

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.

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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 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 microparasites, 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://isi02.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 ($\delta < \gamma$). Directed tests are subject to the constraint that $\delta + \gamma = \alpha$. We followed the guidelines in Rice and Gaines (1994) by setting γ/α to 0.8, giving values of $\gamma = 0.04$ and $\delta = 0.01$.

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).

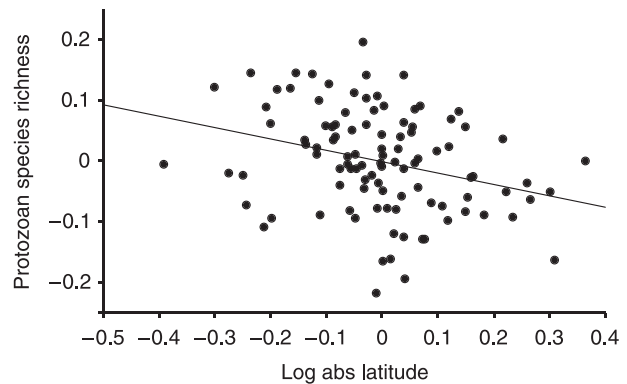


Figure 1 Latitudinal gradients in parasite species richness. Points represent independent contrasts. Increases in median absolute latitude (contrasts) are associated with decreases in the size of the protozoan parasite community. In this plot, parasite species richness was measured as least squares residuals from regression of protozoan species documented for each host species on number of citations for that host in PrimateLit's website (see Methods).

Table 1 Predictors of parasite species richness in multiple regression analyses

Parasite type	Non-phylogenetic tests ($n = 119$)		Phylogenetic tests ($n = 108$)	
	Median latitude	Sampling effort	Median latitude	Sampling effort
Including all transmission modes:				
Protozoa	-2.29*	5.80***	-3.14**	4.17***
Apicomplexa	-1.74	4.80***	-2.19*	4.14***
Euglenozoa	-1.73	2.74**	-1.91*	3.74***
Helminths	0.61	6.25***	0.40	3.65***
Viruses	-1.41	6.18***	-1.55	5.31***
All combined	-1.56	7.87***	-0.88	6.53***
Parasites exhibiting vector-borne transmission:				
Protozoa	-2.42**	4.64***	-1.79*	3.91***
Helminths	-1.59	4.20***	-0.86	2.05*
Viruses	-0.10	3.91***	-0.15	4.19***
All combined	-2.40**	5.84***	-0.78	3.83***

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.

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: $b = -0.28$, $F_{1,107} = 4.21$, $P = 0.04$, two-tailed). This model was statistically significant in analysis of 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 ($b = 0.14$, $F_{3,99} = 7.93$, $P = 0.004$) and a negative effect of latitude ($b = -0.11$, $F_{3,99} = 3.63$, $P = 0.04$) 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 ($F_{4,87} = 11.7$, $P < 0.0001$), with all variables significant at $P < 0.03$. When using independent contrasts with outliers removed, we found statistical support for an effect of latitude ($b = -0.14$, $F_{1,75} = 4.34$, $P = 0.025$), population size ($b = 0.09$, $F_{1,77} = 5.95$, $P = 0.01$), and sampling effort on the diversity of protozoa.

The highly significant association between protozoan diversity and latitude may be a result of the greater proportional representation of vector-borne parasites among protozoa recorded in our

data set. Sixty-four percent of all protozoan species in our study were transmitted by vectors, whereas only 25% of all helminth species and 38% of all viruses were vector-borne (Fig. 2). To investigate the role of transmission mode more directly, we examined patterns among the subset of vector-transmitted parasites. In analyses of vector-borne protozoa, we found that parasite species richness declined significantly with increasing distance from the equator (Table 1). Latitude remained a significant predictor in multiple regression models that controlled for population density, longevity, body mass and sampling effort (independent contrasts: $b_{\text{latitude}} = -0.18$, $F_{1,51} = 10.4$, $P = 0.001$) and total population size, body mass and sampling effort (independent contrasts: $b_{\text{latitude}} = -0.11$, $F_{1,80} = 4.08$, $P = 0.03$), but not in the model with geographic range size ($b_{\text{latitude}} = -0.07$, $F_{1,101} = 2.00$, $P = 0.10$). Phylogenetic analyses of vector-transmitted helminths and viruses produced non-significant results for the effect of latitude (Table 1), with results for helminths approaching significance in non-phylogenetic tests ($P = 0.07$). Combined analyses revealed that the collective diversity of all three types of vector-borne parasites declined significantly with latitude, but this is only significant in non-phylogenetic tests (Table 1).

We also examined latitudinal gradients in the diversity of protozoa with no vector component to their transmission, including those spread by social or sexual contact, fecal to oral routes, or by indirect contact via fomites (inanimate objects that harbour infectious material). Parasite species richness of these protozoa was related to median latitude when six outliers were excluded ($b = -0.11$, $F_{1,100} = 6.01$, $P = 0.01$, directed test). Analyses of parasites without vector transmission using species values produced non-significant results ($b = -0.06$, $F_{1,116} = 1.51$, $P = 0.14$, directed test).

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

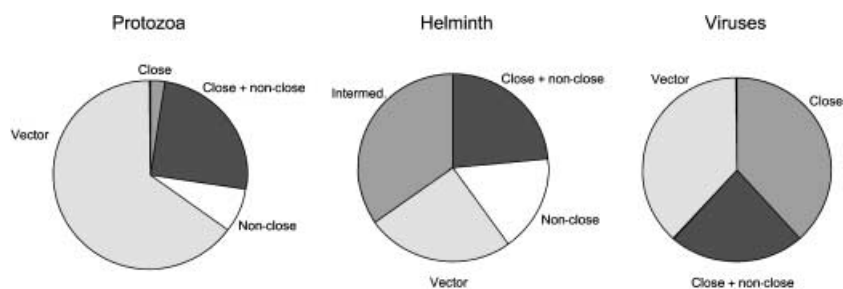


Figure 2 Frequency of transmission strategies within each parasite group, based on information for 84 protozoan species, 169 helminth species, and 92 viruses reported from wild primate populations. Each parasite species was scored according to four major transmission strategies, including close contact, non-close contact (fecal to oral or fomites), vector-borne (spread by biting arthropods), or via intermediate hosts (i.e. parasites with complex life cycles or trophic transmission). Parasites with multiple transmission routes are represented in combinations of these categories.

(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: $t_{49} = -3.11$, $P = 0.002$; Euglenozoa: $t_{53} = -1.81$, $P = 0.048$; controlling for population size, body mass and sampling effort, Apicomplexa: $t_{78} = -1.30$, $P = 0.13$, Euglenozoa: $t_{75} = -2.43$, $P = 0.01$), 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 (Cowlshaw & 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 arachnoides*, *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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REFERENCES

- Ashford, R.W. & Crewe, W. (1998) *The parasites of Homo sapiens: an annotated checklist of the Protozoa, Helminths and Arthropods for which we are home*, Liverpool School of Tropical Medicine, Liverpool.
- Brack, M. (1987) *Agents transmissible from simians to man*, Springer-Verlag, Berlin.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Coatney, G.R., Collins, W.E. & McWilson, W. (1971) *The primate malarialias*, National Institute of Allergy and Infectious Diseases, Bethesda, Maryland.
- Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, **15**, 70–76.
- Corbet, G.B. & Hill, J.E. (1991) *A world list of mammalian species*. Oxford University Press, Oxford.
- Cowlishaw, G. & Hacker, J.E. (1997) Distribution, diversity, and latitude in African primates. *American Naturalist*, **150**, 505–512.
- Cumming, G.S. (2000) Using habitat models to map diversity: pan-African species richness of ticks (Acari: Ixodida). *Journal of Biogeography*, **27**, 425–440.
- Daszak, P., Cunningham, A.A. & Hyatt, A.D. (2000) Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science*, **287**, 443–449.
- Deane, L.M., Ferreira Neto, J.A., Okumura, M. & Ferreira, M.O. (1969) Malaria parasites of Brazilian monkeys. *Revista do Instituto de Medicina Tropical de Sao Paulo*, **11**, 71–86.
- Dobson, A. & Carper, R. (1992) Global warming and potential changes in host-parasite and disease-vector relationships. *Global warming and biodiversity* (ed. by R.L. Peters and T.E. Lovejoy), pp. 201–207. Yale University Press, New Haven, CT.
- Dobson, A. & Foufopoulos, J. (2001) Emerging infectious pathogens of wildlife. *Philosophical Transactions of the Royal Society of London Series B*, **356**, 1001–1012.
- Eeley, H. & Lawes, M. (1999) Large-scale patterns of species richness and species range size in anthropoid primates. *Primate communities* (ed. by J.G. Fleagle, C.H. Janson and K.E. Reed), pp. 191–219. Cambridge University Press, Cambridge.
- Epstein, P.R. (2001) West Nile virus and the climate. *Journal of Urban Health*, **78**, 367–371.
- Ewald, P.W. (1994) *Evolution of infectious disease*, Oxford University Press, Oxford.
- Fiennes, R. (1972) *Pathology of simian primates*. Part II. Infectious and parasitic diseases. S. Karger, London.
- Garnham, P.C.C. (1966) *Malaria parasites and other haemosporidia*, Blackwell Scientific, Oxford.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

- Githeko, A., Lindsay, S., Confalonieri, U. & Patz, J. (2000) Climate change and vector-borne diseases: a regional analysis. *Bulletin of the World Health Organization*, **78**, 1136–1147.
- Gratz, N.G. (1999) Emerging and resurging vector-borne diseases. *Annual Review of Entomology*, **44**, 51–75.
- Gregory, R.D. (1990) Parasites and host geographic range as illustrated by waterfowl. *Functional Ecology*, **4**, 645–654.
- Groves, C.P. (2001) *Primate taxonomy*, Smithsonian Institution Press, Washington, D.C.
- Guernier, V., Hochberg, M.E. & Guegan, J.F. (2004) Ecology drives the worldwide distribution of human diseases. *PLoS Biology*, **2**, 740–746.
- Hafner, M.S. & Page, R.D.M. (1995) Molecular phylogenies and host–parasite cospeciation — gophers and lice as a model system. *Philosophical Transactions of the Royal Society of London Series B*, **349**, 77–83.
- Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J., Hofmann, E.E., Lipp, E.K., Osterhaus, Adme., Overstreet, R.M., Porter, J.W., Smith, G.W. & Vasta, G.R. (1999) Emerging marine diseases — climate links and anthropogenic factors. *Science*, **285**, 1505–1510.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. & Samuel, M.D. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science*, **296**, 2158–2162.
- Harvey, P.H. & Rambaut, A. (2000) Comparative analyses for adaptive radiations. *Proceedings of the Royal Society of London Series B*, **355**, 1–7.
- Hay, S.I., Cox, J., Rogers, D.J., Randolph, S.E., Stern, D.I., Shanks, G.D., Myers, M.F. & Snow, R.W. (2002) Climate change and the resurgence of malaria in the East African highlands. *Nature*, **415**, 905–909.
- Hugot, J.P. (1999) Primates and their pinworm parasites: The Cameron hypothesis revisited. *Systematic Biology*, **48**, 523–546.
- IUCN (2004) *Red list of threatened species*, The World Conservation Union (IUCN), Gland, Switzerland and Cambridge, UK. <http://www.redlist.org>.
- Jetten, T.H. & Focks, D.A. (1997) Potential changes in the distribution of dengue transmission under climate warming. *American Journal of Tropical Medicine and Hygiene*, **57**, 285–297.
- Liang, S.Y., Linthicum, K.J. & Gaydos, J.C. (2002) Climate change and the monitoring of vector-borne disease. *Journal of the American Medical Association*, **287**, 2286–2286.
- Martens, W.J.M., Jetten, T.H., Rotmans, J. & Niessen, L.W. (1995) Climate change and vector-borne diseases: a global modeling perspective. *Global Environmental Change, Part A*, **5**, 195–209.
- Martens, W.J.M., Niessen, L.W., Rotmans, J., Jetten, T.H. & McMichael, A.J. (1997) Potential impact of global climate change on malaria risk. *Environmental Health Perspectives*, **103**, 458–465.
- Mellor, P.S., Boorman, J. & Baylis, M. (2000) *Culicoides* biting midges: their role as arbovirus vectors. *Annual Review of Entomology*, **45**, 307–340.
- Møller, A.P. (1998) Evidence of larger impact of parasites on hosts in the tropics: investment in immune function within and outside the tropics. *Oikos*, **82**, 265–270.
- Morand, S. (2000) Wormy world: comparative tests of theoretical hypotheses on parasite species richness. *Evolutionary biology of host–parasite relationships* (ed. by R. Poulin, S. Morand and A. Skorping), pp. 63–79. Elsevier, Amsterdam.
- Morand, S., Hafner, M.S., Page, R.D.M. & Reed, D.L. (2000) Comparative body size relationships in pocket gophers and their chewing lice. *Biological Journal of the Linnean Society*, **70**, 239–249.
- Morand, S. & Harvey, P.H. (2000) Mammalian metabolism, longevity and parasite species richness. *Proceedings of the Royal Society of London Series B*, **267**, 1999–2003.
- Morand, S. & Poulin, R. (2000) Nematode parasite species richness and the evolution of spleen size in birds. *Canadian Journal of Zoology*, **78**, 1356–1360.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Nunn, C.L. & Altizer, S. (2005) The Global Mammal Parasite Database: an online resource for infectious disease records in wild primates. *Evolutionary Anthropology*, in press.
- Nunn, C.L., Altizer, S., Jones, K.E. & Sechrest, W. (2003) Comparative tests of parasite species richness in primates. *American Naturalist*, **162**, 597–614.
- Nunn, C.L. & Barton, R.A. (2000) Allometric slopes and independent contrasts: a comparative test of Kleiber's law in primate ranging patterns. *American Naturalist*, **156**, 519–533.
- Nunn, C.L. & Barton, R.A. (2001) Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology*, **10**, 81–98.
- Patz, J.A., Epstein, P.R., Burke, T.A. & Balbus, J.M. (1996) Climate change and emerging diseases. *Journal of the American Medical Association*, **275**, 217–223.
- Poulin, R. (1995) Phylogeny, ecology and the richness of parasite communities in vertebrates. *Ecological Monographs*, **65**, 283–302.
- Poulin, R. & Morand, S. (2000) The diversity of parasites. *Quarterly Review of Biology*, **75**, 277–293.
- Poulin, R. & Morand, S. (2004) *Parasite biodiversity*. Smithsonian Institution Press, Washington D.C.
- Poulin, R. & Rohde, K. (1997) Comparing the richness of metazoan ectoparasite communities of marine fishes: controlling for host phylogeny. *Oecologia*, **110**, 278–283.
- Price, T. (1997) Correlated evolution and independent contrasts. *Philosophical Transactions of the Royal Society of London Series B*, **352**, 519–529.
- Purvis, A. (1995) A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London Series B*, **348**, 405–421.
- Purvis, A. & Rambaut, A. (1995) Comparative analysis by independent contrasts (CAIC): an apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences*, **11**, 247–251.
- Rice, W.R. & Gaines, S.D. (1994) Heads I win, tails you lose: testing directional alternative hypotheses in ecological and

- evolutionary research. *Trends in Ecology and Evolution*, **9**, 235–237.
- Rohde, K. & Heap, M. (1998) Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasites of marine teleost fish. *International Journal for Parasitology*, **28**, 461–474.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Ross, C. & Jones, K.E. (1999) Socioecology and the evolution of primate reproductive rates. *Comparative primate socioecology* (ed. by P.C. Lee), pp. 73–110. Cambridge University Press, Cambridge.
- Rowe, N. (1996) *The pictorial guide to the living primates*, Pogonias Press, East Hampton, NY.
- Shanks, G.D., Biomndo, K., Hay, S.I. & Snow, R.W. (2000) Changing patterns of clinical malaria since 1965 among a tea estate population located in the Kenyan Highlands. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **94**, 253–255.
- Smith, R.J. & Jungers, W.L. (1997) Body mass in comparative primatology. *Journal of Human Evolution*, **32**, 523–559.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Woolhouse, M.E.J., Taylor, L.H. & Haydon, D.T. (2001) Population biology of multihost pathogens. *Science*, **292**, 1109–1112.