CHAPTER 4.

FLORISTICS, PRIMARY PRODUCTIVITY AND PRIMATE DIVERSITY IN AMAZONIA: CONTRASTING A EUTROPHIC VÁRZEA FOREST AND AN OLIGOTROPHIC CAATINGA FOREST IN BRAZIL

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Abstract

Several factors such as rainfall, primary productivity, and plant species richness have been hypothesized to affect consumer species richness, possibly explaining differences in species richness among communities and on different continents. Primary productivity in particular has been suggested as important in determining species richness of consumer taxa, such as the primates, in the Neotropics. Here I contrast the floristics and phenological patterns of two Amazonian rainforest sites that differ markedly in primary productivity and yet have the same number of primate species: 1) an oligotrophic site—caatinga forests of Pico da Neblina National Park; and 2) a eutrophic site—várzea forests of Mamirauá. The objective of this comparison is to see how primary productivity interacts with floristics and phenology and ultimately, with primate species richness. With only 4 species each, the compared sites are characterized by low primate species richness. At both sites, low numbers of primate species are associated with an unusually low abundance of important primate food plants such as trees from the Burseraceae, Moraceae, Myristicaceae, Palmae and Sapotaceae. Moreover, in Neblina there is a long period of fruit scarcity and an overall low availability of fleshy fruits, which probably also contributes to the observed low primate species richness. In contrast, productivity in Mamirauá is high and fleshy fruits are abundant. These fruits, however, are mostly small in size and their seeds are most likely dispersed by birds, bats, fish, or water, not by primates. In this case then, primary productivity is not being largely transferred to primates as may be the case in other productive sites where preferred primate plant families are more abundant. Thus, when intertrophic interactions have a mutualistic nature such as the interaction between a fruit and a frugivore, a direct effect of primary productivity on all consumer taxa should not be expected. I suggest that in order to understand the effects of intertrophic interactions on consumer species richness in tropical rainforests it is important to first determine how the primary productivity is funnelled to the second trophic level.

Key words: Brazil, floristics, frugivory, primates, species richness, tropical forests

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INTRODUCTION

One of the main tasks of ecology is to understand the patterns of species diversity among communities and on different continents (Brown, 1995, Rosensweig, 1995). As such, ecologists have been investigating several factors hypothesized to affect species diversity—i.e., abundance and diversity of predators, presence of competitors, food species diversity, primary productivity, rainfall patterns, soil quality, habitat heterogeneity, natural disturbances as well as historical, bigeographical and evolutionary factors (Ashton 1989, Begon et al., 1990, Huston 1994, Rosensweig, 1995).

A relationship between rainfall, plant productivity and plant species diversity has been hypothesized and appointed as important in determining species diversity at the second and subsequent trophic levels (Huston, 1994, Rosensweig, 1995). Kay et al (1997) have considered the effect of 'bottom-up' forces or plant primary productivity on primate species richness. These authors analyzed data from the neotropics and found a tight correlation between rainfall and several relevant variables namely primate species richness, tree species richness, number of wet months and primary productivity. They noticed that the curves for primate richness and productivity had similar shapes: Both increased with rainfall up to a maximum at approximately 2,500 mm/year and then fell off together at higher rainfall levels. They concluded that increased plant productivity led to increased species richness of primates because at higher productivity specialized species could maintain viability.

However, in the Amazon basin, primate species richness appears to follow a biogeographical east-west gradient with more species found near the Andes (west). Whether such pattern of species abundance follows a primary productivity gradient remains to be determined. Here, I contrast the floristics and phenological pattern of two Amazonian rainforest sites that differ markedly in primary productivity but have the same number of primate species: 1) Oligotrophic site—An extremely nutrient starved habitat represented by the white sand forests of Pico da Neblina National Park; and 2) Eutophic site—A nutrient-rich habitat represented by várzea forest of Mamirauá as studied by Ayres (1986, 1993) with rich alluvial soils. The objective of this comparison is to see how is primary productivity interacting with floristics and phenology and thus, with primate species diversity.

Study sites

Pico da Neblina

Pico da Neblina study site (0º24' N/66º18' W) is located in the lowlands of Pico da Neblina National Park, in the Northwestern most part of Brazilian Amazonia on the border with Venezuela (Figure 1). The lowland area of Pico da Neblina is characterized by a high annual average rainfall (2,500 - 3,000 mm/year) and an average temperature of 26º C, with little fluctuation throughout the year (RADAM, 1978). The rainiest months are from May to September. Although, no month can be considered dry, considerably less rain falls from October to April (Figure 2). Soils are extremely acidic at pH = 4 and among the poorest in the Amazon basin consisting of, for the most part, white bleached sands.

Pico da Neblina National Park is covered by dense, tall, evergreen lowland forest, submontane forests, montane forests and upland meadows. In the lowlands (~100 m a.s.l.), the forest is a mosaic of caatinga (forest on white sands *sensu* Klinge *et al*. 1977), terra firme (tall forest on dry land *sensu* Pires and Prance 1985) and chavascal (waterlogged forest). Igapó (seasonally-flooded forest) also occurs but is restricted to small areas along rivers.

This study focussed on an area of 500 hectares along the margins of the Cauaburi river, the main watercourse in the Park. Within this area, terra firme is the predominant forest type covering 44% of the total area with a canopy height of approximately 25 meters and emergents of up to 35 m (Boubli, 1997, 1999).

Chavascal is the second largest forest type covering 29% of the study site. This habitat is low-lying and thus, waterlogged during most of the year. Chavascal is physionomically similar to terra firme forest but has a higher occurrence of lianas (Boubli, 1997, 1999).

Caatinga corresponds to 27% of the study area. This forest is characterized by a dense understorey and a low canopy height of approximately 10 to 15 meters, with emergents of up to 25 m. Lianas are rare in this habitat. Caatinga occurs in the lower and higher parts of the study site, its structure and floristics being most likely determined by the soil. Caatinga is characteristic of areas covered by the acidic and well drained quartz sands; a bleached, white, coarse sandy soil mixed with rolled gravel (Boubli, 1997, 1999).

Figure 1. Location of the two study sites compared

Mamirauá

Mamirauá is located on the margins of Teiu lake in a young Holocene várzea near the mouth of the Japurá river, Amazonas (Figure 1). The area is characterized by several small lakes, streams, channels and swamps. In the height of the flooding season, water covers even the highest ground (Ayres 1986). Annual average rainfall is 2,850 mm with no real dry season (Ayres, 1993). However there is a considerable variation in rainfall with up to 3 times as much rain falling from December to March as compared to the period of July to October (Figure 2). Water level fluctuates as a consequence of rainfall. The total difference in water height registered at the study site was 11 m (Ayres, 1986). Water rise takes 8 months while the drop is quick at 4 months. Maximum height was reached in the months of May and June and the lowest in October.

Vegetation is of two main types: forested areas or restingas located on the higher grounds (30-40% of the area), 2) and open areas, or chavascal, relatively lower grounds (60-70%). Vegetation overlap between lower and higher restingas is only of 37% most probably because floods select against plant species unable to cope with prolonged periods of submersion.

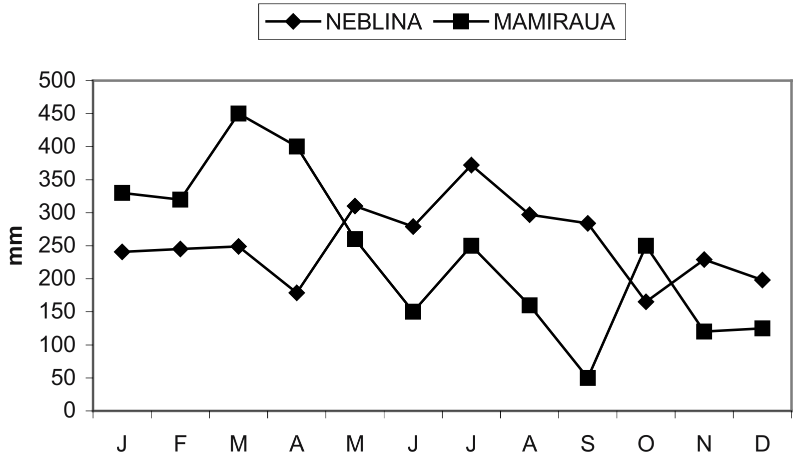

Figure 2. Rainfall at Pico da Neblina in 1995 and at Mamirauá in 1984.

METHODS

In Pico da Neblina, five botanical plots (2 ha total sampled area) in the form of belt transects (*sensu* Ludwig and Reynolds, 1988) were laid out for floristic study of the area. The plots consisted of four 10 x 250 m plots (0.25 ha each - plots 2,3,4,5) and one continuous 10 x 1000 m plot (1 ha - plot 1). Plot 1 was placed haphazardly and was further subdivided into four 0.25 ha sub-plots (plot 1.1 to 1.4). The four smaller plots 2 to 5 were laid out such that all different forest types were represented in proportion to their contribution to the total area of the study site.

Within the plots, all trees with a diameter at breast height (DBH) equal to or greater than 10 cm were marked with aluminum tags and had their DBHs measured with a metric tape. Once a month from October 1994 to October of 1995 (but February), we scanned the crowns of 436 trees ≥ 10 cm DBH with binoculars (10 x 40) to record the presence/absence of young leaves, flowers, buds, and fruits (ripe and unripe). Trees in the phenology were chosen from a total pool of 818 trees with DBH ≥ 10 cm within the long 1 ha transect. Initially, all 818 trees from the botanical plot were used in the phenology. However, because the crowns of many trees were not visible due to thick canopy cover, we decided to reduce the sample to only those trees that offered a reasonable view of their crowns. The inclusion of poorly visible trees can greatly underestimate the production of fruits or flowers in the forest.

In Mamirauá two ha were also sampled. The first ha consisted of 16 25m x 25m quadrats placed within the area of the study site so that areas subjected to different depths were sampled. The second ha was divided into two belt transects randomly placed totaling 1000m x 10 m. All trees ≥10 cm DBH were marked and identified. For the phenology study, all trees from the two ha (i.e. from the 16 quadrats) were observed once a month from July 1983 to December 1984.

Fruits produced by trees in the sample plots of the compared sites were classified as fleshy or dry depending on the presence or absence respectively of animal attractants such as, aril, pulp, fleshy mesocarps etc. These data were obtained directly in the field in Pico da Neblina or, for Mamirauá, from the book *Fruits of the Guianan Flora* (Roosmalen 1985).

Both sites have been intensively studied in terms of their primate fauna. Information on primate diversity and density were obtained from these studies (Ayres 1986, Boubli 1997, 1999).

RESULTS

Floristics

Pico da Neblina

There were 1569 trees with diameter at breast height ≥ 10cm in the sample (minimum of 229 species in 45 families) (Boubli 2002). A minimum of 229 species in 45 families were identified. In plot 1 (1ha) there were at least 161 species. The two tree species *Eperua leucantha* and *Hevea cf. brasiliensis* dominated the forest accounting for 29% of the sampled trees. High species dominance was more evident in the caatinga forest areas where the combined trees *Eperua leucantha, Micrandra* *sprucei* and *Hevea cf. brasiliensis* accounted for 66% of all sampled trees. *Ficus* sp. trees were practically absent from the forest. Compared to Amazonian forests elsewhere, the ranking order of plant families in Pico da Neblina was peculiar in that Leguminosae *sensu latu* and Euphorbiaceae dominated the sample accounting for 52% of all marked trees (Boubli, 2002).

Of the 1569 trees ≥ 10 cm DBH in the two ha plots, at least 1,186 trees (76%) were dry fruit bearers. This high number is explained by the fact that the dominant species produced dry fruits – although more species produced fleshy fruits, the species producing dry fruits were more abundant. The 10 most common species in the two ha sample, representing 50% of all marked trees (780 individuals), produced large-seeded dry fruits protected by hard husks. The top five tree species in Importance Value (*sensu* Mori et al., 1983), *Eperua leucantha, Hevea cf. brasiliensis, Micrandra sprucei, Eschweilera* sp. and *Micrandra spruceana* all produced fruits with hard husks and large seeds that measured from 2 to 4 cm.

Mamirauá

In total there were 996 trees ≥10 cm DBH in the two ha sampled. A total of 174 species in 46 botanical families were present. Species dominance as in Pico da Neblina was not observed in Mamirauá. The most abundant species, *Eschweilera albiflora* (Lecy), *Pterocarpus amazonicus* (Fab) and *Malouetia tamaquarina* (Apo) together represented only 11% of the trees sampled.

Tree family composition also differed from other known Amazonian forests in that Euphorbiaceae was the most abundant family (14%) followed by Annonaceae and Leguminosae *sensu latu* (12% each), Lecythidaceae (6.4%), Apocynaceae (5.3%), Sapotaceae (4.5%) and Myrtaceae (4.3%). Moraceae occupied the 9th position. In the sampled forests, *Ficus* sp. was represented by only one individual.

The great majority of tree species in Mamirauá were adapted to animal dispersal (80%). However, in terms of individuals, 449 trees produced fleshy fruits. Of these, 200 produced small mostly bird, bat or fish dispersed and belonged to Annonaceae, Euphorbiaceae, Myrtaceae, and Meliaceae. Important primate food families such as Sapotaceae, Moraceae, Myristicaceae and Palmae accounted for 113 individuals or 25% of the fleshy fruit trees.

In order to put the floristic composition of both sites into perspective, I plotted in the same graph the results of this study with the combined sample of 48, 1 ha plots summarized by Terborgh and Andressen (1998) (Figure 4). Only the 16 families presented by Terborgh and Adressen were ploted here. Neblina and Mamirauá differed from Terborgh & Andressen's summary sample in that Palmae, Moraceae, Myristicaceae and Burseracea were relatively rare families in these two sites whereas Euphorbiaceae, Guttiferae (not included in Figure 4) and Annonaceae were unexpectedly abundant.

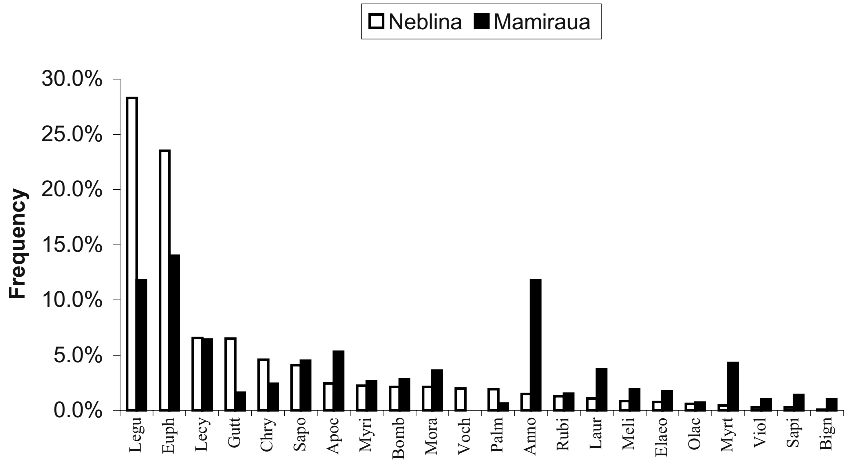

Figure 3. Plant family frequency in Pico da Neblina and in Mamirauá.

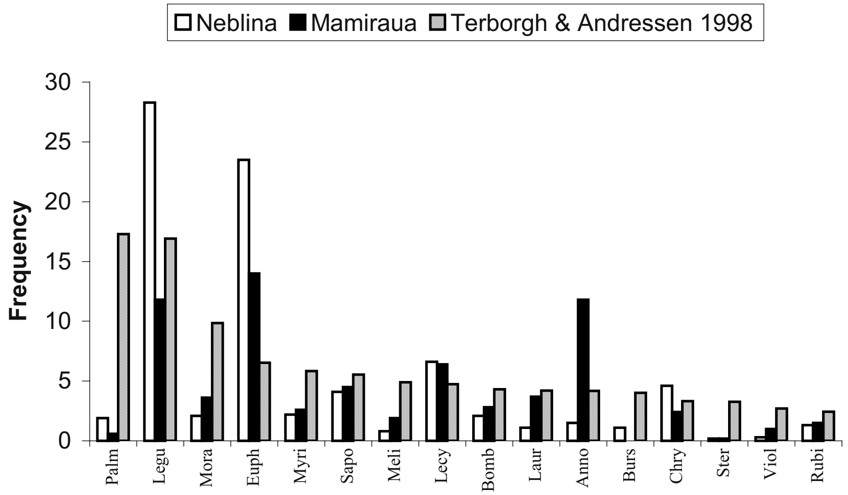

Figure 4. Plant family frequency in Pico da Neblina, Mamirauá and in a combined sample of 16 different 1 ha plots distributed throughout the Amazon basin (Terborgh and Andressen 1998).

Phenology

Pico da Neblina

Of the total sampled trees, 24% (103 individuals) produced 50% or more of their crown capacity of young leaves at least one month of the study. Maximum young leaf production occurred in the beginning of the dry season (October), immediately followed by flowers and young fruits (Boubli 1999). At the community level, leafing preceded flowering by one to two months. By March/April, most of the flushing activity had stopped. We recorded flower production on 143 (33%) trees. Buds and flowers were most abundant in December (59 and 67 individuals, respectively), the dry season. Most fruits were produced from January to July, *.i.e.*, from the end of the dry season through the end of the wet seson (Figure 5). Very few individual trees from the phenology sample produced fruits during the early-dry season (Figure 5). Unripe fruits were produced by 130 (30%) and ripe fruits by only 105 (24%). Unripe fruits were most abundant in the months of January and March (100 and 94 trees, respectively), whereas ripe fruits peaked in April (60 trees), the beginning of the wet season. Unripe fruits were most scarce from July through October; October 1994 being the lowest month with 2 trees with unripe fruits. Ripe fruits were most scarce from August through December; October and November being the lowest months with no trees bearing ripe fruits. There was a smaller peak of ripe fruits in June and July (14 species in each of these months) corresponding to slow-maturing fruits. Unripe fruits were present on individual trees from 1 to 8 months of the study, averaging 3 months per tree. Ripe fruits were available from 1 to 4 months, averaging 1.7 months per tree. At the peak, 13.7% of the trees bore ripe fruits.

Mamirauá

Leaves started to drop after fruiting in May. New leaf production peaked in April. There were two peaks of fruiting, in March-April after the peak in rain and the other in Novemeber-December, prior to the rains (Figure 5). Imature fruits were available from 3 to 5 months. At the peak, 14% of trees bore ripe fruits (Ayres 1993).

Fruit types

Neblina and Mamirauá had similar proportions of tree species producing dry and fleshy fruits with a predominance of the latter (Figure 6). When numbers of trees instead of species were examined however, there was a marked difference in the proportion of fleshy to dry fruit trees (Figure 7). In Neblina, 76% of the trees were dry fruit bearers whereas for Mamirauá this figure was around 40%. In Mamirauá, a large proportion of the fleshy fruits belonged to families such as Annonaceae, Myrtaceae, Melastomataceae, Elaeocarpaceae, Meliaceae, Guttiferae and Euphorbiaceae all producing small fruits dispersed preferably by birds, bats or fish (Figure 8).

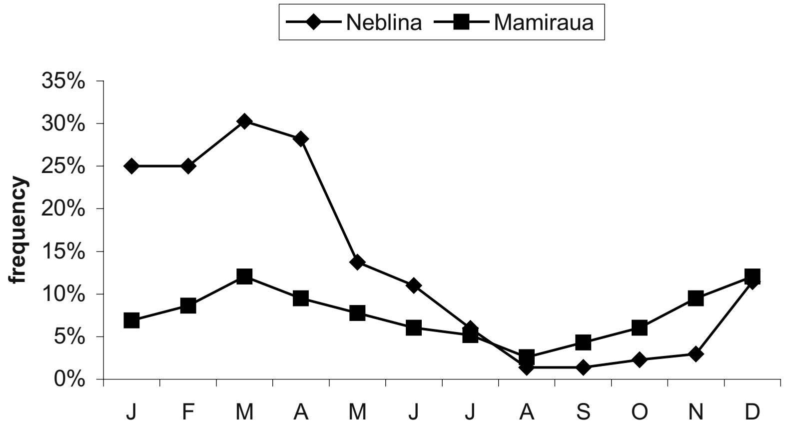

Figure 5. Fruit production in Neblina (1995) and Mamirauá (1984) (ripe and unripe fruits combined).

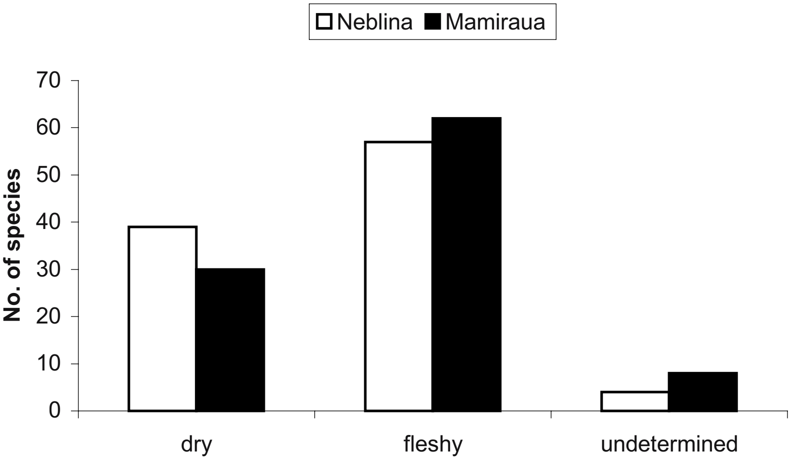

Figure 6. Proportion of tree species producing dry and fleshy fruits in Neblina and Mamirauá.

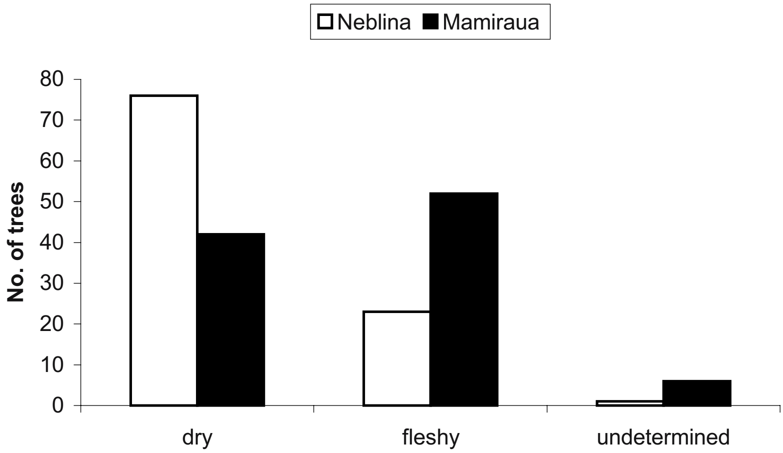

Figure 7. Proportion of individual trees producing dry and fleshy fruits in Neblina and Mamirauá.

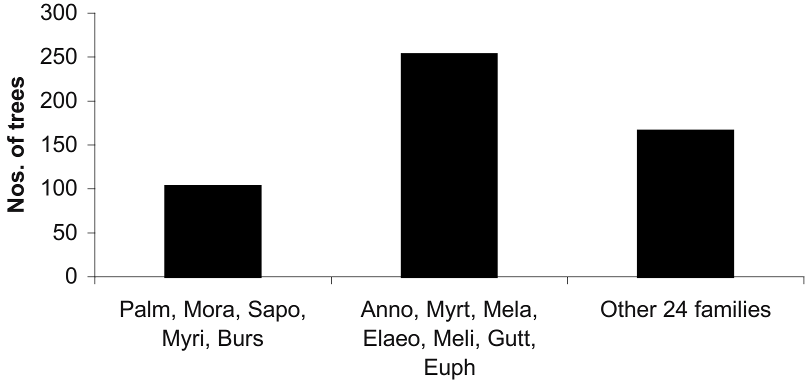

Figure 8. Numbers of trees producing fleshy fruits per family in Mamirauá.

Primary productivity

Primary productivity was not directly measured in either compared sites. However, at San Carlos de Rio Negro, a site near Neblina, and with a forest very similar to the one discussed here, Coomes (1995), found that the foliar concentrations of N were quite low (~ 13.8 mg/g) and average litterfall was 4.5 kg/ha/yr (in contrast to 13.3 kg/ha/yr in Barro Colorado Island, Panama, Foster, 1982) (Coomes, 1995). These data indicate that the San Carlos rainforest (and Neblina by extrapolation) had a low primary productivity.

In várzeas, soils are very rich from sediments brought from the Andes. Thus, nutrients are not limited. High productivity can also be inferred from the high leaf turnover since every year, most trees drop their leaves in the height of the flood (Ayres 1993). Moreover, várzea appears to provide more favorable foliage quality to arboreal folivores such as howlers, sloths hoatzins and iguanas which attain very high biomasses. All these species become rare in oligotrophic forests and are practically absent from Pico da Neblina.

Primate community

Both sites had the same number of primate species and similar primate eco-species (Ayres, 1986, Boubli, 1997). Their densities however, were much higher in Mamirauá. Except for the two small-bodied primates, i.e., titis in Neblina and squirrel monkeys in Mamirauá, the remaining species belonged to the same 3 genera present at both sites: uacaris, howlers and capuchins. Uakaris were the most frugivorous of all primates present but concentrated their diets on unripe seeds. Howlers ate a large proportion of leaves whereas capuchins and squirrel monkeys complemented their fruit diet with insects and small vertebrates (Ayres 1986, Boubli 1997). No information is available on the diet of titis from Neblina but it is possible that, like uacaris, these primates focused on unripe seeds of abundant fruit species. Densities/km^2 however were quite distinct (Table 1).

Neblina (individuals /km^2)	*Mamirauá (individuals /km^2)*
Cacajao melanocephalus (14)	*Cacajao calvus* (14)
Cebus albifrons (1.4)	*Cebus apella* (13)
Alouatta seniculus (2)	*Alouatta seniculus* (40)
Callicebus torquatus (1.6)	*Saimiri vanzolini* (95)

Table 1. Primate densities in Pico de Neblina and Mamirauá

DISCUSSION

In Pico da Neblina, rainfall was high and evenly distributed throughout the year, there was a high tree species and family dominance, fruit availability was quite seasonal and there was an overall low availability of fleshy fruits. Conversely, in Mamirauá, rainfall was more seasonal, no tree species or family dominance was observed, two fruiting peaks were observed and fleshy fruits were relatively more abundant.

Both sites differed considerably from other Amazonian rainforests in plant family composition as suggested by Terborgh and Andressen (1998). Important primate food plants such as trees from Sapotaceae, Moraceae, Palmae and Burseraceae (Peres, 1991, Roosmalen, 1985, Terborgh, 1983) all abundant in other Amazonian rainforests, were relatively scarce in Neblina and in Mamirauá. It is interesting to note that the east-west gradient in primate species diversity in the Amazon maps on a similar gradient in importance of plants of Moraceae, Palmae and to some extent, Sapotaceae (Steege et al., 2000).

In Neblina, low primate species richness might have been associated with the long period of fruit scarcity and the overall low availability of fleshy fruits in particular of Palmae, Moraceae, Sapotaceae, Myristicaceae and Burseraceae. Moreover, the site was possibly unsuited to primates with more folivorous proclivities such as howlers since leaf quality was possibly low (due to the low foliar concentration of N and thus, the resulting high C/N ratio, Milton, 1980).

Coley et al. (1985), hypothesized that plants growing at sites lacking in mineral nutrients would be expected to invest heavily in immobile defences such as tannins and thick cells walls. Janzen (1974) emphasized that caatinga leaves are rich in tannins explaining the scarcity of mammals and birds in the forests. Coomes (1985) found that caatinga forests had more secondary compounds because the tested species had a greater calorific value which he claimed were useful indicators for the presence of these chemicals.

The only primate found in relative abundance was the seed predator black uacari monkey that, due to dental specialization was able to break open the hard pericarps of the dominant fruit species and feed on their seeds.

Low primate species richness in Mamirauá might also have been associated with the low importance of key primate food plant families such as Palmae, Moraceae, Sapotaceae, Myristicaceae and Burseraceae. However, fleshy fruits of different plant families were relatively abundant in Mamirauá. In addition, primary productivity was supposedly high at that site, explaining the high densities attained by arboreal folivores such as howlers and sloths (Queiroz, 1995).

One possibility is that primary productivity in Mamirauá was not being translated into preferred primate fruits in that habitat. In Mamirauá, a large proportion of the fleshy fruits belonged to families such as Annonaceae, Myrtaceae, Melastomataceae, Elaeocarpaceae, Meliaceae, Guttiferae and Euphorbiaceae all producing small fruits dispersed preferably by birds, bats, fish or water.

It has been suggested that one of the most important means of seed dispersal in Amazonian flooded forests is by water. Goulding (1980) found that 35 out of 40 fruits examined in the flooded forests of Rondonia State were able to float for at least a few days. By floating, seeds can travel great distances and attain a relatively even sapatial distribution. For this reason, Ayres (1986) believes that water is possibly more efficient than other agents in dispersing seeds.

Thus, in Mamirauá, primary productivity did not appear to be affecting primate richness although it probably contibuted to their high biomass. In flooded forest habitats, the costs and benefits of seed dispersal may differ from that of Terra firme forests. In this habitat, it might be more efficient for trees to disperse their seeds via water and fish or other small vertebrate then via primates and large mammals.

In conclusion, bottom-up forces (primary productivity) may not always affect the diversity of all taxa when intertrophic interactions have a mutualistic nature such as the interaction between a fruit and a frugivore. The important task, then, is to unravel how is the primary productivity been funneled to the second trophic level.

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