

Tree reproductive phenology determines the abundance of medium-sized and large mammalian assemblages in the Guyana shield of the Brazilian Amazonia

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Abstract

Tree reproductive phenology determines the abundance of medium-sized and large mammalian assemblages in the Guyana shield of the Brazilian Amazonia. Assemblages of medium and large-sized mammals were studied in the Guyana shield of the Brazilian Amazonia. Diurnal and nocturnal line-transect samplings were carried out via the line-transect method in five different forest types along a 10-km transect, along which we also recorded habitat variables, such as tree species diversity, reproductive phenology, and residual fruit productivity. Group density was separately calculated for all mammalian species in the five forest types. Stepwise multiple regression analyses were performed to determine which habitat variables best predicted the mammalian species densities in the sampled forests. The sole determinants of mammalian densities in the forest types studied were basal area of each forest type, total number of tree species in each forest type, and tree reproductive phenology.

Key words: Mammalian assemblages, Group density, Environmental determinants, Forest productivity, Tree reproductive phenology, Amazonia

Resumen

La fenología reproductiva de los árboles determina la abundancia de las comunidades de mamíferos de talla media y grande en el escudo de Guyana de la Amazonia brasileña. Se estudiaron varias comunidades de mamíferos de talla mediana y grande en el escudo de Guyana de la Amazonia brasileña. Se realizaron muestreos en transectos lineales diurnos y nocturnos de 10 km de longitud en cinco tipos distintos de bosque, a lo largo de los que también se registraron variables del hábitat, como la diversidad de especies arbóreas, la fenología reproductiva y la productividad residual de frutos. La densidad del grupo se calculó por separado para todas las especies de mamíferos en los cinco tipos de bosque. Se llevaron a cabo análisis escalonados de regresión múltiple para determinar qué variables del hábitat permitían predecir mejor la densidad de las especies de mamíferos en los bosques muestreados. Los únicos factores determinantes de la densidad de mamíferos en los tipos de bosques estudiados fueron el área basimétrica de cada tipo de bosque, el número total de especies arbóreas en cada tipo de bosque y la fenología reproductiva de los árboles.

Palabras clave: Comunidades de mamíferos, Densidad de grupo, Factores determinantes ambientales, Productividad forestal, Fenología reproductiva de los árboles, Amazonia

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Introduction

For many decades the relationship between body mass and abundance of animals has been a major subject of study (Elton, 1932, 1933). There is a general trend for abundance to decrease with increasing body mass, among different taxa, such as insects and birds (Juanes, 1986; Gaston and Lawton, 1988; Blackburn et al., 1990; Nee et al., 1991; Santini et al., 2017). Studies on mammals from different regions of the Neotropics has also showed that density of tropical mammals decreases with increasing biomass, biomass increases with increasing body weight, and biomass is positively related to home range size (Milton and May, 1976; Clutton-Brock and Harvey, 1977; Eisenberg, 1980; Damuth, 1981; Peters and Wassenberg, 1983; Peters and Raelson, 1984; Robinson and Redford, 1989; Eisenberg, 1990; Santini et al., 2017).

Kinnaird and Eisenberg (1989) highlight, however, the importance of considering the dietary specialisation of the animals, which may cause variation in the relationship between density and biomass. They also show considerable scatter around the regression line, and explain that this is caused by diet and to a lesser extent by phylogeny. These abundance/body mass relationships depend on the availability and divisibility of food in the habitat (Hutchinson and MacArthur, 1959; Brown, 1981; Juanes, 1986; Maurer and Brown, 1988), which is also related to what Brown and Maurer (1986) envisioned, that larger species may monopolise the resources. This also agrees with Lawton's (1989) hypothesis that, through pre-emptive competition (Schoener, 1983), larger species have access to a greater share of the resources, to the detriment of the smaller. Furthermore, generalists should also occur at higher densities than specialists, for they have access to more food items (Brown, 1984; Gaston and Lawton, 1988).

In northernmost Brazilian Amazonia, on the Guyana Shield, lies one of the poorest regions in the Amazon basin for mammalian species diversity. Within it, the poorest area overall is the central zone, where rainfall is low and the dry season protracted (Eisenberg and Redford, 1979; Emmons, 1984; Janson and Emmons, 1990; Mendes Pontes, 2004; Hoorn et al., 2010; Luna et al., 2017). Here the vegetation is a mosaic of campinas (open, scrub vegetation), campinaranas (forests with short thin trees that stand in irregular, floodable terrain), and seasonally-dry to dry forests (Mendes Pontes et al., 2012). In such habitat, terrestrial mammalian abundance may be higher than for arboreal species, and may fluctuate seasonally and yearly due to resource scarcity (Janzen, 1974; Eisenberg et al., 1979; August, 1983; Schaller, 1983; Mendes Pontes, 2004).

Studies of medium- and large-sized mammals in northernmost Brazilian Amazonia are relatively recent and the focus has been mainly on the mammals of protected areas, such as Maracá Ecological Station (Nunes, 1992; Mendes Pontes, 1997, 1999, 2004; Fragoso, 1998; Mendes Pontes et al., 2007), and the Waimiri-Atroari (Mazurek et al., 2000), Yanomami and Macuxi Indian reserves (Fragoso, 2004), although most recently, Melo et al. (2015) and Luna et al. (2017)

studied the impacts on mammal assemblages of recent fishbone human settlements in Roraima state. It was revealed in these studies that the abundance of terrestrial mammal species can be greater than those of the arboreal ones, and that larger species can be more abundant than the smaller ones.

A wide variety of variables may affect the abundance of mammalian assemblages not subjected to human interference, including climate, tectonics, fluvial history, topography (Tuomisto et al., 1995, 2003; Kristiansen et al., 2012; Pomara et al., 2012, 2014; Rossetti, 2014; Higgins et al., 2011, 2015), rainfall (Janson et al., 1981; Terborgh, 1983), site temperature (Peters and Raelson, 1984), plant anti-predator defences (Janzen, 1974; Montgomery and Sunquist, 1978), home range size (Milton and May, 1976), predators (Andrewartha, 1961), competition (Emmons, 1984), among many others.

It has been shown in most studies, however, that mammalian abundance is, above all, a function of soil type, or, of geologically induced edaphic heterogeneity, drier climates, and longer dry seasons (Tuomisto et al., 1995, 2003, 2014; Hoorn et al., 2010; Kristiansen et al., 2012; Pomara et al., 2012, 2014; Rossetti, 2014; Higgins et al., 2011, 2015; Zuquim et al., 2014), and consequently, of forest structure and productivity (Eisenberg et al., 1979; Eisenberg, 1980; Emmons, 1984; Gentry and Emmons, 1987; Eisenberg, 1990; Kay et al., 1997; Hoorn et al., 2010; Marshall et al., 2014). This ultimately determines vegetation cover and complexity, both vertically and horizontally, as well as resource availability (Eisenberg and Thorington, 1973; August, 1983; Eisenberg, 1990; Glanz, 1990; Janson and Emmons, 1990; Malcolm, 1990; Chapman et al., 2002; Marshall and Leighton, 2006).

In this context, the mammalian assemblages should be regulated by the unpredictable, yet recurrent, fluctuations of seasonality, which plays a crucial determining role, since it may cause the species to change diet (MacArthur, 1969; Janson et al., 1981; Terborgh, 1983), habitat use, home range (Peres, 1994; Zhang and Wang, 1995), migrate (Caldecott, 1988; Fragoso, 1998), scatter-hoard (Smythe, 1978), and intensity with which individuals compete for available resources, or ultimately die of starvation (Foster, 1982a, 1982b). In contrast, increased availability of food resources may result in increased species abundance (Eisenberg and Thorington, 1973; August, 1983; Malcolm, 1990; Chapman et al., 2002; Marshall and Leighton, 2006).

Covariates of forest structure and productivity, such as stratification, floristic diversity, and phenology have been proposed as determinants of mammalian abundance (Malcolm, 1995; Gentile and Fernandez, 1999; Grelle, 2003; Marshall et al., 2014; Luna et al., 2017). Gadelha et al. (2017), studying a primate community in a habitat similar to that in the current study, found a significant association between mammalian abundance, and absolute dominance of trees, number of clearings, and vegetation height. No studies to date, however, had tested the effects of the forest structure and productivity covariates on whole assemblages of medium- and large-sized mammals in totally protected areas in the Brazilian Amazonia.

This is the first study for determining the drivers of the abundance of medium- and large-sized mammalian assemblages in highly-seasonal Amazonian forests. Our aim was to calculate the mammalian density in five forest types, and correlate them with the forest structure and the productivity covariates, such as basal area, of tree species diversity, phenology, and residual fruit productivity. Thus, we hypothesised that: (1) mammalian species diversity and densities are one of the poorest in the Amazonia due to the predicted harsher conditions of forest structure and productivity; (2) large-bodied mammals are more abundant than medium-sized ones, and terrestrial species, more abundant than arboreal ones due to the predicted more developed understorey and forest discontinuity of these highly-heterogeneous forest mosaics; and (3) mammalian densities are a function of tree reproductive phenology due to the scarcity and dramatic seasonal fluctuations that occur within, and between, forest types.

Material and methods

Study area

Maracá Ecological Station is located at latitude 3° 15'–3° 35' N and longitude 61° 22'–61° 58' W, comprising 1,013 km² of seasonally-dry forests (Ministério do Interior, 1977). Maracá is a fluvial island formed by the bifurcation of the Uraricoera River into the Maracá Channel (to the south), and Santa Rosa Channel (to the north) (fig. 1), although these channels do not comprise a barrier to most vertebrates, and many species can be seen regularly crossing the river (Mendes Pontes, unpubl. data). Though at least 95% of the island is forested (Milliken and Ratter, 1990) (fig. 2, 3), it lies at the junction between Amazonian forests (Hylea) and the grassland-dominated Rupununi savannas, which lie to the south and east. Mean annual temperature during the study period, 1997/1998, was 31.6 °C and rainfall was 1,577.3 mm, with a sharp decline in the dry season, from September to March (fig. 4).

The trail for this study was cut in the same area used in the Maracá Rainforest Project (National Environment Office–SEMA, and The Royal Geographical Society–UK) (Thompson et al., 1992), where many of the trees studied were already identified and tagged and forest types identified (Milliken and Ratter, 1990). A 10-km trail, 1 m width, was cut from the easternmost point of the forested area towards the northwest in a straight line. The trail was alpha-numerically marked with tags and paint-marks, and debris were regularly removed to minimize the disturbance when walking.

Forest types studied

Five contiguous and sharply-differentiated forest types were identified along the 10-km study transect, according to Milliken and Ratter (1990): the two major types that dominate eastern Maracá, Terra Firme and Mixed forest; the two minor ones that occur in small patches inserted in, and completely surrounded by,

the major ones and have similar height, Pau Roxo and Buritizal; and the very short, shrubby, multi-trunked Carrasco forest.

The main features of the five forest types described by Milliken and Ratter (1990) and complemented by this study (Supp Info 1) are:

Terra Firme forest (fig. 2, 3)

Normally about 25 to 35 m in height, emergent reaching 40 m. During the dry season some trees lose their leaves, including some emergent. Soils are Arenic Distrophic Plinthic Yellow Podzol (Carvalho et al., 1988; Thompson et al., 1992). During this study we increased the former species list of this forest type from 160 (Milliken and Ratter, 1990; Nunes, 1992) to 317 species of emergent, canopy and larger understorey trees. The number of trees with animal dispersed fruit syndrome was 194 (61.2%). The total basal area recorded by Milliken and Ratter (1990) was 182.7 m²/ha. The total area surveyed in this study was 45.5 ha.

Mixed forest (fig. 2, 3)

This has floristic composition and height similar to Terra Firme, but is distinguished by the presence of *Peltogyne gracilipes* Ducke (Leg. Caesalp.), a species absent from the Terra Firme forest, but which is particularly important due to its high density in some locations (Nascimento and Proctor, 1996; Nascimento et al., 1997), and by the large number of specimens of the palm *Oenocarpus bacaba* Mart and the giant herb *Phenakospermum guyannense* (A. Rich.) Endl. ex Miq. (Strelitziaceae) in the better developed ground layer. The soils were classified as Arenic Clayey Dystrophic Yellow and Red–Yellow Argisol (EMBRAPA, 2006). During this study we increased the former species list of this forest type from 201 (Milliken and Ratter, 1990) to 329 species (Mendes Pontes et al., 2013). The number of trees with animal dispersed fruit syndrome was 187 (56.8%). The total basal area recorded by Milliken and Ratter (1990) was 109.7 m²/ha. The total area surveyed in this study was 47.6 ha.

Pau–Roxo forest (fig. 2, 3)

Normally about 30 m in height. It is characterised by a predominance of *Peltogyne gracilipes* (Leg. Caesalp.), with very few other plant species, even being called *Peltogyne*-rich forest by Nascimento and Proctor (1996) and Nascimento et al. (1997). It is considered to be an almost-monodominant forest type, and is one of the tallest forest types in the study area, reaching 40 m (Milliken and Ratter, 1990). The soils were considered very sandy and acid with low concentrations of extractable nitrogen and phosphorous and exchangeable cations, especially for magnesium. It had less sand and more silt than the other forest types and varied from loamy sandy to silt clay (Nascimento et al., 1997). It was considered one of the poorest soils recorded in Amazonian lowland evergreen forests (Carvalho et al., 1988).

It is possible to identify this forest from the air during the dry season when leaves are lost. Frequent canopy discontinuity means that this forest is usually fairly open. During this study we increased the former

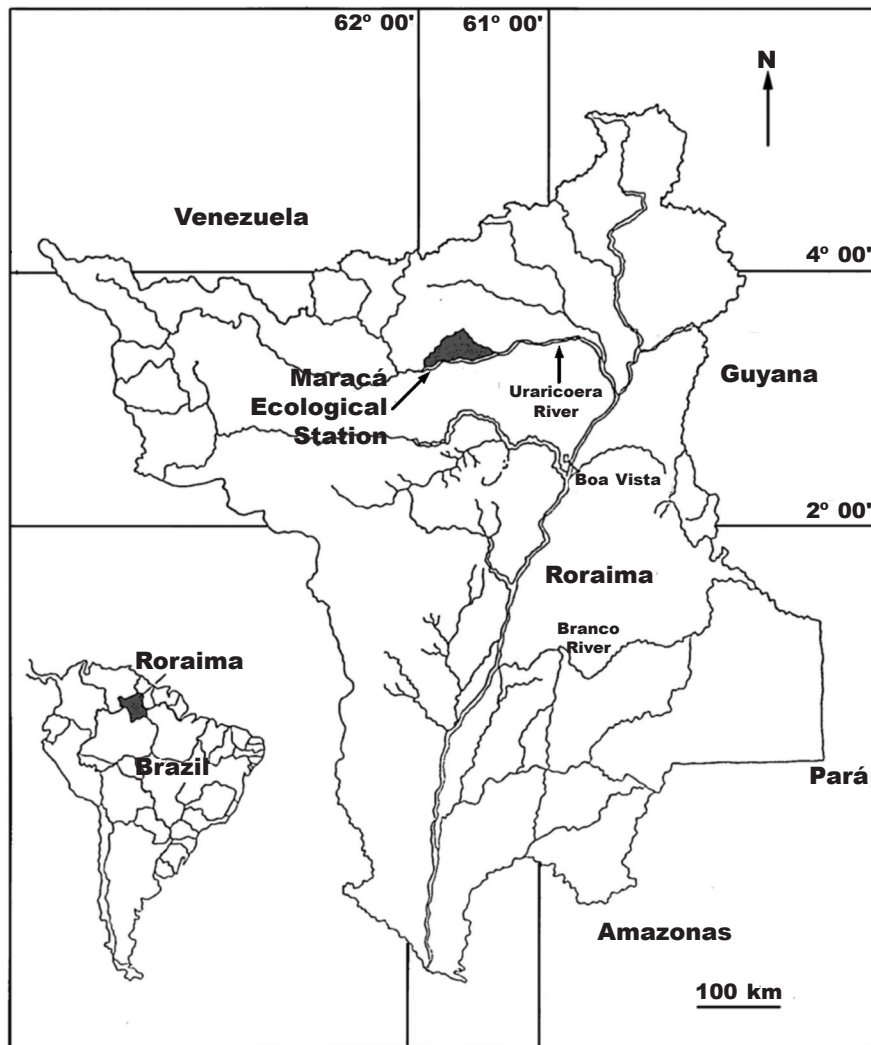


Fig. 1. Maracá Ecological Station, located in the State of Roraima, on the Guyana Shield of Brazilian Amazonia.

Fig. 1. Estación Ecológica de Maracá, situada en el Estado de Roraima, en el escudo de Guyana de la Amazonia brasileña.

species list of this forest type from 26 (Milliken and Ratter, 1990) to 47 species (Mendes Pontes et al., 2013). The number of trees with animal-dispersed fruit syndrome was 34 (72.3%). The total basal area recorded by Milliken and Ratter (1990) was 52.2 m²/ha. The total area surveyed in this study was 1.8 ha.

Buritizal forest (fig. 2, 3)

Occurs exclusively along those streams which flood during the wet season. The commonest plant species is *Mauritia flexuosa* L. (Arecaceae). Trees may reach 23 m in height, forming a discontinuous canopy. Soils are Clayey Dystrophic Red–Yellow Latosol and Clayey Dystrophic Red–Yellow Argisol (EMBRAPA, 2006). During this study we increased the former species list of this forest type from 19

(Milliken and Ratter, 1990) to 48 species (Mendes Pontes et al., 2013). The number of trees with animal dispersed fruit syndrome was 29 (60.4%). The total basal area recorded by Milliken and Ratter (1990) was 9 m²/ha. The total area surveyed in this study was 3.4 ha.

Carrasco forest (fig. 2, 3)

Comprises very small trees that do not exceed 1.5 m in height, all with a very shrubby, multi-trunked form, which makes it almost impossible to penetrate this vegetation formation. Characteristic plant species are the spiny climbing palm *Desmoncus polyacanthos* Mart. and the also very spinore *Bactris maraja* Mart. (Arecaceae). No soil information is available for this forest type. During this study we increased the former

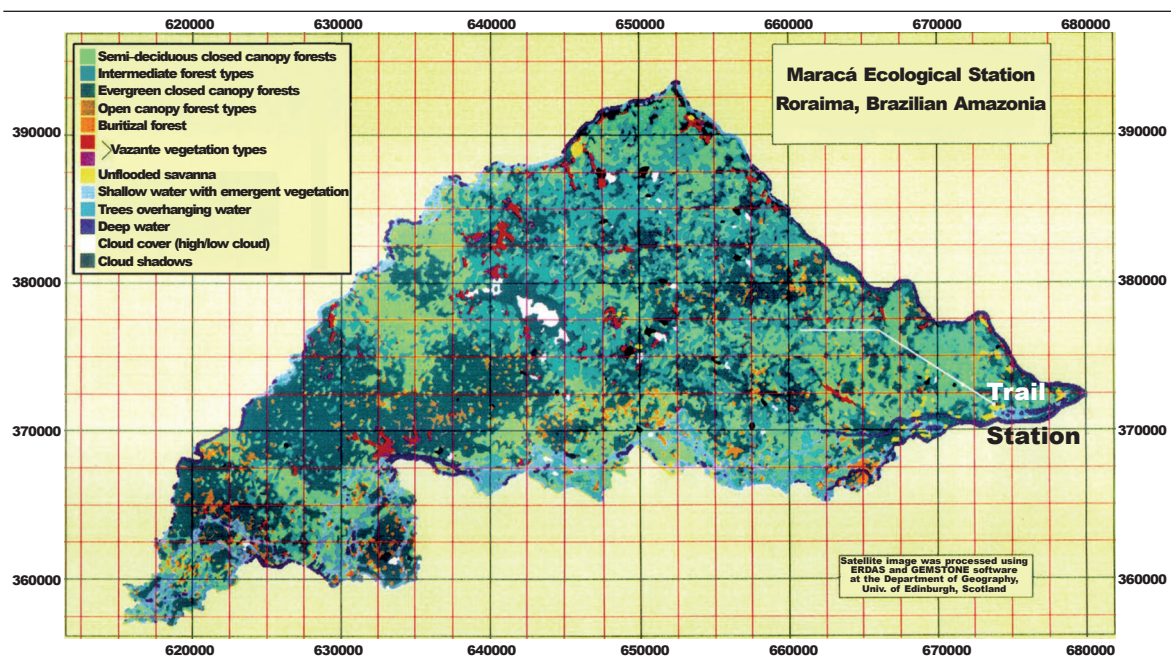


Fig. 2. The forest types at Maracá Ecological Station (according to Milliken and Ratter, 1990) at the landscape scale (10 to 200 km; Peterson et al., 2011), showing the location of the study transect.

Fig. 2. Los tipos de bosque en la Estación Ecológica de Maracá (según Milliken y Ratter, 1990) a escala de paisaje (de 10 a 200 km; Peterson et al., 2011), donde se indica la situación del transecto del estudio.

species list of this forest type from 34 (Milliken and Ratter, 1990) to 45 species (Mendes Pontes et al., 2013). The number of trees with animal dispersed fruit syndrome was 32 (71.1%). The total basal area was 0.23 m²/ha. The total area surveyed in this study was 1.7 ha.

Vegetation survey and forest productivity

Tree species of each forest type were sampled along sections of the study transect by the point-centred quarter (PCQ) transect method (Muller-Dombois and Elleberg, 1974), where, at each pre-established interval of 40 m, the four nearest trees with a DBH of at least 10 cm were marked. Using this method, we marked 504 trees, of which 493 were analyzed across the entire study period. Trees were marked with aluminium tags and vinyl flagging, and monitored monthly for leaves, flowers, and fruits (Mendes Pontes et al., 2013).

Fruit quantities were assessed visually in the forest canopy by counting the number of fruits on an entire branch, or section of the crown, with the help of powerful binoculars, and extrapolating to the number of units of the same size in the whole tree crown. When fruits occurred in bunches, as in palms, we averaged the number of fruits obtained from fallen bunches, which could be counted more accurately. Flowers and fruits were deposited in the Herbarium and carpological collection of the Roraima State Museum, Boa Vista, Brazil (Mendes Pontes et al., 2013).

We also monitored residual fruit production via a raked-ground fruit survey (Sabatier, 1985; Guillotin et al., 1994; Zhang and Wang, 1995), which consisted of surveying all fallen fruits in the same sampling sections of the study transect at regular intervals and removing them all from the sampled areas after each line-transect sampling. Fruits were collected weekly for an entire year, identified, weighed, and samples of each new collection were preserved, and were later deposited in the first fruit collection for Roraima State, built by the authors and housed in the Roraima State Museum (Mendes Pontes et al., 2013).

For each species fruit productivity was calculated by multiplying fruit number by the mean individual fruit weight of each species and total fruit production was obtained by summing up the production of all plant species sampled (Mendes Pontes et al., 2013). Tree-species identifications and fruit-dispersion syndromes followed Van Roosmalen (1985) and Lewis and Owen (1989), and, in all cases, were checked by the following experts: M. Van Roosmalen, L. Lohman, G. Lewis, and T. Pennington.

During the study period, we also collected fruits *ad libitum* whenever they were found within the study area, so that we could sample species that were not registered by any of the previously given methods, although this information was used only to build the checklist of species of each forest type (Mendes Pontes et al., 2013).

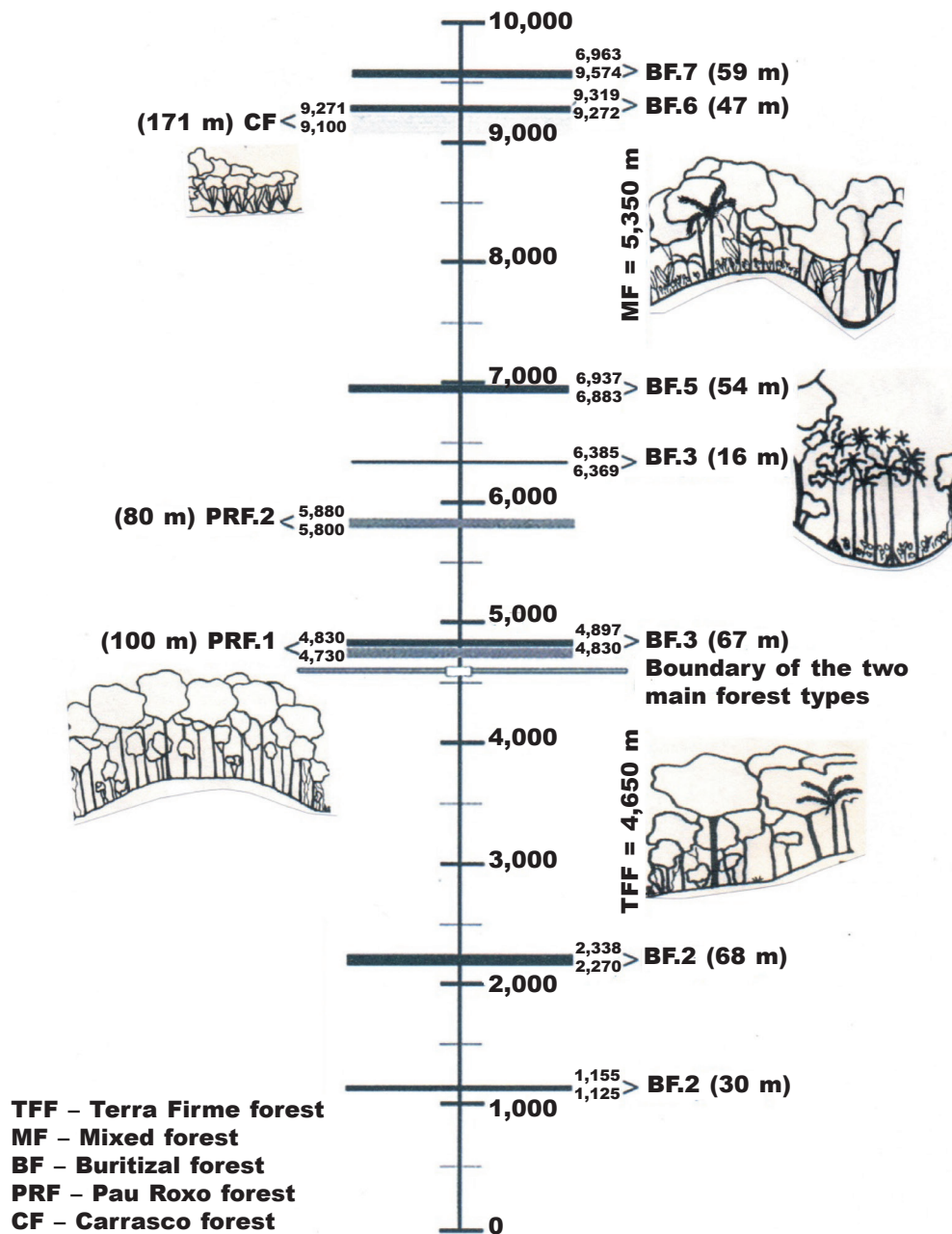


Fig. 3. Study transect with forest types (forest profiles are from Milliken and Ratter, 1990) at a micro-scale (site, or local scale, 10 m to 10 km; Peterson et al., 2011).

Fig. 3. Transecto del estudio con los tipos de bosque (perfiles forestales de Milliken y Ratter, 1990) a microescala (lugar o escala local, de 10 m a 10 km; Peterson et al., 2011).

Vertebrates line transect sampling

The trail was numerically marked at 50 m intervals, and had debris removed monthly to minimize disturbance. Diurnal line transect samplings were carried out for 12 sequential months, from the very beginning of the wet season (April 1997) to the end of the dry season (March

1998). Line-transect walks were carried out four times a week, from 06:00 to 12:00 h when sampling in Terra Firme forest (4,650 m), or from 07:00 to 13:00 h (much further from the station, in Mixed forest, 5,350 m). Average speed was 1 km per hour, with occasional stops of a few seconds to scan the habitat. No sightings were registered beyond 50 m in all forest types. For very large

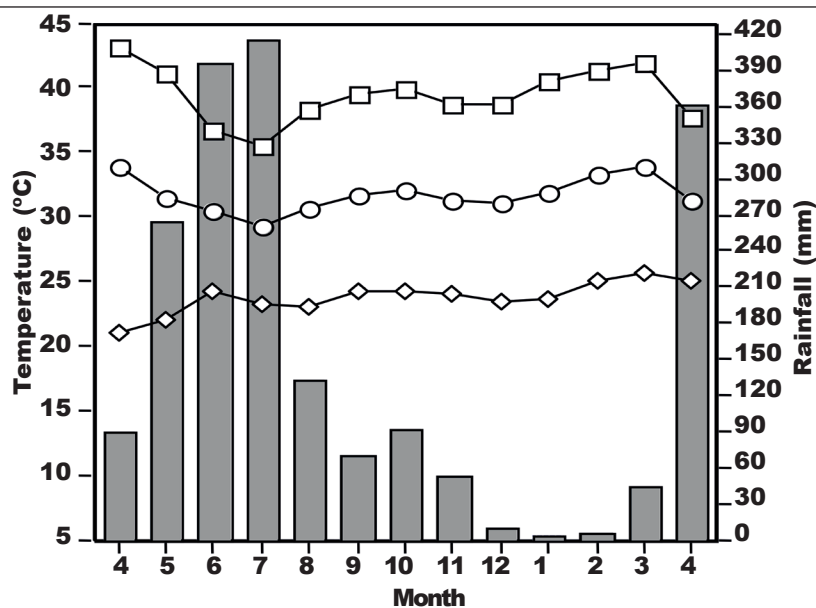


Fig. 4. Minimum, mean, and maximum temperature (lines) and rainfall (bars) at Maracá Ecological Station, Roraima, Brazil, during the study period (1997/1998): 1, January; 2, February; 3, March; 4, April; 5, May; 6, June; 7, July; 8, August; 9, September; 10, October; 11, November; 12, December.

Fig. 4. Valores mínimo, medio y máximo de temperatura (líneas) y precipitación (barras) en la Estación Ecológica de Maracá, en Roraima (Brasil), durante el período del estudio (1997/1998). (Para las abreviaturas de los meses, véase arriba).

groups, counts were considered as minimum counts, and for animals sub-divided into smaller sub-groups, counts were considered as sub-groups (Mendes Pontes, 1999). Special care was taken to avoid double-counting the sighted animals, such as recording the direction the animal/group took after sighted (and even taking their coordinates), and following them for up to 15' to make sure they did not return to the trail.

Nocturnal line-transect samplings were also carried out between April 1997 and March 1998, from 19:00 to 01:00 h, on the same basis as diurnal samplings, with the help of powerful hand spotlights. The data collected when an animal or group was encountered were: species, angle, perpendicular distance, location upon the trail and assumed direction. Date, time started and finished, observers' names and total distance walked were also recorded every day (see Burnham et al., 1980; National Research Council, 1981; Brockelman and Ali, 1987; Buckland et al., 1993; Mendes Pontes, 1997, 1999).

Total diurnal sampling transect length was the summation of all single diurnal walks; for nocturnal samplings it was the total length of the nocturnal walks. For those species active during the day and night, the total trail length was the summation of both diurnal and nocturnal samplings. To calculate group densities, we used the 5.0. version of the DISTANCE program (Buckland et al., 1993), which establishes the maximum effective strip width (ESW). The first step in calculating densities is, therefore, to check the

accuracy of the detection function $g(x)$, which should be a monotonically-decreasing function, although in some cases there are not enough sightings to provide a smooth curve, and in some others, animals might be detected after they have moved a few metres away from the trail. The program DISTANCE considers these constraints, and chooses the most appropriate model to calculate densities (Buckland et al., 1993). Sightings were analyzed for the species in each forest type, during each season.

For species with fewer than 25–30 sightings (the minimum number required to run the program DISTANCE) (Buckland et al., 1993), we combined the sightings of each species in all forest types, after having tested whether there were any statistically significant differences in the distribution of perpendicular distances across forest types, thus achieving enough sightings to run DISTANCE. ESW was calculated from DISTANCE, and densities were then calculated following Chiarello (1999).

For species with very few sightings we used King's method (Robinette et al., 1974), which has provided satisfactory results (Nunes et al., 1988; Malcolm, 1990), in some cases, identical to those obtained via DISTANCE (Mendes Pontes, 1999). Ecological densities were calculated instead of crude densities, which are densities calculated separately for the five forest types. We calculated group densities for all the studied mammals, including the solitary ones, because

Table 1. Phenology of marked trees in the five studied forest types at Maracá Ecological Station, northernmost Brazilian Amazonia: T, total number of marked trees; Tlb, percentage (mean \pm SD) of trees with leaf buds; Tfl, percentage (mean \pm SD) of trees with flowers; Tfr, percentage (mean \pm SD) of trees with fruits; kg, kg of fruit in the tree canopy.

Tabla 1. Fenología de los árboles marcados en los cinco tipos de bosque estudiados en la Estación Ecológica de Maracá, en el extremo septentrional de la Amazonia brasileña: T, número total de árboles marcados; Tlb, porcentaje (media \pm DE) de árboles con brotes de hojas; Tfl, porcentaje (media \pm DE) de árboles con flores; Tfr, porcentaje (media \pm DE) de árboles con frutos; kg, kilogramos de fruta en la copa del árbol.

Forest	T	Season	Tlb (%)	Tfl (%)	Tfr (%)	kg
Terra Firme forest	203	Wet	9.9 (20.2 \pm 17.3)	4.9 (10 \pm 4.6)	13.4 (27.2 \pm 7)	776.7
		Dry	8.3 (16.8 \pm 8.4)	6.0 (12.3 \pm 5.3)	9.8 (20 \pm 3.5)	532.8
Mixed forest	200	Wet	8.25 (16.5 \pm 8.9)	3.1 (6.3 \pm 4)	6.9(13.8 \pm 4.7)	509.5
		Dry	8.3 (16.5 \pm 10.6)	2.6 (5.3 \pm 2.3)	3.6 (7.3 \pm 2.9)	634.5
Buritizal forest	40	Wet	14.2 (5.7 \pm 3)	5.7 (2.3 \pm 2.2)	13.2 (5.3 \pm 1.4)	521.1
		Dry	10.9 (4.3 \pm 3.4)	7.5 (3 \pm 1.1)	12 (4.8 \pm 0.9)	353.7
Pau Roxo forest	40	Wet	9.5 (3.8 \pm 2.6)	2.5 (1 \pm 1.5)	8.2 (3.3 \pm 1.4)	234.2
		Dry	8.7 (3.5 \pm 1)	4.2 (1.7 \pm 1)	6.2 (2.5 \pm 0.8)	129.7
Carrasco forest	11	Wet	22.7 (2.5 \pm 2.2)	11.8 (1.3 \pm 1.2)	9.0 (1 \pm 0.6)	10.4
		Dry	27.3 (3 \pm 2.2)	9.0 (1 \pm 0.9)	6.4 (0.7 \pm 0.8)	1

in some cases, such as in red brocket deer *Mazama americana* Erxleben, we recorded up to three individuals together, the pair plus an infant, or in the case of the puma *Puma concolor* Linnaeus, we recorded 3 sub-adults in a cluster.

Data analysis

Principal components analysis (PCA) was performed with correlation matrices for the means of nine habitat variables calculated for each of the five studied forest types so that the entire set of variables could be reduced parsimoniously into a smaller number of descriptors, those sharing similar principal component scores, and so submitted to the same environmental constraints (Summerville et al., 2006). This allowed us to methodologically encompass as much variability as possible without losing information (Manly, 1986), and yielded uncorrelated composite measures that were used to fit stepwise multiple regressions to model the effects of these habitat variables on the densities of the studied mammalian species.

The following variables were recorded per habitat: (1) tree basal area, (2) total number of tree species recorded during the study, (3) total number of animal dispersed fruit species, (4) mean number of fruit species recorded on the forest floor, (5) kg/ha/year of fruits on the forest floor, (6) mean number of marked trees with leaves, (7) mean number of marked trees with flower, (8) mean number of marked trees with fruits, and (9) kg of fruits in the canopy of marked trees.

As the quality measures of the trait variables were on very different scales, correlation matrices were preferred over covariance matrix, so avoiding biasing the eigenvalues (Jolliffe, 2002; Graham, 2003). PCA factors were tested using Horn's parallel analysis (PA), since it is considered one of the most appropriate methods to select significant principal components (Zwick and Velicer, 1986), comparing PCA factor eigenvalues to threshold eigenvalues in order to find those factors with eigenvalues large enough to be retained.

Factor variable loadings within significant factors were tested by Spearman rank correlation and only significant loadings were used in subsequent stepwise multiple regression analyses between the retained PCA axes and the ranked dependent variables (mammalian species densities) to determine which regression models that best predicted habitat preferences of the mammalian species. We adopted a significance level of 5%. All analyses were performed using the R-program version 2.13.1 (R Core Team, 2012).

Results

Forest productivity: phenology of marked trees

For the two major forest types that dominate eastern Maracá, Terra Firme and Mixed forest, Terra Firme had a higher percentage of trees with leaf buds, both in the wet season (9.9%, n = 203) and in the

Table 2. Raked–ground fruit survey in the five studied forest types at Maracá Ecological Station, northernmost Brazilian Amazonia.

Tabla 2. Estudio de los frutos recolectados en el suelo en los cinco tipos de bosque estudiados en la Estación Ecológica de Maracá, en el extremo septentrional de la Amazonia brasileña.

Forest	Season	Fruit species (mean \pm SD) on the forest floor	Kg/ha/year of fruit on the forest floor
Terra Firme forest	Wet	36 \pm 7.7 (n = 216)	239
	Dry	23.5 \pm 4.3 (n = 141)	45
Mixed forest	Wet	16.7 \pm 5.6 (n = 100)	176
	Dry	10.5 \pm 3.3 (n = 63)	53.5
Buritizal forest	Wet	6.8 \pm 1.8 (n = 41)	2,062.5
	Dry	5.3 \pm 1.4 (n = 32)	3,212.2
Pau Roxo forest	Wet	2.5 \pm 0.84 (n = 15)	750
	Dry	1.5 \pm 0.84 (n = 9)	79.9
Carrasco forest	Wet	2.2 \pm 1.6 (n = 13)	4.16
	Dry	0.7 \pm 0.5 (n = 4)	0.4

dry season (8.3%, n = 203), a higher percentage of trees with flowers (wet season: 4.9%, dry season: 6%, n = 203), and with fruits (wet: season 13.4%, dry season: 9.8%, n = 203). In the case of kilograms of fruits in the canopy of trees, while there were more in the wet season in Terra Firme forest (776.7 kg), there were more in the dry season in Mixed forest (634.5 kg) (table 1).

For the two minor habitats, with similar forest height, Buritizal and Pau Roxo forest, Buritizal had a higher percentage of trees with leaf buds in both the wet (14.2%, n = 40) and dry seasons (10.75%, n = 40), as well as a higher percentage of flowers (wet: 5.7%, dry: 7.5%, n = 40), a higher percentage of fruits (wet: 13.2%, dry: 12%, n = 40), and more kilograms of fruits in the canopy of trees (wet: 521.1 kg, dry: 353.7 kg, n = 40) (table 1).

In the shortest minor forest type, Carrasco, where only 11 trees with DBH \geq 10 cm were recorded, more trees with leaf buds were recorded in the dry season (27.3%, n = 11), whereas more trees with flowers (11.8%, n = 11), with fruits (9%, n = 11), and more kilograms of fruits in the canopy of trees (10.4 kg), were recorded in the wet season (table 1).

Forest productivity: raked–ground fruit survey

For the major forest types, the highest mean number of fruit species on the forest floor was recorded in Terra Firme forest, in both the wet (36 \pm 7.7, n = 216), and dry seasons (23.5 \pm 4.3, n = 141); in the case of the minor forest types of similar height, the highest mean number of fruit species on the forest floor was found in Buritizal forest, also in both the wet (6.8 \pm 1.8,

n = 41), and dry seasons (5.3 \pm 1.4, n = 32); in the lower minor habitat, Carrasco, the greatest number of fruit species was recorded in the wet season (2.2 \pm 1.6, n = 13) (table 2).

In the major forest types, the highest residual amounts of fruit on the forest floor in the wet season were recorded in Terra Firme (239 kg/ha/year), while in the dry season they were recorded in Mixed forest (53.5 kg/ha/year). For the minor forest types, Buritizal had by far the highest amounts of residual fruit on the forest floor in both the wet (2,062.5 kg/ha/year) and dry season (3,212.2 kg/ha/year); In Carrasco the highest residual amounts of fruit on the forest floor occurred in the wet season (4.16 kg/ha/year) (table 2).

Mammalian species densities

During this 12–month study, and across all five habitat types, 33 mammalian species were recorded over a total of 638 hours of line transect samplings, with 599 sightings recorded along the 1,180.2 km walked in a total of five habitat types (1,115.5 in diurnal, and 64.8 in nocturnal sampling).

Density of terrestrial mammals (n = 14) was at least three times higher (1,636.85 groups/km²) than that of the arboreal and scansorial (n = 19) forms (484.05 groups/km²). The most abundant mammal species was Brazilian tapir, *Tapirus terrestris* with an overall density of 626.5 groups/km², followed by red brocket deer, *Mazama americana*, with 449.4 groups/km². The most abundant order was Artiodactyla, with 673 groups/km², in which the largest contribution comes from *M. americana*, followed by *Tayassu pecari*, with 155 groups/km², and *Pecari tajacu*, with

Table 3. Densities (groups/km²) in the different forest types at Maracá Ecological Station, Roraima, Brazilian Amazonia. (For abbreviations of forest types, see fig. 3).

Tabla 3. Densidad (grupos/km²) en los diferentes tipos de bosque en la Estación Ecológica de Maracá, en Roraima, Amazonia brasileña. (Para las abreviaturas de los tipos de bosque, véase fig. 3).

Species	Forest types									
	TFF		MF		BF		PRF		CF	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
O. Artiodactyla										
F. Cervidae										
<i>Mazama americana</i>	11.4	13.3	12	9.7	183.3	85.7	0	1	133	0
F. Tayassuidae										
<i>Tayassu pecari</i>	2	4.1	0.7	1	26.8	119.4	0	1	0	0
<i>Pecari tajacu</i>	2	8.9	0	0.05	25	33.3	0	0	0	0
O. Carnivora										
F. Canidae										
<i>Cerdocyon thous</i>	7.3	3.3	0	0	0	0	0	0	0	0
<i>Sphootos venaticus</i>	0.6	0	0	0	0	0	0	0	0	0
F. Felidae										
<i>Herpailurus yagouaroundi</i>	3.3	0	0	0	0	0	0	0	0	0
<i>Leopardus pardalis</i>	0	0	0	0	0	0	0	0	0	0
<i>L. tigrinus</i>	0	0	0	0	0	0	0	0	0	0
<i>L. wiedii</i>	0	0	0	0	0	0	0	0	0	0
<i>Panthera onca</i>	0.6	1.1	0	0	2.9	2	0	0	0	0
<i>Puma concolor</i>	3.3	6.7	10	0	0	0	0	0	0	0
F. Mustelidae										
<i>Eira barbara</i>	0	0.8	0.2	0.5	0	0	0	0	0	0
<i>Galictis vittata</i>	4	0	0	0	0	0	0	0	0	0
F. Procyonidae										
<i>Bassaricyon beddardi</i>	8.3	4.3	0	0	104.1	0	0	0	0	0
O. Perissodactyla										
F. Tapiridae										
<i>Tapirus terrestris</i>	4.5	8	10	4	150	150	0	0	300	0
O. Primates										
F. Cebidae										
<i>Aotus trivirgatus</i>	66.6	100	0	0	0	0	0	0	0	0
<i>Ateles belzebuth</i>	0.9	0.4	2.1	1.3	9.6	2.6	6	2.8	0	0
<i>Alouatta macconnelli</i>	0.7	0.3	0.4	0.5	0	0	0	0	0	3.7
<i>Sapajus apella</i>	0.4	0.15	0.3	0	0	0	0	0	0	0
<i>Cebus olivaceus</i>	1.6	2.5	1.4	1.3	1.7	5.5	0	1.6	0	0
<i>Saimiri sciureus</i>	0.6	1.2	0.3	0.2	0	0	0	0	3.3	2.4
O. Rodentia										
F. Cuniculidae										
<i>Cuniculus paca</i>	0	0	0	112.3	0	0	0	0	0	0

Table 3. (Cont.)

Species	Forest types									
	TFF		MF		BF		PRF		CF	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
F. Dasyproctidae										
<i>Dasyprocta leporina</i>	4.4	3.5	5.6	6.9	5	4	3.1	2.3	0	3
F. Erethizontidae										
<i>Coendou prehensilis</i>	50	0	0	0	0	0	0	0	0	0
F. Sciuridae										
<i>Sciurus igniventris</i>	3	5.5	4.6	3.8	0	0	0	0	0	20
O. Cingulata										
F. Dasypodidae										
<i>Cabassous unicinctus</i>	0	0	0	0	0	0	0	0	0	0
<i>Dasypus kappleri</i>	0	0	0	0	0	0	0	0	0	0
<i>D. novemcinctus</i>	0	0	0	3.3	0	0	0	0	0	0
<i>D. septemcinctus</i>	0	0	0	3.3	0	0	0	0	0	0
<i>Priodontes maximus</i>	0	0	0	0	166.7	0	0	0	0	0
O. Pilosa										
F. Cyclopedidae										
<i>Cyclopes didactylus</i>	4.5	0.2	0	0	0	0	0	0	0	0
F. Myrmecophagidae										
<i>Myrmecophaga tridactyla</i>	0	1.5	0	0.6	0	0	0	0	0	0
<i>Tamandua tetradactyla</i>	0.2	0.3	0.8	0	16.7	0	0	0	0	0
Total	180.2	166.1	48.4	148.8	691.8	402.5	9.1	8.7	436.3	29.1
Grand total	346.3		197.2		1,094.3		17.8		465.4	

Table 4. Contribution of the components to the abundance of the mammalian species at Maracá Ecological Station, northernmost Brazilian Amazonia.

Tabla 4. Contribución de los componentes a la abundancia de las especies de mamíferos en la Estación Ecológica de Maracá, en el extremo septentrional de la Amazonia brasileña.

Principal component	Proportion of variance (%)	Cumulative proportion (%)
PC1	0.8037	0.8037
PC2	0.1278	0.9315
PC3	0.04135	0.97285
PC4	0.01538	0.98823
PC5	0.00838	0.99661
PC6	0.00309	0.99970
PC7	0.00023	0.99993
PC8	0.00007	1
PC9	0.00000	1

Table 5. Importance of the variables in the components (those significant according to a Spearman rank correlation test are in bold) for the abundance of the mammalian species at Maracá Ecological Station, northernmost Brazilian Amazonia.

Tabla 5. Importancia de las variables en los componentes (las que son significativas según una prueba de correlación por rangos de Spearman están en negrita) para la abundancia de las especies de mamíferos en la Estación Ecológica de Maracá, en el extremo septentrional de la Amazonia brasileña.

Variables	PC1		
1 Basal area	-0.3581	-0.963	< 0.0001
2 Total number of tree species recorded during the study	-0.3536	-0.951	< 0.0001
3 Total number of animal-dispersed fruit species	-0.3583	-0.964	< 0.0001
4 Mean number of fruit species on the forest floor	-0.3510	-0.944	< 0.0001
5 Kg/ha/year of fruit on the forest floor	0.1234	0.332	0.3484
6 Mean number of marked trees with leaves	-0.3661	-0.985	< 0.0001
7 Mean number of marked trees with flowers	-0.3520	-0.947	< 0.0001
8 Mean number of marked trees with fruits	-0.3513	-0.944	< 0.0001
9 Kg of fruit in the canopy of marked trees	-0.3139	-0.844	< 0.0001

69.2 groups/km². The second most abundant order was Perissodactyla, with 626.5 groups/km², with its only species, *T. terrestris* (table 3).

Buritizal was the forest type with the highest overall mammal density, with 1,094.3 groups/km², followed by Carrasco forest, with 465.4 groups/km², and Terra Firme forest, with 346.3 groups/km². The forest with the lowest density was Pau Roxo, with only 17.8 groups/km² (table 3).

Selection of significant habitat variables via principal components analysis

The principal components analysis results, subsequently tested via Horn's parallel analysis, partitioned the 9 species traits into one factor with eigenvalues large enough to be retained (PC1), which explained 80.37% of the total variation contained in the covariates (table 4). Spearman

Table 6. Stepwise multiple regression for the effect of the variables selected via PCA on the abundance of mammalian species at Maracá Ecological Station, northernmost Brazilian Amazonia: SE, standard error.

Tabla 6. Regresión múltiple escalonada para determinar los efectos de las variables seleccionadas a través del análisis de componentes principales de la abundancia de especies de mamífero en la Estación Ecológica de Maracá, en el extremo septentrional de la Amazonia brasileña: SE, error estándar.

Variables / parameters	Coefficient	SE	p-value
1 Basal area	-6.21	2.52	0.0457
2 Total number of tree species recorded during the study	-6.25	2.20	0.0362
6 Mean number of marked trees with leaves	154.60	44.83	0.0183
7 Mean number of marked trees with flowers	109.04	42.95	0.0420
8 Mean number of marked trees with fruits	-33.23	12.91	0.0487
R ²		86.58	
F		6.45	
d.f.		5, 5	
p-value		0.0308	

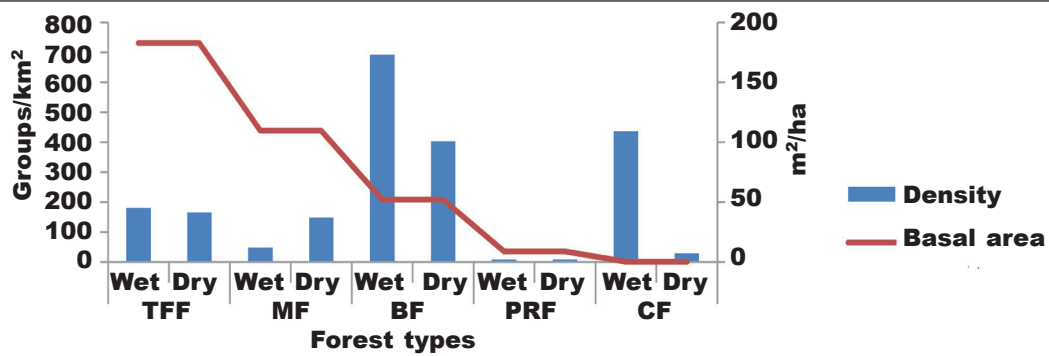


Fig. 5. Relationship between mammalian density (groups/km²) and forest basal area at Maracá Ecological Station, Roraima, Brazil. (For abbreviations of forest types, see fig. 3).

Fig. 5. Relación entre la densidad de mamíferos (grupos/km²) y área basimétrica forestal en la Estación Ecológica de Maracá, en Roraima (Brasil). (Para las abreviaturas de los tipos de bosque, véase fig. 3).

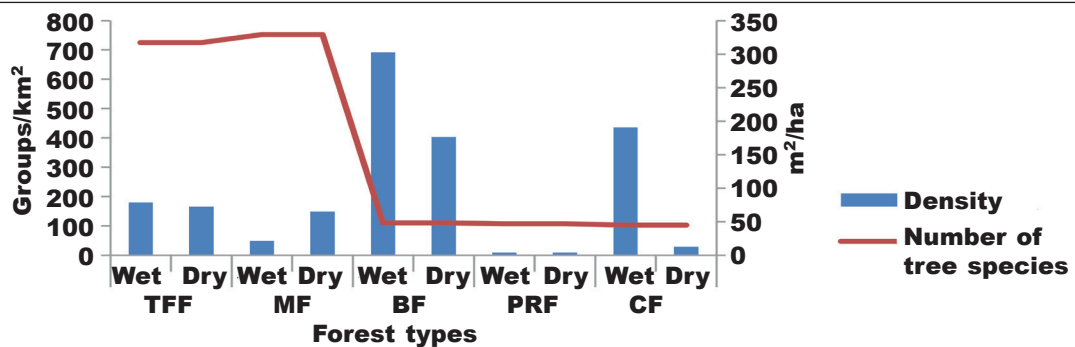


Fig. 6. Relationship between mammalian density (groups/km²) and number of tree species per forest type at Maracá Ecological Station, Roraima, Brazil. (For abbreviations of forest types, see fig. 3).

Fig. 6. Relación entre la densidad de mamíferos (grupos/km²) y el número de especies arbóreas por tipo de bosque en la Estación Ecológica de Maracá, en Roraima (Brasil). (Para las abreviaturas de los tipos de bosque, véase fig. 3).

Rank Correlation tests of loading coefficients of trait variables identified eight significant factor variable loadings ($P < 0.05$) for the first factor (PC1) (table 5).

Stepwise multiple regressions for the effects of environmental variables on mammalian species density

Stepwise multiple regressions identified five of the eight environmental variables selected via PCA as predicting a significantly high amount of the variability in the mammalian species density in the forest types studied ($F = 6.45$, d.f. = 5,5, $P = 0.0308$, $R^2 = 86.6$) (table 6). Density was negatively associated with tree

basal area, total number of tree species registered during the study, and mean number of marked trees with fruits (fig. 5–7, table 6), and positively related to mean number of marked trees with leaves, and mean number of marked trees with flowers (fig. 7, table 6).

Discussion

Maracá Ecological Station is located in the central zone of the Guyana Shield, one of the driest regions in Brazilian Amazonia, with one of the longest dry seasons, most frequent canopy discontinuities, and consequently, a very well-developed understory (Mendes Pontes, 2004; Mendes Pontes et al., 2013).

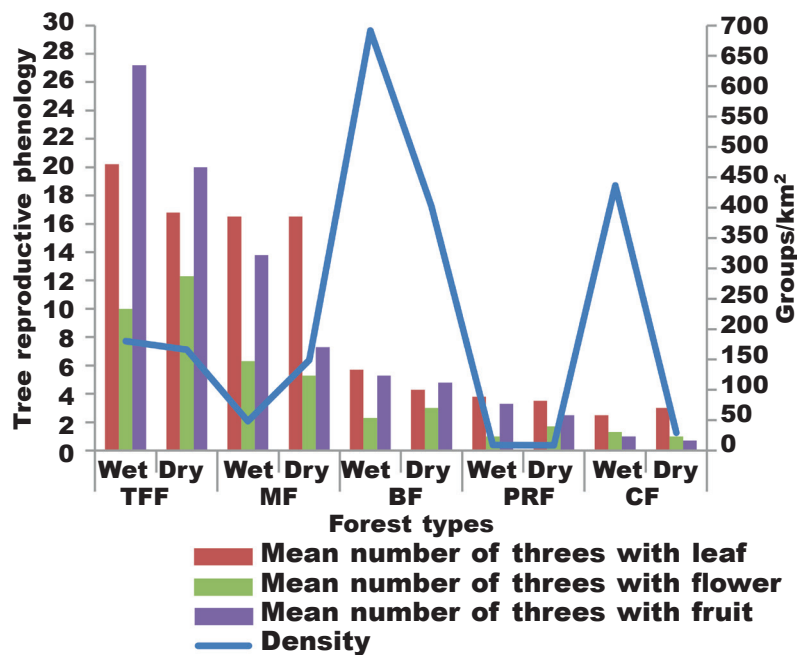


Fig. 7. Relationship between mammalian density (groups/km²) and tree reproductive phenology at Maracá Ecological Station, Roraima, Brazil. (For abbreviations of forest types, see fig. 3).

Fig. 7. Relación entre la densidad de mamíferos (grupos/km²) y la fenología reproductiva de los árboles en la Estación Ecológica de Maracá, en Roraima (Brasil). (Para las abreviaturas de los tipos de bosque, véase fig. 3).

One of the most remarkable features of these seasonally–dry forests was the dramatic seasonal fluctuation on the availability of edible plant parts, both in the canopy and on the floor of the five forest types studied.

As is typical of these regions (Janzen, 1974; Eisenberg and Redford, 1979; Eisenberg et al., 1979; August, 1983; Schaller, 1983; Emmons, 1984), the abundance of the terrestrial mammalian fauna was higher than the arboreal fauna (more than three times higher: see Mendes Pontes, 2004). As the most abundant orders, browsers and grazers (Artiodactyla and Perissodactyla) could benefit most from a well–developed understory. In this scenario, tree reproductive phenology was the sole determinant of the overall abundance in the mammalian assemblages, and in turn it translated into more food resources for the vegetarians/primarily vegetarian species, and indirectly, also for meat eaters.

Thus, we confirmed for this site what had already been suggested in the literature on a much broader scale, that forest productivity is the main determinant of abundance of mammalian assemblages (Eisenberg et al., 1979; Eisenberg, 1980; Gentry and Emmons, 1987; Eisenberg, 1990; Kay et al., 1997; Hoorn et al., 2010; Marshall et al., 2014) more specifically, this being productivity as mediated by tree reproductive phenology (a relationship reported by Marshall et al., 2014).

Indirectly, our findings also support the assumption that soil type is the main determinant of mammalian abundance (Tuomisto et al., 1995, 2003, 2014; Hoorn et al., 2010; Kristiansen et al., 2012; Pomara et al., 2012, 2014; Rossetti, 2014; Higgins et al., 2011, 2015; Zuquim et al., 2014), since it will ultimately determine the structure and productivity of the forests (Eisenberg et al., 1979; Eisenberg, 1980; Emmons, 1984; Gentry and Emmons, 1987; Eisenberg, 1990; Kay et al., 1997; Hoorn et al., 2000; Marshall et al., 2014) via resource availability and seasonality, and hence the intensity of food competition between species (Connell, 1980; Chesson and Huntley, 1989; Chesson and Rosenzweig, 1991).

It has been shown in our previous studies (Gadelha et al., 2017; Luna et al., 2017) that at the regional scale (Peterson et al., 2011), the abundance of the mammalian assemblages can be determined by the physical structure of forests, whether it be in highly–heterogeneous vegetation mosaics, such as in the northern part of the Guyana Shield, or the ombrophilous forests of the southern part, or a transition between them. Now, we have also shown that at the local scale (Peterson et al., 2011), forest structure and productivity, and more specifically food availability and its fluctuations, determined the abundance of the mammalian assemblages.

Basal area, total number of tree species, and total number of tree species with fruits also influenced the recorded mammalian densities, but because in these more open, discontinuous forests of the Guyana Shield the bulk of the mammalian abundance is made up of large, terrestrial, mostly browser and grazer species (at Maracá three times higher than smaller species), the basal area and total number of tree species related negatively to mammalian densities. As a result, Artiodactyla and Perissodactyla, the most abundant orders, favoured more open–canopy forests, which had more abundant undergrowth on which they could feed. The total number of tree species with fruits also showed a negative relationship with mammalian densities, possibly because the most abundant orders/species were primarily browsers and grazers, despite also having a diet containing a considerable proportion of fruits (Emmons and Feer, 1997).

Finally, Maracá Ecological Station is located in the centre of the Guyana Shield and is covered by a mosaic of contiguous forest types that are highly seasonal and have a long dry season. It harbors mammalian assemblages that are one of the poorest in species diversity in the northernmost Brazilian Amazonia, with large-bodied mammals being more abundant than medium-sized mammals, and terrestrial species more abundant than arboreal species. In these assemblages, the mammalian species favoured forest types that were more open and had more zoochorous fruit species. In this scenario, the sole determinant of their densities was the tree assemblage reproductive phenology, confirming what has been previously postulated in the literature, that mammalian abundances should be a function of forest productivity.

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