la resolución taxonómica alcanzada en cada estudio, también es generalmente mayor en hospedadores de las zonas templadas que de las tropicales. Por lo tanto, los estudios de las regiones templadas y tropicales no son del todo comparables por el momento, es por ello que quizás sea prematuro, intentar comprobar a gran escala la hipótesis del gradiente latitudinal de diversidad, así como, el aceptar las conclusiones de estudios previos que han intentado comprobarla.

Palabras clave: biodiversidad - esfuerzo del estudio - helmintos - latitud - resolución taxonómica - trópicos.

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INTRODUCTION

Perhaps the most striking global pattern of biodiversity is the latitudinal gradient in species richness: as a general rule, there are more species in the tropics than at higher latitudes (Gaston, 2000; Willig *et al*., 2003; Hillebrand, 2004). Several non-mutually exclusive processes are believed to have generated this pattern, ranging from the greater input of solar energy at lower latitudes to a greater amount of effective evolutionary time because of fewer geological disruptions (Rosenzweig, 1995). These are all universal processes that should affect all taxa, thus explaining why the latitudinal gradient of diversity applies to the majority of plant and animal groups that have been investigated. Parasites should be no exception; in principle, both the number of parasite species per host species, as well as the total number of parasite species per unit area should also increase toward the equator. However, the various studies focused on parasites have not revealed strong or universal latitudinal gradients in parasite diversity (see reviews in Poulin & Morand, 2000, 2004).

There are several possible explanations for this discrepancy between results on free-living organisms and those on parasites. For instance, perhaps the number of parasite species that can exploit a host is limited by the resources available in this host, so that regardless of local biogeographical conditions, the average or maximum number of parasite species per host species is constrained by host properties. Another explanation might be that there has been a disproportionately low study effort aimed at finding and identifying parasites in animals from tropical areas. Surveys of parasite biodiversity require both taxonomic expertise and a greater investment of time than surveys of free-living organisms, because of the additional effort needed for dissection, finding parasites within the host's body, and preparing them for microscopy. These surveys have a long tradition in North America and Europe, but have only been initiated more recently in tropical areas, which may explain why parasite faunas in tropical areas do not always seem more diverse than those in temperate areas. Discovery and proper identification of parasites is crucial for conservation biology as well as for mitigating the risks of emerging diseases associated with biological invasions and other environmental perturbations (Brooks & Hoberg, 2000, 2001). It is therefore important to obtain some quantitative information on the gap, if any, between the levels of effort invested in parasite diversity surveys between tropical areas and higher latitudes.

This short paper examines trends in parasite diversity and in the scientific effort invested toward discovering parasites as a function of latitude. Here, the focus is on contrasting tropical areas with higher latitudes on a global scale; therefore, the analysis includes not only the Neotropics, but all tropical areas delimited by the Tropic of Cancer (23.4°N) and the Tropic of Capricorn (23.4°S). To provide a quantitative basis for discussion, I use simple analyses on data from a large database compiled by Poulin & Leung (2010). This database consists of data on 950 surveys of helminth communities from 650 different species of fish, bird and mammal hosts studied between the years 1936 and 2009; the full data set, including the list of the original 545 published sources, is available with the online version of Poulin & Leung's (2010) article. Each entry in this dataset corresponds to one parasite survey providing a clear list of all species of trematodes, cestodes, nematodes and acanthocephalans found in one sample of hosts from the same species from one locality, i.e. one local parasite community; some host species have been the subject of a few separate studies, and thus for those host species there are two or more entries in the dataset. The dataset was assembled from studies found with a search of the Web of Science that were available to the authors in electronic or printed form (see Poulin & Leung, 2010, for details). It is therefore likely that it excludes many relevant studies from tropical areas published in local journals. However, this is part of the problem: if data on tropical parasites are unavailable to the international scientific community, it will be difficult for anyone to attempt large-scale tests of latitudinal biodiversity gradients or other patterns. Nevertheless, the dataset does provide a basis for comparisons and discussion.

I will tackle four questions in this article. First, is there some support for a latitudinal gradient of parasite species richness among the studies in the dataset? Second, is there a difference in the cumulative number of parasite surveys over time between the tropics and areas at higher latitudes? Third, is there a difference between the tropics and areas at higher latitudes with respect to the average study effort invested per host species? Four, is the taxonomic resolution achieved during parasite identification as part of diversity surveys the same in the tropics as in areas at higher latitudes? Each of these will be addressed with simple analyses using the database described above, and discussed in relation to the literature to provide a brief overview of the challenges ahead.

LATITUDINAL GRADIENT IN PARASITE DIVERSITY

The available empirical evidence for an association between latitude and parasite species richness is equivocal at best (see Poulin & Morand, 2004). For instance, among mammal species, Poulin (1995) found no relationship between helminth species richness and latitude. In contrast, Nunn *et al*. (2005) found that the number of parasite species, including both metazoans and microparasites, infecting primates increased toward the equator, while Lindenfors *et al*. (2007) found exactly the opposite trend, i.e. greater richness at higher latitudes, for parasites in carnivores. Studies of pathogen richness among human populations tend to show that parasite diversity is greatest in tropical countries, although the challenges of disentangling the respective effects of climatic, ecological, socio-economic and political factors make it difficult to assign causality to any particular factor (Guernier *et al*., 2004; Dunn *et al*., 2010).

The overall picture emerging from studies of fish parasites is equally muddled. Among marine fish species, there seems to exist a latitudinal gradient in ectoparasite species richness. As a rule, the diversity of ectoparasites, in particular monogeneans, is higher in tropical or warm water areas than in temperate regions (Poulin & Rohde, 1997; Rohde & Heap, 1998). This pattern is independent of any differences in host body sizes or of potential phylogenetic influences (Poulin & Rohde, 1997). In contrast, there is no measurable difference in the species richness of endoparasite species between tropical and temperate areas (Rohde & Heap, 1998). Among freshwater fish species, comparative studies have revealed that temperate fish species are hosts to richer assemblages of helminth parasites than tropical fish species (Choudhury & Dick, 2000). This surprising trend persists once we eliminate the potentially confounding effects of differences in sampling effort, host body size, and host phylogenetic affinities (Poulin, 2001). Therefore, there is no consistency among the results obtained for fish hosts: parasite species richness peaks in temperate regions for helminths of freshwater fishes, it peaks in the tropics for ectoparasites of marine fishes, and it shows no latitudinal variation for endoparasites of marine fishes.

Here, I provide an additional empirical test of the latitudinal gradient in parasite diversity, using the database described above. In this database, most available surveys (828 out of 950) came from the Northern Hemisphere. I treated latitude regardless of whether it was north or south, since preliminary analyses indicated that it made no difference whether or not the two hemispheres were differentiated. Endohelminth species richness is defined as the total number of endohelminth species found in a particular survey. Correlations between endohelminth species richness (log-transformed) and latitude of the survey were not statistically significant for bird hosts (r = -0.11, P = 0.13) and mammal hosts (r = -0.01, P = 0.80), but there was a significant positive correlation in fish hosts (r = 0.14, P = 0.002) (Fig. 1). In other words, fish at higher latitudes tend to harbour more species of helminths than those at lower latitudes, i.e. those in the tropics. This is a relatively weak pattern, however, since latitude explained only <3% of the variance in parasite species richness. Thus, there are many fish populations from high latitudes harbouring relatively poor parasite communities (see Fig. 1).

These new results echo those of Choudhury & Dick (2000) and Poulin (2001) by suggesting that fish at higher latitudes might harbour richer parasite assemblages, but the pattern is weak. For bird and mammal hosts, no latitudinal gradient is apparent across the many surveys in the database. These results do not bring us closer to determining whether or not there is a latitudinal gradient in parasite diversity; instead, they just add to the growing list of inconsistent patterns reported to date. The lack of congruence among these past results suggests at least two possibilities. First, maybe there is no latitudinal gradient in species diversity applying to parasites. Solar energy ultimately controls the productivity and diversity of ecosystems, but for parasites the direct determinant of resource availability is the host, and

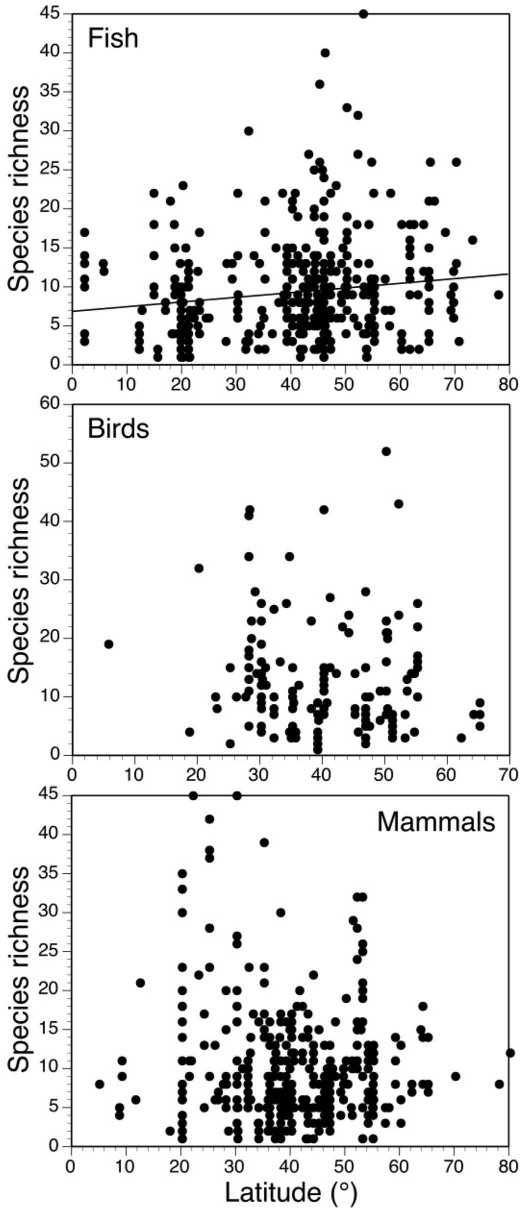

Figure 1. Species richness of endohelminth parasites plotted as a function of the latitude at which a host sample has been collected, for 419 surveys of fish hosts, 161 surveys of bird hosts, and 370 survey of mammal hosts. The best-fit line is shown for the only significant relationship, i.e. that observed in fish hosts.

maybe host properties such as body size, metabolic rate or lifespan, are much more important for parasite diversification than the latitude at which the host lives. There may be a few exceptions, such as ectoparasites of marine fish hosts; Rohde (1992) has proposed that higher water temperature in tropical seas should promote higher mutation rates and shorter generation times in monogeneans, possibly leading to higher rates of diversification. For other parasites in general, however, tropical areas may not necessarily be hotspots of diversity. Latitudinal gradients of species richness indeed tend to be weak for small-bodied taxa (Hillebrand & Azovsky, 2001), and parasites do tend to be small. Second, perhaps there really is a latitudinal gradient in parasite species diversity but we cannot detect it because currently available data are inadequate. It is not farfetched to believe that more data are available from temperate regions of North America and Europe than for tropical regions of the world, simply because (i) North American and European countries have a longer history of scientific research, and (ii) governments of these countries invest a proportionally greater amount of money into science, including basic biological research, than governments of most tropical countries. Therefore, the lack of data may mask a true underlying latitudinal gradient in parasite diversity. The next three sections of this review explore this possibility by examining the evidence that tropical parasite data are not really comparable to temperate parasite data.

CUMULATIVE NUMBER OF SURVEYS

The more we study something, the better we know it. Existing knowledge of parasite diversity is increasing at different rates for different parts of the world, and these differences make it difficult to compare parasite diversity between different geographical areas. For instance, in a comparison between parasite diversity in New Zealand and Canadian fishes, differences in past study effort between the two countries appeared to account for most of the variation found, and suggested that parasite diversity in New Zealand has been severely underestimated (Poulin, 2004). It is therefore important to assess whether surveys of parasite diversity in temperate and tropical areas have been performed at comparable rates.

A look at the cumulative number of parasite surveys in vertebrate hosts published over time reveals some clear patterns (Fig. 2). Firstly, the number of surveys of parasites in tropical vertebrates only started to rise in the 1980s, whereas by that time surveys of parasites in temperate vertebrates were accumulating at a steady rate. Secondly, in the past decade, the rate of increase in the number of published surveys is

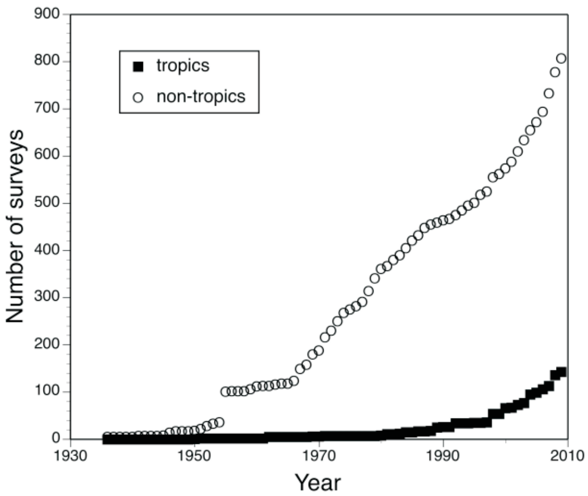

Figure 2. Cumulative number of parasite surveys as a function of year of publication for vertebrate hosts sampled in the tropics (between 23.4°N and 23.4°S) and outside the tropics.

much higher for temperate hosts than for tropical hosts (Fig. 2). These findings suggest that the study effort devoted to tropical parasite assemblages is still lagging behind that devoted to temperate parasites. Of course, these results are derived from a database assembled from studies that were both (i) included in the Web of Science, and (ii) available either electronically or in print via the University of Otago's excellent library. Many parasite surveys published in local journals were no doubt missed, and these may include a disproportionate number of surveys from tropical regions. However, any attempt to test the existence of a latitudinal gradient in parasite diversity will have to be based on internationally available data, and presently, on this international level, research on tropical parasite assemblages is clearly far behind that on their temperate counterparts.

Another difference between surveys in temperate areas and those in tropical areas concerns the frequency at which the same host species is studied more than once. As stated earlier, some host species have been the subject of a few separate studies, and for those host species there are two or more entries in the database. In temperate areas, the database included 807 surveys on 527 host species, among which 146 species, or 27.7%, were the subject of more than one survey. In tropical areas, there were 143 surveys on 123 host species, among which 8 species, or 6.5%, were the subject of more than one survey. Thus temperate host species are about 4 times more likely to be surveyed more than once, generally in different localities, than tropical host species. Since both the composition of parasite communities and the abundance of specific parasite species can vary substantially among localities (Poulin & Morand, 1999; Poulin, 2006; Krasnov *et al*., 2005, 2008), the data currently available for temperate species is more representative simply because for many host species it covers a broader portion of the geographic range.

The available number of surveys of parasite diversity in tropical vertebrates is growing rapidly, but still trailing that for temperate hosts. This is probably only a temporary problem, however, since a large group of very active researchers in Latin America is rapidly closing that gap (see Salgado-Maldonado *et al*., 2000). Indeed, a few very active individuals can speed up parasite discovery in an entire geographical region over a few years of intense work, as illustrated by the history of research on cestodes from Australia (Beveridge & Jones, 2002). Thus, we are fast approaching a time when the discrepancy in available parasite surveys between temperate regions and the tropics will vanish, allowing more robust tests of the latitudinal gradient in parasite diversity.

STUDY EFFORT PER HOST SPECIES

The number of available parasite surveys for a region is not the only measure of how much research effort has been invested in the study of parasitism in that region. There are also many studies on the taxonomy, pathology, life cycles, etc. of parasite species. The combined research effort put into all these aspects of host-parasite relationships must also be comparable between geographical regions if we want to use them in the same analysis, for instance by comparing parasite diversity between temperate and tropical regions.

In the database used here, the relative study effort devoted to parasites in the host species was estimated as the total number of records obtained from a search of the Web of Science using the keywords: Latin binomial name of host species AND (parasit* OR helminth* OR tremat* OR digenea* OR nemat* OR cestod* or acanthoceph*). Although this measure does not perfectly capture all previous work on the taxonomy, pathology, life cycles, etc., of parasites found in the host species, it reflects the extent to which researchers have studied the parasites of that host. This is also a much more relevant measure of study effort than host sample size, since existing knowledge of the biology of parasites in a given host species depends on the extent of previous work rather than on how many individual hosts are examined in a particular survey. Based on this measure, the study effort devoted to parasites of both fish and mammal hosts in the tropics was significantly lower than that devoted to host species outside the tropics (one-way ANOVAs on log-transformed study effort; fish: $F_{1,417} = 36.44$, $P < 0.0001$; mammals, $F_{1,368} = 26.07$, $P < 0.0001$). The difference is substantial: on average, the study effort toward parasites of non-tropical species of fish and mammals is about three times higher than for tropical species (Fig. 3). The difference was not significant for bird hosts, however ($F_{1,159} = 2.47$, $P = 0.11$), most likely because the sample size for tropical bird hosts is very small, i.e. only 6 available surveys of parasites for tropical birds (Fig. 3).

These results indicate clearly that for the two host taxa for which sufficient data are available, i.e. fish

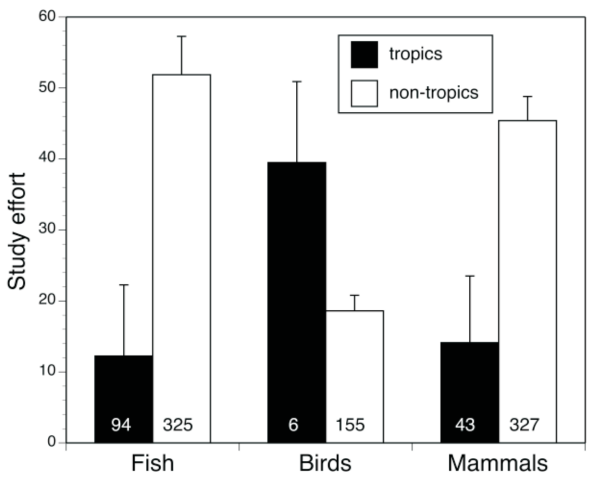

Figure 3. Mean (±SE) study effort devoted to parasites of host species sampled in the tropics (between 23.4°N and 23.4°S) and outside the tropics, shown separately for fish, bird and mammal hosts. Study effort is measured as the total number of relevant records obtained from a search of the Web of Science. Numbers on the bars indicate sample sizes.

and mammals, much more parasitological research is carried out per host species in temperate areas than in the tropics. This is likely to seriously impact our attempts to search for latitudinal gradients in parasite species diversity. For instance, this would mean that there are, on average, more taxonomic studies performed on temperate parasites than on tropical parasites. Taxonomy allows us to distinguish between closely related species, and with better taxonomic knowledge, we can achieve more accurate estimates of parasite species diversity. The next section illustrates how the lower study effort devoted to parasitism in the tropics has seemingly impacted our ability to discriminate among related species.

TAXONOMIC RESOLUTION OF PARASITES

It is becoming increasingly clear that nature is full of cryptic species that cannot be distinguished from each other based on morphology, even by expert taxonomists. In recent years, a large number of studies have used molecular tools to discover new species, with the result that what was previously thought to represent a single species is in fact a complex of two or more closely related species (Poulin & Morand, 2004; Pérez-Ponce de León & Nadler, 2010). This revolution in our understanding of biodiversity is happening at a time when changing funding priorities are threatening the maintenance of taxonomic expertise in museums and universities. The worldwide loss of taxonomic expertise is seen as one of the greatest challenges to current research in parasite biodiversity and ecology (Brooks & Hoberg, 2000, 2001; Cribb, 2004).

There may already be measurable effects of this loss in taxonomic expertise. Among the surveys in the database used here, parasite taxa are often not identified all the way down to species level, but only to genus or family level. A classical example is provided by the nematode *Anisakis*, which is almost always listed only by genus name in numerous surveys of parasites of marine fishes. Recently, Poulin & Leung (2010) have showed that the level of taxonomic resolution achieved per survey has decreased significantly in the past ten years compared to the previous decades. The gradual loss of taxonomic experts mentioned above is one possible explanation. In the context of latitudinal gradients in diversity, it is now important to compare the level of species identification achieved in parasite surveys from temperate and tropical regions.

Here, taxonomic resolution was calculated for each of the 950 surveys in the database as the proportion of endohelminth taxa, out of the total recovered in a survey, that were identified to species level, i.e. given a full binomial Latin name. Thus, for example, a taxonomic resolution value of 1.0 in a given survey means that all species were identified to species level, and a value of 0.5 means that only half of the parasites were identified to species level. Taxonomic resolution for both fish and mammal hosts in the tropics was significantly lower than that for hosts outside the tropics (one-way ANOVAs on arcsine-transformed taxonomic resolution; fish: $F_{1,417} = 7.19$, $P = 0.007$; mammals, $F_{1,368} = 5.23$, $P = 0.022$). The difference is modest, with the resolution achieved in non-tropical species of fish and mammals being not quite 10% higher than for tropical species (Fig. 4). However, the difference was not statistically significant for bird hosts ($F_{1,159} = 1.82$, $P = 0.17$), possibly because the sample size for tropical bird hosts is very small, i.e. only 6 available surveys of parasites for tropical birds (Fig. 4).

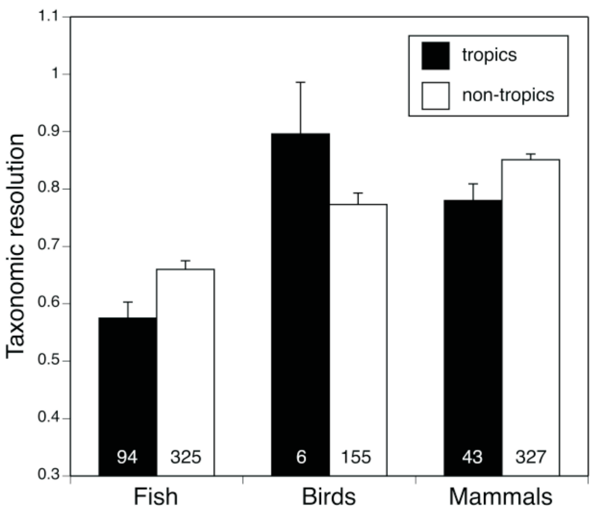

Figure 4. Mean (±SE) taxonomic resolution of parasites in host surveys from the tropics (between 23.4°N and 23.4°S) and outside the tropics, shown separately for fish, bird and mammal hosts. Taxonomic resolution is the proportion of helminth taxa in each survey identified to species level. Numbers on the bars indicate sample sizes.

These results suggest that estimates of parasite species richness cannot be compared between the tropics and temperate areas, because at the moment the lower taxonomic resolution achieved in tropical parasite surveys probably leads to small but systematic errors in richness values. Assuming that some of the taxa identified only to genus or family level often consist of two of more cryptic species, parasite species diversity in the tropics is more likely to be underestimated than in temperate regions.

CONCLUSIONS

Based on a large database compiled from 950 surveys of parasite diversity in vertebrate hosts, the present study has found no consistent or convincing evidence for a latitudinal gradient in parasite species richness. However, analyses of this database also indicate that (i) surveys of parasite diversity are accumulating at a much higher rate in temperate areas than in the tropics, (ii) the overall level of parasitological knowledge per host species is generally higher for temperate vertebrates than for tropical ones, and (iii) the taxonomic resolution achieved per survey is also generally higher for temperate vertebrates than for tropical ones. It is therefore premature to attempt any rigorous large-scale test of the latitudinal diversity gradient hypothesis, because temperate and tropical data are not yet comparable in a quantitative manner. The current rate at which new parasitological knowledge is accumulating in the tropical region, especially in the Neotropics, suggests that such a test will be realistic within just a few years. At present, it would be safer not to consider parasites as exceptions to the almost universal pattern of increasing diversity toward the equator (Gaston, 2000), since the final verdict is still awaiting the data.

ACKNOWLEDGMENTS

I thank Tommy Leung for his invaluable assistance in compiling the database used for the analyses in the present article, and Isabel Blasco-Costa for translating the title and abstract into Spanish.

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Received July 1, 2010.
Accepted October 27, 2010.

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