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# Primate species richness is determined by plant productivity: Implications for conservation

(diversity/*Platyrrhini*/Neotropical forests/litterfall/rainfall)

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**ABSTRACT The explanation of patterns in species richness ranks among the most important tasks of ecology. Current theories emphasize the interaction between historical and geographical factors affecting the size of the regional species pool and of locally acting processes such as competitive exclusion, disturbance, productivity, and seasonality. Local species richness, or alpha diversity, of plants and primary consumers has been claimed to peak in habitats of low and intermediate productivity, which, if true, has major implications for conservation. Here, by contrast, we show that local richness of Neotropical primates (platyrrhines) is influenced by both historical biogeography and productivity but not by tree species richness or seasonality. This pattern indicates that habitats with the highest plant productivity are also the richest for many important primary consumers. We show further that fragmentation of Amazonian rain forests in the Pleistocene, if it occurred, appears to have had a negligible influence on primate alpha species richness.**

Patterns of local animal species richness have been suggested to be causally related to tree species richness, plant productivity, seasonality, habitat heterogeneity, and historical/geographical factors (1–5). However, because there are very few sites for which all variables have been measured, the independent effect of these possible causal factors has so far not been assessed. Here, we circumvent this problem by examining the correlations of these variables with an intermediate variable, local rainfall.

Previous studies from various tropical regions reported a monotonic increase in richness with rainfall (6–9). However, these studies sampled very few sites with annual rainfall of over 2500 mm and/or analyzed the relationship using linear regression and were therefore unable to test more complex hypotheses of relationship. We have gathered new data for Neotropical primate richness through a broader range of rainfall levels. Fig. 1 shows the geographic range of our primate sites. Fig. 2*A* shows local species richness of Neotropical primates as a function of rainfall for a broad sample of equatorial lowland sites with annual rainfall up to 6700 mm. Species richness displays a unimodal relationship with rainfall, rising to a peak at annual rainfall levels of ≈2500 mm and then declining. A similar unimodal pattern is suggested for Madagascar primate faunas (65) and revealed by a reanalysis of Reed and Fleagle's south Asian primate richness data using a nonlinear model (figure 2*D* in ref. 13).

Three factors are hypothesized to explain species richness in relation to rainfall, plant species richness, historical factors, and plant productivity. We consider the merits of each in what follows.

FIG. 1. Map of South America showing the distribution of primate sites sampled for alpha species richness. (Locality data in refs. 10–58 and Di Fiore, A., personal communication, and Digby, L., personal communication; rainfall and seasonality data in site references and in refs. 10 and 59.)

**Plant Species Richness.** If increasing numbers of plant species allow an increase in the diversity of feeding niches, it would be expected that the number of primary consumers, including primates, that can coexist would be related to tree species richness (*cf.* refs. 3 and 66). However, our data do not support this hypothesis. Fig. 2*B* plots tree species richness as a function of rainfall. Tree species richness climbs steadily with increasing rainfall up to the level of 2500 mm/year, in agreement with the primate trends. However, at rainfall above 2500 mm/year, richness reaches a plateau and does not diminish, in contrast with the pronounced decline in primate species richness.

**Seasonality.** Ripe fruit is the major source of energy for many Neotropical primates, and its availability varies seasonally. Seasonality in fruit production increases with the length of the dry season, especially in the Neotropics, thus producing a predictable period of severe fruit scarcity (67). During this lean period, animals tend to specialize on a limited set of keystone resources (68). Interspecific overlap in diet is often lowest during times of food scarcity (69, 70). Because the reliance on keystone resources can be expected to increase with seasonality and because each habitat provides only a limited number of suitable keystone resources,

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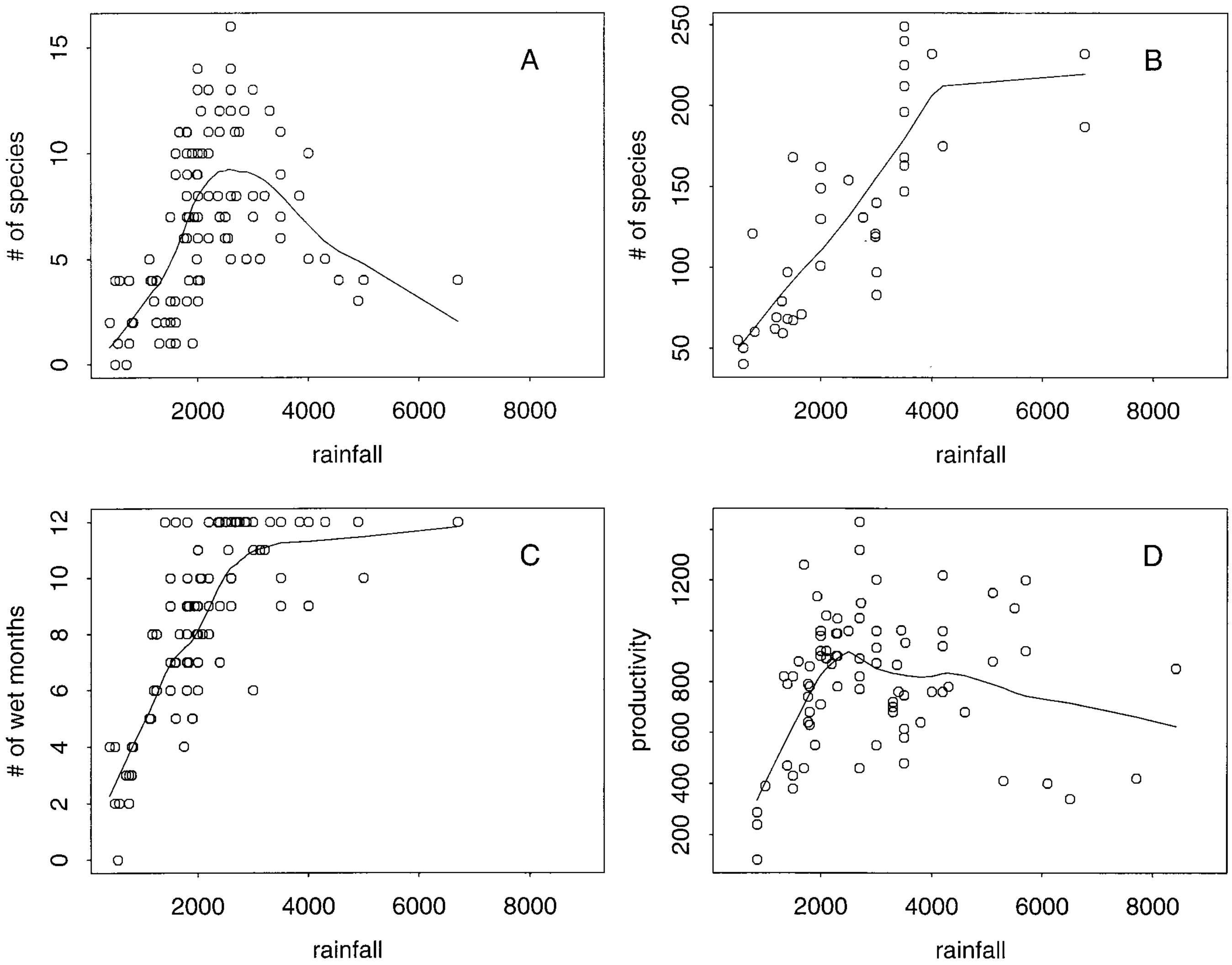

FIG. 2. (*A*) Neotropical primate species richness as a function of rainfall (island data removed). (*B*) Tree species richness as a function of rainfall (data from 37 lowland Neotropical localities in ref. 60). (*C*) Number of wet months [as defined by monthly rainfall exceeding 100 mm (61)] as a function of yearly rainfall. Seasonality estimates were gathered either from reports accompanying the site data or from climatic maps (10). (*D*) Plant productivity (indexed by litter fall) as a function of rainfall [data from 88 lowland tropical localities from Asia and the Neotropics (62)]. Using the loess method for local regression (63, 64), lines are fit for each independent variable given rainfall.

one could predict that the number of primate species that can coexist in a forest area is determined primarily by seasonality. Fig. 2*C* is a plot of seasonality (number of months with rainfall exceeding 100 mm) as a function of rainfall. Seasonality decreases steadily with increased rainfall up to the level of ≈2500 mm/year and then reaches a plateau and does not diminish, in contrast with a decline in primate species richness. Therefore, pronounced seasonality may play a role in limiting the maximum number of sympatric primates but does not explain the decline in primate richness at high levels of rainfall.

**Historical Geography.** Historical and geographic factors clearly have played an important role in shaping platyrrhine faunal richness (Table 1). Holding rainfall levels and dry season lengths nearly constant, there are, on average, more primate species per site in larger than in smaller geographically restricted areas. For example, Amazon localities averaged >9 sympatric species, Orinoco and northern coastal localities have one–half as many species, and the smallest geographic regions (islands and the regions north and west of the Andes) have the fewest species.

In the Pleistocene Refugia hypothesis (71), Pleistocene geographic fragmentation of hitherto more widely distributed Amazonian species into smaller forest fragments promoted genetic divergence and speciation. Then, when the geographic isolation was removed, the newly evolved species could achieve sympatry thereby increasing species richness. New evidence calls into question whether such forest blocks

Table 1. Regional variation in local primate species richness

| Region | Area rank | Localities, *n* | Species, *n* | Rainfall | Dry months, *n* |
|---|---|---|---|---|---|
| Amazon | I | 44 | 9.41 (2.91) | 2358 (624) | 3.22 (2.36) |
| Orinoco and N.E. coast | II | 14 | 4.64 (2.41) | 2277 (851) | 2.71 (2.20) |
| North or west of Andes | III | 6 | 3.33 (1.75) | 2396 (978) | 2.33 (3.20) |
| Island of Trinidad | IV | 1 | 2 | 2400 | NA |
| Maracá Island, Amapá, Brazil | V | 1 | 2 | 1600 | 6 |

Means and SD are given in columns 4–6. NA, not available.

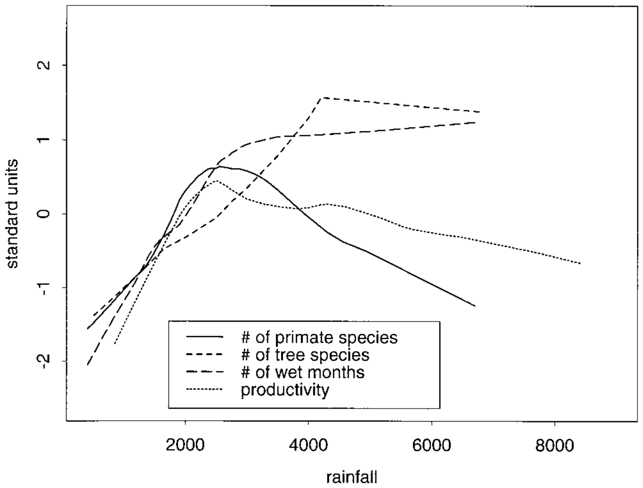

FIG. 3. Local regression lines for primate species richness, tree species richness, seasonality (number of wet months per year), and plant productivity as a function of rainfall. The lines are fit using the loess technique (63, 64). See Table 2 for statistical comparisons.

actually existed (73).‖ Moreover, in the case of platyrrhines, recent evidence of genetic divergence studies suggests that virtually all presently sympatric primate species were phylogenetically separate before 3 million years ago, in other words, before the Pleistocene (72). Thus, the great cladogenic time depth of sympatric platyrrhine species suggests that Pleistocene Refugia, if they existed, played little or no role in explaining platyrrhine species richness.

**Productivity.** Another hypothesis is that increased plant productivity leads to increased species richness of animals because, at higher productivity, specialized species maintain viability (5, 74). Plant productivity in tropical forests is most readily indexed by litterfall. Fig. 2*D* plots litterfall as a function of rainfall. A striking similarity is noted between plant productivity and primate species richness (compare Figs. 2 *A* and *D*). Both increase with rainfall up to a maximum at ≈2500 mm/year and then fall off at higher rainfall levels. An explanation for this linkage may be found in soil nutrient levels and available energy in ecosystems. In areas with very high rainfall, leaching depletes the level of nutrients and depresses plant growth (75). Also, at very high levels of rainfall, cloud cover reduces solar radiation reaching the photosynthetic organs of plants, which limits plant production (67, 76, 77).

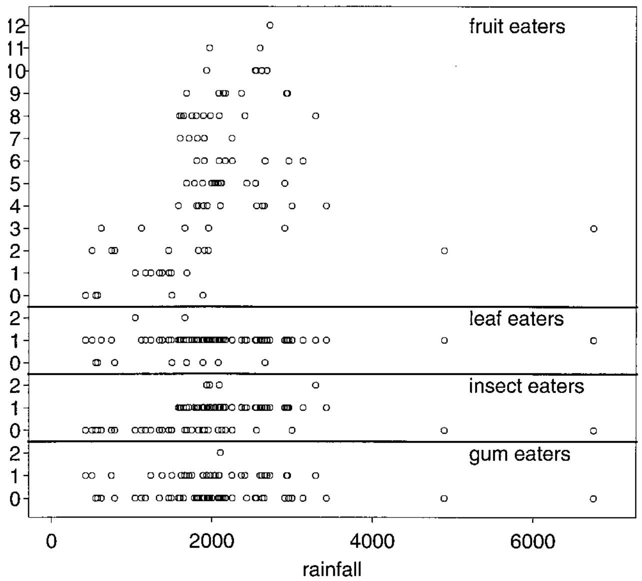

FIG. 4. Species richness of Neotropical primate species that eat primarily fruit, leaves, insects, or gum, as a function of rainfall.

## CONCLUSIONS

Fig. 3 and Table 2 summarize our findings. Fig. 3 reproduces the local regression lines from Fig. 2, only the units for each of the variables have been standardized. Above 2,000 mm/year rainfall, trend lines of local richness of Neotropical primates vs. rainfall closely approximate (and do not differ significantly from) those of productivity whereas they depart widely and significantly from those for tree species richness and seasonality. This tight link between productivity and local species richness in primates also may account for the observed decline in primate species richness with altitude and perhaps also in part for the decline with latitude, both of which also commonly are observed in other taxa.

Biogeography has demonstrable influences within regions of South America (Table 1) but does not affect the underlying unimodal pattern of primate species richness; the pattern is repeated among biogeographic regions of South America and in primate communities from south Asia and Madagascar. The pattern is not observed in African primate faunas because few sites have been sampled with rainfall above 2,500 mm/year.

Preliminary analyses indicate that, within single landscapes in the Neotropics and in tropical Asia, a pattern of higher species numbers and biomass of birds and primates is observed when comparing more productive flood plains with adjacent less productive uplands. Likewise, more productive white water river areas have higher species numbers and biomass of fish than black water river areas (79). An apparent exception to this pattern may be that, in deeply inundated areas along river channels (várzea and igapó), total litterfall is lower than in adjacent terra firme forests (80–82); however, the component of litterfall made up by reproductive parts is still higher near the rivers than in adjacent uplands. This suggests that more light may be shed on the relationship between productivity and species richness by careful analysis at the scale of

Table 2. Correlations between rainfall and each of the variables being studied for localities receiving rainfall over 2,000 mm/year

| Comparison | Localities ⇒ 2,000 mm/year, *n* | Correlation | Approximate 95% confidence interval |
|---|---|---|---|
| Primate species vs. rainfall, *n* | 62 | −0.33 | (−0.53, −0.07) |
| Productivity vs. rainfall | 22 | −0.31 | (−0.57, −0.03) |
| Tree species vs. rainfall, *n* | 60 | 0.48 | (0.29, 0.65) |
| Wet months vs. rainfall, *n* | 58 | 0.51 | (0.33, 0.62) |

Confidence intervals were computed using the bias-corrected nonparametric bootstrap methodology (78). Inference is not sensitive to the choice of the 2,000-mm/year cutoff value used here.

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‖Possible exceptions are two *Cebus* species and two species of *Saguinus* that are often sympatric. These could have diverged in the Pleistocene, but there are no data either way.

single landscapes and discriminating among the components of total litterfall.

A breakdown of platyrrhines by diet (6) reveals that the principal variation in species number with rainfall involves frugivores whereas the numbers of platyrrhine folivores, gumnivores, and insectivores appear to be less affected by total rainfall (Fig. 4). These data suggest that the unimodal pattern of primate species richness with rainfall may be largely a consequence of fruit productivity, either via a reduced variety or absolute amount of edible fruit produced by dry and very wet forests compared with forests at intermediate rainfall levels (83).

If the proportion of the fruit and leaf components of total productivity shows a different relationship with rainfall, the apparent absence of an obvious folivore or insectivore peak among platyrrhines might have an explanation in terms of the components of productivity. Unfortunately, most of the available productivity data simply do not discriminate sufficiently among the components of litterfall. Platyrrhines never radiated extensively into insectivore or folivore guilds (there are never more than two species in any habitat), so the prediction that frugivore, folivore, and insectivore richness should be unimodal with rainfall remains to be tested by considering the guild structure of all mammals. Independent measurements of the production of leaves, reproductive parts, and insects would permit a more detailed examination of the relationship between productivity and the species richness of particular guilds.

Finally, as the most productive areas and habitats are also the most likely to be (and to have been) converted to agriculture, they are usually underrepresented in protected areas (84). Recognition of the important relationship between productivity and species richness should provide an incentive to increase the representation of more productive habitats in protected rain forest areas. Plant productivity and vertebrate species population densities also are highly correlated, so smaller areas of higher productivity may likely protect long term viable populations of a greater number of endangered species.

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