



# The relationship between fruit production and primate abundance in Neotropical communities

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Ecological models predict a positive correlation between fruit production and primate abundance in the Neotropics. To test this relationship, I compiled information on primate abundance and calculated different indexes of fruit production for 30 Neotropical sites. These indexes can be grouped in three categories: (1) Fruit production estimates based on fruit traps, (2) basal area of endozoochorous trees and (3) density of these trees. The first estimate was the best predictor of both primate biomass ( $r^2=0.80$ ) and species richness ( $r^2=0.64$ ). The advantage of using fruit trap estimates is that they take into account production rates (which is not the case for basal area or density estimates), while the advantage of using basal area over density estimates is that it includes some of the expected variation due to tree size. However, using both basal area and density indexes I found a positive correlation between the basal area index and primate biomass for frugivorous monkeys and small platyrrhines, but there was no correlation for folivorous and seed predator primates. I also found a positive correlation between pitheciine biomass and the abundance of *Eschweilera* trees. The analyses gave little support to the importance of suggested keystone resources such as figs and palms. Finally, when including climatic, geographic and plant diversity variables, fruit production continued to be a good predictor of primate biomass in the Neotropics, but primate species richness was best predicted by latitudinal gradients and plant species richness. © 2001 The Linnean Society of London

ADDITIONAL KEYWORDS: fruit production – Neotropical communities – New World monkeys – primate biomass – primate diversity – tropical rain forest.

## INTRODUCTION

There are many factors known to affect species richness and the size of animal populations in a particular habitat, including physical conditions and interspecific interactions. Among these factors, many authors have argued that available energy in the habitat and primary productivity are the most important ones in determining the structure of communities (Hutchinson, 1959; Connell & Orians, 1964; Brown, 1981; Wright, 1983; Currie, 1991). The basic idea is that a fixed fraction of the solar energy is captured by plants and this energy decreases as it is transformed and used by consumers at higher trophic levels (Hutchinson, 1959). This unavoidable physical process generates the common pyramidal patterns in numbers (Elton, 1927), plants being more abundant than primary consumers, herbivores more abundant than secondary consumers,

and so on. This base line idea indicates that plant abundance is determined mainly by the available solar irradiance (when water and essential nutrients are not in short supply) and the abundance of primary consumers will depend on plant productivity and plant resource allocation (Brown, 1981). Thus if more energy is available for production this may result in either larger populations or more species in the environment (Connell & Orians, 1964).

The limited amount of energy available for consumers has to be partitioned in some way among all species present, such that a minimum number of individuals is present to sustain their populations (Currie, 1991). Therefore, in simple bottom-up structured community models, an increase in primary resources may produce three results: (1) an increment in both diversity and biomass of primary consumers (Connell & Orians, 1964); (2) an increment in biomass but a decrease in diversity, when competition favours only few species (Huston, 1979; Rosenzweig, 1992); or (3) a similar biomass per species but an increment of

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diversity, if the species are able to occupy different ecological niches and maintain a fixed degree of ecological overlap (Begon, Harper & Townsend, 1996; Pianka, 1994). This paper explores which of these possibilities occurs in Neotropical primate communities under different regimes of fruit production, which has been shown to be related to available radiation (Wright, 1999).

#### FACTORS THAT MAY AFFECT PRIMATE COMMUNITY STRUCTURE

Several empirical studies have demonstrated that a variety of factors influence primate community structure, including evolutionary history, predation, competition and resource availability. For example, intercontinental comparisons have revealed many differences among primate communities and less variation within the primates in each continent (Bourliere, 1985; Terborgh & van Schaik, 1987; Fleagle & Reed, 1996; Kappeler & Heymann, 1996; Jernvall & Wright, 1998). These studies emphasized the effect of evolutionary history on primate communities, given that different assemblages have evolved in the same biome type (i.e. lowland tropical forests).

The role of predation on primate abundance has been discussed by several researchers, especially the effects of human hunting for bushmeat (Freese *et al.*, 1982; Oates, 1996; Peres, 1997b; Struhsaker, 1981). Although the effect of predation on primate abundance in natural communities is less well documented (i.e. Isbell, 1990; Wright, 1998), drastic changes in population densities and even local extinctions have occurred in areas with heavy predation pressures, such as hunting on large bodied primates (Peres, 1993). Currently, there is little evidence that predation by natural predators has a marked direct effect in reducing primate populations (but see Stanford, 1995). Even less evidence exists to suggest that parasites habitually cause significant mortality relative to other causes of death in natural populations of primates, despite an occasional intriguing example (e.g. Milton, 1996).

Competition for resources among primate species has been invoked to explain the parapatric distributions of related primate species (Waser, 1987) and patterns of overlap in resource use (Terborgh, 1983). Some studies have also suggested that primates might compete with other animals outside their order, such as ants or sloths (Bourliere, 1985; Estrada & Coates-Estrada, 1985; Rockwood & Glander, 1979). At least for the Neotropics, however, there is no evidence of complementarity or compensation in species diversity among mammals of distinct orders (Emmons, 1999). It is difficult, however, to assess the influence of competition in community structure, because ecological

studies that fail to detect competition (i.e. aggression or large niche overlap) may simply reflect the effect of past competition between the species (Fleming, 1979).

Increased food production is likely to increase the abundance of primary consumers such as primates. Some attempts have been made to predict primate species richness and biomass from presumed climatic or biotic correlates of primary plant productivity. For instance, it was found that primate diversity increases linearly with rainfall, but this relationship does not hold for very wet tropical forests (Reed & Fleagle, 1995). In a recent study (Kay *et al.*, 1997) argued that the effect of rainfall on primate diversity in the New World was driven by parallel variation in habitat-wide productivity, but the direct relationship between primate species richness and productivity was not evaluated.

Total primary production may not be the best measure of food abundance for some primates. For instance, in Africa, Asia and Madagascar, where the majority of primate species rely extensively on foliage, the quality of leaves (e.g. protein to fibre ratio) seems to be a very good predictor of primate biomass (Oates *et al.*, 1990; Ganzhorn, 1992). In contrast, overall levels of plant productivity (as indexed by rainfall, see Kay *et al.*, 1997) are negatively related to total primate biomass in these communities (Janson & Chapman, 1999). It is also likely that total plant production is not a good measure of food availability for seed-consuming primates, the diets of which are typically restricted to a relatively few species, the seeds of which are not (or only slightly) toxic (e.g. van Roosmalen, Mittermeier & Fleagle, 1988). Indeed, the biomass of seed-consuming mammals in one Neotropical community was a tiny fraction of that which could theoretically be supported by the annual production of seeds (Janson & Emmons, 1990). Despite the possible complication of food quality, it is valuable to test the potential importance of total plant productivity on primate biomass, which is currently undocumented for more than a pair of sites on any continent (Ganzhorn, Wright & Ratsimbazafy, 1999).

Whatever determines the abundance and diversity of entire primate communities, particular taxa of primates (despite their diverse diets) do not consume more than about one tenth of the plant species available to them in tropical forests. Thus, it is reasonable to expect that the biomass or diversity of taxonomically or ecologically restricted subsets of primates would be best correlated with the abundance of their preferred plant food species. In some cases, these species fall into a relatively few families (Milton, 1980; McFarland Symington, 1988).

Finally, the distribution of resources in time has been proposed as the major factor determining the carrying capacity of primate communities (Terborgh,

1983). Terborgh proposed that the survival of primate species in a community depends on a few keystone resources (including figs and palms) that are available during periods of food shortage (Terborgh, 1986). For instance, the energetic demands of the total fruit-eating mammalian community in one Neotropical forest was shown to match well the minimum level of fruit production during the year (Janson & Emmons, 1990).

Given the evidence reviewed above, any study attempting to relate primate community structure directly to plant productivity should fulfill several criteria. First, it should be restricted to a single primate radiation. Second, it should focus on protected areas where hunting was not a significant factor depressing primate populations at the time biomass data were measured. Third, it should control for or examine the effects of biogeographic factors, seasonality, and local differences in plant species composition. The study reported here attempts to meet all these requirements.

#### PREDICTIONS FOR NEOTROPICAL COMMUNITIES

Neotropical primate communities are composed of mainly frugivorous primates (Bourliere, 1985; Terborgh & van Schaik, 1987; Kappeler & Heymann, 1996). Not surprisingly, it has been suggested that primate diversity and population densities may be affected by community wide patterns of fruit production or the abundance of particular fruit-bearing plant species (Kay *et al.*, 1997; McFarland Symington, 1988), but no large-scale attempts have been made to look at these relationships. The purpose of this study is to analyze this relationship and the correlation between fruit production and the abundance of particular primate guilds (e.g. folivores, highly insectivorous primates, and seed predators). In addition, the association between the relative abundance of particular monkey species and keystone or preferred plant resources will be discussed.

The main difficulty of this kind of analysis is data availability, because it is difficult to find sites with adequate information on both community wide primate densities and estimates of fruit production. To partially overcome this problem I used different indexes of fruit and tree abundance (see Methods), in order to include as many sites as possible (total  $n=30$ ). By breaking down tree abundance by type of fruit produced and by family, more detailed relationships between resource availability and primate abundance could be examined.

Assuming that these primate communities rely mainly on fruits and that predation and parasitism play a minor role (see above), the following predictions were examined: (1) There is a better correlation between fruit production and primate abundance (biomass and/or diversity) for frugivorous primates than

for folivorous species or seed predators (see above). (2) This relationship is also tighter for large frugivorous primates than for small more insectivorous ones. (3) The production and abundance of fig species (a keystone plant group) is positively correlated with primate abundance (Terborgh, 1986). (4) The density of palms is positively correlated with monkey abundance, especially for *Cebus apella*, for which palms are both preferred and keystone resources (Izawa, 1975; Terborgh, 1983; Janson, 1987). (5) The abundance of howler monkeys is correlated with the abundance of one of their preferred plant families: Moraceae (Braza, Alvarez & Azcarate, 1983; Gaulin & Gaulin, 1982; Glander, 1978); and (6) the abundance of pitheciines is associated with the occurrence of one of their primary seed sources, the monkey pots, *Eschweilera* spp. (Ayres, 1989; Fontaine, 1981; Prance & Mori, 1978; van Roosmalen, Mittermeier & Milton, 1981).

#### METHODS

I collected information on body size and primate densities from the literature and the data on Neotropical forest fruit productivity, structure and composition was gathered from published articles, as well as from data bases sent directly by the authors. The data for analyses were limited to New World sites with no or low human disturbance (see Table 1), in order to minimize the known influence of hunting on primate biomass (following Peres, 1999). All sites were forested and most were in lowlands (<400 m elevation), but span a wide range of rainfall values (Table 1). Old secondary and young successional forests (>20 yr) were included in the analysis because forests of this age are already able to produce large amounts of fruit for primate consumption (for instance, in old riverine forests).

Metabolic biomass was calculated for every species in each site, as the product between population density and the body weight to the 0.75 power (see Peres, 1993 for justification). For the body weight, I used the average value between adult males and adult females (from different sources, see Appendix 1). All species with average body weight above 6.0 kg were categorized as large-bodied; the remainder were small-bodied. It was assumed that half of the population corresponds to immature animals, whose weight is half that of adults (as in Freese *et al.*, 1982). Population densities were taken directly from the literature (Table 1). I selected the studies reporting population densities for the largest number of species in that community, using a single methodology. When different estimates were available from a single site, I used those estimated from long term data of group composition, home range size and home range overlap (NRC, 1981). In studies that reported results from different census methods, I

**Table 1.** List of Neotropical sites included in the study. Some geographic and climatic variables are shown. The first reference for each site corresponds to the source for primate densities, and the other citations correspond to vegetation and fruit production data. EAS = Elevation above sea level

Site (State, Country)	Latitude	Ann. Rain	Dry months	Avg. Temp.	EAS	Reference <sup>1</sup>
Los Tuxtlas (Veracruz, Mexico)	18.40°N	4953	3	27	425	1, 2, 3, 4*
Tikal National Park (Petén, Guatemala) <sup>2,3</sup>	17.55°N	1500	6	25	175	5
Santa Rosa National Park (Guanacaste, Costa Rica)	11.00°N	1614	6	27.4	300	6, 7, 8
La Selva Biological Station (Heredia, Costa Rica) <sup>6,4</sup>	10.43°N	3994	0	27	137	9, 10
Barro Colorado Island (Canal Zone, Panamá)	9.15°N	2656	4	27	30	11, 12, 13*
Hato Masaguaral (Guarico, Venezuela) <sup>2,3,5,6</sup>	8.58°N	1450	6	28	—	21, 22, 23*
Magdalena Valley (Colombia) <sup>3,5</sup>	8.58°N	2705	3	27.5	81	14, 15
Parque Timigua (Meta, Colombia)	2.67°N	2604	3	26.1	350	16, 17, 18, 19, 20*
Middle Essequibo River (Central Guyana) <sup>6,7</sup>	5.22°N	2950	5	25	—	24, 25, 26
Demerara Region (Northern Guyana) <sup>8</sup>	6.40°N	3500	4.5	26	30	27, 28*
Saut Parare (Central French Guiana) <sup>6,5</sup>	4.30°N	3125	3	26.5	—	29, 30, 31*
Noragues Reserve (Central French Guiana) <sup>2,3</sup>	4.80°N	3125	3	26.5	—	32, 33*
Raleighvallen (Central Surinam) <sup>8</sup>	5.00°N	2200	3.5	26.1	100	34, 35, 36
Cocha Cashu (Madre de Dios, Peru)	11.90°S	2028	3	24	350	57*, 58
Manaus Area (Amazonas, Brazil)	3.25°N	3000	3	24	290	59, 60
Tambopata (Madre de Dios, Peru) <sup>3</sup>	12.81°S	1783	7	30	325	42, 43
Maraca Island (Roraima, Brazil)	2.42°S	2535	5	27.2	80	37, 38, 39
Manaus Area (Amazonas, Brazil)	2.95°S	2850	1	26	250	40, 41
Lake Teiú (Amazonas, Brazil) <sup>3</sup>	3.83°S	1754	3	25	175	44, 45, 46
Tapajós National Park (Para, Brazil)	4.83°S	3256	3	26	71	47
Urucu River (Amazonas, Brazil) <sup>8</sup>	5.90°S	2116	4	26.3	700	48, 49
Purucui River (Para, Brazil) <sup>5</sup>	8.30°S	2300	5	24	—	50, 51
Samuel Reserve (Rondonia, Brazil) <sup>5</sup>	15.10°S	1600	6	21.5	1100	52, 53
Brasilía Area (Distrito Federal, Brazil) <sup>5</sup>	22.67°S	1263	6	21.5	480	54, 55, 56*
Barreiro Rico (Sao Paulo, Brazil) <sup>2,3,5,6</sup>	22.50°S	2289	7	17.5	1100	61, 62
Parque El Rey (Salta, Argentina) <sup>5</sup>	24.25°S	1500	7	19.5	1000	61, 63, 64*
Riacho Pílagra (Formosa, Argentina)	25.00°S	1375	3	22.1	65	65
Parque Iguazú (Misiones, Argentina)	25.35°S	1700	3	20	200	66, 67, 68, 69*
Guacacara Island (Corrientes, Argentina)	27.33°S	1200	3	21.6	50	61, 70
Riachuelo River (Corrientes, Argentina)	27.50°S	1200	3	21.6	60	61, 70

<sup>1</sup> Source data: (1) Estrada & Coates-Estrada (1985); (2) Bongers *et al.* (1988); (3) Alvarez (1984); (4) Sanchez & Alvarez-Sanchez (1995); (5) Coelho *et al.* (1976); (6) Pedigan *et al.* (1985); (7) Chapman (1988); (8) Burnham (1997); (9) Fishkind & Sussman (1988); (10) Hartshorn & Hammel (1994); (11) Glanz (1990); (12) Hubbell *et al.*, unpubl.; (13) Foster (1982); (14) Green (1978); (15) Folster & las Salas (1976); (16) Stevenson (1996); (17) Stevenson *et al.* (1999); (18) Takehara & Stevenson (1997); (19) Stevenson *et al.* (1998); (21) Eisenberg (1978); (22) Robinson (1986); (23) Colonello (1991); (24) Muckenhirn *et al.* (1975); (25) Johnston & Gillman (1995); (26) Steege *et al.* (1993); (27) Sussman & Philipsonroy (1995); (28) Cooper (1982); (29) Guillotin *et al.* (1994); (30) Mori & Boom (1987); (31) Puig & Delobelle (1988); (32) Kessler (1998); (33) Zhang & Wang (1995); (34) Mittermeier (1977); (35) Schulz (1960); (36) Roosmalen van (1985b); (37) Rylands & Keoughlian (1988); (38) Prance *et al.* (1976); (39) Klinge (1968); (40) Ayres (1995); (42) Mendes-Pontes (1999); (43) Milliken & Ratier (1983); (44) Branch (1983); (45) Ferreira & Prance (1998); (46) Pereira de Carvalho (1981); (47) Peres (1991); (48) Johns (1986); (49) Paiva Salomao *et al.* (1988); (50) Lemos de Sa (1995); (51) Paiva Salomao & Lisboa (1988); (52) Queiroz (1991); (53) Felili & Claudio da Silva Jr. (1993); (54) Torres de Assupcao (1983); (55) Milton (1984); (56) Morellato (1992); (57) Terborgh (1983); (58) Terborgh, unpubl.; (59) Emmons (1984); (60) Phillips *et al.* (1993); (61) Brown & Zunino (1994); (62) Grau *et al.* (1999); (63) Brown *et al.* (1985); (64) Brown cited in 69; (65) Arditi & Placci (1990); (66) Di Bitetti & Janson, pers. comm.; (67) Placci & Giorgis (1993); (68) Placci *et al.* (1992); (69) Placci *et al.* (1994); (70) Rumiz *et al.* (1986).

\* Production estimates based on fruit traps.

<sup>2</sup> No basal area available.

<sup>3</sup> No information on tree densities was included.

<sup>4</sup> Basal area based on the most important species, assuming that the proportion of BAE holds for the less common species.

<sup>5</sup> Some of the vegetation data comes from a near by site.

<sup>6</sup> Only the proportion of endozoochorous trees was available.

<sup>7</sup> Using the pooled estimate for the whole region.

<sup>8</sup> Fruit-fall estimates estimated as assuming that 62.5% of the production of both flowers and fruits corresponds to fruits. This is the average among other Neotropical studies that report both estimates independently (SD = 10.5,  $n = 11$ ).

<sup>9</sup> For the following plant families it was assumed that basal area was proportional to tree density: Apocynaceae, Euphorbiaceae, Lecythidaceae, Leguminosae, and Rubiaceae.

used that recommended by the author. Finally, to choose among different estimates from line transect methods I selected the estimate derived from the longest total transect length.

Different primate guilds and taxa were used in different analyses. For the purposes of this paper I used (1) folivorous monkeys as *Alouatta* spp., (2) frugivorous monkeys as all Neotropical primates but the folivorous species, and (3) seed predators as all pitheciine species. I also separated the large fruit-eating ateline monkeys (including *Brachyteles* spp.) from all other species (small monkeys and *Alouatta*).

Fruit production estimates based on fruit traps were taken also from the literature (Table 1). Given the small sample size for this analysis, in four cases I used estimates from nearby sites in the same biogeographical region, within the same forest type (see footnote to Table 1). In all cases, fruit trap studies covered at least a full continuous year.

To look for community-wide patterns, I also estimated three different indexes of fruit abundance based on the basal area of trunks of particular plant species in vegetation quadrants. These indexes are based on observations made for a variety of species for which the diameter at breast height (DBH) of individual trees is positively correlated with their fruit production (Leighton & Leighton, 1982; Chapman *et al.*, 1992). Also, the basal area of fruiting trees in the whole community has been shown to be correlated with the weight of fruits falling in traps in one Neotropical forest (Stevenson, Quiñones & Ahumada, 1998). The first index (BAE) included the basal area of all trees belonging to species that produce fleshy fruits with seeds dispersed by endozoochory (van der Pijl, 1969). The fruit type (endozoochorous vs. not, primate vs. other type of disperser) for each species was assigned based on personal knowledge, published data (Ridley, 1930; van Roosmalen, 1985a; Croat, 1978; Gentry, 1993; Stevenson, Quiñones & Castellanos, 2000) and from voucher specimens at the New York Botanical Garden. I excluded the basal area of some plant species with large seeds that are not ingested by primates but on occasion are dispersed by them by carrying (e.g. *Hymenaea courbaril*). The second index (BAW) is similar to the first one, but it excludes the basal area of plants that are almost exclusively consumed by birds, fish or bats (Appendix 2, based on van Roosmalen, 1985a; Stevenson *et al.*, 2000). The third index is intended to correct for the fact that male trees in dioecious species do not produce fruit. The index correcting for dioecious species (BAD) was calculated assuming that half of the total basal area of dioecious species contributes to fruit production. A sex ratio of 1:1 is assumed for practical reasons, as the true population sex ratio is not known in the vast majority of cases. Information about sexual systems for the

species was taken from the original sources, my personal experience in Tinigua National Park, and the botanical literature (Croat, 1978; Kress & Beach, 1994; van Roosmalen, 1985a). In many cases I did not find information on sexual systems for a particular species, so I assigned the prevalent type for that genus.

Four additional indexes were calculated to test the association between some plants that play very important or keystone roles and particular primate guilds. The first one includes the basal area of fig trees (BAF), which have been proposed to be very important for all frugivorous primates during periods of fruit scarcity (Terborgh, 1986). The second one includes the basal area of all palm species (BAP) that also are known to be very important resources during lean periods, especially for brown capuchin monkeys (Terborgh, 1986; Placci *et al.*, 1992). The third index comprises all plants belonging to the family Moraceae (BAM), which in many Neotropical sites are the principal component in the diet of howler monkeys (e.g. Milton, 1982; Stevenson, Quiñones & Ahumada, 2000). The final index (BAL) includes the basal area of all trees in one genus (*Eschweilera* spp.) belonging to the family Lecythidaceae, that is heavily used by Pitheciine species, who usually prey upon their seeds.

Given that the number of fruiting trees has been shown to be correlated with fruit production in one Neotropical forest (Stevenson *et al.*, 1998), I used density estimates for the same seven categories of plants listed above (DE = endozoochorous, DW = without bird or bat fruits, DD = correction for dioecy, DF = figs, DM = Moraceae, DP = Palmae and DL = *Eschweilera*), in addition to total density of trees of all dispersal types (DT).

For these indexes based on vegetation composition and size classes, plots totaling at least 1 ha were used for each corresponding site ( $n = 24$ , Table 1), but plots were not necessarily contiguous. These studies included all woody plants with DBH equal to or greater than 10 cm. In two cases, vegetation plots excluding DBH 10–15 cm were used and a correction was made assuming the same frequency distribution of endozoochorous basal area for other sites (DBH > 10 cm). In general, vegetation plots were located in the same areas used by the monkeys, except for seven sites, where I used vegetation plots of forested areas relatively nearby (<100 km), within the same rainfall and temperature regime (see Table 1). Finally, plant species richness (average number of species per hectare) was also estimated and included in the analysis as a measure of resource range availability, to test the importance of plant species richness on animal diversity (MacArthur & MacArthur, 1961). Some abiotic factors (Table 1) were also used as covariates in multiple regression analyses.

I performed Pearson correlations and multiple regression analyses to test the different hypotheses. When the assumptions of the former tests were not met, I calculated nonparametric Spearman correlation coefficients ( $r_s$ ). All statistical tests were produced in Microsoft Excel spreadsheets.

## RESULTS

### FRUIT TRAP ESTIMATES

Fruit production estimated by fruit traps was positively related to both Neotropical primate biomass ( $F=43.9$ ,  $P<0.001$ ,  $n=13$ ) and species richness ( $F=18.2$ ,  $P=0.001$ ,  $n=13$ ). This analysis indicates that a large proportion of the variance in biomass ( $r^2=0.80$ , Fig. 1A) and in species richness ( $r^2=0.64$ , Fig. 1B) may be explained by the variation in fruit production. This relationship was not uniform across primate guilds: frugivorous monkeys and small monkeys showed all significant positive correlations between primate biomass and fruit production, whereas, as expected, this was not the case for the folivorous and seed predator guilds (Table 2). The positive linear slope was also significant for the regression between the biomass of the large ateline species and fruit production estimates ( $F=16.8$ ,  $P=0.002$ ), but not for ateline species richness ( $F=2.45$ ,  $P=0.14$ ).

A multiple regression analysis trying to explain primate biomass by production trap estimates of fruit and small litter other than fruit (leaves, flowers and twigs) showed that only the partial coefficient of fruit production, holding small litter constant, was positively correlated to primate biomass ( $P=0.005$ ,  $n=10$ ). A similar analysis showed that only fruit production was positively correlated to primate species richness when controlled statistically by small litter production ( $P=0.007$ ,  $n=10$ ).

As fruit production increased among sites, mean biomass per species increased only slightly and not significantly for either total species or only frugivorous species ( $P=0.12$ ,  $P=0.34$ , respectively). Total primate biomass increased significantly with both fruit production and primate species richness (multiple regression,  $P=0.014$ ,  $P=0.05$ , respectively), whereas primate species richness did not increase with fruit production after controlling for primate biomass (multiple regression,  $P=0.83$ ,  $P=0.05$ , respectively).

### BASAL AREA ESTIMATES

I found a positive correlation between the total basal area of endozoochorous species and primate biomass (Fig. 2A). Using the total sample there was no significant correlation ( $F=3.05$ ,  $P=0.09$ ,  $n=23$ ), but when a site with an unusual high density of howler monkeys (Guascara Island, Argentina, 237 ind/km<sup>2</sup>)

was treated as an outlier, a significant correlation resulted ( $F=8.8$ ,  $P<0.01$ ). Among basal area estimates for particular resources, only the basal area of trees belonging to the family Moraceae was positively correlated with total primate biomass ( $F=8.7$ ,  $P<0.01$ ,  $n=22$ ).

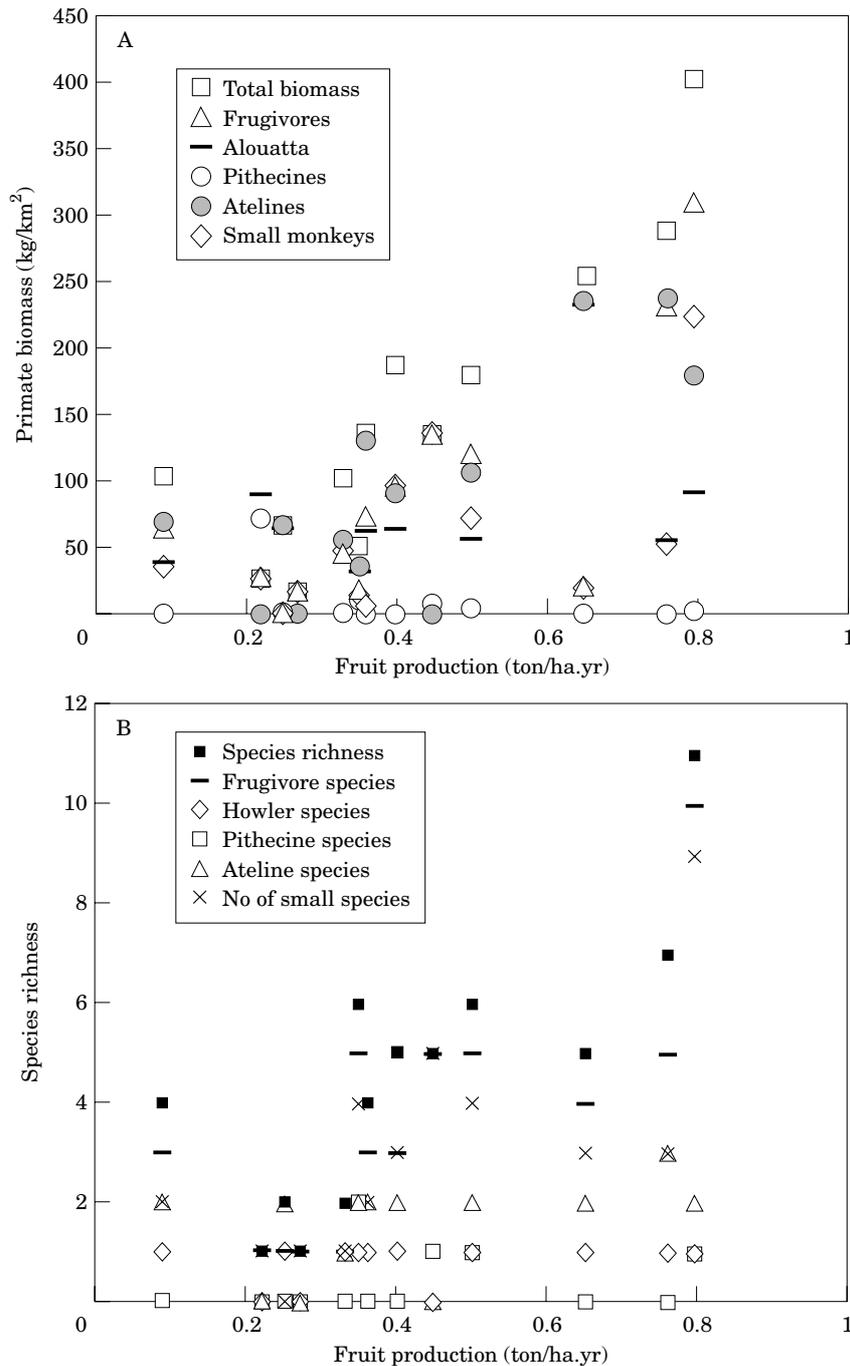
The biomass of frugivorous primates was positively correlated with the basal areas of (1) endozoochorous plants ( $F=5.0$ ,  $P=0.04$ , Fig. 2B), (2) primarily primate fruits ( $F=4.5$ ,  $P=0.05$ ) and (3) female trees producing fleshy fruits (BAD,  $F=4.5$ ,  $P=0.05$ ). On the other hand, none of the basal area estimates of fruit abundance were positively correlated with the biomass of folivorous monkeys (*Alouatta*), seed-eating species or small monkeys (Table 3). The biomass of large ateline monkeys was positively related to the basal area of endozoochorous trees and of female trees producing fleshy fruits (Table 3). The total basal area per hectare (including trees without fleshy fruits) was not correlated with the biomass of any primate guild.

I did not find any significant correlation between the basal area of suggested keystone resources (figs, palms) and the abundance of any primate guild except for a weak effect of the basal area of figs on the biomass of large atelines (Table 3). However, the biomass of seed predators in the subfamily Pitheciinae, which was not correlated with any of the fruit basal area estimates, was positively correlated to the basal area of their preferred resource *Eschweilera* trees ( $F=10.6$ ,  $P<0.001$ ,  $n=23$ , Fig. 3). Similarly, basal area of the preferred plant family Moraceae was positively related to total primate biomass, frugivorous primate biomass, and the biomass of large atelines (Table 3).

Neither total primate species richness nor the diversity of different guilds were associated with most of the fruit basal area estimates ( $P>0.05$ ,  $n=23$ ). The only exception was found for the basal area of *Eschweilera* trees, which was positively correlated with the number of total primate species, frugivorous species, ateline species, pitheciine species, and small-bodied primates (respectively, Spearman's  $r=0.82$ ,  $0.81$ ,  $0.53$ ,  $0.86$ ,  $0.82$ , all  $P<0.01$ ).

### DENSITY OF FRUIT RESOURCES

I found a positive correlation between total primate biomass and the density of trees with endozoochorous fruits (DE,  $F=6.9$ ,  $P=0.02$ ,  $n=21$ ). However, this relationship was not significant for the density of female trees (DD,  $F=1.3$ ,  $P=0.26$ ) or total tree density per hectare (DT,  $F=2.9$ ,  $P=0.11$ ). The biomass of frugivorous primates was also positively correlated with the density of endozoochorous trees (DE,  $F=4.4$ ,  $P=0.05$ ) and with the density of palms (DP,  $F=6.6$ ,  $P=0.02$ ). No other consistent associations were found for density estimates. For example, the density of trees



**Figure 1.** Relationship between fruit production estimates based on traps and (A) the biomass of Neotropical primates ( $n = 13$ ), (B) species richness. The biomass and number of species in two different primate guilds are also shown in the figures. The biomass and species richness of their guilds can be derived by subtraction from the data shown, except for the pitheciine monkeys, which form a small fraction of the biomass in all communities and never exceed a species richness of 2.

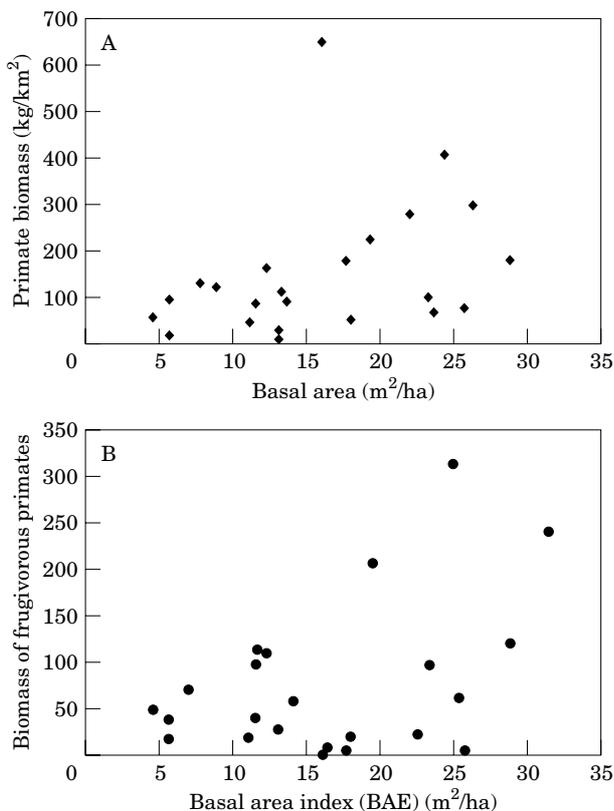
belonging to the Moraceae was positively correlated to total primate and folivorous primate biomass, although the regression coefficient was not significant if the Argentinian outlier was removed from the analysis.

In general, the density of fruit trees was not a good predictor of primate species richness. However, the density of *Eschweilera* trees was positively correlated with the number of pitheciine species (Spearman's  $r =$

**Table 2.** Regression statistics for the analyses between fruit production according to trap estimates and different attributes of primate communities in the Neotropics ( $N = 13$ )

	Regression coefficient	$F$	$P$
Total primate biomass	475.1	43.9	***
Biomass of frugivores	330.1	14.8	**
folivores	145.8	3.9	ns
seed predators	1.7	0.1	ns
small monkeys	171.7	5.4	*
large atelines	158.2	7.5	*
Total species richness	10.3	18.2	**
Number of frugivore species	9.1	15	**
folivore species	0.6	0.9	ns
seed predator species	0.7	0.6	ns
small primate species	7.68	10.5	**
large ateline species	1.39	3.5	ns

ns = not significant.

\* $P < 0.05$ .\*\* $P < 0.01$ .\*\*\* $P < 0.001$ .**Figure 2.** Relationship between Neotropical primate biomass and the basal area of trees with endozoochorous fruits. (A) Total biomass and (B) biomass of frugivorous species. For regression statistics, see Table 3.

0.84,  $P < 0.001$ ,  $n = 21$ ), frugivorous species ( $r_s = 0.73$ ,  $P < 0.001$ ), ateline species ( $r_s = 0.43$ ,  $P = 0.055$ ), small monkeys ( $r_s = 0.75$ ,  $P < 0.001$ ), and total primate species richness ( $r_s = 0.73$ ,  $P < 0.001$ ). Palm density was positively correlated to the number of small primates ( $r_s = 0.64$ ,  $P = 0.002$ ), number of frugivorous monkeys ( $r_s = 0.60$ ,  $P = 0.004$ ) and total species richness ( $r_s = 0.52$ ,  $P = 0.02$ ). None of the other density parameters were correlated with primate species richness of any of the guilds included.

#### CLIMATIC, GEOGRAPHICAL AND PLANT DIVERSITY VARIABLES

Among these independent variables (see Table 3), total primate biomass was positively correlated only with plant species richness [ $F = 11.9$ ,  $P = 0.002$ ,  $n = 23$  (excluding Guascara Island)]. This correlation was found also for the biomass of frugivorous primates ( $F = 18.9$ ,  $P < 0.001$ ,  $n = 24$ ), but for them there is also a negative correlation between biomass and latitude ( $F = 5.4$ ,  $P = 0.03$ ). Latitude is also negatively correlated to the biomass of pitheciine monkeys ( $F = 10.5$ ,  $P = 0.003$ ).

Some of the climatic estimates are inter-correlated (see Table 5), making it difficult to tease apart the most important variables to predict primate biomass. A multiple regression analysis to predict Neotropical biomass from all of these variables and from fruit trap production estimates showed that 87% ( $r = 0.93$ ,  $n = 13$ ) of the variance in primate biomass can be explained by the model. Fruit production based on fruit traps was the only significant partial coefficient in the analysis,

**Table 3.** *F* statistics for linear regression analyses, testing that the slope of the line is different from zero. The analyses are between primate biomass of different guilds and various estimates of abundance of fruit resources (see methods for abbreviations), climatic variables (mm = mean annual rainfall, T° = mean annual temperature and Dry Mo = number of dry months), latitude, and plant species richness per hectare (PSR)

	Total Biomass <sup>1</sup>	Frugivores	Folivores	Seed predators	Large atelines	Small monkeys
Basal area estimates						
BAE	8.8**	5.0*	0.3 ns	1.2 ns	6.2*	1.8 ns
BAW	9.6**	4.5*	0.6 ns	0.5 ns	4.0 ns	2.4 ns
BAD	9.7**	4.5*	0.5 ns	0.7 ns	4.5*	2.1 ns
Total BA	0.5 ns	3.2 ns	0.1 ns	0.2 ns	1.9 ns	2.6
Basal area of particular resources						
BAL	0.2 ns	1.3 ns	0.6 ns	21.9***	0.1 ns	2.6 ns
BAF	2.7 ns	0.7 ns	0.0 ns	3.6 ns	6.5*	0.3 ns
BAP	0.6 ns	1.0 ns	0.3 ns	0.8 ns	1.5 ns	0.3 ns
BAM	8.7**	6.1*	0.0 ns	1.6 ns	14.1**	0.9 ns
Climatic and plant diversity variables						
mm	0.1 ns	0.4 ns	1.2 ns	1.2 ns	0.0 ns	0.8 ns
Dry Mo	4.0 ns	0.6 ns	2.2 ns	2.7 ns	0.0 ns	0.9 ns
T°	2.4 ns	2.0 ns	0.3 ns	1.7 ns	2.2 ns	0.3 ns
Latitude	2.3 ns	5.4*	3.0 ns	10.5**	1.5 ns	3.7 ns
PSR	11.9**	18.9***	0.6 ns	1.6 ns	4.9*	14.4***

NA = Not adequate data for the analysis.

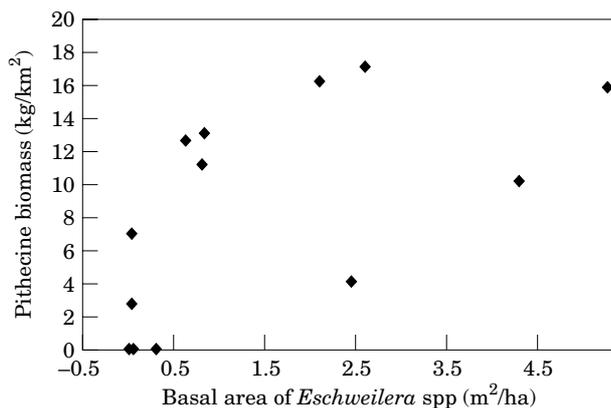
ns = not significant.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

\*\*\* $P < 0.001$ .

<sup>1</sup> Guascara Island is removed as an outlier in the analyses of total biomass.



**Figure 3.** Relationship between the biomass of pitheciine monkeys and the basal area of *Eschweilera* trees. For statistics, see Table 3.

explaining about 80% of the variance in primate biomass. A similar model to predict primate biomass using the basal area of endozoochorous trees as an

independent variable showed a lower multiple correlation coefficient. Climatic variables were as important as the basal area estimate in predicting total biomass (rainfall:  $F = 5.8$ , dry months:  $F = 5.7$ , basal area:  $F = 5.7$ ,  $P = 0.02$  for all,  $r^2 = 0.63$ ,  $n = 23$ ).

Total primate species richness was positively correlated with plant species diversity, temperature and annual rainfall, and negatively correlated with latitude (Table 4). Similar relationships were found for frugivorous and small monkeys, but the effects of temperature were weaker. The number of folivorous primates was correlated only with mean annual temperature ( $r_s = 0.44$ ,  $P = 0.014$ ). The number of pitheciine species was negatively correlated with latitude ( $r_s = -0.60$ ,  $P < 0.001$ ). The number of ateline species was negatively related to latitude, but positively related to temperature (Table 4).

In a multiple regression analysis using fruit trap estimates, climatic and latitudinal variables to explain primate species richness, only fruit production estimates resulted in a significant partial correlation coefficient ( $P = 0.004$ ,  $n = 13$ ). Together, fruit production

**Table 4.** Spearman rank correlation coefficients for analyses between primate species richness in different guilds and four independent variables: MAR=mean annual rainfall (mm), Dry Mo=number of dry months and T°=mean annual temperature, latitude, and plant species richness per hectare (PSR)

	Total no. species	Frugivores	Folivores	Seed predators	Large atelines	Small monkeys
MAR	0.43*	0.49**	0.01 ns	0.35 ns	0.34 ns	0.42*
Dry Mo	-0.10 ns	-0.08 ns	-0.31 ns	-0.06 ns	-0.07 ns	-0.04 ns
T°	0.36*	0.34 ns	0.44*	0.22 ns	0.42*	0.25 ns
Latitude	-0.67***	-0.67***	-0.27 ns	-0.60***	-0.55**	-0.60***
PSR	0.69***	0.63***	0.16 ns	0.35 ns	0.25 ns	0.64***

ns = not significant.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

\*\*\* $P < 0.001$ .

and latitude were able to explain 73% of the variation in primate species richness. In a similar regression analysis using basal area estimates of endozoochorous fruits, the explanatory power of fruit abundance was not significant, but latitude and plant species richness showed highly significant partial correlation coefficients (Basal area:  $F = 0.8$ ,  $P = 0.39$ ; Latitude:  $F = 10.6$ ,  $P < 0.001$ ; Plant species richness:  $F = 5.4$ ,  $P = 0.004$ ,  $n = 23$ ).

## DISCUSSION

### EFFECTS OF FRUIT PRODUCTION ON PRIMATE BIOMASS

Primate densities are variable in time (e.g. Milton, 1982), even within years in regions where the monkeys track feeding resources over large areas (Peres, 1994). There are also several studies showing differences in primate densities among different forest types at the scale of the area covered by a single group (Mendes-Pontes, 1999; Stevenson, 1996). Furthermore, plant diversity in Neotropical lowland forests (especially in western South America) is very high (Gentry, 1988), making it very difficult to characterize vegetation attributes, even when using plots of at least 1 ha. For example, the basal area index of endozoochorous trees in our study site at Tinigua National Park tended to reach a stable value only after sampling at least 1.5 ha. Similarly, our annual fruit production estimate based on 300 fruit traps changed as much as 9% if a biweekly datum from a single trap was excluded from the overall calculation (Stevenson *et al.*, 1998). Given all these natural sources of variation, the fact that all estimates of fruit abundance or fruit tree density were positively correlated with primate biomass in this set of Neotropical forests suggests a strong effect of fruit production on Neotropical primate communities. The importance of fruit production, but not overall plant production, is highlighted by the results that neither

total litterfall production (excluding fruits), total basal area, nor total tree densities were correlated with primate biomass, when statistically controlled by the respective estimate of fruit abundance.

The different estimates of fruit production or density of fruit resources were all positively correlated with each other (Table 5). However, the predictive power of the estimates based on fruit traps on primate biomass was better than when using basal area estimates or density. Although a larger sample size is desirable to reach concrete conclusions, these results suggest two possible alternatives. First, basal area may not be a good predictor of fruit abundance because of differences in reproductive output per unit basal area among plant families and habitats. For example, it is expected that plants in nutrient poor environments would not allocate as much energy to reproduction than those in nutrient rich habitats (Chapin, 1980). Therefore, basal area indexes may not be appropriate estimates when comparing areas with different soil fertility, as is the case in the Neotropics. Second, the even lower predictive power of density estimates probably reflects that size is important when assessing reproductive output.

In spite of all the caveats, the analyses confirmed the predictions that the relationship between the biomass of frugivorous monkeys and fruit production should be tighter than that of folivores and seed predators. This correlation was also significant for small monkeys, which suggest that for them, fruit resources are also important as energy sources.

The corrected basal area indexes (BAW and BAD) were highly correlated to the overall basal area index ( $r = 0.96$  and  $r = 0.97$ ), and they were not better predictors of primate biomass than the total uncorrected index. In the first case (BAW), it is important to note that assigning fruit species to different categories of consumers is somewhat arbitrary. Some plant species,

**Table 5.** Correlation coefficients among the different independent variables used in this study. Dry Mo = number of dry months, T° = mean annual temperature, PSR = plant species richness per hectare, BAE = basal area of endozoochorous trees, DE = density of endozoochorous trees per hectare, Ton FR/ha/yr = fruit production based on fruit trap estimates and  $n$  = sample size. Bold numbers represent significant coefficients ( $P < 0.05$ )

	Rainfall	Dry Mo	T°	Latitude	PSR	BAE	DE	$n$
Dry Mo	<b>-0.48</b>							31
T°	0.25	-0.13						31
Latitude	<b>-0.42</b>	0.14	<b>-0.82</b>					31
PSR	<b>0.41</b>	-0.31	0.34	<b>-0.53</b>				24
BAE	0.39	-0.19	0.30	-0.22	<b>0.62</b>			23
DE	-0.01	-0.36	-0.02	0.07	<b>0.60</b>	<b>0.64</b>		21
Ton FR/ha/yr	-0.09	-0.21	0.22	-0.33	<b>0.74</b>	0.64	0.65	7-13

primarily consumed by birds and bats, are ingested by primates in areas where other plant resources are not available. For example, in the subtropical site at Iguazu National Park, brown capuchin monkeys consume fruit species belonging to *Cabralea*, *Casearia*, *Miconia*, *Piper*, *Rapanea*, *Solanum* and *Tetracera* (Di-Bitetti, pers. comm.), which are generally consumed by birds and bats. In the second case (BAD), it is possible that the correction for the lack of fruit production by male trees is either incorrect or is overwhelmed by the fact that even within this set of largely mammal-dispersed species, certain predominantly dioecious families such as Moraceae and Lauraceae are strongly preferred taxa in the monkey's diet.

#### SPECIES OR DENSITY COMPENSATION UNDER INCREASED PRODUCTIVITY?

As fruit production increased among sites, both primate biomass and species diversity increased. Primate biomass increased significantly with fruit production even after controlling for species richness, suggesting that fruit production had a direct effect on primate biomass. However, species diversity did not increase with fruit production when biomass was controlled statistically. This result suggests that greater biomass mediates the increase in species diversity in areas of higher production. One mechanism to produce this outcome would be if species with narrow niches could maintain viable populations only when the potential biomass of that niche exceeded a critical value.

#### EFFECTS OF KEYSTONE OR PREFERRED FOOD TAXA ON BIOMASS

Contrary to the expectations, the basal area indexes for fig or palm plants were not good predictors of total primate biomass or that of any primate guild. In the case of figs, there are two points that make it difficult to reach a decisive conclusion. First, the sample size

problem mentioned above is accentuated if one is interested in cases of low-density resources, as usually is the case for figs. Second, for some fig species with predominantly hemiepiphytic forms, taking the basal area as an index of fruit productivity may underestimate production and makes the comparisons with tree species difficult. Basal area of palms was not a good predictor of frugivorous or total primate biomass, but the density of palms was correlated with the biomass of frugivorous primates. However, the low explanatory power of this correlation ( $r^2 = 0.26$ ) suggests that many other fruit resources are also important in determining primate biomass for frugivorous monkeys in the Neotropics. This seems to be the case for the brown capuchin monkeys (*Cebus apella*), which rely heavily on palm fruits, but whose biomass was not correlated with the basal area of palms.

The basal area of Moraceae, a preferred food plant family, was significantly related to total biomass, frugivore biomass and ateline biomass. Given the weak relationship of the basal area of Moraceae to other primate guilds, its effects on total and frugivore biomass are almost certainly caused by its strong relationship to ateline biomass. Because ateline biomass was only weakly related to the basal area of fig trees, other genera of plants in the Moraceae (e.g. *Brosimum*) may be more important for determining ateline biomass (but see caveats above concerning estimates of fig tree basal area).

It was expected that the basal area of Moraceae would be related to the biomass of *Alouatta* spp., based on their frequent use of plants of this family in at least some areas, yet no clear relationship was found. Although it is clear that the density of howler monkeys is affected by the degree of hunting pressure, soil fertility, forest heterogeneity, patterns of rainfall and latitude (Peres, 1997a), all of these variables except hunting should exert their effects indirectly through food abundance and quality. The lack of correlation

between *Alouatta* biomass and the abundance of Moraceae plants failed, probably because of the ample range of resources that *Alouatta* can use (including leaves of many other plant families). It would be interesting to look at the quality of their foods and long term changes as already suggested (Chapman & Balcomb, 1998; Janson & Chapman, 1999).

Within the set of particular plant species examined for this study the most striking result was the association between the abundance of pitheciine species and *Eschweilera* trees. Positive correlations were found between pitheciine biomass and the basal area index (BAL) and the density of *Eschweilera* trees (DL). DL was also correlated with the number of pitheciine species. The density and basal area of *Eschweilera* trees were also related to the species richness of other primate guilds (except *Alouatta*), but never as strongly as for the pitheciines. Many studies of these seed predators indicate the importance of these Lecythidaceae trees on their diet (Ayres, 1989; Fontaine, 1981; Mittermeier, 1977; Prance & Mori, 1978; van Roosmalen *et al.*, 1981; van Roosmalen *et al.*, 1988). Thus, the trends found here may reflect a causal relationship explaining the abundance of this primate guild. Recently, it was pointed out that pitheciines lack any ecological counterpart outside the Amazon basin (Peres & Janson, 1999), and these analyses indicate that the main reason for this pattern is the reduced abundance of Lecythidaceae in other Neotropical sites outside central and eastern Amazon regions (Terborgh & Andresen, 1998).

Finally, some relationships like the one between the density of *Eschweilera* trees and total primate species richness merits some cautionary comments. None of these analyses done in this study prove causality, and it is possible that primate species richness is indeed determined by another factor that co-varies with density and basal area of *Eschweilera* trees. The results of this study suggest that plant species richness is a very important factor, given the high positive correlation between primate and plant species richness ( $r=0.69$ ,  $n=21$ ). Indeed, the significant effect of *Eschweilera* basal area or density on total primate species diversity become non-significant when total plant species diversity among sites is controlled statistically in a multiple regression.

#### EFFECTS OF FRUIT PRODUCTION ON PRIMATE SPECIES RICHNESS

Primate species richness for this set of Neotropical sites was positively correlated with fruit production based on trap estimates. However, primate diversity was not correlated with either basal area or density of endozoochorous trees. Instead, two other variables were more important than basal area measures of

fruit production in explaining primate species richness: latitude and plant species richness. The possible factors affecting species richness on latitudinal gradients have been addressed on several occasions, and recently reviewed for primates (Eeley & Lawes, 1999; Peres & Janson, 1999).

The smallest data base used in this study showed that fruit production based on fruit traps may influence primate species richness in the Neotropics (as suggested by Kay *et al.*, 1997). However, there was a strong correlation between latitude and fruit production using trap estimates ( $r=-0.84$ ), so the causal relationship between fruit production and primate diversity is not certain. For instance, it is possible that seasonality of fruit production (related to latitude) is as important as total annual production in affecting which primate species can survive in a given area. Nevertheless, in the multiple regression of primate species richness against both fruit production and climatic/geographic variables, only the fruit production variable retained a significant partial correlation coefficient. Seasonality, as gauged by the number of dry months per year, was not correlated significantly with total primate species richness or that of any subgroup analysed here. However, direct estimates of the variability of food production were not used in this analysis. It remains possible that the biomass of primates is determined by the minimum level of fruit production (e.g. Janson, 1984; Janson & Emmons, 1990), which could be highly correlated with total annual production measures.

#### BIOGEOGRAPHIC FACTORS, HISTORY, AND PRIMATE SPECIES DIVERSITY

Species richness values for all primates and most primate guilds were strongly related to latitude. However, the multiple regression analysis including fruit production and climatic variables suggested that fruit production was the primary correlate of species diversity. If correct, then the apparent effect of latitude on primate species diversity is mediated by the latitudinal reduction in fruit production. The longitudinal differences in floristic composition between western and central-eastern Amazonia may also be important in determining fruit production in the Neotropics (Terborgh & Andresen, 1998) because of the abundance of usually inedible fruit trees for primates in the latter region (e.g. Lecythidaceae). On the other hand, the high correlation between plant and primate species richness suggests that an increase in plant species richness may allow the coexistence of more sympatric primate species, especially in the smaller size classes.

This study did not assess the effect of other biogeographic factors, such as fragment area or distance from other species sources. Both the latter variables would be influenced by the extent of forest cover in

the region surrounding each study site, a variable which has been shown to affect Neotropical species diversity even after controlling for latitude and habitat type (Peres & Janson, 1999). Given that fruit production alone explained 64% of the variation in primate species diversity, it seems unlikely that fragment area and isolation measures will account for much more of the variance in primate species diversity, unless fruit production is coincidentally correlated with these measures.

#### CONSERVATION IMPLICATIONS

If the goal of conservation efforts is to preserve the largest possible number of primate species in the Neotropics, the results of this study suggest one should concentrate efforts on lowland forest close to the equator with high plant species richness and high levels of fruit production. In cases when conservation efforts are focused on particular primate taxa, the basal area of preferred plant resources of these taxa may provide a rapid and reliable guide to areas of high potential biomass and diversity.

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## APPENDIX 1

Ecological data for the primate species included in the analyses. ABW = average body weight. Under diet, Fr + In = fruits + insects, which are included in text as frugivorous. Under taxon, species are grouped according to the categories used in the data analysis.

Primate species	ABW(Kg)	Metabolic mass (Kg)	Diet	Taxon	Reference*
<i>Alouatta belzebul</i>	6.40	4.02	Leaf	<i>Alouatta</i>	1
<i>Alouatta caraya</i>	5.62	3.65	Leaf	<i>Alouatta</i>	1
<i>Alouatta fusca</i>	6.06	3.86	Leaf	<i>Alouatta</i>	1
<i>Alouatta palliata</i>	6.20	3.93	Leaf	<i>Alouatta</i>	1
<i>Alouatta seniculus</i>	6.50	4.07	Leaf	<i>Alouatta</i>	2
<i>Aotus azarae</i>	0.94	0.95	Fr + In		1
<i>Aotus brumbacki</i>	0.94	0.95	Fr + In		1
<i>Aotus nigriceps</i>	1.00	1.00	Fr + In		2
<i>Aotus trivirgatus</i>	0.94	0.95	Fr + In		1
<i>Ateles belzebuth</i>	7.50	4.53	Fruit	ateline	3
<i>Ateles geoffroyi</i>	7.80	4.67	Fruit	ateline	1
<i>Ateles paniscus</i>	7.78	4.66	Fruit	ateline	4
<i>Brachyteles arachnoides</i>	10.79	5.95	Leaf	ateline	1
<i>Cacajao calvus</i>	3.20	2.39	Seed	pithecine	2
<i>Callicebus brunneus</i>	0.85	0.89	Fr + In		1
<i>Callicebus cupreus</i>	1.20	1.15	Fr + In		3
<i>Callicebus moloch</i>	1.08	1.06	Fr + In		5
<i>Callicebus personatus</i>	1.32	1.23	Fr + In		1
<i>Callicebus torquatus</i>	1.20	1.15	Fr + In		2
<i>Callimico goeldii</i>	0.59	0.67	Fr + In		2
<i>Callithrix emiliae</i>	0.34	0.45	Fr + In		1
<i>Callithrix flaviceps</i>	0.41	0.51	Fr + In		1
<i>Callithrix geoffroyi</i>	0.22	0.32	Fr + In		1
<i>Callithrix jacchus</i>	0.25	0.35	Fr + In		1
<i>Callithrix penicillata</i>	0.20	0.30	Fr + In		1
<i>Cebuella pygmaea</i>	0.15	0.24	Fr + In		2
<i>Cebus albifrons</i>	2.70	2.11	Fr + In		2
<i>Cebus apella</i>	2.90	2.22	Fr + In		2
<i>Cebus capucinus</i>	3.25	2.42	Fr + In		5
<i>Cebus olivaceus</i>	2.54	2.01	Fr + In		1
<i>Chiropotes satanas</i>	2.99	2.27	Seed	pithecine	4
<i>Lagothrix lagotricha</i>	8.70	5.07	Fruit	ateline	2
<i>Pithecia albicans</i>	2.80	2.16	Seed	pithecine	2
<i>Pithecia irrorata</i>	2.20	1.81	Seed	pithecine	2
<i>Pithecia monachus</i>	2.20	1.81	Seed	pithecine	2
<i>Pithecia pithecia</i>	1.87	1.60	Seed	pithecine	4
<i>Saguinus fuscicollis</i>	0.39	0.49	Fr + In		2
<i>Saguinus geoffroyi</i>	0.54	0.63	Fr + In		1
<i>Saguinus imperator</i>	0.51	0.60	Fr + In		2
<i>Saguinus labiatus</i>	0.46	0.56	Fr + In		1
<i>Saguinus leucopus</i>	0.44	0.54	Fr + In		1
<i>Saguinus midas</i>	0.49	0.59	Fr + In		4
<i>Saguinus mystax</i>	0.51	0.60	Fr + In		2
<i>Saimiri boliviensis</i>	0.94	0.95	Fr + In		2
<i>Saimiri sciureus</i>	0.94	0.95	Fr + In		2
<i>Saimiri vanzolinii</i>	0.80	0.85	Fr + In		1

\* References for body weights: (1) Rowe (1996), (2) Peres (1997b), (3) Robinson & Redford (1986), (4) Fleagle & Mittermeier (1980), (5) Harvey, Martin & Clutton-Brock (1987).

## APPENDIX 2

List of plant genera (or species) not included in the BAW index (Basal area of fleshy fruit species, excluding those predominantly consumed by birds, fish or bats).

<i>Alchornea</i>	<i>Cestrum</i>	<i>Hasseltia</i>	<i>Myrrhinium</i>	<i>Piper</i>	<i>Solanum</i>
<i>Andira</i>	<i>Clusia</i>	<i>Ilex</i>	<i>Myrsine</i>	<i>Psychotria</i>	<i>Stylogyne</i>
<i>Banara</i>	<i>Connarus</i>	<i>Inga vera</i>	<i>Pentapanax</i>	<i>Rapanea</i>	<i>Xylosma</i>
<i>Cabralea</i>	<i>Curatella</i>	<i>Lacistema</i>	<i>Pera</i>	<i>Rhamnidium</i>	<i>Tetracera</i>
<i>Carpotroche</i>	<i>Davilla</i>	<i>Margaritaria</i>	<i>Phenakospermum</i>	<i>Sambucus</i>	<i>Tovomita</i>
<i>Casearia</i>	<i>Erythroxylum</i>	<i>Miconia</i>	<i>Picramnia</i>	<i>Sapium</i>	<i>Vismia</i>