

## Primate community structure at twenty western Amazonian flooded and unflooded forests

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**ABSTRACT.** This paper presents data from a standardized series of line-transect censuses on the species and subspecies composition, population density, and crude biomass of western Amazonian primate communities occurring at eight flooded (= várzea) and 12 unflooded (= terra firme) forests. These were located primarily along one of the largest white-water tributaries of the Amazon (= Solimões), the Juruá river. On average, terra firme forests contained twice as many primate species, lower population densities, and less than half of the total community biomass than did adjacent várzea forests. There was a clear habitat-dependent positive association among primate species, particularly within várzea forests, as well as marked shifts in guild structure between forest types. Species turnover between these two forest types involved primarily understory insectivores (e.g. *Saguinus* sp.), which do not occur in seasonally inundated forest. These were consistently replaced by squirrel monkeys (*Saimiri* sp.), which are extremely abundant in annually flooded várzea forests. Similarly, large-bodied folivores such as red howler monkeys (*Alouatta seniculus*) were uncommon or rare in terra firme forests, but very abundant in várzea forests, even though they are hunted less intensively in the former than in the latter. This can be largely explained by the nutrient-rich alluvial soils of young floodplains, compared to the heavily weathered terra firme soils occurring even within short distances of major white-water rivers. This study clearly shows a reversed diversity/density pattern resulting from the lower species richness, but high overall community biomass of seasonally flooded Amazonian forests, which can now be generalized for a wide range of terrestrial vertebrate taxa, including amphibians, birds, and several other orders of mammals.

**KEY WORDS:** Amazon, Brazil, primate communities, primate biomass, primate density, seasonal flooding, terra firme forest, várzea forest

**RESUMO.** Este trabalho descreve a composição de espécies e sub-espécies, densidades populacionais, e biomassa bruta para comunidade de primatas da amazônia ocidental em 8 sítios de floresta inundável (várzea) e 12 sítios de floresta de terra firme, localizadas principalmente ao longo do Rio Juruá, um dos maiores afluentes de água branca do Rio Solimões–Amazonas. Matas de terra firme em média contém o dobro do número de espécies, mas densidades populacionais e uma biomassa de comunidade consideravelmente mais baixas, que matas de várzea inundadas anualmente. Houve uma forte associação positiva dependente do habitat na ocorrência de certos grupos de espécies, particularmente em matas de várzea, assim como mudanças bem demarcadas na estrutura de guildas claramente associadas a ambientes de várzea ou de terra firme. A rotatividade de espécies entre estes tipos de floresta envolve principalmente o desaparecimento de insetívoros de sub-bosque (e.g. *Saguinus* sp.) em matas alagadas, os quais são substituídos funcionalmente por macacos-de-cheiro (*Saimiri* spp.), os quais são extremamente abundantes em florestas de várzea sujeitas a enchentes sazonais prolongadas. Da mesma forma, folívoros de grande porte como guaribas vermelhas (*Alouatta seniculus*) são conspicuamente raros em matas de terra firme, mas tornam-se muito comuns em matas de várzea, mesmo quando submetidos a uma pressão de caça mais intensa. Isto pode ser atribuído a alta disponibilidade de nutrientes em solos aluviais de planícies inundáveis, em relação a solos de terra firme, mesmo num raio relativamente próximo a rios de água

branca. Resultados apresentados aqui são claramente consistentes com um padrão invertido de baixa diversidade de espécie, mas alta biomassa de comunidade, que pode ser generalizado a partir de vários grupos de vertebrados terrestres (e.g. anfíbios, aves, outras ordens de mamíferos) para florestas amazônicas inundadas sazonalmente, e sob a influência de rios transportando uma alta carga de sedimentos.

#### INTRODUCTION

The remarkable primate species richness of Amazonian forests is illustrated by the fact that they safeguard 66% (58/88) of the species and 88% (14/16) of the genera described to date for the neotropics (updated from Mittermeier *et al.* 1988), and perhaps an even greater proportion of as yet undescribed infraspecific taxa. Amazonian primate assemblages range from the poorest to the most species-rich anywhere in the tropics, consisting of as few as three species in tidal gallery forests of the Amazon estuary (eastern Marajó Island: Peres 1989), and as many as 14 sympatric species in unflooded forests of western Amazonia (west bank of the Rio Juruá: Peres 1988). Large differences in primate species packing have also been documented in other tropical forest regions sharing a common source fauna (see Bourlière 1985). Yet the environmental and biogeographic factors determining differences in primate community structure and diversity remain poorly understood (but see Ganzhorn 1992, Terborgh & van Schaik 1987). This apparent lack of interest in primates at the community level is at odds with the recent exponential growth of single-species studies, which nevertheless clearly aids the interpretation of multiple responses to environmental gradients. In addition, studies on the ecological determinants of primate abundance, diversity, and guild structure have largely emphasized processes of anthropogenic disturbance – including selective logging (Johns & Skorupa 1987), subsistence hunting (Peres 1990), and forest fragmentation (Rylands & Keuroghlian 1988) whereas comparatively little attention has been placed on habitat differences in soil fertility, resource productivity, and natural disturbance regimes (but see Oates *et al.* 1990, Peres in press).

This paper documents intrinsic differences in primate species composition and abundance between flooded and unflooded forests of Amazonia, which account for the main heuristic dichotomy in terrestrial macrohabitats across an otherwise largely continuous closed-canopy forest region. I focus on a series of standardized line-transect censuses of primate communities at 15 forest sites located along a major turbid (or white-water) tributary of the Amazon, the Rio Juruá. This represents the largest effort in quantifying primate abundance and diversity for an entire Amazonian river basin. Primate abundance is expressed in terms of a kilometric index, and population density and biomass estimates are derived for individual species, and then compared with data from other studies (Ayres 1986; Peres 1988, 1993a; Soini 1986). Community-wide shifts between flooded and unflooded forests in species richness, abundance, and biomass are then interpreted in light

of the overall differences in seasonal flooding régime, soil fertility, and habitat structure.

#### STUDY AREAS

##### *Habitat terminology*

Seasonally inundated forests (hereafter, várzea forests) are defined as those which are partially immersed into the broadened, meandering channels of suspension-rich white-water rivers of Amazonia for as long as half of the year, corresponding to the mid-wet to the early-dry seasons. The sedimentary soils of várzea forests along the Rio Juruá are thought to be mainly of Pleistocene origin (Irion 1978), although they continue to receive on a seasonal basis a heavy load of fresh alluvial sediments of Andean origin, which appear to more than replace previously deposited nutrients lost to plant growth and water run-off (e.g. Campbell *et al.* 1992, Duivenvoorden & Lips 1995). Such typical várzea forests are distinguished from irregularly inundated floodplain forests (*sensu* Prance 1979), which are subject to occasional, supra-annual floods occurring every 4–8 y. These ephemeral flash-floods are induced by exceptional surges in water-level that spill over adjacent floodplain leveés, and last from a few days to several weeks. This forest type is typical of the headwater section of the Rio Juruá (Figure 1), where it replaces seasonal várzea forests influenced by increasingly larger catchment areas as one moves farther downriver. Unflooded (hereafter, *terra firme*) forests, on the other hand, are never subject to inundation, and have, therefore, been long deprived of nutrient-rich alluvial sediments carried by seasonal floods. Terra firme forests considered here are, however, within relatively short distances of up to 6 km from areas directly affected by floodwaters, and their soil nutrient status is likely to be intrinsically different from those in remote interfluvial regions of Amazonia farther inland (see Peres 1993a).

##### *Sampling sites*

A brief characterisation of the 20 forest sites considered in this study is presented in Table 1. The 15 forest sites sampled along the Rio Juruá of western Brazilian Amazonia span linear distances of up to 962 km and elevations of 65–250 m a.s.l. This river has an annual discharge of  $10^{12}$  m<sup>3</sup> (Gibbs 1967), and spans a longitudinal axis of almost 1300 km, in terms of linear segments of 10 km measured from RADAM charts with a resolution of 1 : 250,000. This length more than doubles considering distances along the river's highly meandering course, thus making the Juruá one of the longest white-water affluents of the Amazon (Figure 1). The annual water level amplitude along the mid to lower Rio Juruá was usually 8–12 m, but more dramatic seasonal fluctuations were known for the upper Juruá, reaching 15 m. The fluviodynamic character of the Juruá and other meandering rivers of western Amazonia is such that the broad floodplain belt consists of a complex forest mosaic interspersed with

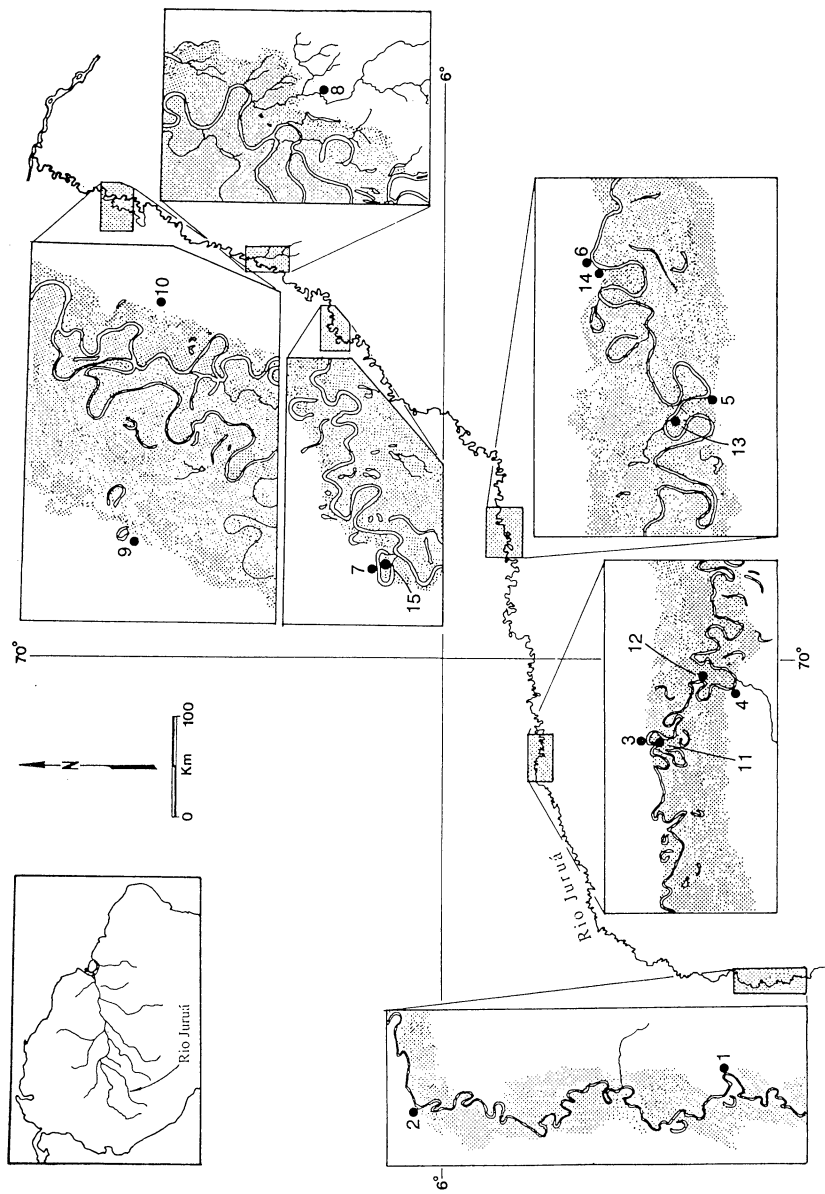


Figure 1. Location of forest sites along the Rio Juruá, western Brazilian Amazonia, where 15 line-transect censuses reported here were conducted. Shaded areas indicate headwater floodplain forests (box on far left) and the gradually wider belt of várzea forest (other boxes) along the meandering course of the river. Unshaded areas represent terra firme forests. Census locality numbers refer to those listed in Table 1.

Table 1. Profile of key habitat features of forest sites considered in this study, ordered from the headwaters to lower stretches of the Juruá watershed. Numbers for sites along the Rio Juruá refer to those shown in Figure 1.

FOREST TYPES Site localities	Latitude (S), Longitude (W)	Key sources <sup>1)</sup> of disturbance	River <sup>2)</sup> type	Flood level (m) <sup>3)</sup> duration (mo)	Hunting <sup>4)</sup> pressure	Transect length, km	Census distance, km
<b>TERRA FIRME FORESTS</b>							
1. Porongaba	8°40', 72°47'	B (m), G (l)	W (hw)	—	H	4.6	115.0
2. Sobral	8°22', 72°49'	B (l)	W (hw)	—	H	5.0	109.4
3. Condor	6°45', 70°51'	T (l)	W (c)	—	L	4.2	119.4
4. Penedo	6°50', 70°45'	B (l), G (m)	W (c)	—	H	4.0	102.1
5. Altamira	6°35', 68°54'	—	W (c)	—	L	4.0 + 0.8	112.9
6. Barro Vermelho I	6°28', 68°46'	—	W (c)	—	M	4.2	116.8
7. Fortuna	5°05', 67°10'	—	W (c)	—	M	4.5	56.0
8. Igarapé Jaraquí	4°21', 66°31'	G (l)	B (l)	—	M	4.2	50.0
9. Vira Volta	3°17', 66°14'	G (l), L (l)	W (l)	—	L	5.0	110.0
10. Vai Quem Quer Kaxinawá Reserve <sup>5)</sup> Riozinho <sup>6)</sup>	3°19', 66°01' 9°23', 71°52' 4°38', 66°54'	BW (l) T (l) G (m)	W (l) W (hw) B (c)	— — —	M H L	4.2 4.2 + 3.5 4.0	106.7 91.5 44.0
<b>VÁRZEA FORESTS</b>							
11. Sacado	6°45', 70°51'	F (l)	W (c)	0.7–1.0, 3–4	L	4.2	92.4
12. Nova Empresa	6°48', 70°44'	F (l)	W (c)	0.5–0.8, 3–4	L	3.6	96.0
13. Boa Esperança	6°32', 68°55'	F (m)	W (c)	0.8–1.2, 4–5	L	3.8	101.8
14. Barro Vermelho II	6°28', 68°46'	F (l), L (l)	W (c)	0.5–0.8, 4–5	M	4.3	91.4
15. Lago da Fortuna	5°05', 67°10'	F (m)	W (c)	1.0–2.0, 4–5	M	4.0	48.0
Lago Mimirauá <sup>7)</sup>	2°59', 64°55'	F (m)	W (l)	3–5, 4–6	L	?	98.0
Lago Teitú <sup>7)</sup>	2°58', 64°55'	F (m)	W (l)	1–3, 3–5	L	?	98.0
Cajauana Island <sup>8)</sup>	5°30', 74°10'	F (m)	W (c)	c. 1.0, 2–4	L	?	?

<sup>1)</sup> Indicates most important sources of natural or anthropogenic sources of forest disturbance: (B) bamboo regeneration cycles; (L) selective logging; (G) small canopy gaps; (B) larger gaps generated by wind blowdowns; (BW) backwater palm swamps; (F) prolonged seasonal flooding. Classes of intensity are: none (—), light (l), moderate (m), and heavy (h).

<sup>2)</sup> Indicates geochemical characteristics of nearest river (W: white-water, B: black-water rivers), and geographic position of survey sites along a given watershed: (hw) headwaters, and (c) central, and (l) lower sections of the rivers.

<sup>3)</sup> Represented by the high water mark in typical years above the soil level, as indicated by a band of discoloration on tree trunks.

<sup>4)</sup> Hunting pressure: (—) none, (L) light, (M) moderate, and (H) heavy.

<sup>5–8)</sup> Data for unnumbered sites, located outside the Juruá river basin, were obtained from Peres (1990, unpubl. data)<sup>5–6)</sup>, Ayres (1986)<sup>7)</sup> and Soini (1986)<sup>8)</sup>.

abandoned channels (oxbow lakes), swales, erosional riverbanks, and strips of colonizing and successional vegetation in young landforms. These Pleistocene várzea forests, however, are physiognomically distinguished from the Holocene várzeas of the upper Amazon (Rio Solimões) in that they tend to be on higher ground (equivalent to high *restingas* of the lower Japurá: Ayres 1993), subject to shallower floods at high water which last fewer weeks, and are defined at low water by sharp cutbanks of up to 12 m created by active river channel migration (Table 1). Várzea transects were entirely confined to continuous expanses of várzea forests, but in one case confined to the concave bank of an oxbow lake (Lago da Fortuna) and in another case within a peninsula delineated by the meandering river channel (Boa Esperança).

Forest sites, located along the (i) upper (or headwaters), (ii) central, and (iii) lower sections of the Rio Juruá, were surveyed between 1987 and 1992, which included a one-year fluvial expedition (July 1991–June 1992) aiming to document the vertebrate fauna on both banks of this river (Malcolm *et al.* 1992, Patton *et al.* 1994, Peres 1993*b*). Surveys consisted of a standardized series of line-transect censuses which, combined with a selective museum collection of certain small-bodied species (Peres 1993*b*), represents the first attempt to survey primate communities along an entire Amazonian river basin. It also complements earlier efforts to survey mammals of the Juruá (Carvalho 1957, Ollala 1938, Vieira 1948), making this one of the best sampled primate faunas in the entire Amazon.

An additional headwater terra firme forest (Kaxinawá Reserve, Acre, Brazil) is located *c.* 128 km southeast of Porongaba (site 1), using transects on both banks of the upper Rio Tarauacá, a right-bank tributary of the upper Rio Juruá. I also reanalyse and report census data obtained previously (Peres 1990) at a terra firme forest on the right bank of the Riozinho river, a right-bank black-water tributary of the Jutáí river, which flows parallel with the west bank of the Juruá. In total these localities include 12 terra firme and five várzea forests. Because of this pronounced sampling asymmetry, primate densities at three additional flooded forests were incorporated in the analysis from (i) a fluvial island forest studied by Soini (1986) within the Pacaya-Samiria Reserve of eastern Peru (Cahuana Island), and (ii) two younger (Holocene) várzea forests (Lago Teiú and Lago Mamirauá) studied by Ayres (1986) near the mouth of the Japurá river, a northern tributary of the western Amazon. Although quantitative data on primate communities are available from several Amazonian unflooded forests elsewhere (for a review see Peres 1997), primate density estimates for flooded forests are largely restricted to the eight sites considered here.

## METHODS

### *Line-transect censuses*

Each site census consisted of a cumulative transect distance of 44–119 km (mean = 92 km, SD = 26; Table 1), giving a total of 1564 km walked at the 17

sites in the Juruá basin. Because night surveys undertaken at a small number of sites were insufficient to calculate densities of owl monkeys (*Aotus nigriceps*), data on this relatively ubiquitous species are restricted to presence or absence. Data presented here thus focuses on the diurnal primate community, which accounted for all, or all but one, species occurring at any given site. Censuses at each site were conducted on most months of the year (see Table 1) from early morning to mid-day (0600–1130 h) by the author and one previously trained observer operating independently. Linear or near-linear forest transects of 3.6–5.0 km in length – which had been cut and marked every 50 m prior to each survey – were walked (or canoed) slowly ( $1.25 \text{ km h}^{-1}$ ) mostly by single observers. All but one of the várzea sites were censused on foot during the low-water season of the year. The only exception was Lago da Fortuna, which was sampled during the high-water season. This site was, therefore, censused using a dugout canoe paddled by a second observer through a near-linear transect 2 m above ground. In order to avoid any possible local disturbance effects caused by trail-cutters, fresh transects were left to ‘rest’ for at least one day following trail preparation before census walks could be initiated. Survey methodology was standardized according to weather conditions (e.g. no censuses were conducted on rainy mornings), walking velocity, and previous experience of observers, and were usually completed within 30 consecutive days.

I used a kilometric index in terms of number of primate groups encountered per 10 km walked (hereafter, sighting rates) to control for overall differences in sampling effort. Group density estimates were derived from either the hazard rate or uniform models with a cosine adjustment (Buckland *et al.* 1993) using ungrouped perpendicular distances from the sampling transect to the first animal sighted. These models provided better fits for species-specific data sets than the fourier series and half-normal models, as determined by the minimum Akaike Information Criterion (see Buckland *et al.* 1993). In order to avoid unrealistic distortions of detection curves due to small sample sizes, I truncated a small proportion of outlying perpendicular data (5%), and performed a pooled analysis of all surveys yielding fewer than 40 independent group sightings for a given species – the minimum recommended by Burnham *et al.* (1980). Unrealistically inflated density estimates, which might have been caused by a greater detection probability of species exhibiting large, uncohesive groups (e.g. *Saimiri* spp., *Cacajao calvus*, *Lagothrix lagotricha*) were corrected by adding one third of the mean group spread (gs) of each species to its probabilistic strip width estimate (ESW), as in  $ESW_{\text{corr}} = ESW + 0.33 \text{ gs}$  (cf. Brockelman & Ali 1987, Janson & Terborgh 1980). Group spread estimates, defined as the distance between the most polarized group members, were obtained whenever possible during observation periods of up to 15 min following sightings. I was then able to calculate group density estimates for each species based on the number of groups sighted, their  $ESW_{\text{corr}}$ , and the total one-way distance walked along transects at each census site. This procedure was justified since between-site variances in perpendicular distances – which could have resulted from potential differences in habitat-dependent detectability – were no greater

than those within sites (ANOVAs,  $P > 0.05$  in all cases). Moreover, measurements of understorey density at each forest site, which could have affected lateral visibility and detection probabilities, failed to uncover a significant difference in understorey structure (mean density at terra firme sites:  $82.1 \pm 20.7\%$ ,  $N = 168$ ; várzea:  $84.5 \pm 19.2\%$ ,  $N = 200$ ; one-factor ANOVA,  $F_{1,366} = 1.38$ ,  $P = 0.24$ ). This was carried out based on 40 counts per site of the 10-cm sections of a 250-cm marked pole held vertically at random points along a 500-m section of each sampling transect. Counts were based on the number of sections visible to an observer positioned perpendicularly to the transect and at 20 m from the marked pole. Relative understorey density was then calculated as an inverse function of the number of 10-cm pole sections entirely visible to the observer.

Population densities (D) were then calculated using mean group sizes at each site from the fraction of total group counts considered to be accurate. In order to calculate crude population biomass (B), I used the mean body mass of an individual in a given population, defined as 80% of the average between the mean adult male and the mean adult female body weight, as derived from Ford & Davies (1992) and Peres (1993b). A few cases of local extinctions were documented for the two large-bodied atelines – *Ateles paniscus* and *Lagothrix lago-tricha*. These species were assumed to be locally extinct ( $D = 0$ ) at a given site if local hunters interviewed during surveys agreed unanimously that they had once been common, but had not been sighted for a period of at least 5 y prior to surveys.

Species nomenclature and taxonomic arrangements follows Hill (1960) and Mittermeier *et al.* (1988) with appropriate modifications based on Hershkovitz (1990) and Peres (1993b).

### *Statistical analysis*

The overall site-by-species abundance matrix considered here was examined by ordination using CANOCO (ter Braak 1988). Detrended correspondence analysis (DCA), an indirect gradient analysis which reduces the dimensionality of  $n$  species across  $m$  forest sites to a few ordination axes, proved to be the most appropriate ordination technique for this matrix. The performance of other techniques applied to the same matrix was consistently poor and showed systematic distortions of the first axis (arch effect). Species occurrences were weighed by their respective untransformed density estimates at each site. Points in the joint plots corresponding to forest sites are thus located at the centre of gravity of the species that occur there, particularly the most abundant and frequently occurring ones. Species were entered in the ordination according to discrete functional groups (hereafter, ecospecies), corresponding to a single species and subspecies, or a few ecologically equivalent (and mutually exclusive) congeners representing parapatric replacements across opposite banks of major rivers.

Ecospecies classification, however, clearly relies on detailed knowledge of



the ecology of individual species, which fortunately has been reasonably well documented for all species considered here (Ayres 1986, Defler 1979, Peres 1993c, 1993d, 1994a, Pook & Pook 1981, Rylands 1987, Soini 1988, Terborgh 1983, and references therein). A total of 15 ecospecies, ordered by increasing adult body mass, are recognized for the purposes of this paper:

Pygmy marmosets, *Cebuella pygmaea* (0.15 kg);  
 Saddle-back tamarins, *Saguinus fuscicollis* ssp. (0.39 kg);  
 Moustached and emperor tamarins, *Saguinus mystax* ssp. and *S. imperator* (0.51 kg);  
 Goeldi's monkeys, *Callimico goeldii* (0.59 kg);  
 Gray-cap and black-cap squirrel monkeys, *Saimiri sciureus* and *S. boliviensis* (0.94 kg);  
 Red-neck owl monkeys, *Aotus nigriceps* (1.0 kg);  
 Red titis, *Callicebus cupreus* (1.05 kg);  
 Collared titis, *Callicebus torquatus* ssp. (1.2 kg);  
 Buffy, bold-face, and monk sakis, *Pithecia albicans* (2.8 kg) *P. irrorata* (2.2 kg) and *P. monachus* (2.2 kg), respectively;  
 White-fronted capuchins, *Cebus albifrons* (2.7 kg);  
 Brown capuchins, *Cebus apella* (2.9 kg);  
 White uakaries, *Cacajao calvus* (3.2 kg);  
 Red howlers, *Alouatta seniculus* (6.5 kg);  
 Lowland woolly monkeys, *Lagothrix lagotricha* ssp. (8.7 kg); and  
 Black spider monkeys, *Ateles paniscus chamek* (9.0 kg).

In addition, I used normal association analysis of the presence/absence matrix of each primate ecospecies at each site to test the null hypothesis that species composition did not covary among census sites (Schluter 1984). Simultaneous associations between all pairs of species were then used to sort out census sites into homogeneous groups, defined whenever  $\chi^2$  values between any species pair in that group exceeded the critical  $\chi^2$  at one degree of freedom (Ludwig & Reynolds 1988). This analysis also produced a hierarchical classification, which identified the most important divisor species splitting apart groups of sites containing the most similar sets of species occurrences.

## RESULTS

### *Species richness and abundance*

Terra firme forests of western Amazonia on average contained over twice as many primate species ( $12.2 \pm 1.3$  species, range = 10–14) than did annually flooded várzea forests ( $5.3 \pm 1.5$  species, range = 3–7; Mann-Whitney U,  $z = 3.73$ ,  $P < 0.001$ ; Figure 2a). This resulted in terra firme sites having significantly higher richness and diversity indices than those of várzea sites (Table 2). Considering primate communities along the Rio Juruá, várzea forests combined included a total of nine primate ecospecies belonging to 11 species, whereas terra firme forests contained a total of 15 ecospecies and 19 species. A total of 10 species occurring in terra firme forests did not occur at any várzea site, whereas none of primate taxa in várzea failed to occur in terra firme forests. Moreover, the maximum sympatric species packing for várzea forests (7), was only half of that for the most species-rich terra firme community (14). Pleistocene várzea forests along the Rio Juruá (4–7 species per site) contained

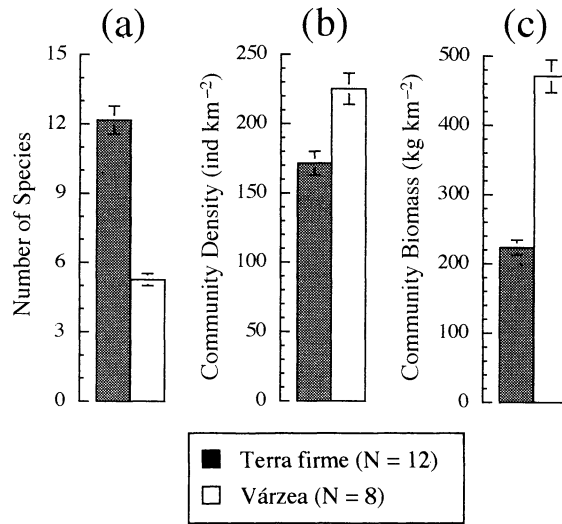


Figure 2. Mean  $\pm$  SE number of species (a), overall density (b), and overall crude biomass (c) of primate communities censused at terra firme and várzea forest sites of western Amazonia.

Table 2. Summary of primate community characteristics at 12 terra firme and eight várzea forests of western Amazonia.

FOREST TYPES Site localities	No. of <sup>1)</sup> species	Richness <sup>2)</sup> (R <sub>i</sub> )	Diversity <sup>3)</sup> (H')	Density (ind. km <sup>-2</sup> )	Biomass (kg km <sup>-2</sup> )
<b>TERRA FIRME FORESTS</b>					
Porongaba	12	2.043	1.941	209	158
Sobral	11	1.924	1.489	174	117
Kaxinawá Reserve	12	2.130	1.834	145	173
Condor	11	1.858	1.896	194	274
Penedo	10	1.805	1.563	129	118
Altamira	12	2.004	1.960	227	463
Barro Vermelho I	13	2.327	2.220	165	261
Fortuna	14	2.407	2.161	216	297
Riozinho <sup>4)</sup>	14	2.541	2.322	157	225
Igarapé Jaraquí	13	2.428	1.915	137	131
Vira Volta	13	2.285	2.185	182	282
Vai Quem Quer	11	2.049	2.032	124	176
<b>VÁRZEA FORESTS</b>					
Sacado	4	0.611	1.110	126	245
Nova Empresa	6	0.938	1.397	185	410
Boa Esperança	5	0.671	1.366	355	953
Barro Vermelho II	7	1.097	1.343	213	361
Lago da Fortuna	7	0.999	1.342	358	627
Lago Mamirauá <sup>5)</sup>	3	0.358	0.740	270	429
Lago Teiú <sup>5)</sup>	4	0.581	1.081	175	352
Cajuana Island <sup>6)</sup>	6	1.044	1.459	120	389

<sup>1)</sup> Species known to occur in the local source fauna whether or not they were actually detected during censuses.

<sup>2)</sup> Margalef's index of richness.

<sup>3)</sup> Shannon's index of diversity.

<sup>4-6)</sup> Data from other studies (4: Peres 1990; 5: Ayres 1986; 6: Soini 1986).

nearly twice as many primate species as those in Holocene várzeas on the lower Rio Japurá (3–4 species: Ayres 1986). This can be explained by the fact that the former rest on higher ground formed by older alluvial deposits, and are invariably contiguous with adjacent terra firme forests, whereas the latter consist of vast expanses of várzea forests (up to 90 km wide) separated from the nearest terra firme forests by anastomosing river channels, and thus could not be used by species requiring terra firme habitats for at least part of the year.

Conversely, the primate abundance of the species-rich terra firme forests was in general considerably lower than that of the species-poor seasonally flooded várzeas (Table 2). The community-wide diurnal primate density of várzea forests ( $225 \pm 94$  ind. km<sup>-2</sup>) tended to be higher, albeit not significantly so, than those of terra firme forests ( $172 \pm 35$  ind. km<sup>-2</sup>, Mann-Whitney U test,  $z = 1.08$ ,  $P = 0.28$ , Figure 2b). The small bodied tamarins (*Saguinus* spp.) and squirrel monkeys (*Saimiri* spp.) were by far the most numerous taxa in terra firme and várzea forests, respectively (Figure 3; see Table 3 and 4). All callitrichids (i.e. *Cebuella*, *Saguinus* sp., and *Callimico*), *Callicebus torquatus*, and *Lagothrix lagotricha*, which are hallmarks of terra firme forests, virtually dropped out of várzea sites in the central and lower stretches of the Juruá river. Of those ecospecies occurring in both forest types, however, only *Alouatta*, *Saimiri*, and *C. albifrons* had significantly higher densities in várzea forests (Mann-Whitney U-tests,  $P < 0.01$ ).

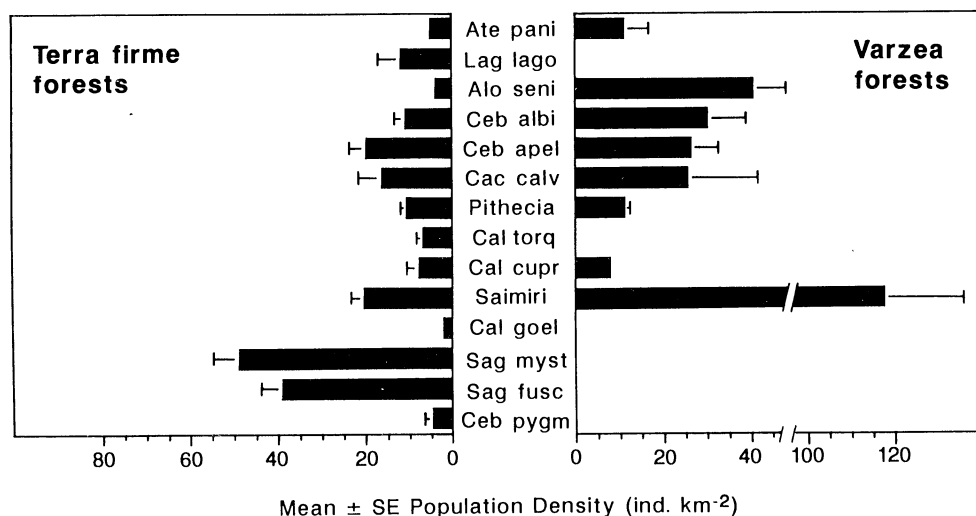


Figure 3. Comparison of population densities of primate ecospecies occurring at 12 terra firme and eight várzea forests. English names and classification of the ecospecies listed above are described in the text.

Low crude densities and species rarity in terra firme forests appeared to result from basically two distinct mechanisms. Groups of several species tended to occur in low ecological densities throughout the main upland forest matrix, largely represented by high-ground terra firme forests (e.g. *Pithecia* sp., *Cebus*

Table 3. Primate sighting rates (SR: sightings/10 km walked), population densities (D: ind km<sup>-2</sup>) and biomass (B: kg km<sup>-2</sup>) at 12 terra firme forest sites<sup>1)</sup>.

Primate species	Porongaba			Sobral			Kaxinawá Reserve			Condor			Penedo			Altamira				
	SR	D	B	SR	D	B	SR	D	B	SR	D	B	SR	D	B	SR	D	B		
<i>Cebus pygmaea</i>	1.2	15.9	1.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Saguinus f. fuscicollis</i>	—	—	—	5.1	51.4	16.0	—	3.9	43.2	13.5	—	—	—	—	—	—	—	—	—	
<i>S. fuscicollis melanoleucus</i>	6.3	65.1	20.3	—	—	3.6	36.7	11.5	—	—	—	—	—	—	—	—	—	—	—	
<i>S. mystax mystax</i>	—	—	—	6.4	87.8	35.8	—	3.9	54.5	22.2	—	—	—	—	—	—	—	—	—	
<i>S. mystax pileatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>S. imperator subgriseus</i>	6.3	58.6	23.9	—	—	—	2.6	25.2	10.3	—	—	—	—	—	—	—	—	—	—	
<i>Callimico goeldii</i>	0.2	2.9	1.4	—	—	—	P	P	P	—	—	—	—	—	—	—	—	—	—	
<i>Saimiri sciureus macrodon</i>	—	—	—	0.2	5.9	4.5	—	1.3	36.1	27.1	—	—	—	—	—	—	—	—	—	
<i>S. boliviensis boliviensis</i>	0.4	11.3	8.5	—	—	—	1.1	36.4	27.4	—	—	—	—	—	—	—	—	—	—	
<i>Aotus ? nigriceps</i>	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	
<i>Callicebus cupreus cupreus</i>	3.7	22.8	19.1	0.2	1.1	1.0	0.8	4.3	3.6	P	P	P	0.8	4.9	4.1	0.9	5.5	4.6	—	
<i>Callicebus torquatus purinus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Pithecia irrorata irrorata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Pithecia irrorata vanzolinii</i>	1.0	9.9	17.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Pithecia monachus monachus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Cacajao calvus</i>	—	—	—	0.9	8.0	14.1	—	1.5	13.8	24.2	—	—	—	—	—	—	—	—	—	
<i>Cebus apella</i>	—	—	—	0.2	5.8	14.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Cebus albifrons unicolor</i>	0.2	2.9	6.7	0.6	9.0	21.0	1.0	15.7	36.4	1.5	24.8	57.8	0.8	12.9	30.0	3.0	49.6	115.5	—	
<i>Alouatta seniculus jamaica</i>	0.7	16.8	36.3	0.2	4.4	9.6	0.4	12.6	27.2	0.2	4.1	8.8	0.2	4.7	10.2	0.4	8.6	18.5	—	
<i>Lagothrix lagotricha cana</i>	P	P	P	P	P	P	0.8	9.2	48.2	P	P	P	0.2	2.6	13.3	0.4	4.6	24.0	—	
<i>Atetes paniscus chamek</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	0.2	3.1	22.3	†	†	†	†	†	†	0.3	11.1	77.6	—	—	—	1.1	26.2	182.2	—	
	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Total	—	209.3	157.9	—	173.6	116.7	—	144.7	172.7	—	193.5	274.2	—	129.2	117.5	—	—	—	226.5	462.9

Table 3. (continued).

Primate species	Barro Vermelho I			Fortuna			Igarapé Jaraqui			Vira Volta			Vai Quem Quer			Riozinho		
	SR	D	B	SR	D	B	SR	D	B	SR	D	B	SR	D	B	SR	D	B
<i>Cebuella pygmaea</i>	0.2	2.2	0.3	0.4	4.7	0.6	P	P	P	—	—	—	—	—	—	0.2	4.3	0.5
<i>Saguinus f. fuscicollis</i>	2.1	20.0	6.2	2.5	29.7	9.3	—	—	—	—	2.4	28.1	8.8	—	—	2.5	24.4	7.6
<i>S. fuscicollis avilapresi</i>	—	—	—	—	—	—	3.3	31.5	9.8	—	—	—	—	—	—	—	—	—
<i>Saguinus mystax mystax</i>	2.2	29.8	12.2	2.5	34.7	14.2	3.3	49.2	20.1	4.0	55.4	22.6	2.8	34.4	14.0	2.5	36.4	14.9
<i>Saimiri sciureus macradon</i>	0.5	16.7	12.5	0.7	23.2	17.4	—	—	—	0.6	17.7	13.3	—	—	—	0.7	20.8	15.7
<i>S. boliviensis boliviensis</i>	—	—	—	—	—	—	0.2	7.7	5.8	—	—	—	—	—	—	—	—	—
<i>Aotus ? nigriceps</i>	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
<i>Calliцеbus cupreus cupreus</i>	1.7	10.7	9.0	4.8	30.1	25.3	0.7	4.5	3.7	0.2	1.1	1.0	0.2	1.2	1.0	0.5	4.5	3.8
<i>Calliцеbus torquatus purinus</i>	—	—	—	—	—	—	7.7	5.8	—	—	—	—	—	—	—	—	—	—
<i>Calliцеbus torquatus regulus</i>	0.7	7.0	6.7	0.4	2.8	2.7	—	—	—	0.9	7.2	6.9	—	—	—	0.7	6.9	6.6
<i>Pithecia irrorata irrorata</i>	—	—	—	—	—	—	1.2	11.3	19.9	—	—	—	—	—	—	—	—	—
<i>Pithecia monachus monachus</i>	0.9	8.1	14.3	0.7	6.8	12.0	—	—	—	0.7	7.5	13.1	—	—	—	0.9	10.2	18.0
<i>Pithecia albicans</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cacajao calvus</i>	—	—	—	0.7	31.5	79.9	—	—	—	0.4	15.1	38.3	—	—	—	0.2	11.8	29.9
<i>Cebus apella</i>	2.4	28.3	65.9	2.3	38.2	89.0	0.5	7.8	18.3	1.3	21.0	48.8	0.8	12.4	28.7	0.7	12.7	29.6
<i>Cebus albifrons unicolor</i>	1.4	33.1	71.6	0.4	8.6	18.7	0.2	5.8	12.4	0.6	13.2	28.5	0.2	4.5	9.8	0.5	12.6	27.1
<i>Alouatta seniculus jurua</i>	0.1	1.0	5.2	0.2	5.3	27.6	0.2	5.5	28.6	0.4	4.7	24.7	0.1	1.0	5.2	0.7	8.4	43.7
<i>Lagothrix lagotricha cana</i>	0.2	5.0	34.7	†	†	†	†	†	†	0.2	4.7	32.5	—	—	—	†	†	†
<i>Ateltes paniscus chamek</i>	0.2	3.1	22.0	†	†	†	†	†	†	0.4	6.0	43.2	0.4	9.6	69.2	0.2	3.9	28.1
Total	—	164.9	260.5	—	215.6	296.7	—	136.5	131.3	—	181.6	281.6	—	123.6	176.3	—	156.9	225.4

<sup>1)</sup> All sites are located along the Rio Juruá, except for Kaxinawá Reserve and Riozinho which are located on the upper Rio Tarauacá and Rio Riozinho, respectively. Symbols: (p) present at the survey site, but not detected during actual censuses; (†) locally extinct (see text for definition); (—) does not occur.

Table 4. Primate sighting rates (SR: sightings/10 km), population densities (D: ind km<sup>-2</sup>) and biomass (B: kg km<sup>-2</sup>) at five várzea forest sites along the Juruá river.

Primate species	Sacado do Condor			Nova Empresa			Boa Esperança			Barro Vermelho II			Lago da Fortuna		
	SR	D	B	SR	D	B	SR	D	B	SR	D	B	SR	D	B
<i>Saimiri sciureus macrodon</i>	—	—	—	1.9	73.8	55.5	—	—	—	—	109.5	82.3	5.0	189.8	142.7
<i>S. boliviensis boliviensis</i>	1.7	70.7	53.2	—	—	—	3.9	149.2	112.2	—	—	—	—	—	—
<i>Aotus ? nigriceps</i>	—	—	—	p	p	p	—	—	—	—	—	—	p	p	p
<i>Callitrichus cupreus cupreus</i>	—	—	—	—	—	—	—	—	—	—	7.4	6.2	1.3	8.5	7.1
<i>Pithecia irrorata irrorata</i>	1.1	13.3	23.3	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pithecia monachus monachus</i>	—	—	—	0.6	7.7	13.5	—	—	—	—	10.7	18.9	—	—	—
<i>Cacajao calvus</i>	—	—	—	—	—	—	—	—	—	—	—	—	1.3	55.2	139.8
<i>Cebus apella</i>	1.1	17.4	40.5	2.9	55.7	129.8	3.3	53.7	124.9	1.3	21.4	49.9	1.3	20.1	46.8
<i>Cebus albifrons unicolor</i>	—	—	—	0.4	12.2	26.2	1.4	40.1	86.6	1.5	44.7	96.5	1.7	48.6	105.0
<i>Alouatta seniculus jurua</i>	1.7	24.7	128.4	2.5	35.7	185.4	6.3	89.7	466.2	1.1	15.6	81.1	2.5	35.7	185.4
<i>Ateltes paniscus chamek</i>	—	—	—	—	—	—	1.4	2.6	163.2	0.2	3.6	26.0	—	—	—
Total	—	126.1	245.4	—	185.0	410.4	—	355.2	953.1	—	212.9	360.9	—	357.8	626.8

Symbols: (p) present at the survey site, but not detected during actual censuses; (—) does not occur.

*albifrons*). Other rare species, on the other hand, were necessarily confined to minor habitat enclaves – subject to higher rates of natural disturbance – which were patchily distributed in an otherwise largely undisturbed, closed-canopy forest landscape. This was the case, for example, of *Cebuella pygmaea* and *Callicebus cupreus* on the edges of large canopy gaps, and *Callimico goeldii* in small forest patches regenerating from massive die-offs of giant Amazonian bamboo (*Guadua* sp.) stands. Indeed, observed densities of these spatially restricted ‘gap-phase’ habitat specialists could have been much higher provided that forest structural heterogeneity was to be maintained by appropriate levels of natural disturbance, such as blowdowns and bamboo regeneration dynamics.

There was a pronounced shift in body size towards large-bodied species, such as *Alouatta seniculus*, from terra firme to várzea forests (Table 3 and 4). The average body mass of a diurnal monkey was  $1277 \pm 395$  g for all terra firme sites and  $2142 \pm 563$  g for all várzea sites (Mann-Whitney,  $z = 3.32$ ,  $P < 0.001$ ). This combined with differences in population densities resulted in the overall community biomass of várzea forests ( $471 \pm 222$  kg km<sup>-2</sup>) being on average more than twice that of terra firme forests ( $223 \pm 100$  kg km<sup>-2</sup>,  $z = 2.93$ ,  $P = 0.003$ , Figure 2c). It thus becomes clear that there is a sharp decline in primate species richness and a sharp increment in the overall community biomass as one moves from terra firme to adjacent várzea forests (see Table 2).

### Species associations

Considering the composition of each primate community, there was a strong trend towards positive species associations among all forest sites (Schluter’s variance test for overall association,  $V = 5.43$ ,  $W = 108.6$ ,  $P < 0.001$ ). This could be shown on the basis of species occurrences alone (Table 4 and 5), regardless of their abundances. Homogeneity within four site groupings was reached after two divisive cycles showing a clear split between terra firme and várzea sites (Table 5). Penedo (site 4) was the only outlier in the first attempt to separate all sites, for its species composition was somewhat similar to that of várzea

Table 5. Site groupings based on normal association analysis of primate species composition at all forest sites. The most important ecospecies in each divisive cycle are shown in parentheses.

	First divisive cycle	Second divisive cycle (Homogeneous groups)
All sites	All terra firme sites, except Penedo  ( <i>Saguinus mystax/imperator</i> )	Porongaba and Kaxinawá Reserve ( <i>Callimico goeldii</i> )
		Terra firme sites 2–3, 5–11, and Riozinho
	All várzea sites, plus Penedo	Terra firme site 4 (Penedo) ( <i>Cebuella pygmaea</i> )
		All várzea sites

forests. The twelve terra firme sites thus formed three homogeneous groups: Penedo, two headwater sites containing mixed patches of regenerating bamboo where *Callimico goeldii* occurred (Porongaba and Kaxinawá Reserve), and all other sites. In contrast, all eight várzea sites were grouped together in a separate homogeneous group. Tamarins (*Saguinus* spp.) presented the highest species loadings in the first divisive cycle, for they consistently occurred at terra firme forests but never at várzea forests subjected to prolonged inundations. The split between Penedo and all várzea sites was largely caused by the occurrence of *Cebuella pygmaea* in the former, for this species was never detected in the latter. *Callimico goeldii* and *Callicebus torquatus* were also among a few habitat specialists which may or may not occur at terra firme sites but were never found in typical várzea forests. Várzea forests, on the other hand, did not contain a single species which could not be found in at least one terra firme site suggesting a moderate species turnover between these two macrohabitats.

#### *Community convergence and divergence*

Ecospecies dimensionality in a detrended correspondence analysis (DCA) was largely attributed to the first two axes, out of a cumulative proportion of 70.4% of the total variation explained by the first four axes (axes I: 49.1, II: 11.7, III: 6.1, IV: 3.5%). Because the first two axes alone uncovered 61% of the total variance, other dimensions were disregarded in assessing the overall matrix of 20 sampling sites by 15 ecospecies.

On the basis of primate species densities, terra firme and várzea forest sites formed two distinctively clustered natural groups diverging primarily along the first DCA dimension (Figure 4). While terra firme sites were somewhat more variable in the overall structure of their primate assemblages – which is to be expected given their higher species richness and larger number of sites – those of várzea sites were markedly cohesive. Clearly, centres of gravity of forest sites were largely influenced by numerically dominant or ubiquitous species such as tamarins and squirrel monkeys within terra firme and várzea, respectively, and brown capuchins in both forest types.

In the overlaying ecospecies scatter of the DCA plot, rare or patchily distributed taxa were largely peripheral in relation to those which were either numerically abundant or widespread. Species restricted to, or occurring primarily in, either terra firme or várzea forests were displaced to either the left or to the right hand side of the plot, respectively (Figure 4). As expected, a few habitat generalists thriving to varying degrees in both habitats, such as *Cebus apella*, *C. albifrons*, *Ateles paniscus*, and *Cacajao*, fell intermediately between typical terra firme and várzea species.

Reasons to account for between-species differences in overall abundance include population declines and local extinctions due to subsistence hunting in the case of atelines (*Ateles* and *Lagothrix*; see Table 3), dietary and habitat specialization in certain callitrichids (*Cebuella* and *Callimico*), and in the case of a pitheciine living in large groups (*Cacajao calvus*), what appears to amount to



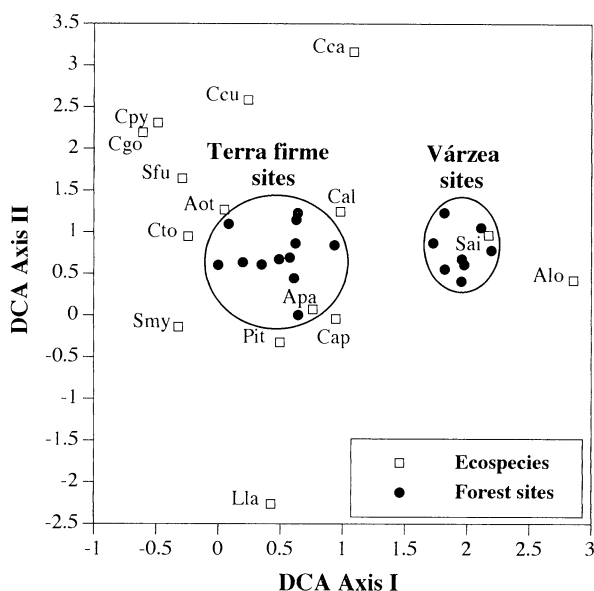


Figure 4. Detrended correspondence analysis plot showing the centres of gravity of primate ecospecies (open squares) and forest sites (solid circles) along the first two ordination axes. The two ellipses delineate terra firme and várzea forest clusters. Ecospecies abbreviations are: (Cpy) *C. pygmaea*, (Sfu) *S. fuscicollis*, (Smy) *S. mystax* or *S. imperator*, (Cgo) *C. goeldii*, (Sai) *Saimiri* spp., (Aot) *Aotus* sp., (Ccu) *C. cupreus*, (Cto) *C. torquatus*, (Pit) *Pithecia* spp., (Cca) *C. calvus*, (Cap) *C. apella*, (Cal) *C. albifrons*, (Alo) *A. seniculus*, (Lla) *L. lagotricha*, (Apa) *A. paniscus*.

high natural rates of local extinctions leading to one of the most puzzling hit-or-miss distributions for any Amazonian primate.

#### DISCUSSION

Amazonian flooded forests – which have been selected to tolerate exceptional water level amplitudes of up to 20 m and standing water for as long as half of the year – represents one of the most seasonal forest environments in the lowland, low-latitude tropics. The frequency, duration, amplitude, and geochemistry of floodwaters are perhaps the most important abiotic variables determining the main divergences in soil fertility, intensity of natural disturbance processes, habitat structure, and floristic composition for Amazonian forests (c.f. Campbell *et al.* 1992, Junk 1989, Terborgh & Petren 1991). Moreover, crude distinctions in river types and seasonal inundation régimes are primary considerations in standard classifications of Amazonian forest types (Pires & Prance 1985, Prance 1979).

It is not surprising, therefore, that severe seasonality imposed by a large flooding régime should determine substantial spatiotemporal shifts in Amazonian vertebrate faunas (c.f. Ayres 1986, Bodmer 1990, Peres *in press*, Remsen & Parker 1983). That prolonged seasonal inundation has a major effect on vertebrate patterns of habitat use would obviously be expected for

taxa which are exclusively terrestrial, and hence unable to cope with large fluctuations in water level. This rationale would also predict that seasonal flooding should have fewer consequences to arboreal and volant species, which are physically capable of tolerating environments lacking a dry ground substrate. However, this paper shows that predictable flooding patterns bring about profound changes to the species richness and abundance of strictly arboreal vertebrates, such as platyrrhine primates, even if some structural similarities between flooded and unflooded forests are maintained. Less can be said about large systems of igapó flooded forests (e.g. Rio Negro basin) – inundated by black-water rivers that are rich in humic acids but poor in suspended and dissolved soils (Furch & Klinge 1989) – for little census data are available for their vertebrate communities. It would be reasonable to speculate, however, that the physical consequences of a flooding régime to igapó vertebrates are similar to those of várzea forests, even though these two systems may diverge profoundly in their geochemical effects on forest phytochemistry and resource abundance.

#### *Species associations and habitat use*

Assuming little interspecific interactions, such as mutualisms and competition, the strongly positive species associations among survey sites shown here would suggest a common response to changes in the supply of different sets of resources associated with different habitats (Schluter 1984). This can be illustrated by the high density of *Saguinus* in terra firme forest, or the strong covariance of *Saimiri* and *Alouatta* in várzea forests. Yet the moderate species turnover between these forest types resulted mainly from the apparently prohibitive nature of várzea habitats for a guild of understorey and midstorey insectivores, which in Amazonian primates are chiefly represented by callitrichids (e.g. *Cebuella*, *Saguinus*, *Callimico*). These taxa consistently dropped out of large extensions of várzea forests, where they were largely replaced by *Saimiri* spp., the smallest bodied cebids. This was consistently the case despite the fact that callitrichids often thrive in disturbed habitats (Rylands 1987), which are more common in várzea than in terra firme forest mosaics. Prolonged inundation is likely to severely disrupt the availability of understorey arthropods, or suitable prey foraging substrates, even if the ‘boom and bust’ periodicity of várzea forests results in large seasonal pulses in harvestable prey items, such as understorey orthopterans (C. A. Peres, *pers obs.*). Similar responses were obvious in the várzea understorey avifauna, which is dramatically simplified in its species and foraging guild diversity, compared to that of adjacent terra firme sites (C. A. Peres & A. Whittaker, unpubl. data). One can only surmise, therefore, that seasonal flooding *per se* has a far greater effect on understorey species which are directly affected by rising floodwaters, rather than their canopy counterparts. However, callitrichids are often found at the edges of inundated floodplain forest, which may constitute the ‘optimum habitat’ for *Cebuella pygmaea* (Soini 1988). This is probably because this species is intimately associated with structurally heterogeneous forest sites subject to high rates of natural disturbance,

and often entirely missing from structurally uniform closed-canopy forests (e.g. Peres 1993a).

Several other points can be made regarding the use of flooded and unflooded forests by Amazonian primates. *Saimiri* – a frugivore and leaf-gleaning insectivore specializing on live, dead, or rolled leaves (Mitchell 1990, Terborgh 1983) – was clearly the numerically most dominant primate at all várzea sites. This is in sharp contrast with the conspicuous absence of squirrel monkeys in terra firme forests of remote Amazonian interfluvial regions (Peres 1993a), and their gradually lower densities as one moves beyond a few kilometres from large rivers and perennial forest streams. The exceptional ecological success of *Saimiri* in várzea and floodplain forests can be attributed to their almost exclusive small-body size of the frugivore-insectivore primates within this forest type, their wide vertical range of foraging activity, and their special relationship with large-crowned fig trees (*Ficus* spp.), which are far more abundant in these habitats than in terra firme forests (Ayres 1993, Balslev *et al.* 1987, Campbell *et al.* 1992, Silva *et al.* 1992, Terborgh 1983, C. A. Peres unpubl. data). This is relevant because prolonged seasonal inundations, with high flood depths of up to 2 m, clearly affects understorey structure. Even if suitable prey substrates can be found at the lower levels of the forest, they remain submerged and thus unavailable for as long as half of the year. Moreover, the highly variable understorey density of várzea forest is inversely correlated with floodwater depth (J. R. Malcolm & C. A. Peres, unpubl. data). This may explain why understorey insectivores, such as *S. fuscicollis*, could be found in fringe várzea habitats and in headwater floodplain forests subject to supra-annual or exceptionally rare floods, but were never found in typical várzea forests subject to prolonged inundation on a seasonal basis (see also Peres *et al.* 1996).

This series of primate censuses confirms Defler's (1994) recent findings from Colombian populations of *Callicebus torquatus* that this species cannot be described as a white-sand specialist, as had been previously hypothesized (Kinzey & Gentry 1979). None of the seven terra firme sites in which collared titis were found (Table 2) contained significant amounts of podzolic soils. The clay loams at these sites can be generally described as poorly structured, having high fractions of kaolinitic materials, and apparently of low to moderate fertility. Moreover, it is unlikely that this poorly known species elsewhere in western Amazonia can be found in densities higher than those reported here (cf. Peres 1993a). *C. torquatus* could be found in entirely undisturbed forest and did not require natural or man-made forest edges, or other forms of disturbance, typical of the optimal habitat of its sympatric congener, *C. cupreus*. Although *C. torquatus* can be occasionally observed in 'well-developed floodplain forest' (Defler 1994), the underlying causes of the relatively patchy distribution of this species remains poorly understood, and its conspicuous absence from some apparently suitable forest sites cannot be explained by any obvious reasons.

Groups of *Cacajao calvus* were sighted in the early wet season at Riozinho, a terra firme site within a black-water drainage system some 60 km from the nearest white-water river (Rio Juruá). This contradicts previous findings that

this species is a várzea specialist (Ayres 1986, 1989). These observations are also consistent with survey data from eastern Peru, where large groups of *Cacajao c. ucayalii* were invariably sighted at least 2 km from the nearest river (Aquino 1988). Indeed the only genera consistently associated with inundated forests in disproportionately large numbers were *Alouatta* and *Saimiri*, which are in fact the best várzea specialists of all primate taxa in Amazonia (see Figure 4).

*Lagothrix* appears to avoid várzea and igapó forests (cf. Peres 1993a, Stevenson *et al.* 1994), although brief seasonal incursions into these habitats by groups in abutting terra firme forests are reported in many areas. The occurrence of *L. lagotricha poeppigii* at Cahuana Island, Peru (Soini 1986) could be simply explained by the fact that this site shares characteristics that are intermediate between floodplain and typical várzea forests.

#### *Community structure*

The low primate richness in várzea forests could be intuitively understood considering how impoverished their plant communities are compared to terra firme forests (Ayres 1993, Balslev *et al.* 1987, Campbell *et al.* 1992, Junk 1989, C. A. Peres & J. R. Malcolm, unpubl. data). Despite the sharp collapse in species richness from terra firme to várzea forests, the crude biomass of all species combined was over twice as high in the latter. This reversed density/diversity pattern is the opposite to that most frequently found in natural communities, in which high overall abundance is often correlated with high diversity. This is also remarkable considering the physical proximity between the terra firme and várzea forests surveyed here, which suggests that these differences could be even greater for more remote upland forests far removed from the influence of major rivers. On the other hand, primate communities within irregularly inundated floodplain forests in the headwater section of the Juruá (opposite site 1; opposite site 2) had a species composition just as rich as that of terra firme forests (C. A. Peres, *pers. obs.*). Such headwater floodplain sites further supported high densities of *Saguinus* spp. – one of the most várzea-adverse of all primate genera – and were structurally intermediate between várzea or terra firme sites farther downriver. Genera typical of either várzea or terra firme forests (e.g. *Saimiri* and *Saguinus*, respectively) were found at these sites coexisting side-by-side and in good numbers, a pattern consistent with other floodplain forests of upper Amazonia studied in far greater detail (Cocha Cashu, Peru: Terborgh 1983).

Discrepancies between várzea and terra firme forests cannot be attributed to between-site variation in hunting pressure (Table 1), which targets primarily the large-bodied species (>4 kg) that account for the greatest contribution to the overall community biomass (Freese *et al.* 1982, Peres 1990). If that were the case, one should expect an *inverse* response to that observed here because várzea sites were subject to *stronger* hunting pressure in terms of game offtake per unit area (Peres 1997). This is explained by the higher human densities in

várzea forests, and the shorter distances and convenient access to the areas sampled from nearby extractive households. Indeed várzea rubber-tappers along the Juruá largely turn to non-aquatic sources of protein such as primates for as long as half of the year, when the water level becomes prohibitively high for subsistence fishing.

In relation to certain wide-ranging species which may exhibit long-distance bilateral movements between flooded and unflooded forests, it could be argued that some qualitative differences in this cross-site comparison might result from the time of year that censuses were conducted (Branch 1981, Peres 1993a, see Table 1). However, possible seasonal shifts in primate community structure are unlikely to have played a significant role in this study because the timing of várzea census was kept relatively constant (coinciding with the low water season at all but one site), and community composition at terra firme sites is likely to be relatively stable throughout the year (Peres 1993a).

The high primate biomass of várzea forests, particularly with respect to folivores, is best explained by the high fertility of the young alluvial soils, which in turn are related to high levels of fruit production (Ayres 1986) and possibly low levels of secondary phytochemical defense allocated to young and mature foliage (Herrera *et al.* 1978, McKey *et al.* 1978). Chemical analyses of soil macronutrients important to plants (N, P, K, Na, Ca and Mg) have consistently shown that várzea floodplain soils have elemental concentrations far greater than those of terra firme forests (Irion 1978). This is particularly the case for phosphorus and potassium (19 and 6 times greater, respectively), and calcium (as much as 190 times greater: Furch & Klinge 1989), which have the greatest effects on tropical forest productivity (Vitousek & Sanford 1986). These patterns are clearly consistent with data from Cocha Cashu, Manu National Park, Peru, where soils under typical mature floodplain forest contain 1.5–3.0 times as much carbon, nitrogen, and potassium, and 2–60 times as much calcium and magnesium, as soils in adjacent areas supporting typical terra firme forests (M.P. Riley, *pers. comm.*). Using mean body weights as described here, the diurnal primate community at this un hunted floodplain forest (12 species comprising a biomass of 588 kg km<sup>-2</sup>: Terborgh 1983) – is clearly comparable to that of Pleistocene várzea forests along the Rio Juruá, despite the effects that selective hunting has had on the latter. For example, the lightly hunted várzea forest at Boa Esperança (site 13) attained the record high primate biomass (953 kg km<sup>-2</sup>) for any neotropical forest site sampled to date (C. A. Peres, unpubl. data).

The greater primate biomass in várzea forests is probably related to differences in forest structure, plant reproductive phenology, and floristic composition. Flood-disturbed forests are more deciduous, structurally heterogeneous, and have many large canopy gaps, which presumably allow higher rates of vegetative productivity, and more favourable foliar nutrient levels, particularly in the form of renewed young foliage (Klinge *et al.* 1983). Higher foliage quality in terms of lower levels of secondary compounds and fibre content is expected

to favour leaf-eaters, which is consistent with the much higher biomass of *Alouatta* and several other arboreal folivores, including iguanas (*Iguana iguana*), hoatzins (*Opisthocomus hoatzin*), horned screamers (*Anhima cornuta*), and both genera of sloths (*Bradypus* and *Choloepus*), compared to terra firme forests (Queiroz 1995, C. A. Peres in press). A more detailed discussion of the dietary quality and ecological success of arboreal folivores in flooded forests is presented elsewhere (Peres 1997).

The overall fruit production in várzea forests is also apparently higher than that of terra firme forests, although little comparative data is available on adjacent plant communities straddling the upper reaches of high floodwaters. A 12-mo study in the lower Japurá river indicated that on average 7.6 and 9.6% of 982 trees and lianas within high- and low-ground várzea forest plots, respectively, produced fruits in any given month (Ayres 1993). The comparative figure from a 14-mo study of a set of 996 trees  $\geq 10$  cm DBH in a remote terra firme forest was 5.0% (Peres 1994b). The annual period of greatest fruit scarcity also appears to have less severe effects in the former than in the latter, partly because frugivores can move around into adjacent plant communities with staggered fruiting peaks, which is more likely to take place in successional floodplain habitats such as várzea forests (c.f. Terborgh 1983). It remains unclear, however, how these differences relate to fleshy fruits consumed by a wider range of generalist frugivores, for both the floristic diversity and the proportion of gut-dispersed plant species is lower in várzea than in terra firme forests (Ayres 1993, Kubitzky & Ziburski 1994).

This study provides substantial support for the fact that the reduction in species diversity from terra firme to várzea forests – which has been reasonably well documented for trees (e.g. Ayres 1993, Junk 1989) – can be extended to primates (Ayres 1986). Results from the Juruá Project indicate that several other vertebrate taxa, including amphibians, undertorey birds, and terrestrial rodents and marsupials also follow the same pattern (Malcolm *et al.* 1992; C. A. Peres & A. Whittaker, unpubl. data). A number of other, usually terrestrial, non-volant mammal taxa with flood-intolerant lifestyles are conspicuously lacking in várzea forests, which may nevertheless be used on a seasonal basis (Bodmer 1990, Peres in press). This should by no means imply that the comparatively impoverished communities of várzea forest should be neglected by conservation efforts, for this unique ecosystem greatly contributes with increments in species  $\beta$ -diversity in a given river basin along an axis perpendicular to the main river channel. Indeed the relatively small proportion of Amazonia covered by várzea and igapó forests (5–7%) safeguard a disproportionately large fraction of the region's biota, for as much as one fifth of the species in several higher taxonomic groups may be restricted to flooded forests (Junk 1989). The water-stressed plant and animal communities of Amazonian inundated forests should thus be seen as a unique complement to those of terra firme forests.

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