Latitudinal gradients of parasite species richness in primates

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ABSTRACT

Infectious disease risk is thought to increase in the tropics, but little is known about latitudinal gradients of parasite diversity. We used a comparative data set encompassing 330 parasite species reported from 119 primate hosts to examine latitudinal gradients in the diversity of micro and macroparasites per primate host species. Analyses conducted with and without controlling for host phylogeny showed that parasite species richness increased closer to the equator for protozoan parasites, but not for viruses or helminths. Relative to other major parasite groups, protozoa reported from wild primates were transmitted disproportionately by arthropod vectors. Within the protozoa, our results revealed that vector-borne parasites showed a highly significant latitudinal gradient in species richness. This higher diversity of vector-borne protozoa near the tropics could be influenced by a greater abundance or diversity of biting arthropods in the tropics, or by climatic effects on vector behaviour and parasite development. Many vector-borne diseases, such as leishmaniasis, trypanosomiasis, and malaria pose risks to both humans and wildlife, and nearly one-third of the protozoan parasites from free-living primates in our data set have been reported to infect humans. Because the geographical distribution and prevalence of many vector-borne parasites are expected to increase because of global warming, these results are important for predicting future parasite-mediated threats to biodiversity and human health.

Keywords

Biodiversity, latitudinal gradient, parasite richness, primates.

INTRODUCTION

Understanding the factors responsible for latitudinal gradients in species richness has been a major research focus in evolutionary ecology (Rosenzweig, 1995). Latitudinal variation in species richness has been documented for a wide range of taxonomic groups and may be caused by multiple factors, including climatic limits on organismal life cycles, increased productivity near the equator and geometric constraints of continental landmasses (Brown, 1995; Rosenzweig, 1995; Colwell & Lees, 2000; Gaston, 2000). Global patterns of parasite diversity have received less attention than biodiversity gradients among free-living species, but a few studies focusing on avian, fish and mammalian hosts have shown that direct and indirect measures of parasite pressure and diversity increase closer to the equator (e.g. Poulin & Rohde, 1997; Møller, 1998; Rohde & Heap, 1998; Cumming, 2000; Poulin & Morand, 2004). More recently, Guernier et al. (2004) showed that the global diversity of parasites and infectious diseases that are reported to infect humans increased in areas closer to the equator, and that this pattern closely corresponded to climatic variables, including annual variation in rainfall and temperature.

A fundamental measure of disease risk is the number of parasite species to which an individual host is potentially exposed, as assayed by the observed parasite species richness in a given host taxon (Morand & Poulin, 2000; Poulin & Morand, 2000). Increased parasite species richness is expected in the tropics for several reasons. Mortality as a result of temperate winters may represent a major source of mortality for parasites with life history stages that occur outside of vertebrate hosts (Harvell et al., 2002). In addition, increased geographical range overlap among host species closer to the equator may lead to greater cross-species infection opportunities for parasites (Morand, 2000), especially for generalist parasites that can infect a wide range of host species. Finally, intermediate hosts and arthropod vectors might show latitudinal gradients in abundance and diversity, with secondary effects on parasite biodiversity and transmission rates. These vectors and intermediate hosts represent important limits on the distribution of some parasites with multihost life cycles, including those that cause schistosomiasis, malaria, Chagas’ disease, dengue fever, and St. Louis encephalitis (e.g. Patz et al., 1996; Jetten & Focks, 1997; Martens et al., 1997; Githeko et al., 2000). Thus, both collectively and individually, all of these processes predict latitudinal gradients in parasite diversity.
diversity that mirror patterns found in free-living species, with greater parasite diversity expected in tropical versus temperate regions (Brown, 1995; Rosenzweig, 1995; Gaston, 2000).

In this work, we tested whether parasite species richness increases near the equator in free-living primate hosts. We focused on primates as a model system because the behaviour, life history, phylogeny and ecology of this group of mammals have been relatively well studied, and as a group, they are widely distributed. Because of their close evolutionary relationships to humans, much is known about the parasites that infect primates, including macroparasites, such as viruses, protozoa, bacteria and fungi, and macroparasites, such as helminths and arthropods. Moreover, several host characteristics are known to affect parasite diversity in primates, including population density, body mass and geographic range size (Nunn et al., 2003). This information is readily available for primate species, allowing us to control potentially confounding variables in our comparative tests.

Because many reported parasites of wild primates can infect human hosts, results of our study are also relevant to human health concerns. Furthermore, much attention has focused on the potential role of climate warming in the spread and severity of infectious diseases in both marine and terrestrial systems (Harvell et al., 1999, 2002). Thus, understanding the factors associated with the global patterns of parasitic organisms represents one step towards predicting the impact of large-scale climate changes on the geographical distribution of infectious diseases.

METHODS

To investigate latitudinal gradients in parasite species richness, we compiled information from the published literature on parasites that infect free-living primates. We recorded micro or macroparasites reported from free-living primate species by using primate Latin binomials as search keywords in the major online reference databases (Biological Abstracts, AGRICOLA, Medline, Web of Science). We also searched by primate genus name and by common taxonomic variants (based on Rowe, 1996; Groves, 2001). In addition to using electronic Bibliographic databases, we examined edited volumes and reviews (e.g. Fiennes, 1972; Brack, 1987) and studies that were cited by publications that we located in our first round of searches. For each parasite or infectious disease reported from a wild primate population, we recorded the type of parasite (virus, protozoan, fungi, arthropod, helminth, bacteria), its genus and species names, the host’s genus and species names (later revised according to Corbet & Hill, 1991), and information on the location and method of sampling. We ultimately restricted our analyses to protozoa, helminths and viruses, as these are the best studied parasites of primates (Nunn et al., 2003) and represent a diverse array of parasite life cycles and transmission strategies. Host species were included only if they had been sampled for parasites. Parasites with clear synonyms were collapsed into one species, taxonomic records were scanned in current textbooks and online databases, and parasites identified to only the genus level were included in the analysis if they represented a unique record for that genus in a host species. Data from these three parasite groups collectively represented 825 unique host–parasite combinations involving 330 parasite species reported from 119 primate host species. Further details on how this database was constructed are reported in Nunn et al. (2003) and Nunn and Altizer (2005).

Analyses were based on the absolute value of median latitude for each primate species, which ranged from 38.84° S to 31.51° N. We predicted a negative association between parasite species richness and latitude north or south of the equator. We obtained data on the median latitude of primate hosts using geographically rectified range maps for each of the primate species, as compiled in a geographical information system (GIS, W. Sechrest, unpublished data). We used median latitude of the host rather than information on the collecting localities because our analyses were conducted at the species level, and geographical coordinates could be identified for only 63% of the references used in the database.

In a set of three multivariate analyses, we included information on host body mass, population density, geographic range size, total population size, and longevity. Body size was estimated as mean female body mass (Smith & Jungers, 1997), and longevity was measured as maximum recorded longevity in years (Ross & Jones, 1999). We obtained estimates of population density based on field studies of local populations, measured as the mean number of animals per square kilometre. Geographic range size was compiled using the published literature to establish a digitized map of occurrence for each species (W. Sechrest & J.L. Gittleman, unpublished data). Population size was estimated as the product of geographic range size and mean population density. Based on previously published theoretical and empirical work, we predicted that parasite richness should exhibit a positive association with each of these five host traits (e.g. Morand, 2000; Nunn et al., 2003).

Regional or taxonomic sampling biases pose a challenge to studies of parasite diversity, with host species that are better studied having more parasites reported in the literature (Gregory, 1990; Poulin & Morand, 2000). To address this issue, we followed previous researchers (Gregory, 1990; Poulin, 1995; Morand & Harvey, 2000; Morand & Poulin, 2000) by including a measure of sampling effort as a covariate in all analyses reported here. As the primary measure of sampling effort, we used the number of citations from an online database, PrimateLit, which can be accessed at <http://primatelit.library.wisc.edu/>. This source provides the most complete reference information for journal articles, books and book chapters on primates. In addition, this citation index most closely matches the sampling period (1940 up to present) during which most of the studies in our database were published. Use of an alternative citation index, the Web of Science (<http://isist02.isiknowledge.com/portal.cgi>), produce generally congruent results in a subset of tests.

We conducted multiple regression analyses with and without controlling for host phylogeny. Using information on primate phylogeny (Purvis, 1995), we calculated independent contrasts with the computer program CAIC (Purvis & Rambaut, 1995) to investigate whether phylogenetic differences in parasite diversity are correlated with differences in absolute median latitude. Because
an alternative model of evolution has been shown to produce inflated type I error rates when using independent contrasts (Price, 1997; Harvey & Rambaut, 2000), we also present results from non-phylogenetic analyses that used species values (Harvey & Rambaut, 2000). To best meet the assumptions of independent contrasts, all data and branch lengths were log-transformed prior to running phylogenetic and non-phylogenetic tests, and we conducted analyses after removing outlying contrasts (Nunn & Barton, 2000, 2001).

We followed recent comparative studies of parasite richness by correcting for host phylogeny, thus treating parasite species richness as characteristic of the host (e.g. Poulin, 1995; Morand & Harvey, 2000; Nunn et al., 2003). We did not incorporate information on parasite phylogeny because the goal of our study was to investigate ecological patterns of parasitism rather than parasite evolution. Moreover, a strict phylogenetic approach based on cospeciation (Hafner & Page, 1995; Hugot, 1999; Morand et al., 2000) is impossible to implement when generalist parasites infect a wide range of host species. Indeed, 56% of the parasites in our database were classified as generalists, meaning they were reported to infect a range of hosts at the taxonomic level of family or above, and in many cases, also infecting non-primate hosts.

When testing specific predictions, we used directed tests rather than one-tailed tests, as these enable detection of patterns that are opposite to predictions while retaining much of the statistical power of one-tailed tests (Rice & Gaines, 1994). Directed tests allocate a disproportionate probability under the null hypothesis to the tail of the distribution in the predicted direction (γ), while retaining a smaller probability in the other tail to detect unexpected deviations in the opposite direction (δ < γ). Directed tests are subject to the constraint that δ + γ = α. We followed the guidelines in Rice and Gaines (1994) by setting γ/α to 0.8, giving values of γ = 0.04 and δ = 0.01.

### RESULTS

Median latitude and sampling effort together explained 24.5% of the variation in the number of protozoan parasite species per host species ($F_{1,116} = 17.5, P < 0.0001$) in non-phylogenetic analyses. Both independent variables were statistically significant, with parasite richness declining with distance from the equator and increasing with sampling effort (Table 1). In phylogenetic tests using independent contrasts, both latitude (Fig. 1) and sampling effort were statistically significant predictors of protozoan parasite diversity. In analyses of helminths and viruses, however, only sampling effort explained significant variation in parasite diversity, and latitude was not a significant predictor of variation in the diversity of all parasites combined (Table 1).

#### Table 1

<table>
<thead>
<tr>
<th>Parasite type</th>
<th>Non-phylogenetic tests ($n = 119$)</th>
<th>Phylogenetic tests ($n = 108$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median latitude</td>
<td>Sampling effort</td>
</tr>
<tr>
<td>Protozoa</td>
<td>−2.29*</td>
<td>5.80***</td>
</tr>
<tr>
<td>Apicomplexa</td>
<td>−1.74</td>
<td>4.80***</td>
</tr>
<tr>
<td>Euglenozoa</td>
<td>−1.73</td>
<td>2.74**</td>
</tr>
<tr>
<td>Helminths</td>
<td>0.61</td>
<td>6.25***</td>
</tr>
<tr>
<td>Viruses</td>
<td>−1.41</td>
<td>6.18***</td>
</tr>
<tr>
<td>All combined</td>
<td>−1.56</td>
<td>7.87***</td>
</tr>
<tr>
<td>Protozoa</td>
<td>−2.42**</td>
<td>4.64***</td>
</tr>
<tr>
<td>Helminths</td>
<td>−1.59</td>
<td>4.20***</td>
</tr>
<tr>
<td>Viruses</td>
<td>−0.10</td>
<td>3.91***</td>
</tr>
<tr>
<td>All combined</td>
<td>−2.40**</td>
<td>5.84***</td>
</tr>
</tbody>
</table>

Values are $t$-statistics, with sign of the $t$-statistic corresponding to the sign of the regression coefficient. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, directed tests (Rice & Gaines, 1994). Sample sizes differ in non-phylogenetic and phylogenetic analyses because of polytomies in the phylogeny used to calculate contrasts (Purvis & Rambaut, 1995; Purvis, 1995) and removal of outliers.

![Figure 1](image_url)
To control for potentially confounding variables, we performed three sets of multivariate tests involving the diversity of protozoa. First, we controlled for population density, longevity and body mass based on three host traits shown to be significant in a previous analysis of protozoan diversity (Nunn et al., 2003). When the effects of latitude were examined together with these variables in a multiple regression model, latitude remained a significant predictor of protozoan parasite species richness in both non-phylogenetic ($b = -0.17, F_{1,55} = 4.59, P = 0.023$, directed test) and phylogenetic tests ($b = -0.18, F_{1,50} = 6.12, P = 0.011$, directed test). Population density, longevity, and sampling effort also remained significant in many of these analyses, which is consistent with previous results (Nunn et al., 2003).

Second, we examined the effects of geographic range size, latitude and sampling effort on the diversity of protozoa, based on the finding that primate geographical range increases close to the equator (independent contrasts: $b = -0.28, F_{1,100} = 4.21, P = 0.04$, two-tailed). This model was statistically significant in analysis of species values ($F_{1,115} = 13.5, P < 0.001$) and independent contrasts ($F_{1,99} = 10.8, P < 0.0001$), although latitude failed to reach significance in the non-phylogenetic test ($b = -0.09, F_{1,115} = 2.38, P = 0.08$). In the contrasts analysis, we found a positive effect of geographic range ($b = 0.14, F_{5,99} = 7.93, P = 0.004$) and a negative effect of latitude ($b = -0.11, F_{5,99} = 3.63, P = 0.04$) on the diversity of protozoa when outliers were excluded.

In a final multivariate model, we investigated whether the combined effects of density and geographic range might in fact reflect an influence of total population size, which we estimated as geographic range multiplied by population density. A multivariate model that included population size, latitude, body mass, and sampling effort as predictor variables was statistically significant when using species values ($F_{3,115} = 13.5, P < 0.001$) and independent contrasts ($F_{3,99} = 10.8, P < 0.0001$), although latitude failed to reach significance in the non-phylogenetic test ($b = -0.09, F_{1,115} = 2.38, P = 0.08$). In the contrasts analysis, we found a positive effect of geographic range ($b = 0.14, F_{5,99} = 7.93, P = 0.004$) and a negative effect of latitude ($b = -0.11, F_{5,99} = 3.63, P = 0.04$) on the diversity of protozoa when outliers were excluded.

Finally, to further investigate factors that account for the latitudinal gradient in protozoan parasite richness, we examined patterns within the two major protozoan phyla infecting wild primates, Apicomplexa and Euglenozoa. These two phyla differ in their relative degree of host specificity, with 28/46 (61%) of the Apicomplexa specific at the level of host species or genus, but only 5/17 (29%) of the Euglenozoa exhibiting the same level of host specificity. In fact, most Euglenozoa in our data set were classified as generalists at the level of host order or higher.
(S.M. Altizer, unpublished data). Parasites in both of these phyla were dominated by vector-borne species, including all of the Euglenozoa in our dataset and 75% of the Apicomplexa. Both groups exhibited a significant latitudinal gradient in parasite diversity when using independent contrasts (Table 1), and non-phylogenetic results approached significance at $P < 0.06$. Latitude was statistically significant in many of the multivariate tests using independent contrasts (controlling for population density, body mass, longevity and sampling effort, Apicomplexa: $t_{100} = -3.11, P = 0.002$; Euglenozoa: $t_{100} = -1.81, P = 0.048$; controlling for population size, body mass and sampling effort, Apicomplexa: $t_{100} = -1.30, P = 0.13$, Euglenozoa: $t_{100} = -2.43, P = 0.01$), but not when we included geographic range size in the statistical model (Apicomplexa: $t_{100} = -0.39, P = 0.44$, Euglenozoa: $t_{100} = -1.89, P = 0.11$). Similar results were obtained in multivariate non-phylogenetic analyses using species values.

**DISCUSSION**

Our results revealed a significant latitudinal gradient in the diversity of protozoan parasites reported from wild primate populations, with strongest results obtained for protozoa that are transmitted by arthropod vectors. This pattern is consistent with the hypothesis that an increasing abundance or diversity of arthropod vectors close to the equator leads to increased diversity of protozoan parasites within each primate host species. The pattern that we found could also be caused by changes in vector behaviour or development of the pathogens themselves, so that higher vector biting rates or more rapid parasite development may occur at warmer latitudes (Dobson & Carper, 1992; Liang et al., 2002). Indeed, several studies have identified temperature, and rainfall to a lesser degree, as major components of vectorial capacity and epidemic potential (Martens et al., 1995; Harvell et al., 2002), although some recent studies have disputed the impacts of climate on the distribution of vector-borne diseases (Shanks et al., 2000; Hay et al., 2002). In their study of infectious diseases of humans, Guernier et al. (2004) also found links between multiple climatic variables, including temperature and annual variation in rainfall, and patterns of parasite species diversity.

Explanations involving vector transmission fail to account for the lack of significance for other parasite groups that exhibit vector transmission. Thus, the species richness of vector-borne protozoa declined significantly with latitude, as compared to nearly significant effects for vector-borne helminths and non-significant results for vector-borne viruses. Moreover, non-vector transmitted protozoa were significantly related to latitude in some analyses, suggesting that factors other than vector transmission might account partially for the latitudinal gradient in protozoan richness. Further research is needed to test whether significant results for protozoa reflect that a higher proportion of protozoa are vector-borne, which could possibly give us greater statistical power to detect correlations among the vector-borne protozoa, and consistent with the nearly significant results for vector-borne helminths. Alternatively, the latitudinal gradient in protozoan species richness may reflect an unidentified aspect of protozoan biology that leads to increased diversity and prevalence or probability of coinfection at lower latitudes. For example, climate-induced developmental restrictions could be more severe for vector-borne protozoa that complete sexual reproduction or asexual cycles of replication within arthropod vectors, relative to vector-borne viruses and helminths.

Latitudinal gradients in parasite diversity could also be caused by geographical variation in host species richness. For example, ‘collective’ parasite species diversity may be higher near the equator simply because more host species are present at lower latitudes. Primate species diversity has been shown to increase near the equator (Cowlishaw & Hacker, 1997; Eeley & Lawes, 1999), but this process alone is unlikely to generate the patterns observed here for at least three reasons. First, associations between parasite species richness and latitude were only significant for protozoa. Second, our analyses examined effects of latitude on the diversity of parasites on a host species basis, so that increased parasite species richness was not simply as a result of a collective effect of pooling parasites across multiple host species in a given location. Finally, latitudinal patterns hold for both relatively host specific (Apicomplexa) and non-specific (Euglenozoa) phyla of protozoa, indicating that latitudinal gradients in the diversity or abundance of particular vertebrate hosts are not driving this pattern.

We also considered the possibility that latitudinal gradients in parasitism may be driven by characteristics of the host species themselves, so that variation in host body size, population density, or geographic range may drive observed patterns of parasitism (e.g. if population sizes increase closer to the equator). With the exception of some analyses involving geographic range size, latitude remained a significant predictor of protozoan parasite species richness in most multivariate tests that controlled for host traits that are likely to influence patterns of parasitism.

Characterizing the global distribution of vector-transmitted parasites, and understanding processes driving these patterns, are important to both human health and wildlife conservation for several reasons. Vector transmission is expected to confer greater opportunities for pathogens to cross species boundaries (Woolhouse et al., 2001), as compared to parasites transmitted by direct contact. Many vector-borne diseases, such as leishmaniasis, trypanosomiasis, and malaria are zoonotic and thus pose risks to both humans and wildlife species. In fact, 32% of the protozoan parasites reported from free-living primates in our data set have also been reported to infect humans under natural conditions (Ashford & Crewe, 1998), and latitudinal gradients observed in human cases may parallel those from wild host species. Moreover, vector-transmission is predicted to correlate with general increases in parasite virulence relative to many other transmission modes (Ewald, 1994). Thus, increased parasite richness at low latitudes may also be associated with elevated severity of vector-transmitted protozoa through intrahost competition among different parasite species (Woolhouse et al., 2001).

Understanding geographical variation in parasite diversity is also important for predicting how infectious disease risk may change with climate warming. Evidence from diverse taxa and geographical regions points to the impacts of human-induced climate change on parasite species’ distributions and ecology.
(Harvell et al., 2002; Walther et al., 2002). Following release from climate limitations in temperate zones, global warming may shift the abundance and geographic range of a suite of parasites, including those that cause vector-borne and water-borne diseases (Harvell et al., 2002; Liang et al., 2002). For example, rising temperatures and increased rainfall are predicted to increase the population size, geographic range, and biting rates of arthropod vectors, and could also increase rates of pathogen development within vector species (Dobson & Carper, 1992). Multiple vector-borne pathogens of humans and wildlife have recently increased their geographic ranges into regions of higher latitude and altitude, probably as a result of combined effects of human activity, climate change, and expansion in the ranges of arthropod vectors (Gratz, 1999; Mellor et al., 2000). Even the recently introduced West Nile virus is thought to be favoured by warm winters and spring droughts, possibly accounting for patterns of spread of West Nile virus in the United States and Europe (Epstein, 2001). The fact that our analyses showed stronger links between protozoa and latitude indicates that this group of parasites may be unusually sensitive to climatic variables therefore these parasites are and more likely to respond to future climate change than other groups of parasites.

Managing parasites and infectious disease has increasingly become a focus in conservation biology, partly because parasites can trigger catastrophic declines in wild host populations, and because human activities are predicted to influence disease emergence and impact on wildlife (Daszak et al., 2000; Dobson & Foufopoulos, 2001). Among threatened primate taxa (IUCN, 2004), risks posed by parasites remain largely unquantified, yet many of the biodiversity hotspots (Myers et al., 2000) where primates are in danger of extinction lie in close proximity to the equator, such as the Atlantic coastal forest of Brazil. Moreover, vector-borne protozoa have been documented in several threatened primate species (e.g. Brachyteles arachnoids, Pan troglodytes, Garnham, 1966; Deane et al., 1969; Coatney et al., 1971). Hosts in geographical areas with high parasite pressure may be at greater risk of disease-induced declines or extinction, particularly those caused by generalist parasites that persist in domestic animal reservoirs (Daszak et al., 2000; Dobson & Foufopoulos, 2001). Thus, parasites, in combination with other drivers of global change, may have profound effects on threatened species of primates and other mammals. Increased monitoring of a wide range of parasites will improve our understanding of the links between climate, latitude, and infectious disease, thereby increasing our ability to predict future risks to humans and biodiversity.

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