

STRUCTURE AND FLORISTIC COMPOSITION OF ONE OF THE LAST FOREST FRAGMENTS CONTAINING THE CRITICALLY ENDANGERED NORTHERN MURIQUI (*BRACHYTELES HYPOXANTHUS*, PRIMATES)

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Abstract. This study presents results from the first systematic botanical investigation of the RPPN Feliciano Miguel Abdala (RPPN-FMA, formerly Caratinga Biological Station), a semi-deciduous forest fragment in southeastern Brazil that supports nearly a third of the remaining population of the critically endangered northern miquiqui (*Brachyteles hypoxanthus*). Here we describe the structure, diversity, and floristic composition of this forest. Our goal was to provide the scientific basis for a management plan that will take into consideration the factors involved in the unusually high miquiqui carrying capacity in this fragment. Our sample comes from six 500 x 10-m plots, totaling 3 ha. We marked and identified all trees with DBH \geq 10 cm in all of the plots, and all trees of $5 \leq$ DBH $<$ 10 cm in half of the plots (1.5 ha). Forest structure was consistent with secondary forest characteristics, inasmuch as large trees were rare, total basal area was small, canopy was discontinuous, average tree height was low, and liana load was heavy. Top-ranking families, based on Importance Value, were Fabaceae, Euphorbiaceae, Annonaceae, Rubiaceae, and Moraceae. Compared with other forests where northern miquiquis occur, the RPPN-FMA forest was more floristically diverse ($H' = 4.6$) and even ($J = 0.85$). In addition, top-ranking species were known miquiqui foods. These factors might contribute to the unusually high density of the primate found at this site.

Key words: Atlantic forest, *Brachyteles*, botanical inventory, habitat structure, primate conservation.

INTRODUCTION

The Atlantic Forest is one of the 34 biodiversity hotspots, yet it is among the most threatened ecosystems in the world (Mittermeier *et al.* 2004). According to current estimates only 11% of this forest remains, most of which is highly fragmented and at some stage of secondary succession (Galindo-Leal & Câmara 2003, Ribeiro *et al.* 2009). Such habitat loss and fragmentation, together with overhunting, have caused local extinctions of large vertebrates and in particular primates (e.g., Peres 1997a, Chiarello 2000). Of the 23 species of primates found in the Atlantic Forest, 20 are endemic and under some degree of threat (Hirsh *et al.* 2006, IUCN 2010).

Brachyteles (miquiquis) is the largest New World primate genus and the only member of its family endemic to the Atlantic Forest. Before the arrival of

the Europeans in Brazil in 1500, miquiquis had a vast distribution spanning several degrees of latitude from Bahia to Paraná states in Brazil (Aguirre 1971). With an original estimated population of 400,000 individuals, today less than 1% of this total remains distributed in isolated, mostly small forest fragments (Aguirre 1971, Mendes *et al.* 2005). Of the two known species, the northern miquiqui, *B. hypoxanthus* is Critically Endangered (IUCN 2010). One of the last strongholds of this species is the Reserva Particular do Patrimônio Natural Feliciano Miguel Abdala (RPPN-FMA, formerly Caratinga Biological Station). The RPPN-FMA has gained international recognition due to its importance in supporting one of the largest populations of northern miquiquis (Strier 1993/94, 2000; Mendes *et al.* 2005). Despite its relatively small size and past history of fires, agriculture, and selective logging, this forest also has sustained viable populations of brown howler monkeys, black-horned capuchins, and buffy-headed

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marmosets, and several other vertebrates including some cats such as ocelot (Bianchi & Mendes 2007). In particular, the miqui population has been increasing steadily since scientific studies began in this forest more than 30 years ago (Strier & Boubli 2006). Today, the density of howler monkeys (50 ind/km²) and miquis (29 ind/km²) are exceptionally high (Almeida-Silva *et al.* 2005) if we consider the relatively small size, isolation, and disturbed state of this forest and the landscape around it (e.g., Chiarello 2000, Metzger *et al.* 2009, Pardini *et al.* 2010); so the situation at our study site seems unusual.

For arboreal primary consumers such as primates, habitat attributes like primary productivity, forest total basal area per hectare, connectivity, tree species diversity, total rainfall, and soil fertility are known to affect population abundances (August 1983, Ganzhorn 1995, Hirsh 1995, Kay *et al.* 1997, Peres 1997a,b; Janson & Chapman 1999, Terborgh *et al.* 2001, Felton *et al.* 2003, Boubli 2005, Silva-Junior *et al.* 2009, Boubli *et al.* 2010). Although primary productivity has been considered to be one of the most important determinants of abundances and diversity in the second trophic level and above ('bottom up forces' *sensu* Power 1992, Peres 1997a, Boubli 2005), in tropical forests this relationship is complicated by the fact that only part of the total primary production is passed on to herbivores in the form of edible fruits and palatable leaves. Tropical trees vary in the type of fruits produced and palatability of their plant parts, and not all tree species produce edible fleshy fruits or the protein-rich palatable leaves that are low in tannins and alkaloids and preferred by primary consumers (Milton 1980, van der Pijl 1982, Gautier-Hion *et al.* 1985, Boubli 2005). Thus fine grained analyses of the floristic composition of tropical forests are necessary to interpret the carrying capacity of consumer populations at a given site.

The relationship between tree species diversity and consumer abundance has been attributed to the greater feeding alternatives during times of scarcity that high tree species availability provide (Ganzhorn 1995). However, plant diversity has also been correlated with other variables such as soil fertility, rainfall, and primary productivity (Gentry 1988, Ashton 1989), which can also indirectly affect consumer population abundances (Peres 1997a).

Whereas forest structural attributes do not influence food availability *per se*, they may nonetheless affect consumer populations in indirect ways. For

example, for large arboreal primates such as the northern miqui, high canopy connectivity and large substrates (large branches in large trees) permit safe and easy travel between food patches (Fimbel 1994). In addition, social primates such as miquis often prefer large food patches that can accommodate many individuals at the same time, offering greater protection against predators and advantages in intergroup and interspecific competition (Milton 1984, Strier 1986, 1989; Lemos de Sá & Strier 1992, Moraes *et al.* 1998).

Here we provide a detailed description of forest structure, floristic diversity, and tree species composition of the RPPN-FMA. This forest is vital to the conservation of the critically endangered northern miqui. Our goal with this study was to create a scientific base for evaluating the carrying capacity of this miqui population and its possible determining factors. These data will help design management strategies for this reserve and species that will take into account threats/risks due to (e.g.) possible change in tree species composition following natural regeneration, climate change, changes in patch resilience due to greater disturbance of the surrounding landscape (Lindenmayer *et al.* 2008, Metzger *et al.* 2009, Pardini *et al.* 2010).

METHODS

Study site. The RPPN-FMA is part of the Rio Doce Basin and is an isolated fragment with roughly 1000 + ha of forest surrounded by pastures and plantations located 52 km east of the town of Caratinga, in eastern Minas Gerais, Brazil, (19°50'S, 41°50'W; Fig. 1). The forest is classified as Tropical Atlantic Morphoclimatic Domain (Ab'Saber 1977), but even the most intact areas have suffered for many years from selective logging and fires and there is little or no primary forest evident at present. The RPPN-FMA forest consists of a network of hills and valleys, with altitudes ranging from 318 to 682 m a.s.l., and a mosaic of disturbed forests at different stages of regeneration (Strier & Boubli 2006, Strier 1999). There are three main water drainage systems: Matão, Sapo, and Jaó; the present study was conducted in the Jaó Valley area (c. 490 ha), corresponding to the northern half of the forest (Fig.1).

The Köppen Classification climate type is "Aw," with total mean annual rainfall of around 1168 ± 286 mm. There is a distinct rainy season from November to April, when > 80% of precipitation falls (rainfall data updated from Strier *et al.* 2001).

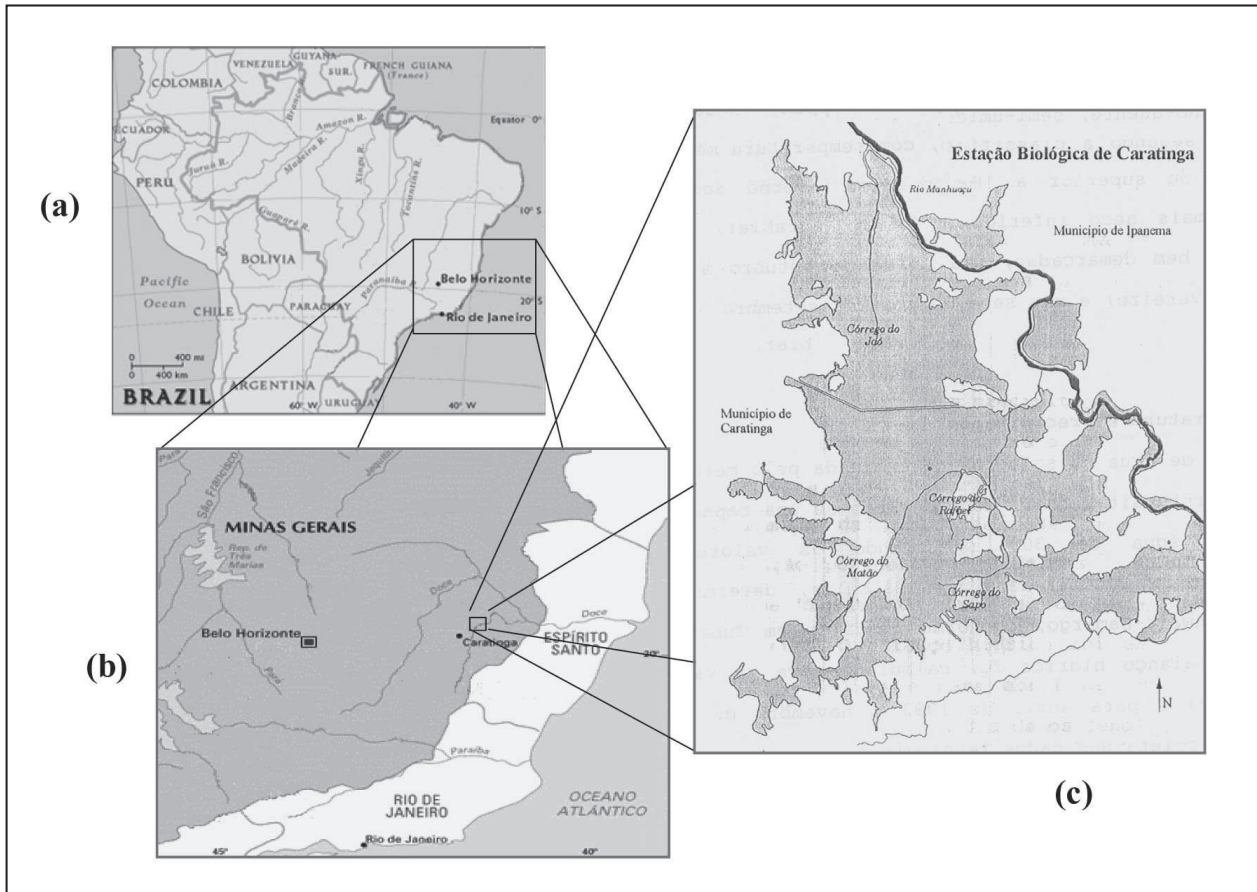


FIG. 1. Maps showing the location of the study area and site: (a) Minas Gerais State in Brazil; (b) The city of Caratinga; (c) The RPPN-FMA forest with the Jaó, Matão, and Sapo valley areas.

Botanical study. In October 2001 we laid out six 10 x 500-m (0.5 ha each) plots (sensu Ludwig & Reynolds 1988) at randomly selected locations in the Jaó Valley. Our intention with this random placement of 3-km transects was to sample the diversity of microhabitats (i.e., hilltop, hillside, and valley) in proportion to their presence in this portion of the forest. We further subdivided all plots in 10 x 10-m subplots to accurately locate and map each marked tree. During a mortality and recruitment tree study from 2001-2004, we measured the diameter at breast height (DBH) of trees and marked all trees with $DBH \geq 10$ cm within each plot with aluminum number tags. We also tagged trees with $DBH \geq 5$ cm that grew only on half of the plot area (5 x 500 m, totaling 1.5 ha). In our samples, several trees had multiple trunks in which case we calculated the quadratic DBH according to the formula $DBH = \sqrt{DBH_i^2 + DBH_j^2}$. We grouped DBHs into classes previously defined by the Sturges formula $[\log_2(n) + 1]$, implicitly basing bin widths on the range of the data (Sturges 1926).

We visually estimated the heights of tagged trees. We made a histogram of height classes to characterize the vertical structure of RPPN-FMA forest. The final number of layers was defined as equal to the number of possible distribution curves (Martins 1991). In a first attempt to investigate the influence of lianas in the forest's regeneration process, we visually estimated the percentage of the crown of our marked trees that were obstructed (covered) by lianas.

All tagged trees in the six plots were initially identified in the field by their common names by an experienced local assistant. Later, three voucher specimens from tagged trees were collected and dried in the field and later sent to the Herbarium of the University of Minas Gerais in Belo Horizonte (BHCB Herbarium), Brazil, to obtain the scientific identification and to be deposited in the existing reference collection for the area. When identification was not obtained at BHCB, voucher specimens were sent to specialists in taxonomic groups. All species identification followed the Angiosperm Phylogeny Group II (APG II 2003).

We calculated tree species diversity index by relating the total number of species to the total number of individuals in the sample. We used the Shannon-Wiener diversity index for comparative purposes (Pielou 1974). The evenness component of species diversity, J , was also calculated according to the formula $J = H'/\ln(S)$, where H' is the number derived from the Shannon-Wiener diversity index and S is the total number of species in our sample. We estimated the similarity between samples of trees with $DBH \geq 10$ and $5 \leq DBH < 10$ (for the presence and absence of species) with the Sørensen's Similarity Index (SI), according to Mueller-Dombois & Ellenberg (1974).

To test if a reduction of 50% in our sample affected its capacity to represent the community structure of the forest, we calculated a floristic dissimilarity matrix (Bray-Curtis) for trees $DBH \geq 10$ in 3 ha and in only 1.5 ha (half sample). We used Mantel's test to determine the relationship between the total sample and the half sample.

We compared the diversity of our tree community sample by constructing mean species accumula-

tion curves (SAC) and their standard deviations from 100 randomizations of sample order (Gotelli & Colwell 2001). To estimate extrapolated species richness we used four presence/absence estimators: Chao, first and second order jackknife, and bootstrap (Palmer 1990, Colwell & Coddington 1994).

We calculated the relative and absolute density, the dominance, and the frequency of each tree species following Mori *et al.* (1983), and Importance Value Indices (IV) (Cain *et al.* 1956). For the analyses of frequency distributions we subdivided all six plots (of 500 x 10 m) into 30 smaller 100 m x 10-m plots (0.1 ha), and treated each of these smaller plots as one sample unit (SU). Finally, we performed a Kruskal-Wallis Rank Sum test (KW) with a Multiple Comparison post hoc test to contrast the structure and floristics of trees occurring on hilltops, hillsides, and in valleys.

Soil fertility. We collected soil samples along the six plots with a soil corer. In each plot, sampling blocks 50 m in length were spaced by a 50-m interval where no coring was done. Within each block, we obtained

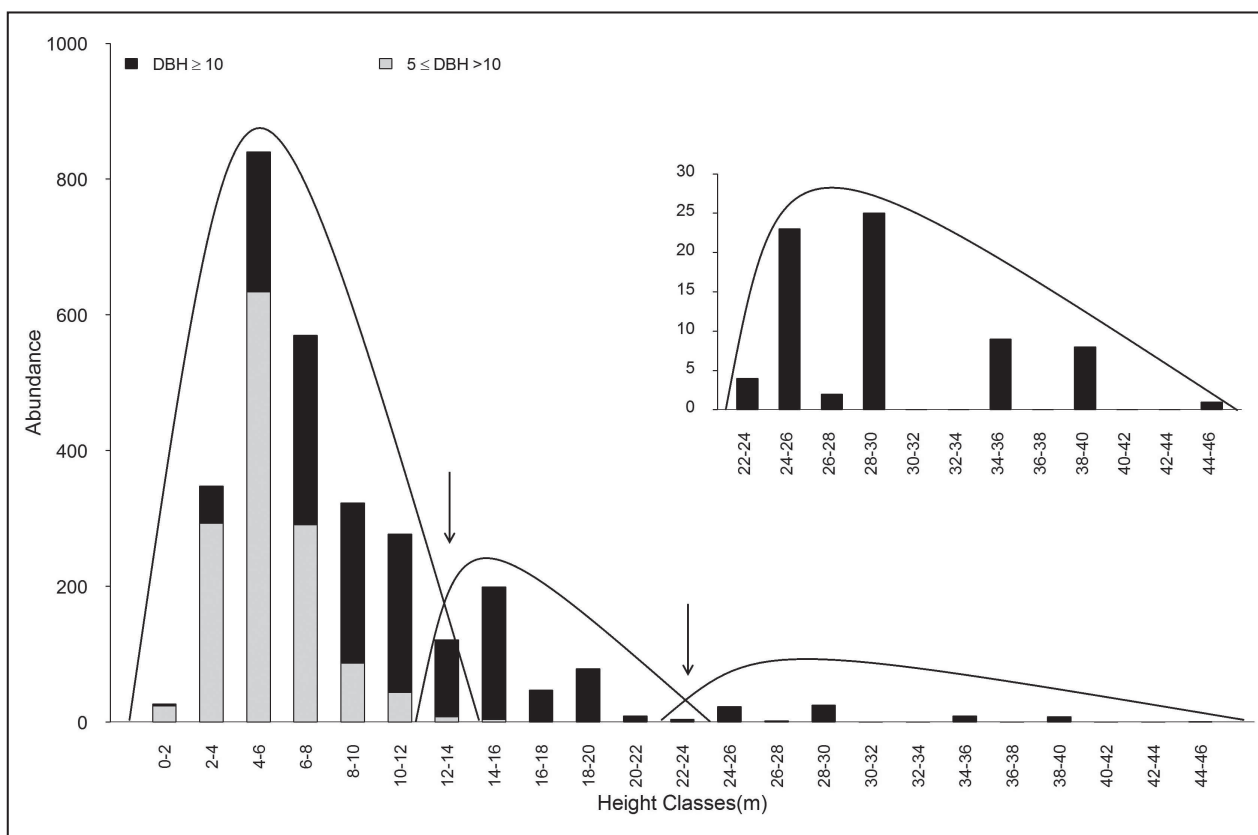


FIG. 2. Height class frequency distribution of trees of $DBH \geq 5$ cm in 3.0 ha in RPPN-FMA forest ($n = 2912$). Arrows indicate top boundary of lower and middle layer heights. Inset represents an enlargement of the corresponding part of the graph.

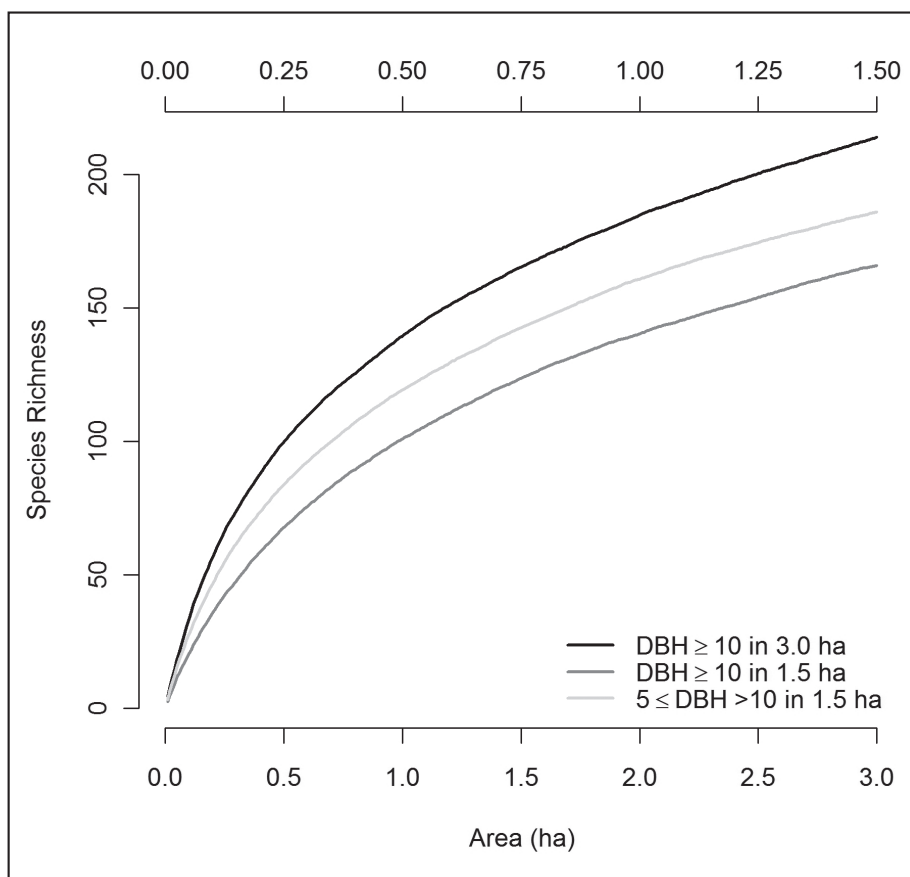


FIG. 3. Mean species accumulation curves for trees of different DBH sizes and subplot area at RPPN-FMA. For trees with DBH ≥ 10 cm in 3.0 ha (black line) subplot sizes 100m², while for trees with DBH ≥ 10 and $5 \leq \text{DBH} < 10$ cm in 1.5 ha (dark and light gray line, respectively) subplot sizes 50m². Total sampled subplots = 300.

three samples separated by 20-m intervals. Each of these samples was composed of a mixture of four subsamples of 15-cm depth collected at each sample point, coring the four corners of a square of 20 cm per side. We combined the samples to obtain a single sample per 50-m block, resulting in five samples per plot and a total of 30 samples in the six plots. Soil chemical properties (pH in H₂O, Al³⁺, H⁺, Ca²⁺, Mg²⁺, Na⁺, K⁺, P) were analyzed at the Soil Laboratory of EMBRAPA (Brazilian Agricultural Research Corporation) and the sum of bases (S), cation exchange capacity (T), base saturation (V), and potential acidity (H + Al) were calculated following EMBRAPA (1997) methodology.

RESULTS

In total, we marked 2930 trees (including those of DBH ≥ 5 cm) in our 3-ha sample. We were able to obtain species level identifications for 2587 (88.3%) of them, genus level for 137, family level for 37, common regional name for 19, and 150 individual trees remained undetermined. DBH showed an inverted J' distribution with most trees in the total sample (92%) having a DBH ≤ 20 cm and only 2%

with a DBH ≥ 40 cm. The average (\pm SD) estimated height for 2912 of the 2930 marked trees with DBH ≥ 5 cm was 9.00 ± 5 m. The histogram of height classes indicated the presence of two well defined and continuous tree layers: a lower layer with a mode of 4–6 m, a middle layer with a mode of 14–16 m and a top layer harder to define, comprising a more discontinuous layer with the majority of trees measuring between 28 and 30 m in height (Fig. 2). In addition, there were some scattered emergent trees with heights > 30 m, such as *Cariniana legalis*, *Gallesia integrifolia*, *Apuleia leiocarpa*, *Platypodium elegans*, *Virola gardneri*, *Andradea floribunda* and *Plathymenia foliolosa*. The great majority of our sampled trees were found in the lower layer (86%).

A total of 1276 lianas were recorded in the entire 3 ha of plots sampled, and 52.21% of all marked trees had one or more lianas obstructing their crowns. On average $22.50 \pm 29.90\%$ of the crown surface of trees ≥ 10 cm DBH was obstructed by lianas.

Mean species accumulation curves followed an asymptotic trend in both DBH sample plots, i.e., 3 ha and 1.5 ha. Considering only the smaller sample (1.5 ha), richness was greater for trees of $5 \leq \text{DBH} < 10$ cm than for trees DBH ≥ 10 cm (Fig. 3). The

TABLE 1. Extrapolated species richness estimated by four different methods. Standard errors of the estimates are in brackets.

	N subplots	Observed Species Richness	Extrapolated Species richness			
			Chao	Jackknife 1 st order	Jackknife 2 nd order	Bootstrap
DBH ≥ 10 (3.0 ha)	300	214	288.13 (23.35)	284.76 (9.72)	321.63	246.00 (5.43)
5 ≤ DBH < 10 (1.5 ha)	300	186	269.77 (27.91)	251.78 (10.07)	291.59	215.00 (5.38)

nonparametric estimators confirm these results (Table 1).

The soil analysis data are summarized in Table 2. Overall, soils in Caratinga were dystrophic, acidic and relatively nutrient poor and with slightly high Al^{+3} concentration. An unexpected high concentration of sum of bases may be a result of previous use of fertilizers when parts of the forest were cleared for coffee plantations. Plots varied in soil fertility, in the following order $P3 < P5 < P2 < P6 < P1 < P4$ according to the sum of bases values (K^+ , Ca^{+2} , Mg^{+2} , NA^+). Plot 3 stands out as the poorest with a high concentration of Al^{+3} .

Trees of DBH ≥ 10 cm. There were 1539 trees with DBH ≥ 10 cm in the 3-ha plots, or roughly 513 trees with DBH ≥ 10 cm/ha. Average diameter was 17.80 ± 12.00 cm (range: 10 to 178, median = 14.30 cm); 79% of the trees had a DBH < 20 cm and 5% a DBH ≥ 40 cm. Total basal area was 55.90 m², or 18.63 m²/ha.

At least 214 species (including morphospecies) in 49 families were identified. The Shannon-Wiener diversity index was $H' = 4.6$ and evenness $J = 0.86$. We found that a 50% reduction in the area sampled resulted in a 22% loss in the total number of species sampled (48 species). However, the correlation between the floristic dissimilarity matrix of Bray-Curtis based on the total sample and on the subsample with reduced area was high and significant (Mantel $R = 0.96$, $p < 0.001$). This strong correlation indicates that even with the reduction of sampling effort, species composition and structure of the community would continue to be well represented.

The most diverse plant families were Fabaceae (including all subfamilies) ($n = 42$ species), Rubiaceae (14), Myrtaceae (12), Lauraceae (10), and Euphorbiaceae (9). Fabaceae and Euphorbiaceae had the greatest number of individuals in the sample ($n = 413$ and $n = 175$ respectively), comprising nearly 40% of

all trees of DBH ≥ 10 cm. Other abundant plant families in our plots were Annonaceae, Rubiaceae, and Moraceae (Fig. 4).

Although we found no dominant species in our samples (see Table S1 in supplemental online material), a few had a large number of individuals. In particular *Mabea fistulifera* (Euphorbiaceae) was very abundant, accounting for 9% of all marked trees. This species was followed in abundance by *A. leiocarpa* (Fabaceae Caesalpinioideae; 5%), *Anadenanthera colubrina* (Fabaceae Mimosoideae; 4%), and *Dalbergia nigra* (Fabaceae Faboideae; 3%).

Because most species in tropical forests are represented by only a few individuals, a frequency index is usually of little value (Mori *et al.* 1983). However this index is important to differentiate those abundant tree species that are evenly spread throughout the sample plots from tree species that are abundant but patchily distributed. The most abundant species, *M. fistulifera*, was found in only 33% of our samples in comparison to the less abundant *D. nigra*, *A. colubrina* and *Astronium fraxinifolium* that occurred in c. 60% of the sample units (Table S1, supplemental online material). The three highest indices for relative dominance were 4.7% for *A. leiocarpa*, and 4.5% for *M. fistulifera* and *Ficus sp.*, the latter corresponding to only one very large tree.

Trees of DBH ≥ 5 cm and 5 cm ≤ DBH < 10 cm. In the 1.5-ha sample there were 2190 trees with DBH ≥ 5 cm (c. 1460 trees with DBH ≥ 5 cm/ha) of which 1391 were trees with $5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$. The average DBH for the 2190 trees with DBH ≥ 5 cm was 8.40 ± 8.99 (range 5 to 155.50, median = 8.40 cm).

There were 186 species in 47 families for trees with $5 \leq \text{DBHs} < 10$ cm in the 1.5-ha sample. The most diverse families were the same as those in the DBH ≥ 10 cm sample; Fabaceae ($n = 33$ species), Rubiaceae (15), Myrtaceae (10), and Lauraceae (9).

TABLE 2. Soil chemical analysis (mean ± SD) at RPPN-FMA by plot (n = 5 samples per plot) and overall. S = sum of bases, T = cation exchange capacity, V = base saturation, and $H^+ Al^{+3}$ = potential acidity.

	P1	P2	P3	P4	P5	P6	RPPM-FMA
pH (H ₂ O)	4.88±0.95	4.46±0.48	3.88±0.25	5.54±0.60	4.36±0.34	4.18±0.79	4.55 ± 0.78
Al ⁺³ (c.mol.dm ⁻³)	0.82±1.08	1.02±0.31	1.76±0.31	0.10±0.22	1.00±0.46	1.14±0.97	0.97 ± 0.81
Ca ⁺² (c.mol.dm ⁻³)	2.58±2.90	1.10±0.22	0.10±0.22	4.14±1.67	0.44±0.98	1.52±2.10	1.65 ± 2.12
Mg ⁺² (c.mol.dm ⁻³)	1.16±0.61	0.74±0.15	0.44±0.15	1.22±0.36	0.74±0.53	0.90±0.55	0.87 ± 0.49
Na ⁺ (mg.dm ⁻³)	0.40±0.89	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.07 ± 0.37
K ⁺ (mg.dm ⁻³)	67.80±23.64	44.60±10.72	32.00±10.72	98.20±9.83	53.20±19.29	46.00±27.88	56.97 ± 27.55
H ⁺ Al ⁺³ (c.mol.dm ⁻³)	7.52±4.08	7.88±1.41	10.30±1.41	4.34±1.68	6.94±1.36	8.74±2.63	7.62 ± 2.87
P ^r (mg.dm ⁻³)	2.56±2.07	1.42±0.95	1.98±0.95	2.62±1.04	1.40±0.00	2.14±0.75	2.02 ± 1.15
S(c.mol.dm ⁻³)	3.92±3.54	1.96±0.35	0.62±0.35	5.62±1.96	1.30±1.53	2.56±2.60	2.66 ± 2.61
T(c.mol.dm ⁻³)	11.44±2.13	9.84±1.08	10.92±1.08	9.96±1.40	8.24±1.55	11.28±1.79	10.28 ± 1.79
V%(c.mol.dm ⁻³)	35.00±28.87	20.20±4.06	6.00±4.06	56.00±17.20	14.60±15.39	21.80±22.44	25.60 ± 23.93

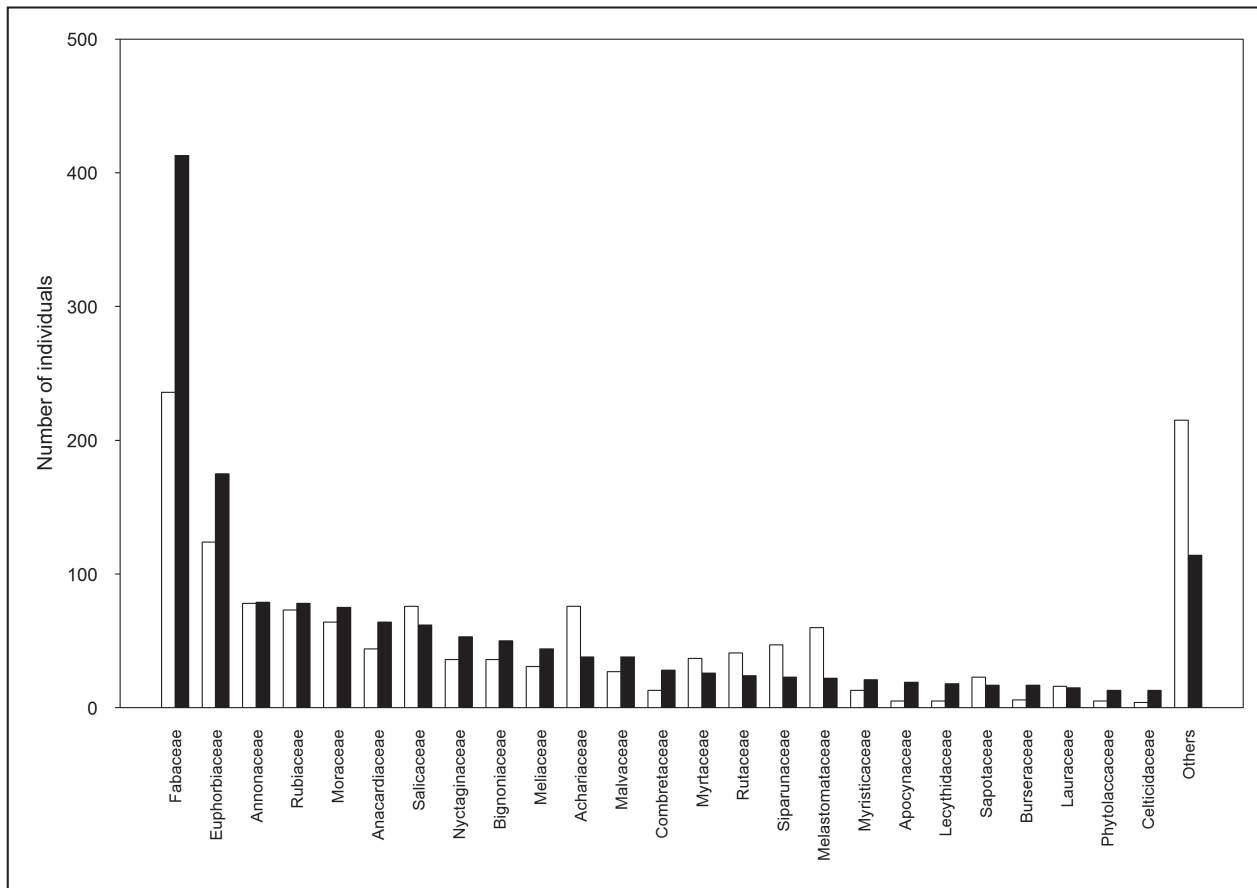


FIG. 4. Tree family abundances for trees in RPPN-FMA with DBH ≥ 10 cm in 3.0 ha (solid bars) and trees $5 \leq$ DBH < 10 cm in 1.5 ha (open bars).

Most abundant families were Fabaceae ($n = 236$ individuals), Euphorbiaceae (124), Annonaceae (78), Salicaceae (76), Achariaceae (76), and Rubiaceae (73).

The top two most abundant trees with DBHs of between 5 and 9.9 cm were *M. fistulifera* ($n = 81$ individuals) and *Carpotroche brasiliensis* ($n = 76$ individuals), which together accounted for 11% of the sampled trees. Other abundant trees in this size class were *A. leiocarpa* (55 individuals), *Siparuna guianensis* (43), *A. colubrina* (36), *Astronium fraxinifolium* (33), and *D. nigra* (31).

Floristic comparison between DBH ≥ 10 and $5 \leq$ DBH < 10 cm samples. Table 3 shows the most abundant tree species in the DBH ≥ 10 cm (3 ha, $n = 1539$ trees) sample and in the $5 \leq$ DBH < 10 cm sample (1.5 ha, $n = 1,391$ trees). The Sørensen Similarity Index was high (SI = 0.7). Of the 262 species present in our total sample, 138 species were common to both small and large DBH trees sampled, 48 occurred exclusively in the sample of trees with small DBHs, and 76 occurred exclusively in trees ≥ 10 cm DBH. The majority of the species that were exclusive to one or

the other sample were found at low densities. A few exceptions were *Almeidea rubra*, *C. brasiliensis*, *Casearia* spp., *Erythroxylum pelleterianum*, *Miconia* spp., and *S. guianensis*, which were all relatively abundant in the small, and scarce or absent in the large DBH sample. These are small understory trees that rarely reach DBH > 10 cm. At the family level, differences in tree abundances were less evident between the two samples. Among the exceptions were trees of Achariaceae, Melastomataceae, Siparunaceae, and Salicaceae, which included the above mentioned species and therefore were proportionally more abundant in the $5 \leq$ DBH < 10 cm sample. Species that were exclusive or relatively more abundant in the large DBH sample included *M. fistulifera*, *A. leiocarpa*, *A. colubrina*, *Banara kuhlmanni*, *Clarisia racemosa*, and *Pseudopiptadenia contorta*. Their low representation in the small DBH sample possibly indicates their reduced recruitment as secondary succession progresses at the RPPN-FMA.

Comparison between hilltop and valley habitat. Of the three habitat types represented in our sample plots, 1.36 ha (45%) corresponded to areas of hillside, 0.76

TABLE 3. Most abundant tree species in the DBH ≥ 10 cm sample (3 ha, n = 1539 trees) and in the 5 ≤ DBH <10 sample (1.5 ha, n = 1391 trees).

Species	DBH ≥10 (n = 1539)	5 ≤ DBH <10 (n = 1391)
<i>Mabea fistulifera</i> Mart.	133	81
<i>Apuleia leiocarpa</i> (Vog.) J.F.Macbr.	83	55
<i>Anadenanthera colubrina</i> (Vell.) Altschul var. <i>colubrina</i>	66	36
<i>Dalbergia nigra</i> (Vell.) Allemão ex. Benth.	49	31
<i>Astronium fraxinifolium</i> Schott	43	33
<i>Carpotroche brasiliensis</i> (Raddi) A.Gray	38	76
<i>Guateria campestris</i> R.E. Fr.	32	27
<i>Sorocea guilleminiana</i> Gaudich.	27	26
<i>Acacia polyphylla</i> DC.	27	8
<i>Terminalia phaeocarpa</i> Eichler	24	8
<i>Guapira hirsuta</i> (Choisy) Lundell	23	23
<i>Alseis floribunda</i> Schott	23	21
<i>Jacaranda puberula</i> Cham.	23	9
<i>Lonchocarpus aff. guilleminianus</i> (Tul.) Malme	21	6
<i>Clarisia racemosa</i> Ruiz & Pav.	21	0
<i>Virola gardneri</i> (A. DC.) Warb.	17	9
<i>Platypodium elegans</i> Vog.	17	8
<i>Crepidospermum atlanticum</i> Daly	17	6
<i>Miconia ligustroides</i> (DC.) Naudin	16	28
<i>Ephedranthus sp.1</i>	15	29
<i>Casearia guianensis</i> (Aubl.) Urb.	15	19
<i>Casearia ulmifolia</i> Vahl ex Vent.	15	13
<i>Luehea grandiflora</i> Mart.	15	8
<i>Tapirira guianensis</i> Aubl.	15	8
<i>Banara kuhlmannii</i> (Sleumer) Sleumer	15	2
<i>Tabebuia serratifolia</i> (Vahl) G.Nicholson	14	19
<i>Molopanthera paniculata</i> Turcz. var. <i>burchellii</i> K.Schum.	14	10
<i>Ramisia brasiliensis</i> Oliv.	14	3
<i>Galipea jasminiflora</i> (A.St.-Hil.) Engler	13	27
<i>Trichilia pallida</i> Sw.	13	19
<i>Xylopia sericea</i> A.St.-Hil.	13	11
<i>Celtis orthacanthos</i> Planch.	13	4
<i>Gallesia integrifolia</i> (Spreng.) Harms	13	4
<i>Siparuna guianensis</i> Aubl.	12	43
<i>Brosimum guianensis</i> (Aubl.) Huber	12	25
<i>Senefeldera verticillata</i> (Vell.) Croizat	12	21
<i>Pseudobombax sp.1</i>	12	7
<i>Albizia polycephala</i> (Benth.) Killip ex Record	12	5
<i>Amaioua sp.1</i>	12	5
<i>Tabernaemontana laeta</i> Mart.	12	4

Species	DBH ≥10 (n = 1539)	5 ≤ DBH <10 (n = 1391)
<i>Piptadenia gonoacantha</i> (Mart.) J.F.Macbr.	12	3
<i>Pseudopiptadenia contorta</i> (DC.) G.P. Lewis & M.P. Lima	12	0
<i>Myrcia splendens</i> (Sw.) DC.	11	24
<i>Inga aff. marginata</i> Willd.	11	6
<i>Guarea guidonia</i> (L.) Sleumer	11	3
<i>Siparuna reginae</i> (Tul.) A. DC.	11	0
<i>Machaerium nictitans</i> (Vell.) Benth.	10	12
<i>Pogonophora schomburgkiana</i> Miers ex Benth.	10	11
<i>Casearia arborea</i> (Rich.) Urb.	9	20
<i>Casearia mariquilenensis</i> Kunth	0	17
<i>Paradrypetes ilicifolia</i> Kuhlm.	8	15
<i>Almeidea rubra</i> A.St.-Hil.	0	11
<i>Miconia holosericea</i> (L.) DC.	1	10
<i>Erythroxylum pelleterianum</i> A.St.-Hil.	0	10

ha (25%) to areas of valley, and 0.78 ha (26%) to areas of hilltop. The remaining 0.10 ha (4%) was not classified. Although we did not intentionally stratify our sample, the proportion at which each of these 3 habitat types occur in the RPPN-FMA is estimated to be roughly comparable (i.e. *c.* 50% hillside, *c.* 25% hilltop and *c.* 25% valley; JPB pers. obs.).

Considering only trees with DBH ≥ 10 cm, basal area per tree was significantly different between habitats type (KW = 18.4011, df = 2, *p* < 0.001) and was much higher in the valley (mean = 530 ± 1748 cm²) than in the hilltop habitats (248 ± 433 cm²), confirmed by multiple comparison post hoc test. There were 351 individual trees representing 81 species in the hilltop habitats. Two species, *M. fistulifera* and *A. colubrina*, comprised 32% of all trees in this habitat. There were 400 trees representing 119 species in the valley habitats. No species dominated the valley areas sampled, and the top three most abundant species, *Acacia polyphylla*, *Alseis floribunda* and *Terminalia phaeocarpa*, were each represented by only 15 individuals. Although a total of 39 species was found in common in both hilltop and valley habitats, their densities differed in most cases. Forty-three tree species were exclusive to hilltop habitats and 81 tree species were exclusive to the valley sample.

DISCUSSION

The structural attributes of the RPPN-FMA forest found in this study are consistent with those of a disturbed secondary forest where *B. hypoxanthus* still

persists (Boubli *et al.* 2010). In our plots there was a high density of small trees with DBH of between 5 and 10 cm, and average DBH and basal area per hectare for trees with DBH ≥ 10 cm was relatively small compared with other tropical forests including Atlantic Forest sites (e.g., Richards 1996, Lopes *et al.* 2002, Guilherme *et al.* 2004, Boubli *et al.* 2010, Silva-Junior *et al.* 2010). The top canopy layer was discontinuous and large emergent trees were rare, all consistent with a long history of selective logging. This situation was more pronounced in the hilltops, possibly due to greater exposure to strong winds and lightning. Humidity is also expected to be lower on the hilltops (Oliveira-Filho *et al.* 2001). In this respect, hilltop habitats present comparable “edge conditions” found in lowland forest fragments (*sensu* Laurance *et al.* 2002).

As a result of a history of fires, in some hilltop areas bracken covered the forest floor leaving large (more than 20 m in diameter) gaps in the canopy. Forest regeneration is arrested in these areas because bracken encroachment and shading hinders tree sapling growth (Tolhurst & Turvey 1992). High liana infestation represents another problem for forest regeneration at the RPPN-FMA. The density of lianas in the study area was very high, to the extent that in some areas it was nearly impossible to walk through the forest without a machete. High densities of lianas are typical of disturbed or high-light areas (Oliveira-Filho *et al.* 1997) or non-mature forests (Ballé & Campbell 1990).

Liana infestation may promote forest degradation causing tree death (Putz 1984) and it arrests the natural regeneration of trees (Naturales 2001). Silva-Junior *et al.* (2010) described a similar phenomenon in another Atlantic Forest fragment at the Parque Estadual Serra do Brigadeiro (PESB), where they report a decrease in basal area and stem density of trees in areas dominated by bamboo. These authors recommend a management of bamboo stands in order to increase the availability of suitable habitat for *Brachyteles hypoxanthus* in that forest. In the RPPN-FMA, managing lianas and bracken could help increase total forest basal area and the closure of the upper canopy layer, leading to a faster regeneration of the forest with an increase in the conditions necessary for the establishment of shade tolerant, climax species (e.g., Tabarelli & Mantovani 1999).

In spite of its disturbed state, the RPPN-FMA forest was unexpectedly very diverse ($H' = 4.6$). The evenness component J was relatively high, indicating that no tree species dominated our sample. Such high diversity and evenness indices are comparable to wetter and more pristine Atlantic Rain Forest sites in São Paulo and Rio de Janeiro (Silva & Leitão Filho 1982, Leitão Filho 1993, 1994; Melo & Mantovani 1994, Sztutman & Rodrigues 2002) and unusual for dry and semideciduous disturbed tropical forests (Richards 1996, Ivanauskas *et al.* 1999, Lopes *et al.* 2002). Phytosociological surveys conducted in the wetter Atlantic Rain Forest in São Paulo show tree diversity indices ranging from 4.07 to 4.31 (Silva & Leitão Filho 1982, Leitão Filho 1993). Diversity of trees in the large semideciduous forest of Parque Estadual do Rio Doce, MG, approximately 200 km west of Caratinga, is lower ($H' = 3.98$; Lopes *et al.* 2002). Data from several 1-ha plots throughout the Neotropics reveal that the number of tree species with DBH ≥ 10 cm varies from 60 to 150 and, in very rich areas such as western Amazonia, this figure goes up to 200 – 300 species (Gentry 1990, Richards 1996). With *c.* 150 species per hectare, the RPPN-FMA forest falls at the upper end of the floristic diversity documented throughout the Neotropics. Although the correlation between tree species diversity and soil fertility is controversial, Gentry (1988) believed that the richest forests in Amazonia occur on the richer soils of the Andean foothills. Ashton (1989), on the other hand, suggested that on rich soils competitive exclusion would come into effect, lowering overall diversity as competitive superior species would dominate the sample. At our site, soils were acidic

and dystrophic, comparable with other lowland tropical rainforests.

One possible factor contributing to tree species diversity in the RPPN-FMA is the heterogeneity of habitat types present there. Hilltop and valley habitat differed not only in forest structure but also in plant species composition. Just as hilltop habitat resembles edge habitat in its structural attributes, it is also likely richer in pioneer and early succession trees than valley habitats, which are better able to support the establishment of a mature, late succession tree community. This species difference between hilltop and valley is a source of overall species diversity in the RPPN-FMA.

Another possibility that remains to be tested is the role played by the abundant primate fauna in maintaining the high tree species diversity in the RPPN-FMA by their seed-dispersing services. Some support for this idea comes from the high absolute frequency of the most abundant tree species and the high evenness index, indicating that most abundant trees were not spatially clumped. Even in pristine primary forests of Amazonia, trees tend to have clumped distributions (Hubbell & Foster 1986) and absolute frequency indexes are low overall (e.g., Boubli 2002), to the extent that Mori *et al.* (1983) consider all frequency indexes to be of little value. However, it would have to be established that seeds are viable post-dispersal and that a substantial percentage of them survive to adulthood for seed dispersal by primates to be considered as important in contributing to the observed tree diversity and evenness.

Abiotic seed dispersal might also play an important role in the non-clumped plant distribution in RPPN-FMA. However, abiotically dispersed trees did not outnumber animal dispersed trees in our sample it represents *c.* 45% of the most abundant species (Couto-Santos *et al.* 2007). *Mabea fistulifera* is a good example of these abiotically dispersed trees; although not dominant it was the most abundant species in our sample but showed a clumped distribution.

Seeds of *Mabea fistulifera* are dispersed by an explosive mechanism (*sensu* van der Pijl 1982), with its three seeds per fruit dropping to the ground near the parent tree. The high abundance of *M. fistulifera* is a peculiarity of the RPPN-FMA; it does not tend to be so abundant in other sites where northern muriquis occur (Lopes *et al.* 2002, Silva-Junior *et al.* 2010). *M. fistulifera* is a pioneer and is commonly found in areas of severe disturbance, where it colo-

nizes open abandoned pastures. The distribution of *M. fistulifera* in our sample at the RPPN-FMA is associated with the regeneration process of areas that have been clear-cut for pasture and agriculture, or in areas that have suffered frequent fires such as on hilltops, where they are presently most abundant. The nectar of *M. fistulifera* is consumed by the miquis and other primates in the RPPN-FMA and may represent a critical resource at times of food scarcity (Ferrari & Strier 1992, Mourthé 2006). Yet the relatively small number of *M. fistulifera* in the $5 \leq \text{DBH} < 10$ cm relative to their numbers in the $\text{DBH} \geq 10$ sample suggests a decline in the recruitment of trees of this species, perhaps as a consequence of the decline in forest disturbances at the site and the regeneration of these areas.

The floristic composition of RPPN-FMA showed some other peculiarities compared with overall Atlantic Forest patterns as presented by Oliveira-Filho & Fontes (2000). For example, the commonest plant families, Myrtaceae and Lauraceae, ranked relatively low in abundance (although not in species richness), and other common Atlantic Forest genera such as *Eugenia*, *Euterpe*, *Myrcia*, and *Ocotea* (Oliveira-Filho & Fontes 2000) were relatively scarce in our samples. However, these differences may be characteristic of other semideciduous secondary forests of Minas Gerais as well, for many abundant species at the RPPN-FMA (e.g., *Apuleia leiocarpa*, *Dalbergia nigra*, *Anadenanthera colubrina*, *Pseudopiptadenia contorta*, *Piptadenia gonoacantha*, *Carpotroche brasiliensis*, *Aca-cia polyphylla*, *Xylopia sericea*, *Sorocea* spp., *Brosimum guianensis*, *Casearia sylvestris*, *Siparuna guianensis*, *Virola gardneri*, *Cariniana legalis*) are found in relative abundance in these other neighboring forests (e.g., Lopes *et al.* 2002, Silva *et al.* 2003, Silva-Junior *et al.* 2010).

In terms of factors involved in the high carrying capacity of the miquis population at our site, of the 54 top-ranking species in our total sample (with at least 10 individuals in either the $5 \leq \text{DBH} < 10$ cm or $\text{DBH} \geq 10$ cm sample), only 15 are not known to be consumed by the northern miquis (Strier 1991, Rímoli & Ades 1997, Boubli *et al.* unpublished). In addition, top ranking dietary species such as *A. leiocarpa*, *C. brasiliensis*, *M. fistulifera*, *M. holosericea*, or *S. guianensis* are also among the most abundant tree species sampled. Thus we believe that the floristic composition of the RPPN-FMA forest, regardless of structural attributes, is an important factor explaining the observed high northern miquis numbers in

RPPN-FMA. Support for this idea comes from Parque Estadual do Rio Doce (PERD), where Silva-Junior *et al.* (2010) have attributed the comparatively low density of northern miquis to the fact that the dominant species *Senefeldera multiflora* is not food for the monkeys. This is a dense tree species responsible for the low evenness index ($J = 0.70$) in their sample (Silva-Junior *et al.* 2010), and which they suggest might result in increased locomotion requirements for foraging and a corresponding lower density of northern miquis. The highest density of miquis in that comparative study was also the site (Mata do Sossego) that had the highest evenness index ($J = 0.87$).

In summary, our study shows that the secondary forest at the RPPN-FMA is composed of a very diverse and even tree community with a floristically unique tree species assemblage, including top-ranking species that are important miquis foods. This forest is a mosaic of patches at different stages of regeneration with abundant pioneer species. Although structurally RPPN FMA should not be expected to offer ideal substrate for the locomotion of a large arboreal primate, overall conditions in this forest are favorable to miquis as their population has been growing steadily since research began in this site more than 30 years ago, achieving its highest known density today. It has been shown in forests elsewhere that primates that include substantial amounts of leaves in their diet (as is the case in northern miquis: 51% of the annual diet, Strier 1991) may occur at higher densities in disturbed habitats where palatable and nutritious leaves with high protein to fiber ratios are more abundant (Johns & Skorupa 1987, Ganzhorn 1995, Strier 2000, Pinto *et al.* 2009). Rapidly growing pioneer plants, characteristic of secondary forests, may be more palatable because these plants contain fewer chemical and structural defenses (Coley *et al.* 1985, Ganzhorn 1995). Thus if early stages of secondary succession mean there is more food available to northern miquis, then these monkeys should thrive in these types of forests (but see Silva-Junior *et al.* 2010).

Unfortunately, as has been shown in other fragmented landscapes, maintaining the status quo in fragmented habitats is insufficient to guarantee the long-term survival of key species such as the northern miquis (e.g., Krauss *et al.* 2010). If the high carrying capacity of the miquis population is a consequence of current favorable conditions in a secondary forest habitat, as this forest matures it can be expected that

these conditions will change. As shown above, there is already an indication that the recruitment of the important muriqui feeding tree, *Mabea fistulifera*, is declining. Although the RPPN FMA forest fragment may stay a secondary forest patch because of the way it is sized and configured within the landscape (see Groeneveld *et al.* 2009), other factors such as changes in climate and land use may affect RPPN FMA resilience in yet unpredictable ways (Metzger *et al.* 2009, Pardini *et al.* 2010), posing a threat to the survival of northern muriquis there. We recommend that a management plan for this reserve should include mitigation measures that take such threats into account, but also that put in place a monitoring program to detect any changes in species diversity and composition that may indicate a regime shift (*sensu* Pardini *et al.* 2010) where the erosion in biodiversity may be irreversible and detrimental to muriquis.

Apart from implementing a monitoring system, we also believe that the next most important step is to increase RPPN FMA connectivity with remaining fragments in this landscape. Despite some controversy, corridors are usually considered to be one of the most important landscape elements to facilitate movement of individuals and gene flow through fragmented landscapes (Simberloff *et al.* 1992, De Lima & Gascon 1999). Connecting fragments would foster the formation of metapopulations for northern muriquis, a desirable situation for primate populations such as the one in RPPN-FMA that remain vulnerable to natural and human-induced catastrophes such as fires and diseases (see Mendes *et al.* 2005, Strier *et al.* 2005, Tabacow *et al.* 2009).

Finally, we believe that without northern muriquis or other large seed dispersers neighboring forest fragments are likely to undergo a collapse in tree diversity, becoming dominated by a few tree species that produce abiotically dispersed seeds (e.g., Tabarelli *et al.* 1999, Laurence *et al.* 2002, Tabarelli & Peres 2002, Redford & Feinsinger 2003, Peres & Palacios 2007, Terborgh *et al.* 2008). Introducing northern muriquis into these isolated empty fragments by creating a network of ecological corridors would help reestablish this ecological interaction and restore the local ecosystem dynamics.

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Additional material available on the ECOTROPICA homepage (http://www.gtoe.de/?page_id=113):

TABLE S1. Phytosociological descriptors of tree species with DBH \geq 10 cm sampled in 3 ha of lowland Atlantic Rain Forest, RPPN-FMA, Minas Gerais, Brazil.

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