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# Mammal assemblage structure in Amazonian flooded and unflooded forests

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**Abstract:** Few studies have contrasted faunal communities between flooded and unflooded tropical forests, and such attempts have largely been restricted to a few taxonomic groups. We present the first comparison of the composition and structure of an entire assemblage of mid-sized to large-bodied mammals in adjacent unflooded (terra firme) and flooded (várzea) forests of central-western Amazonia. We extend this comparison to 13 other terra firme and várzea forest sites in order to examine the fundamental dichotomy between mammal communities in these Amazonian environments. We found a consistently impoverished fauna in várzea environments both in terms of primates and other non-volant mammals, although primate density and biomass was substantially higher in várzea than in terra firme. The average Bray–Curtis mammal community dissimilarity between terra firme and várzea forests was 74%, whereas mean dissimilarity within várzea and terra firme samples was 40% and 39%, respectively. The results seem to be largely a function of high habitat heterogeneity and floristic diversity in terra firme and the physical connectivity and proximity of várzeas to adjacent terra firme forests. We suggest that inundated forests should be set aside as a crucial complement to Amazonian reserves dominated by terra firme forests in future biodiversity conservation planning.

**Key Words:** Amazonia, assemblage structure, conservation, flooded forest, large-bodied mammals, mammal assemblage, Neotropical forests, primates, terra firme, várzea

## INTRODUCTION

The Amazon basin covers around 7 million km$^2$ and includes the largest remaining tract of tropical forest, harbouring one of the richest faunas and floras of the world. The highest levels of local diversity of most plant and vertebrate taxa, including trees (Gentry 1988), amphibians (Dixon & Soini 1986), reptiles (Rodriguez & Duellman 1994), birds (Terborgh *et al.* 1990) and primates (Peres & Janson 1999), occur in the western Amazon. Most of this diversity is found in unflooded (hereafter, terra firme) forests. Upland terra firme forests are those above the maximum flood level of Amazonian rivers. Consequently, these unflooded forests lie on well-drained terrains that tend to be heavily leached and nutrient-poor because they have long been deprived of alluvial sediments. This represents the main forest type across the region. However, several plant communities can be found embedded within the closed-canopy forest, as confirmed by satellite images (Tuomisto & Ruokolainen 1994, Tuomisto *et al.* 1995) and floristic variation (Terborgh & Andresen 1998, ter Steege *et al.* 2000). This is consistent with studies suggesting that the exceptional levels of diversity of western Amazonia is a consequence of high habitat heterogeneity derived from different edaphic and ecological conditions (Salo *et al.* 1986, Terborgh 1985, Tuomisto *et al.* 1995) caused by a range of historical, geographical and ecological factors (Ayres & Clutton-Brock 1992, Liu & Colinvaux 1985, Patterson *et al.* 1998, Peres & Janson 1999, Peres *et al.* 1996, Räsänen *et al.* 1987, Voss & Emmons 1996).

Seasonally inundated forests comprise a second major vegetation type in the Amazon. The low-lying topography of the basin and rainfall seasonality inundate these floodplains for up to 6 mo of the year as the annual water level fluctuation of the Amazon river and its tributaries can reach 14 m in amplitude. These forests can be divided into several types based on hydrochemical (Sioli 1968) and floristic differences (Prance 1979). However, floodplain forests along white-water rivers (hereafter, várzea forests) account for the main type of flooded forest in Amazonia and cover about 180 000 km$^2$ (2.6%) of the Amazon basin (Bayley & Petrere 1989). These rivers drain mostly geologically young and easily erodable

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landscapes (Räsänen *et al.* 1987) and carry large amounts of nutrient-rich suspended sediments. These forests are eutrophic due to the seasonal influx of nutrients and remain exceptionally productive (Junk & Piedade 1993).

Although many plant and animal inventories are available, very few have described the contrasting biological assemblages between terra firme and várzea forests. For example, only two previous studies provide a quantitative comparison of tree assemblages in flooded and unflooded forest. Campbell *et al.* (1986) conducted a quantitative inventory of adjacent terra firme and flooded forest along the Rio Xingú and Balslev *et al.* (1987) contrasted terra firme and várzea forest at Añagu in Amazonian Ecuador.

Faunal studies are also scarce and have been restricted to a few taxonomic groups. For example, Patton *et al.* (2000) contrasted small-mammal communities in terra firme and várzea forests along the Rio Juruá, and similar comparisons are available for leaf-litter frogs (Gascon 1996) and primates (Gascon *et al.* 2000, Peres 1997a). Despite these attempts to explore the differences in flora and fauna between terra firme and várzea forest, the environmental and biogeographic determinants of assemblage structure and diversity remain poorly understood.

However, it is possible to make a number of predictions concerning mammal diversity in várzea and terra firme forests. Firstly, several factors could depress species richness in várzea forests. For example, stress factors such as persistent flood pulses, anoxic or hypoxic water conditions, and interruption of photosynthesis by complete submergence of many trees are possible causes for the lower floristic diversity of várzea forests (Kubitzki 1989). As a result of flooding, várzea environments also have a considerably simplified forest structure by the lack of understorey and dry ground for much of the year. A combination of these factors could reduce animal diversity and abundance, particularly in the case of terrestrial and understorey vertebrates. Terra firme mammal species richness should therefore be higher compared with that in várzea, reflecting the high floristic diversity and structural heterogeneity of the forest. Seasonal flooding should, however, have fewer consequences for strictly arboreal mammals which are expected to tolerate environments lacking dry ground for several months of the year.

Secondly, if nutrient input is an important determinant of primary productivity, the lack of seasonal influx of nutrient-rich sediments should limit the availability of macronutrients to plants on terra firme soils and, in turn, affect the overall primary productivity available to primary consumers (Peres 1997a). Plants may be forced to invest more in protection against primary consumers on nutrient-poor soils, packing leaves with elevated amounts of secondary metabolites (e.g. condensed tannins) or fibre making them unpalatable or indigestible (Janzen 1974). Due to low nutrient availability, mammal density and biomass should therefore be expected to be lower in terra firme particularly in terms of primary consumers.

Here we present the first comparison of the composition and structure of an entire assemblage of mid-sized to large-bodied mammals in adjacent terra firme and várzea forests in order to examine the fundamental dichotomy between these major Amazonian environments. We also extend this comparison to 13 other sites of varying hydrological regimes in central-western Amazonia from which density estimates of primates and other non-volant mammals are available. Community-wide shifts in species richness, density and biomass between the different forest types are then interpreted in light of the differences experienced by seasonal flooding, soil fertility and habitat structure. Finally, we draw some general implications from the environmental transitions between juxtaposed terra firme and várzea forests to the conservation of Amazonian biota.

## STUDY AREA

The study took place at Lago Uauaçú (04°20′S, 62°28′W) in the lower Rio Purús region of central-western Brazilian Amazonia, about 350 km south-west of Manaus (Figure 1). The main study areas where population censuses were carried out consisted of terra firme (sites A–C) and várzea forests (sites D–F; Figure 1). The várzea forests in sites D and E were separated from terra firme by a *c.* 50-m-wide river channel, whereas study area F consisted of várzea forest that was physically connected to terra firme. Lago Uauaçú itself is a 32-km-long crescent-shaped black-water lake fed entirely by rainfall collected in an internal catchment consisting primarily of terra firme forest. The entire study area retains a full complement of vertebrate species and remains virtually undisturbed, but was occupied by 30 extractive *caboclo* (non-tribal) households who depend primarily on the collection of Brazil nuts from natural *castanhais* (clusters of Brazil nut trees, *Bertholletia excelsa* Humboldt & Bonpland – Lecythidaceae) in addition to small-scale fishing, and highly selective logging and hunting.

## METHODS

### Line-transect censuses

All sites were surveyed using a standardized line-transect census protocol described in Peres (1999a). In brief, census walks were conducted from 07h00–11h00 and 13h00–17h00. During rain censuses were terminated. Upon a detection event, the time, species identity, group size, perpendicular distance to the animal, sighting location along the transect and detection cue was recorded. Data on the Uauaçú mammal fauna were collected during a preliminary survey carried out in terra

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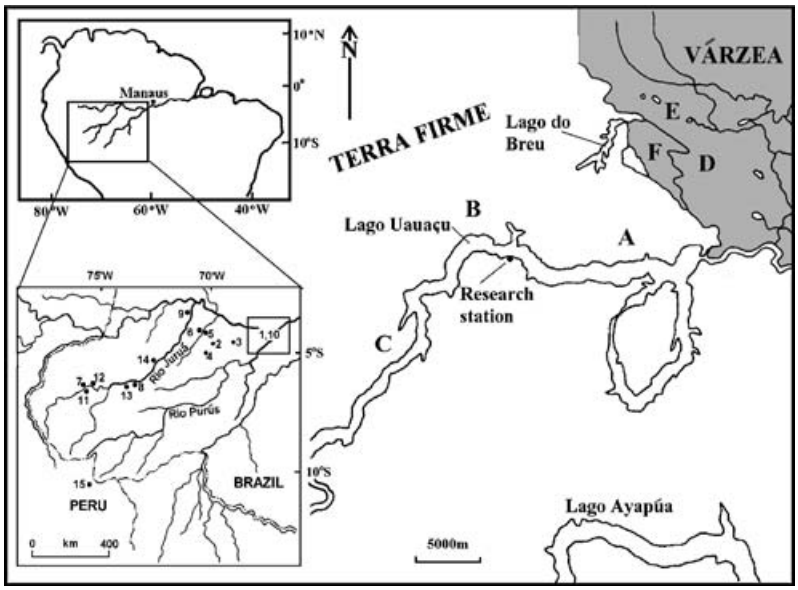



**Figure 1.** Map of the study area in the lower Rio Purús region of central-western Brazilian Amazonia. The main forest types occurring in the region are terra firme and várzea forest and the letters A–F represent the main focal areas censused in these environments. Inset shows the placement of the 15 sites used in the cross-site comparison. Site numbers correspond to those in Table 1.

firme in July–August 1998, followed by extensive surveys in both várzea and terra firme in January–December 2002. The latter survey was carried out in four sampling blocks of 2 mo, coinciding with the late wet, early dry, late dry and early wet seasons. In total, this study is based on a two-way census effort of 1227 km in terra firme and 965 km in várzea walked along 11 transects ranging 4–5 km in length (= 52.5 km of transects). To our knowledge, this amounts to the largest survey effort allocated to a single central-western Amazonian study area, especially in várzea forest.

Replicate census walks within each sampling block were systematically alternated between terra firme and várzea forests in order to minimize any confounding effects of seasonality. In the high-water season, censuses along the várzea transects were conducted by canoe. In addition, all incidental observations outside census walks were noted and appropriate data recorded. Night surveys were not carried out, and thus the data presented here focus on diurnal mammals. This excludes only one primate species (night monkeys, *Aotus* cf. *nigriceps*) and a few other nocturnal mammal species such as paca (*Agouti paca*) and kinkajou (*Potos flavus*).

Information on vertical use of the forest and body mass data were compiled from previous studies (Peres 1999b, Peres & Dolman 2000, Robinson & Redford 1986), and in order to calculate population biomass we used the average body mass of males and females defined as 80% of the adult mean weight of a species. Trophic classification follows Janson & Emmons (1990) and Peres (1999b; Appendix 1). Scientific nomenclature in this paper follows Wilson & Reeder (1993).

### Other survey sites

Additional data used here were compiled from flooded and unflooded forests from which relatively robust line-transect census effort and density estimates for all large diurnal mammals were available (Janson & Emmons 1990, Peres, unpubl. data). We also restricted our analysis to central-western Amazonia (Figure 1) because although várzea forests are associated with white-water rivers throughout the basin, they are most prominent in the central-western Amazon. By excluding the Guiana Shield and eastern Amazonia, several potentially confounding variables such as soil and geochemical factors were also eliminated. The source fauna in central-western Amazonia is also very similar, thereby simplifying the comparative analysis. Similarly, the prominent east–west species diversity gradient observed for at least some taxa (e.g. primates: Peres & Janson 1999) is less likely to influence the comparative analysis. However, we also include a mature floodplain site from southern Peru in the analysis, which is irregularly inundated by flash-floods spilling over the typical maximum flood level and depositing silt and nutrients on a supra-annual basis (normally every 7–10 y; J. Terborgh, pers. comm.). The soils of these sites are therefore also characterized by rich alluvial sediments but are intermediate in terms of fertility between seasonally flooded and unflooded forests.

Finally, we selected forest sites with minimal levels of anthropogenic disturbance including hunting pressure, which can have profound effects on Amazonian vertebrate assemblage structure (Peres 2000). We therefore assume that the large mammal assemblages of different

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**Table 1.** Summary of the non-volant mammal assemblage characteristics at 15 forest sites in central-western Amazonia. The table only includes the number of species for which density estimates are available.

| | | | No. of species | | Density (ind. km$^{-2}$) | | Biomass (kg km$^{-2}$) | | |
|---|---|---|---|---|---|---|---|---|---|
| Site number | Site localities | River basin | Non-primates | Primates | Non-primates | Primates | Non-primates | Primates | Source[1] |
| Terra firme | | | | | | | | | |
| 1 | Uauaçú, Brazil | Purús | 15 | 11 | 19 | 123 | 171 | 259 | 1 |
| 2 | Urucú, Brazil | Juruá | 10 | 11 | 27 | 137 | 494 | 324 | 2 |
| 3 | Igarapé Açú, Brazil | Juruá | 10 | 10 | 34 | 106 | 380 | 313 | 2 |
| 4 | SUC-1, Brazil | Juruá | 10 | 10 | 34 | 77 | 400 | 217 | 2 |
| 5 | Oleoduto, Brazil | Juruá | 10 | 9 | 23 | 103 | 292 | 253 | 2 |
| 6 | Curimatá, Brazil | Juruá | 10 | 12 | 27 | 79 | 418 | 222 | 2 |
| 7 | Condor, Brazil | Juruá | 10 | 9 | 34 | 195 | 367 | 279 | 2 |
| 8 | Altamira, Brazil | Juruá | 10 | 11 | 43 | 227 | 325 | 463 | 2 |
| 9 | Vira Volta, Brazil | Juruá | 8 | 11 | 18 | 182 | 233 | 282 | 2 |
| Várzea | | | | | | | | | |
| 10 | Uauaçú, Brazil | Purús | 6 | 7 | 10 | 201 | 27 | 325 | 1 |
| 11 | Sacado, Brazil | Juruá | 4 | 4 | 18 | 126 | 74 | 245 | 2 |
| 12 | Nova Empresa, Brazil | Juruá | 7 | 6 | 15 | 185 | 38 | 410 | 2 |
| 13 | Boa Esperança, Brazil | Juruá | 6 | 5 | 11 | 355 | 145 | 953 | 2 |
| 14 | Lago da Fortuna, Brazil | Juruá | 4 | 6 | 10 | 344 | 39 | 552 | 2 |
| Mature floodplain | | | | | | | | | |
| 15 | Cocha Cashu, Peru | Manu | 8 | 13[2] | 48 | 255 | 364 | 655 | 3 |

[1] 1 = this study; 2 = C. A. Peres, unpubl. data; 3 = Janson & Emmons (1990).
[2] Only 10 species reside at Cocha Cashu; three species are considered to be vagrant (Janson & Emmons 1990) and occasionally using the census area.

sites are largely representative of their respective habitats, reflecting intrinsic differences in forest structure and composition, flooding regime and soil fertility rather than varying degrees of anthropogenic disturbance. A brief profile of the 15 sites considered in this study is presented in Table 1.

### Data analysis

Census data were analysed using DISTANCE 4.0 software (Thomas *et al.* 2002). All visual and acoustic detection events were included in the analyses. In several cases, however, the perpendicular distance data were truncated to remove outliers, which provided a better fit to the various estimator models. Group density estimates were derived from Half-Normal models with either cosine or polynomial adjustments or using King's method where sample sizes were too small. Population density estimates were then calculated on the basis of group densities and mean group sizes in each forest type, which were based on the total number of reliable group counts.

Detection data for sympatric congeners of three genera (tamarins, *Saguinus* spp.; squirrels, *Sciurus* spp.; and brocket deer, *Mazama* spp.) were pooled because these congeners could not always be unambiguously distinguished in the field. This also increased sample sizes, allowing more robust model fits. In these cases, individual density and biomass estimates were extrapolated from the number of detection events in which each species were reliably identified.

Independent-samples t-tests were used to examine the differences in species richness, density and biomass between terra firme and várzea forest in the cross-site comparison.

Non-metric multidimensional scaling (MDS) was considered the most appropriate ordination technique to examine the cross-site variation in species composition and abundance. Using the computer software PRIMER v. 5 (Clarke 1993) all species were entered in the ordination as single entities. However, ecologically analogous species occurring at different sites were pooled together under a common functional group (e.g. *Saguinus mystax* and *Saguinus imperator*, *Pithecia albicans* and *Pithecia monachus*). Forest sites are thus positioned in the ordination space according to their mammal species composition and abundance. An index of multivariate dispersion (Warwick & Clarke 1993) was calculated to investigate the variability among replicate terra firme and várzea forest samples. Average Bray–Curtis dissimilarity between groups of samples was also calculated.

## RESULTS

### The Uauaçú large-mammal community

In total, 45 large-mammal species occur at Uauaçú including 13 primates, 13 carnivores, eight xenarthrans, six rodents and five ungulates (Appendix 2). Of these, 34 species were encountered during census walks, another six were detected visually or acoustically outside the census routine, three were confirmed to be present

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by local hunters, and two remain unconfirmed but their geographic distribution suggest that they occur in the study region.

Reliable population density estimates could be calculated for 23 of the 34 species observed during censuses in terra firme forest, and 12 of the 20 species observed in várzea forest. Reliable estimates for most carnivores and some primates were not calculated due to their natural rarity or low frequency of detection events at these sites.

### Species richness and abundance

*Primates.* Terra firme forest at Uauaçú supported a higher number of primate species than várzea (Table 1). The maximum number of sympatric species observed in terra firme sites was 11, whereas the várzea sites supported at most 7 species. Four primate species were restricted to várzea site F which was physically connected to terra firme, and all encounters with these species occurred in the late wet season. The species richness of várzea sites D and E, which were isolated from terra firme by a river channel, never exceeded three species. A total of four primate species occurring in terra firme did not occur in várzea, whereas all várzea species also occurred in terra firme. Howler monkeys (*Alouatta seniculus*), however, were far more common in várzea than in terra firme forest (Appendix 2).

Conversely, primate abundance in the species-rich terra firme forest was considerably lower than the species-poor várzea. The overall primate density in várzea forest was nearly twice that of the terra firme forest, which reflects the number of group encounters in this forest type. Golden-backed squirrel monkeys (*Saimiri* cf. *ustus*) comprised the most abundant primate species in várzea, whereas brown capuchins (*Cebus apella*), closely followed by moustached tamarins (*Saguinus mystax*), were most abundant in terra firme (Appendix 2). Consequently, the aggregate primate biomass was also higher in várzea compared with that of terra firme. The high density of the small-bodied squirrel monkeys in várzea forest means that this difference was not as great as could be expected from that in numerical abundance. In summary, várzea forests were characterized by low primate species richness and high assemblage biomass compared with that of adjacent terra firme forests.

*Other non-volant mammals.* The species richness of other non-volant mammals in terra firme forest was twice that of várzea (Table 1). This difference was more pronounced in unconnected várzea forest sites, where another four strictly terrestrial species were missing. The remaining species occurring on both banks of the river channel consisted of six arboreal or scansorial species (southern tamandua *Tamandua tetradactyla*, pale-throated three-toed sloth *Bradypus tridactylus*, southern two-toed sloth *Choloepus didactylus*, southern Amazon red squirrel *Sciurus spadiceus*, South American coati *Nasua nasua* and tayra *Eira barbara*), two terrestrial (Brazilian tapir *Tapirus terrestris* and jaguar *Panthera onca*) and one semi-aquatic species (Neotropical otter *Lontra longicaudis*). However, as the area of dry land contracted with the rising waters in the rainy season, all remaining strictly terrestrial species were forced to abandon the várzea forest. Only the two-toed sloths were observed in the várzea but never in terra firme, whereas a total of 14 species occurring in terra firme were never observed in várzea (Appendix 2). All of these were strictly terrestrial.

Consequently, the aggregate abundance of other large non-volant mammals in terra firme forest was twice that of the várzea. The most abundant of these was the black agouti (*Dasyprocta fuliginosa*) in terra firme forest and the semi-arboreal coati in várzea forest (Appendix 2).

The lower primate-assemblage biomass in terra firme compared with that of várzea is more than compensated for by other mammal species. This was mainly due to the greater abundance of terrestrial browsers, frugivores and seed predators such as ungulates and rodents. However, some large mammals such as the tapir and giant anteater (*Myrmecophaga tridactyla*) account for a large proportion of the total assemblage biomass despite their low densities.

*Trophic guilds.* The mid-sized to large-bodied mammal community at Uauaçú is dominated by frugivores and seed predators. Carnivores are rare, as are browsers and insectivores. Additionally, there seems to be a clear distinction between várzea and terra firme. Folivores and generalists were more common in várzea, whereas terra firme appears to allow a higher degree of specialization.

Arboreal mammals accounted for 88% of the total of 142 individuals $km^{-2}$ in terra firme forest, whereas terrestrial species accounted for only 12%. Consequently, arboreal species represented 260 kg $km^{-2}$ and a large proportion (58.6%) of the total assemblage biomass, despite the larger body size of many terrestrial species. In the várzea, arboreal mammals accounted for more than 203 individuals $km^{-2}$ of the total of 211 individuals $km^{-2}$. As a result, the terrestrial mammal contribution to the aggregate biomass of várzea forest was only 7.3% of 328 kg $km^{-2}$. However, this proportion is considerably overestimated because sloths, which account for most of the arboreal mammal biomass in Amazonian várzea forests (Peres 1999b), cannot be surveyed through standardized line-transect censuses.

### Cross-site comparison

*Species richness and abundance.*

*Primates.* Terra firme forests of central-western Amazonia contained significantly more primate species

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**Table 2.** Mean (± SE) number of species, aggregate density and biomass of primates and other non-volant mammals at different central-western Amazonian terra firme (n = 9) and várzea/mature floodplain (n = 6) forest sites. * = difference between forest types significant at the 0.05 level.

| | Primates | | Other non-volant mammals | |
|---|---|---|---|---|
| | Terra firme | Várzea | Terra firme | Várzea |
| No. of species | 10.8 ± 0.5 | 5.6 ± 0.51* | 10.1 ± 0.4 | 5.4 ± 0.6* |
| Total density (ind. km$^{-2}$) | 136.6 ± 17.8 | 242.4 ± 45.5 | 28.8 ± 2.7 | 12.8 ± 1.6* |
| Total biomass (kg km$^{-2}$) | 290.2 ± 24.74 | 497.0 ± 124.8 | 342.2 ± 32.9 | 64.6 ± 21.6* |

than várzea forests (t = 7.06, df = 12, P < 0.001; Table 2). The highest species packing at a single várzea site was at Uauaçú where as many as seven sympatric primate species were observed. The most diverse site had 12 sympatric species (Curimatá; Table 1). Cocha Cashu is listed with 13 species, however, three of these species are vagrant and only occasionally use this area.

Conversely, várzea forests had a much higher primate abundance than terra firme forests, however, this difference was not significant (t = −2.17, df = 5.3, P = 0.08). Similarly, várzea forests contained a considerably greater primate biomass than terra firme, although this difference was not significant (t = −1.63, df = 4.3, P = 0.174; Table 2).

*Other non-volant mammals.* The species richness of non-volant mammals was significantly higher in terra firme forests (t = 6.5, df = 12, P < 0.001; Table 2). The highest number of species observed in a várzea site was six (Uauaçú and Boa Esperança), while mature floodplain forests again contained a higher richness with eight species (Table 1).

This resulted in a significantly greater assemblage-wide density in terra firme forests (t = 4.1, df = 12, P = 0.001). Consequently, terra firme sites supported a significantly greater biomass of non-volant mammals than várzea forests (t = 5.8, df = 12, P < 0.001; Table 2).

*Community convergence and divergence.* On the basis of the mammal species composition and density at different sites, terra firme and várzea forests formed two clearly distinct clusters to the left- and right-hand side of the MDS ordination plot, respectively, diverging primarily along the first axis (Figure 2). As expected, the mature floodplain forest site was intermediate between typical terra firme and annually flooded várzea sites (Figure 2), but was more similar to flooded-forest sites. This is supported by the Bray–Curtis dissimilarity measure: várzea and mature floodplain sites had an average dissimilarity of 46%, whereas terra firme sites and the mature floodplain site had an average dissimilarity of 58%. Terra firme and várzea sites were most dissimilar, with an average dissimilarity of 74%. Sites at opposite ends of the ordination thus had few species in common.

The index of dispersion shows that there is no difference in variability between groups of terra firme (0.985) and

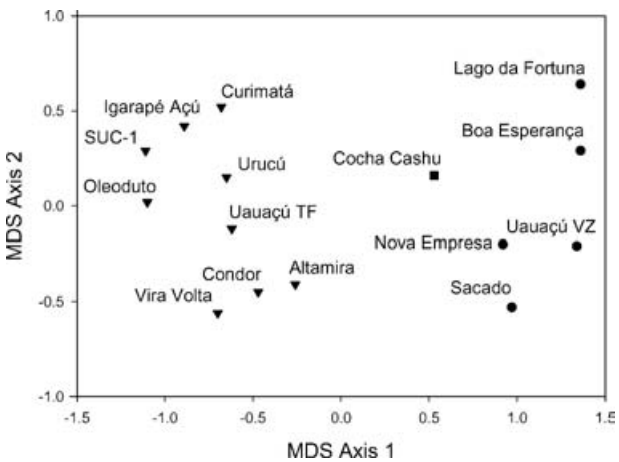



**Figure 2.** Non-metric multi-dimensional scaling (MDS) ordination of the large-mammal fauna at 15 central-western Amazonian sites of varying hydrological regimes. A brief description of each site can be found in Table 1. Stress = 0.06.

várzea (1.055) forest samples. This is also indicated by the MDS ordination, and further supported by the Bray–Curtis dissimilarity, where várzea and terra firme samples had a mean between-site dissimilarity of 40% and 39%, respectively.

## Trophic guilds

The aggregate density and biomass of medium- to large-bodied mammals in central-western Amazonian forests was clearly dominated by arboreal frugivores and there was no significant difference in these summaries between terra firme and várzea forests (Table 3).

The strongest contrast between forest types is the significantly higher density and biomass of terrestrial frugivores and granivores in terra firme forest compared with those of várzea forest, and the significantly higher densities and biomass of folivores in várzea (Table 3). The mature floodplain forest shows a community profile that is intermediate between terra firme and annually flooded várzea forests. This site had a high density of arboreal frugivores, but also supported a high biomass of terrestrial frugivores, granivores and arboreal folivores. The similarity between terra firme and várzea for terrestrial insectivores/vertebrate predators is probably best explained by the inclusion of the semi-arboreal coati in this guild.

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**Table 3.** Mean (±SE) density and biomass of the non-volant mammal assemblage among different trophic guilds in Amazonian terra firme and várzea forest along with the observed values at one mature floodplain forest. Independent t-test results show differences between terra firme and várzea forest. df = 1,12 in all cases.

| Foraging position and trophic guild | Terra firme (n = 9) | Várzea (n = 5) | Mature floodplain (n = 1) | t | P |
|---|---|---|---|---|---|
| Density (ind. $km^{-2}$) | | | | | |
| Arboreal folivores | 3.5 ± 0.9 | 39.5 ± 14.1 | 21.3 | −3.5 | 0.004 |
| Arboreal frugivores | 119.4 ± 16.0 | 179.3 ± 30.3 | 267.0 | −1.9 | 0.076 |
| Arboreal granivores/frugivores | 18.9 ± 3.9 | 24.5 ± 10.9 | 25.0 | −0.6 | 0.564 |
| Arboreal insectivores | 0.01 ± 0.01 | 0.08 ± 0.08 | 0 | −1.2 | 0.27 |
| Terrestrial granivore/frugivores | 18.0 ± 1.0 | 1.8 ± 0.3 | 19.1 | 12.2 | < 0.001 |
| Terrestrial frugivore/folivores | 3.0 ± 0.4 | 0.8 ± 0.2 | 4.1 | 3.8 | 0.003 |
| Terrestrial insectivores/vertebrate predators | 0.02 ± 0.02 | 1.2 ± 1.2 | 0 | −1.4 | 0.198 |
| Biomass (kg $km^{-2}$) | | | | | |
| Arboreal folivores | 18.2 ± 4.6 | 196.6 ± 75.5 | 156.0 | −3.3 | 0.007 |
| Arboreal frugivores | 244.2 ± 23.3 | 269.6 ± 64.3 | 431.3 | −0.5 | 0.659 |
| Arboreal granivores/frugivores | 23.1 ± 5.7 | 39.4 ± 26.5 | 12.0 | −0.8 | 0.444 |
| Arboreal insectivores | 0.04 ± 0.04 | 0.3 ± 0.3 | 0 | −1.1 | 0.277 |
| Terrestrial granivore/frugivores | 214.3 ± 19.5 | 30.0 ± 9.3 | 210.7 | 6.7 | < 0.001 |
| Terrestrial frugivore/folivores | 105.9 ± 11.2 | 27.5 ± 15.8 | 140.8 | 4.1 | 0.001 |
| Terrestrial insectivores/vertebrate predators | 0.06 ± 0.06 | 3.0 ± 3.0 | 0 | −1.4 | 0.198 |

## DISCUSSION

Aggregate biomass was similar between várzea and terra firme forests, however, while mammal species assemblages in várzea forests contained consistently fewer species than those in terra firme forests, the former had a substantially higher aggregate density than the latter. These trends cannot be attributed to different forms of anthropogenic disturbance such as selective logging and hunting, as these were controlled for in the selection of study sites examined here. One possible caveat is that seasonal movements and habitat shifts by some species could lead to qualitative differences between sites depending on the time of the year the census was conducted. Although such movements certainly occur, it seems unlikely that they affected our results, which included repeated census walks during the same seasons and throughout the year. Furthermore, the results from the cross-site comparison were very consistent with those found at Uauaçú, and there was a high congruence in species composition, density and biomass within each forest type. We are thus confident that our observations reflect intrinsic environmental differences between the two forest types rather than sampling artefacts. The possible determinants of the large-mammal community structure are discussed below.

### Environmental factors

Differences in floristic composition, habitat structure and soil fertility may comprise the most plausible explanations for the dramatic differences in large-mammal assemblage structure between várzea and terra firme forests. For example, the persistent inundation period in várzea forest of up to 6 mo, dominated by deep standing water, have profound physiological, morphological and anatomical consequences in várzea trees (Junk 1989, Parolin 2001, Worbes 1997). Phenological and reproductive patterns may also be adapted to flooding, as highlighted by the fruiting synchrony of many várzea trees during the high-water season and their ichthyochorous or hydrochorous (modes of dispersal by fish or water) fruits or seeds (Gottsberger 1978, Goulding 1980, Kubitzki & Ziburski 1994, Worbes 1997). The recent evolutionary origin of várzea forests (Irion *et al.* 1997) and the extreme evolutionary adaptations needed to tolerate flooding, has probably led to the well-documented lower floristic diversity of várzea compared with terra firme (Ayres 1993, Balslev *et al.* 1987, Campbell *et al.* 1986). As a result of flooding, várzea environments also have a considerably simplified forest structure as the understorey and ground layers are completely submerged for much of the year. It is also clear from chemical analyses of soil macronutrients that are crucial to plants (N, P, K, Na, Ca and Mg), that várzea forest soils are far more fertile than those of terra firme forests (Irion 1978).

Soil properties in different forest types could affect plant communities in several ways. For example, the high fertility of the young alluvial soils renewed in várzea forest every year, may increase overall fruit production in this forest type. Comparable data sets from a terra firme (Urucu: Peres 1994) and a várzea site (Mamirauá: Ayres 1993) at the same longitude (65° W) show that the latter on average have a higher number of trees bearing fruit during any given month of the year. Similarly, the flood disturbance may generate a more heterogeneous environment containing a greater diversity of successional habitats, which tend to fruit at different times of the year. As the bulk of the large mammal fauna was frugivorous (Table 3), seasonal use by mammals of these habitats may be vital in periods of fruit scarcity. On the other hand, habitat diversity in the

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terra firme forest matrix tends to be lower, and the lack of alternative fruit resources during periods of scarcity may severely limit the carrying capacity of this forest type.

Furthermore, levels of phytochemical defences may decrease in várzea forest due to less-limiting nutrient uptake. Foliage quality may therefore be more favourable to folivores, as plants are more likely to replace leaf tissue lost to herbivores rather than invest in secondary metabolites (Janzen 1974). The overwhelming density and biomass of many folivores such as howler monkeys, hoatzins (*Opisthocomus hoazin*), horned screamers (*Anhima cornuta*), iguanas (*Iguana iguana*) and the two genera of sloths (*Bradypus* and *Choloepus*) in várzea compared with terra firme (Peres 1997a, Queiroz 1995, T. Haugaasen, unpubl. data) support these predictions. This is also supported by evidence from the mature floodplain site (Cocha Cashu), which not only supported a full complement of terrestrial and understorey mammals, but also a large abundance of arboreal folivores (see Table 3), resulting in its intermediate positioning in the MDS. Although Cocha Cashu only experiences occasional supra-annual flood pulses, this may result in more fertile soils than those of terra firme and the mature floodplain site therefore bears most resemblance to várzea in terms of numbers of folivores. Klinge *et al.* (1983) also showed that várzea forest is more deciduous than terra firme forest. This resulted in lower leaf longevity and a higher abundance of young foliage, which have a more favourable nutrient level and contain reduced levels of chemical defences compared with mature foliage (Klinge *et al.* 1983).

### Broad patterns in species richness and habitat use

The consistently impoverished mammal fauna in várzea environments in central-western Amazonia and at Uauaçú, which appears to be typical of the lower Rio Purús region, is consistent with other studies in flooded and unflooded forests on plant (Ayres 1993, Balslev *et al.* 1987, Campbell *et al.* 1986, Gentry 1982) and animal communities (Patton *et al.* 2000, Peres 1997b, 1999b). Strictly terrestrial mammals were conspicuously absent in várzea forests cut off from adjacent upland habitats by river channels (Table 3). Prolonged seasonal inundation alone prohibits terrestrial and understorey species from using this forest type for much of the year, and this is perhaps the simplest reason to explain the lower mammal species richness in várzea. A select set of terrestrial mammals, however, may be able to use várzeas at certain times of the year (Bodmer 1989, this study), temporarily boosting the vertebrate species richness of this habitat. However, this seems to be largely a function of physical connectivity and proximity to adjacent terra firme forests, as there was a dramatic loss of species across the river channel from site F, which abutted terra firme terraces, to sites D and E which did not. This suggests that this *c.* 50-m-wide paranã channel provides an effective barrier to dispersal and movements by many species including primates and terrestrial mammals. Even when the water level at várzea forest sites D and E had receded, only a handful of large-mammal species – which were arboreal (primates), semi-arboreal (coati and tayra) or adept swimmers (tapir, red brocket deer *Mazama americana* and jaguar) – could be observed at these unconnected sites.

The channel barrier aside, the success of the species found in várzea forest may be due to their ability to digest leaves (howler monkeys) or their generalized diets (squirrel monkeys and brown capuchins). These latter species use all forest strata from the ground to the canopy and feed on a mixture of fruit and arthropods. Brown capuchins also consume a variety of flowers and other non-reproductive plant material (Terborgh 1983, T. Haugaasen, unpubl. data). They may therefore be better adapted to the seasonal disruption of certain food supplies by flooding. Small-bodied understorey primates consuming large arthropod prey, such as pygmy marmoset (*Cebuella pygmaea*), tamarins (*Saguinus* spp.) and Goeldi's monkey (*Callimico goeldii*), do not occur in large expanses of annually flooded várzea forests along the Rio Juruá, presumably due to the seasonal submersion or lack of understorey foraging substrates (Peres 1997b). Seasonal floods can therefore have considerable impact also on arboreal mammals, and this partly contradicts the prediction that floods should have little or no impact on such mammals.

The overall higher abundance of arboreal compared with terrestrial mammals (Table 3) may be due to the ability of arboreal mammals to take advantage of the fruit resources as they ripen in the canopy. Terrestrial mammals must make a living from the residual fruitfall, in other words the excess fruit produced or the scraps left behind by arboreal mammals. Similarly, the fact that terrestrial species tend to be larger may cause this discrepancy, as population density is inversely related to the average adult body mass of a given species, with larger animals occurring at lower densities than smaller animals (Damuth 1981, Eisenberg 1980, Peters & Raelson 1984, Robinson & Redford 1986).

In summary, our results suggest that broad patterns of species richness, abundance and biomass in Amazonian mammal assemblages partly reflect the combined effects of forest structure and connectivity, habitat heterogeneity and floristic diversity which differ markedly between terra firme and várzea environments (ter Steege *et al.* 2003). However, there may still be less apparent and poorly understood relationships between the idiosyncrasies of different species and their habitats, which affect mammal assemblage structure.

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### Conservation implications

The consistently lower species richness in várzea should not imply that this major Amazonian forest type should be neglected in future conservation planning (cf. Goulding *et al.* 2003, Peres & Terborgh 1995). We have demonstrated that várzea forests differ profoundly from adjacent terra firme forests in terms of mammal species composition, abundance and biomass. Evidence from elsewhere similarly suggests that a large number of bird (Remsen & Parker 1983) and tree (Balslev *et al.* 1987, Kubitzki 1989) species are endemic or show a strong preference to várzea forest. Data provided here and elsewhere also show that several vertebrate species may use flooded forests on a seasonal basis, suggesting that habitat complementarity is crucial to the long-term population viability of wide-ranging species. This has been clearly shown for aquatic organisms (Gottsberger 1978, Goulding 1980, 1983, 1985; Junk *et al.* 1997). These results suggest that várzea forests comprise an important complement to terra firme forest in terms of regional-scale biodiversity conservation and that conservation planning in Amazonian forests must be considered on a landscape scale.

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## LITERATURE CITED

AYRES, J. M. 1993. *As matas de várzea do Mamirauá*. Sociedade Civil Mamiraua, Belém. 96 pp.

AYRES, J. M. & CLUTTON-BROCK, T. H. 1992. River boundaries and species range size in Amazonian primates. *American Naturalist* 140:531–537.

BALSLEV, H., LUTEYN, J., ØLLGARD, B. & HOLM-NIELSEN, L. B. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botanica* 92:37–57.

BAYLEY, P. N. & PETRERE, M. 1989. Amazon fisheries: assessment methods, current status and management options. *Special Publications of the Canadian Journal of Fisheries and Aquatic Sciences* 106:385–398.

BODMER, R. E. 1989. *Frugivory in Amazon ungulates*. Ph.D. Thesis, University of Cambridge, Cambridge.

CAMPBELL, D. G., DALY, D. C., PRANCE, G. T. & MACIEL, U. N. 1986. Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingú, Brazilian Amazon. *Brittonia* 38:369–393.

CLARKE, K. R. 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.

DAMUTH, J. 1981. Population density and body size in mammals. *Nature* 290:699–700.

DIXON, J. R. & SOINI, P. 1986. *The reptiles of the upper Amazon Basin, Iquitos Region, Peru*. Milwaukee Public Museum, Milwaukee. 154 pp.

EISENBERG, J. F. 1980. The density and biomass of tropical mammals. Pp. 35–55 in Soulé, M. E. & Wilcox, B. A. (eds). *Conservation biology – An evolutionary-ecological perspective*. Sinauer Associates, Sunderland.

GASCON, C. 1996. Amphibian litter fauna and river barriers in flooded and non- flooded Amazonian rain forests. *Biotropica* 28:136–140.

GASCON, C., MALCOLM, J. R., PATTON, J. L., DA SILVA, M. N. F., BOGART, J. P., LOUGHEED, S. C., PERES, C. A., NECKEL, S. & BOAG, P. T. 2000. Riverine barriers and the geographic distribution of Amazonian species. *Proceedings of the National Academy of Sciences of the USA* 97:13672–13677.

GENTRY, A. H. 1982. Patterns of Neotropical plant-species diversity. *Evolutionary Biology* 15:1–85.

GENTRY, A. H. 1988. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the USA* 85:156–159.

GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of Huamaita, Amazonia. *Biotropica* 10:170–183.

GOULDING, M. 1980. *The fishes and the forest. Explorations in Amazonian history*. University of California Press, Berkley. 280 pp.

GOULDING, M. 1983. The role of fishes in the seed dispersal and plant distribution in Amazonian flood plain ecosystems. Pp. 271–283 in Kubitzki, K. (ed.). *Dispersal and distribution*. Verlag Paul Parey, Hamburg.

GOULDING, M. 1985. Forest fishes of the Amazon. Pp. 267–276 in Prance, G. T. & Lovejoy, T. E. (eds). *Amazonia*. Pergamon Press, Oxford.

GOULDING, M., BARTHEM, R. & FERREIRA, E. J. G. 2003. *The Smithsonian Atlas of the Amazon*. Smithsonian Institution Press, Washington. DC. 256 pp.

IRION, G. 1978. Soil infertility in the Amazonian rain forest. *Naturwissenschaften* 65:515–519.

IRION, G., JUNK, W. J. & DE MELLO, J. A. S. N. 1997. The large central Amazonian river floodplains near Manaus: geological, climatological, hydrological and geomorphological aspects. Pp. 23–46 in Junk, W. J. (eds). *The Central Amazon floodplain: ecology of a pulsing system*. Springer-Verlag, Berlin.

JANSON, C. H. & EMMONS, C. H. 1990. Ecological structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. Pp.314–338 in Gentry, A. H. (ed.). *Four neotropical rainforests*. Yale University Press, New Haven.

JANZEN, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6:69–103.

JUNK, W. J. 1989. Flood tolerance and tree distribution in Central Amazonian floodplains. Pp. 47–64 in Nielsen, L. B., Nielsen, I. C. &

https://doi.org/10.1017/S026646740400207X Published online by Cambridge University Press

Balslev, H. (eds). *Tropical forests: botanical dynamics, speciation and diversity*. Academic Press, London.

JUNK, W. J. & PIEDADE, M. T. F. 1993. Biomass and primary-production of herbaceous plant communities in the Amazon floodplain. *Hydrobiology* 263:155–162.

JUNK, W. J., SOARES, M. G. M. & SAINT-PAUL, U. 1997. The fish. Pp. 385–408 in Junk, W. J. (ed.). *The Central Amazon flood plain. Ecology of a pulsing system*. Springer-Verlag, Berlin.

KLINGE, H., FURCH, B., HARMS, E. & REVILLA, J. D. 1983. Foliar nutrient levels of native tree species from Central Amazonia. 1. Inundation forest. *Amazoniana* 8:19–45.

KUBITZKI, K. 1989. The ecogeographical differentiation of Amazonian inundation forests. *Plant Systematics and Evolution* 162:285–304.

KUBITZKI, K. & ZIBURSKI, A. 1994. Seed dispersal in flood-plain forests of Amazonia. *Biotropica* 26:30–43.

LIU, K. B. & COLINVAUX, P. A. 1985. Forest changes in the Amazon Basin during the last glacial maximum. *Nature* 318:556–557.

PAROLIN, P. 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. *Oecologia* 128:326–335.

PATTERSON, B. D., STOTZ, D. F., SOLARI, S., FITZPATRICK, J. W. & PACHEO, V. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593–607.

PATTON, J. L., DA SILVA, M. N. F. & MALCOLM, J. R. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History* 244:1–306.

PERES, C. A. 1994. Primate responses to phenological changes in an Amazonian terra firme forest. *Biotropica* 26:98–112.

PERES, C. A. 1997a. Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp.). *Folia Primatologica* 68:199–222.

PERES, C. A. 1997b. Primate community structure at twenty western Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* 13:381–405.

PERES, C. A. 1999a. General guidelines for standardising line-transect surverys of tropical forest primates. *Neotropical Primates* 7:11–16.

PERES, C. A. 1999b. The structure of nonvolant mammal communities in different Amazonian forest types. Pp. 564–578 in Eisenberg, J. F. & Redford, K. H. (eds). *Mammals of the Neotropics: the central Neotropics*. The University of Chicago Press, Chicago.

PERES, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14:240–253.

PERES, C. A. & DOLMAN, P. M. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122:175–189.

PERES, C. A. & JANSON, C. H. 1999. Species coexistence, distribution and environmental determinants of neotropical primate richness: a community-level zoogeographic analysis. Pp. 55–74 in Fleagle, J. G., Janson, C. H. & Reed, K. E. (eds). *Primate communities*. Cambridge University Press, Cambridge.

PERES, C. A. & TERBORGH, J. W. 1995. Amazonian nature reserves – an analysis of the defensibility status of existing conservation units and design criteria for the future. *Conservation Biology* 9:34–46.

PERES, C. A., PATTON, J. L. & DA SILVA, M. N. F. 1996. Riverine barriers and gene flow in Amazonian saddle-back tamarins. *Folia Primatologica* 67:113–124.

PETERS, R. H. & RAELSON, J. V. 1984. Relations between individual size and mammalian population density. *American Naturalist* 124:498–517.

PRANCE, G. T. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia* 31:26–38.

QUEIROZ, H. L. 1995. *Preguiças e guaribas: os mamiferos folivoros arboricolas do Mamirauá*. Sociedade Civil Mamirauá, Belém. 161 pp.

RÄSÄNEN, M. E., SALO, J. S. & KALLIOLA, R. J. 1987. Fluvial perturbance in the Western Amazon Basin – regulation by long-term sub-Andean tectonics. *Science* 238:1398–1401.

REMSEN, J. V. & PARKER, T. A. 1983. Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica* 15:223–231.

ROBINSON, J. G. & REDFORD, K. H. 1986. Body size, diet, and population density of Neotropical forest mammals. *American Naturalist* 128:665–680.

RODRIGUEZ, L. B. & DUELLMAN, W. F. 1994. Guide to the frogs of the Iquitos region, Amazonian Peru. *The University of Kansas Natural History Museum Publication* 22:1–80.

SALO, J., KALLIOLA, R., HAKKINEN, I., MAKINEN, Y., NIEMELA, P., PUHAKKA, M. & COLEY, P. D. 1986. River dynamics and the diversity of Amazon lowland forest. *Nature* 322:254–258.

SIOLI, H. 1968. Hydrochemistry and geology in the Brazilian Amazon region. *Amazoniana* 1:267–277.

TERBORGH, J. 1983. *Five new world primates – A study in comparitive ecology*. Princeton University Press, Princeton. 260 pp.

TERBORGH, J. 1985. Habitat selection in Amazonian birds. Pp. 311–338 in Cody, M. L. (ed.). *Habitat selection in birds*. Academic Press, New York.

TERBORGH, J. & ANDRESEN, E. 1998. The composition of Amazonian forests: patterns at local and regional scales. *Journal of Tropical Ecology* 14:645–664.

TERBORGH, J., ROBINSON, S. K., PARKER, T. A., MUNN, C. A. & PIERPONT, N. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60:213–238.

TER STEEGE, H., SABATIER, D., CASTELLANOS, H., VAN ANDEL, T., DUIVENVOORDEN, J., DE OLIVEIRA, A. A., EK, R., LILWAH, R., MAAS, P. & MORI, S. 2000. An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology* 16:801–828.

TER STEEGE, H., PITMAN, N., SABATIER, D., CASTELLANOS, H., VAN DER HOUT, P., DALY, D. C., SILVEIRA, M., PHILLIPS, O., VASQUEZ, R., VAN ANDEL, T., DUIVENVOORDEN, J., DE OLIVEIRA, A. A., EK, R., LILWAH, R., THOMAS, R., VAN ESSEN, J., BAIDER, C., MAAS, P., MORI, S., TERBORGH, J., VARGAS, P. N., MOGOLLON, H. & MORAWETZ, W. 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodiversity and Conservation* 12:2255–2277.

THOMAS, L., LAAKE, J. L., STRINDBERG, S., MARQUES, F. F. C., BUCKLAND, S. T., BORCHERS, D. L., ANDERSON, D. R., BURNHAM, K. P., HEDLEY, S. L. & POLLARD, J. H. 2002. Distance 4.0 Release 1. University of St. Andrews. Research Unit for Wildlife Population Assessment. http://www.ruwpa.st-and.ac.uk/distance/.

https://doi.org/10.1017/S026646740400207X Published online by Cambridge University Press

TUOMISTO, H. & RUOKOLAINEN, K. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain-forest. *Journal of Vegetation Science* 5:25–34.

TUOMISTO, H., RUOKOLAINEN, K., KALLIOLA, R., LINNA, A., DANJOY, W. & RODRIGUEZ, Z. 1995. Dissecting Amazonian biodiversity. *Science* 269:63–66.

VOSS, R. S. & EMMONS, L. H. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American Museum of Natural History* 230:3–115.

WARWICK, R. M. & CLARKE, K. R. 1993. Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology* 172:215–226.

WILSON, D. E. & REEDER, D. M. (eds). 1993. *Mammal species of the world*. Smithsonian Institution Press, Washington. DC. 1206 pp.

WORBES, M. 1997. The forest ecosystem of the floodplains. Pp. 223–266 in Junk, W. J. (eds). *The Central Amazon flood plain. Ecology of a pulsing system*. Springer-Verlag, Berlin.

**Appendix 1.** Characteristics of the different species included in the analysis of assemblage structure at different central-western Amazonian sites of varying forest types. Species are ordered according to body mass within families.

| Species | Mean body mass (kg)[1] | Trophic classification[1,2] | Forest level[1,3] |
|---|---|---|---|
| Primates | | | |
| Callitrichidae | | | |
| *Cebuella pygmaea* | 0.15 | Ex/In | U, Sc |
| *Saguinus fuscicollis* | 0.39 | Fr/In | U, Sc |
| *Saguinus mystax/imperator* | 0.51 | Fr/In | Sc, U |
| *Callimico goeldii* | 0.59 | | |
| Cebidae | | | |
| *Saimiri ustus/boliviensis* | 0.94 | Fr/In | Sc, C |
| *Callicebus cupreus* | 1.05 | Fr/Sp | U, Sc |
| *Callicebus torquatus* | 1.2 | Fr/In | Sc, U |
| *Pithicia albicans/monachus* | 2.2 | Sp/Fr | Sc, C |
| *Cebus apella* | 2.91 | Fr/Sp/In/Vp | Sc, C, U |
| *Cebus albifrons* | 2.7 | Fr/Sp/In/Vp | Sc, U, T |
| *Cacajao calvus* | 3.17 | Sp/Fr | C, Sc |
| *Alouatta seniculus* | 6.5 | Fo/Fr | C, Sc |
| *Lagothrix lagotricha* | 8.71 | Fr/Fo | C, Sc |
| *Ateles chamek* | 9.02 | Fr | C, Sc |
| Xenarthra | | | |
| Myrmecophagidae | | | |
| *Tamandua tetradactyla* | 4.6 | A/In | Sc, U, T |
| *Myrmecophaga tridactyla* | 27.0 | A/In | T |
| Rodentia | | | |
| Sciuridae | | | |
| *Microsciurus flaviventer* | 0.1 | Sp/Fr | U, Sc |
| *Sciurus ignitus* | 0.22 | Sp/Fr | Sc, U |
| *Sciurus spadiceus* | 0.6 | Sp/Fr | U, T |
| Dasyproctidae | | | |
| *Myoprocta pratti* | 0.75 | Sp/Fr | T |
| *Dasyprocta fuliginosa* | 4.5 | Sp/Fr | T |
| Carnivora | | | |
| Procyonidae | | | |
| *Nasua nasua* | 3.1 | In/Vp | T, U |
| Mustelidae | | | |
| *Eira barbara* | 4.8 | Fr/In/Vp | T, U |
| Perissodactyla | | | |
| Tapiridae | | | |
| *Tapirus terrestris* | 150.0 | Fr/Fo | T |
| Artiodactyla | | | |
| Tayassuidae | | | |
| *Pecari tajacu* | 25.0 | Sp/Fr/Vp | T |
| *Tayassu pecari* | 32.0 | Sp/Fr/Vp | T |
| Cervidae | | | |
| *Mazama gouazoubira* | 18.0 | Fr/Fo | T |
| *Mazama americana* | 30.0 | Fr/Fo | T |

[1]Mean body mass, trophic classifications and stratification use were derived from Peres & Dolman (2000), Peres (1999b) and Robinson & Redford (1986).
[2]Diet: Ex = Exudate feeder; Fr = Frugivore; In = Insectivore; Sp = Seed predator; Vp = Vertebrate predator; Fo = Folivore; A = Anteater.
[3]Forest levels: T = terrestrial; C = canopy; U = understorey; Sc = sub-canopy. Listed in order of preference.

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**Appendix 2.** Summary of the non-volant mammal community in terra firme (TF) and várzea (VZ) forests at Uauaçú. Species are ordered according to body mass within families.

| | Group size[1] | | N[2] | | Groups[3] ($km^{-2}$) | | Individuals ($km^{-2}$) | | Biomass[4] ($kg\ km^{-2}$) | | Detection[5] | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | TF | VZ | TF | VZ | TF | VZ | TF | VZ | TF | VZ | TF | VZ |
| Primates | | | | | | | | | | | | |
| Callitrichidae | | | | | | | | | | | | |
| *Cebuella pygmaea* | – | – | – | – | – | – | – | – | – | – | I | – |
| *Saguinus mystax pileatus*[6,7] | 9.25 | 4.3 | 107 | 8 | 2.93 | 0.33 | 27.1 | 1.4 | 10.8 | 0.56 | C | C |
| *Saguinus fuscicollis avilapiresi*[6] | 5.25 | 2.4 | 107 | 8 | 2.93 | 0.33 | 15.4 | 0.8 | 4.6 | 0.24 | C | C |
| Cebidae | | | | | | | | | | | | |
| *Saimiri* cf. *ustus* | 26.9 | 10.5 | 11 | 240 | 0.85 | 11.0 | 22.9 | 116.0 | 18.3 | 92.8 | C | C |
| *Aotus* cf. *nigriceps* | – | – | – | – | – | – | – | – | – | – | A | – |
| *Callicebus cupreus* | – | – | 5 | – | – | – | – | – | – | – | C | – |
| *Callicebus torquatus purinus* | 3.0 | – | 7 | – | 0.19* | – | 0.57 | – | 0.6 | – | C | – |
| *Pithecia albicans* | 3.9 | 3.0 | 36 | 15 | 0.82 | 0.19 | 3.2 | 0.6 | 5.8 | 1.1 | C | C |
| *Cebus apella* | 7.2 | 6.1 | 139 | 298 | 4.19 | 11.4 | 30.2 | 69.9 | 69.5 | 160.8 | C | C |
| *Cebus albifrons versicolor* | 10.3 | – | 12 | 2 | 0.32 | – | 3.3 | – | 7.3 | – | C | C |
| *Alouatta seniculus seniculus* | – | 3.8 | 3 | 123 | – | 3.5 | – | 13.4 | – | 69.7 | C | C |
| *Lagothrix lagotricha cana* | 14.7 | – | 27 | – | 1.38 | – | 20.3 | – | 142.1 | – | C | – |
| *Ateles chamek* | – | – | 5 | – | – | – | – | – | – | – | C | I |
| Total primates | | | 352 | 686 | 10.7 | 26.4 | 123.0 | 201.1 | 259.0 | 325.2 | | |
| Xenarthra | | | | | | | | | | | | |
| Myrmecophagidae | | | | | | | | | | | | |
| *Cyclopes didactylus* | – | – | – | – | – | – | – | – | – | – | A | – |
| *Tamandua tetradactyla* | 1.0 | 1.0 | 6 | 7 | 0.12 | 0.36 | 0.12 | 0.4 | 0.4 | 1.5 | C | C |
| *Myrmecophaga tridactyla* | 1.25 | – | 4 | – | 0.33* | – | 0.41 | – | 8.6 | – | C | |
| Bradipodidae | | | | | | | | | | | | |
| *Bradypus tridactylus* | 1.0 | 1.0 | 1 | 2 | – | – | – | – | – | – | C | C |
| Megalonychidae | | | | | | | | | | | | |
| *Choloepus didactylus* | – | 1.0 | – | 1 | – | – | – | – | – | – | – | C |
| Dasypodidae | | | | | | | | | | | | |
| *Dasypus novemcinctus* | 1.0 | – | 1 | – | – | – | – | – | – | – | V | – |
| *Dasypus kappleri* | 1.0 | – | 1 | – | – | – | – | – | – | – | V | – |
| *Priodontes maximus* | 1.0 | – | 1 | – | – | – | – | – | – | – | C | – |
| Rodentia | | | | | | | | | | | | |
| Sciuridae | | | | | | | | | | | | |
| *Sciurus spadiceus*[6] | 1.16 | 1.16 | 32 | 32 | 0.99 | 1.62 | 1.15 | 1.9 | 0.6 | 1.0 | C | C |
| *Sciurus ignitus*[6] | 1.0 | – | 32 | – | 0.08 | – | 0.08 | – | 0.02 | – | C | – |
| *Microsciurus flaviventer* | 1.8 | – | 5 | – | 0.34* | – | 0.61 | – | 0.06 | – | C | – |
| Dasyproctidae | | | | | | | | | | | | |
| *Agouti paca* | 1.0 | 1.0 | 3 | 1 | – | – | – | – | – | – | C | V |
| *Dasyprocta fuliginosa* | 1.04 | 1.03 | 224 | 32 | 7.69 | 1.07 | 8.0 | 1.1 | 28.8 | 4.0 | C | C |
| *Myoprocta pratti* | 1.06 | – | 65 | – | 2.8 | – | 2.97 | – | 1.78 | – | C | – |
| Carnivora | | | | | | | | | | | | |
| Procyonidae | | | | | | | | | | | | |
| *Nasua nasua* | 2.5 | 8.42 | 2 | 19 | 0.07* | 0.71 | 0.18 | 6.0 | 0.5 | 15.0 | C | C |
| *Potos flavus* | 1.0 | – | 1 | – | – | – | – | – | – | – | V | – |
| Mustelidae | | | | | | | | | | | | |
| *Pteronura brasiliensis* | – | – | – | – | – | – | – | – | – | – | H | – |
| *Lontra longicaudis* | 1.5 | 1.0 | 2 | 2 | – | – | – | – | – | – | C | C |
| *Eira barbara* | 1.5 | 1.33 | 3 | 6 | 0.33* | 0.12* | 0.5 | 0.16 | 1.9 | 0.8 | C | C |
| *Galictis vittata* | 1.0 | – | 1 | – | – | – | – | – | – | – | C | – |
| Canidae | | | | | | | | | | | | |
| *Atelocynus microtis* | 1.0 | – | 1 | – | – | – | – | – | – | – | C | – |
| *Speothos venaticus* | – | – | – | – | – | – | – | – | – | – | H | – |
| Felidae | | | | | | | | | | | | |
| *Panthera onca* | 1.0 | 1.0 | 1 | 1 | – | – | – | – | – | – | C | C |
| *Puma concolor* | 1.33 | – | 3 | – | 0.12* | – | 0.16 | – | 5.92 | – | C | – |
| *Leopardus pardalis* | 1.0 | – | 1 | – | – | – | – | – | – | – | V | – |
| *Leopardus wiedii* | – | – | – | – | – | – | – | – | – | – | I | – |
| *Herpailurus yaguarondi* | – | – | – | – | – | – | – | – | – | – | I | – |

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**Appendix 2.** Continued.

| | Group size[1] | | N[2] | | Groups[3] ($km^{-2}$) | | Individuals ($km^{-2}$) | | Biomass[4] ($kg\ km^{-2}$) | | Detection[5] | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | TF | VZ | TF | VZ | TF | VZ | TF | VZ | TF | VZ | TF | VZ |
| Perissodactyla | | | | | | | | | | | | |
| Tapiridae | | | | | | | | | | | | |
| *Tapirus terrestris* | 1.22 | – | 9 | 4 | 0.19 | – | 0.23 | – | 25.6 | – | C | C |
| Artiodactyla | | | | | | | | | | | | |
| Tayassuidae | | | | | | | | | | | | |
| *Pecari tajacu* | 3.43 | – | 21 | 5 | 0.61 | – | 2.09 | – | 41.8 | – | C | C |
| *Tayassu pecari* | 103.3 | – | 3 | – | 0.02* | – | 2.48 | – | 63.48 | – | C | – |
| Cervidae | | | | | | | | | | | | |
| *Mazama gouazoubira*[6] | 1.0 | – | 40 | – | 0.08 | – | 0.08 | – | 1.15 | – | C | – |
| *Mazama americana*[6] | 1.0 | 1.0 | 40 | 7 | 0.16 | 0.16* | 0.16 | 0.16 | 3.84 | 4.8 | C | C |
| Total | | | 782 | 801 | 24.6 | 30.4 | 142.2 | 210.8 | 443.5 | 352.1 | | |

[1]Mean group size obtained from all visual detection events.
[2]Number of individual detection events.
[3]All densities derived with DISTANCE (Thomas *et al.* 2002) using the Half-Normal model except *where King's method was used.
[4] Biomass estimates calculated using data presented in Peres & Dolman (2000), Peres (1999b) and Robinson & Redford (1986).
[5]Documented as following: C = observed during census; I = interviews with locals; A = acoustic detection; V= visual detection at other times than censuses; H = hypothetical.
[6]Pooled in the analysis.
[7]Although moustached tamarins at Uauaçú occur within the geographic range of the reddish-capped *Saguinus mystax pileatus*, these are more similar to the epiphenotype of the black-capped *Saguinus mystax mystax*.

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