

Geographic and climatic control of primate diversity

(species–area relationship/rainfall/primate evolution)

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Communicated by Elwyn L. Simons, Duke University, Durham, NC, May 5, 1995

ABSTRACT Although the comparative ecology of primates has been relatively well studied and there have been a number of outstanding studies of individual primate communities, the factors determining primate species diversity on either a local or regional level are largely unexplored. Understanding the determinants of species abundance is an important aspect of biodiversity and is critical for interpreting the comparative ecology of these different communities and for designing effective strategies of conservation. Comparative analysis of species diversity in more than 70 primate communities from South America, Africa, Madagascar, and Asia shows that on major continental areas and large tropical islands, there is a high positive correlation between the number of primate species and the area of tropical forest. Within major continental areas, the species diversity at individual sites is highly correlated with mean annual rainfall for South America, Africa, and Madagascar, but not Asia.

As relatively large, often brightly colored, diurnal mammals, primates are among the best studied mammals. In addition to numerous studies of autoecology, there have been outstanding studies of the comparative ecology of sympatric species in many different parts of the world that have contributed greatly to our understanding of the comparative ecology and competitive interactions of sympatric species in local communities (1–4). In contrast, there have been few comparisons of the composition of primate communities between major continental regions or attempts to understand the factors underlying species diversity at either the local or continental level (5, 6). This is in striking contrast with many other groups of vertebrates (especially, birds, lizards, and among mammals, bats) for which there are numerous studies of the geographical and climatic factors underlying species diversity (7–9). Knowledge of the broad factors controlling present patterns of biodiversity is critical for understanding the history of living faunas and for designing strategies of effective conservation of this diversity. We have compiled data from the literature on the number of primate species on different continental areas and large islands and at individual study sites or survey sites in South America, Africa, Madagascar, and Asia (10, 11). We examine the relationship between regional primate species diversity and area of tropical rain forest for major geographical areas and between local diversity and annual precipitation.

Species–area relationships are one of the most universal of biogeographic relationships and have been well documented for many groups of organisms (7–9, 12). The roughly 200 species of primates are largely restricted to tropical forests (10), with relatively few species adapted to either temperate or nonforest habitats, and it seems likely that primate diversity at a continental level is and has been historically determined largely by the amount of forest rather than overall continental area. Therefore, we have used regression analysis to compare

the numbers of forest-dwelling primate species against the area of tropical rain forest on the larger islands and major continental areas currently inhabited by primates. Regression analyses of the number of forest species and area of tropical rain forest (either raw or logged data) yield a high positive correlation ($R^2 = 0.87$; Fig. 1). Similar relationships have been reported for rain-forest bats (9). It is notable that the Asian “areas” fall below the regression line, emphasizing the relatively low primate species diversity on that continent, as noted by several other authorities (5, 6). Madagascar falls well above the regression line for the area of rain forest on that island. For comparability we included only rain-forest primate species and an estimated area of rain forest in the recent past. Inclusion of species found in dry forests or the numerous subfossil species would have placed Madagascar even further above the line (4, 10).

Within geographical regions, there is a high correlation between the number of primate species at any site and mean annual rainfall for South America, Africa, and Madagascar (Fig. 2). Rainfall has been correlated with primary productivity in many climates (35) and with diversity of tree species in the Neotropics (36). The slopes for South America and Africa are not significantly different from one another, while the slope for Madagascar is roughly half that of either South America or Asia. This lower slope probably reflects the recent extinction of a very diverse primate megafauna (4, 10) but may also indicate a lower overall available diversity on this island compared with the larger continental areas. Asia shows no relationship between rainfall and primate species on a continental level. There are several possible reasons for this lack of correlation between rainfall and number of primates at Asian sites. Partly this may reflect the fact that the continent of Asia includes many separate islands. Since each of these islands has a relatively low species diversity as a result of its small area, this may place an upper limit on the potential primate diversity at many sites, regardless of rainfall. In addition, it is worth noting that much of Asia is subject to monsoonal climates with very high rainfall limited to a short period of time each year, a distribution that should yield very different patterns of plant productivity than that found on other continents. Botanists have specifically noted a lack of any correlation between rainfall and tree diversity in Asia (36) and other workers have noted striking discrepancies in the primate abundances at different localities correlated with idiosyncratic differences in plant species compositions (13). However, with a more extensive data set, it should be possible to examine the relationship of rainfall, floral diversity, and primate diversity within individual islands and isolated peninsular areas to evaluate some of these hypotheses.

These studies demonstrate that for most tropical areas, primate diversity at a continental or local level is highly correlated with relatively simple factors of geography (area of tropical rain forest) and climate (rainfall). However, at this stage we can only speculate about how these broad geographic and climatic variables relate to the proximate factors controlling the biogeographical distribution of individual species or to macroevolutionary phenomena related to these patterns. The

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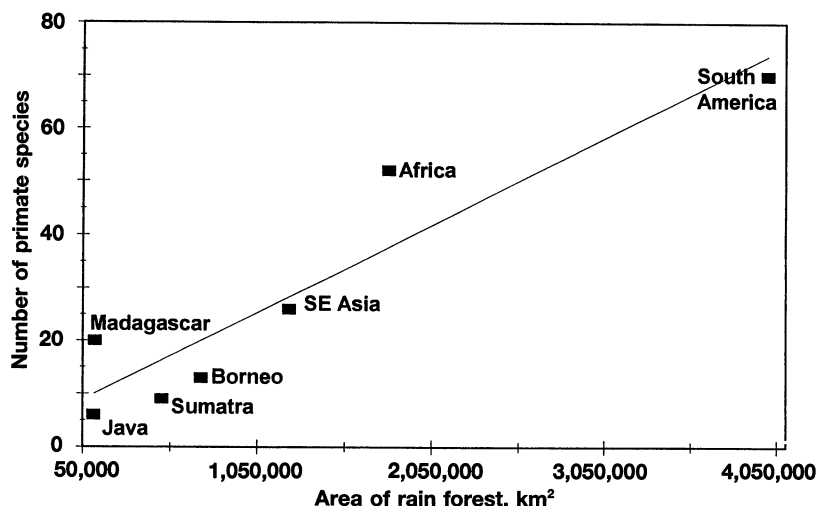


FIG. 1. Least squares regression analysis of the number of rain-forest primate species as a function of the area of tropical rain forests for major continents and large islands. The area for Madagascar is the estimated area at initial human contact. $R^2 = 0.87$; $y = 0.000016x + 8.10$; $P = 0.006$; $n = 7$.

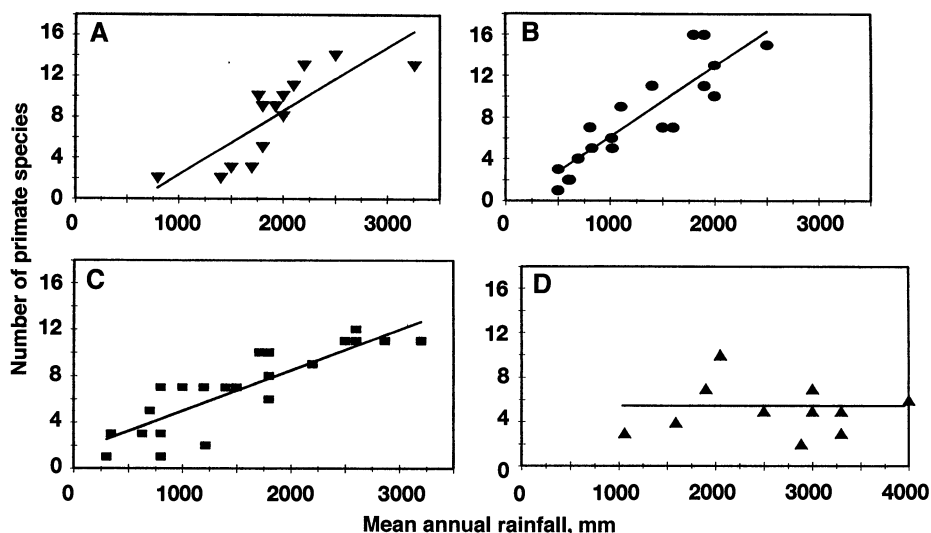


FIG. 2. Least squares regression analyses of the number of primate species as a function of mean annual rainfall for numerous primate sites in South America ($n = 14$) (A), Africa ($n = 20$) (B), Madagascar ($n = 28$) (C), and Asia ($n = 11$) (D). Note that there is a high correlation between the variables and a positive slope for South American, Africa, and Madagascar and that there is no significant correlation between these variables in Asia. (A) $R^2 = 0.67$; $y = 0.006x - 3.90$; $P < 0.001$. (B) $R^2 = 0.75$; $y = 0.007x - 0.59$; $P < 0.001$. (C) $R^2 = 0.70$; $y = 0.0035x + 1.49$; $P < 0.001$. (D) $R^2 = 0$; $y = 5.23x$. Data are from multiple sources (2, 13–34).

role of competitive relationships (both within primates and other mammals) and the composition of species at particular sites deserve closer study. In addition, there are striking differences in both the numbers of different phylogenetic clades and the diversity of individual clades of primates found on different continents. The relationships of these phylogenetic differences in diversity to patterns of Pleistocene climate change and to the ecological characteristics of different continental floras should provide valuable insights into the evolutionary history of primate communities throughout the world.

We thank Charles Janson, William Jungers, Richard Kay, Alfred Rosenberger, Bob Martin, and Jeffrey Walker for discussions and suggestions concerning the contents of this paper. This work was supported in part by funds from the National Science Foundation, The John D. and Catherine T. MacArthur Foundation, and the American Association of University Women.

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