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# Analysis of floristic composition and structure as an aid to monitoring protected areas of dense rain forest in southeastern Brazil

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**ABSTRACT**

To study forest composition and structure, as well as to facilitate management plans and monitoring programs, we conducted a phytosociological survey in the PE Caverna do Diabo State Park and the Quilombos do Médio Ribeira Environmentally Protected Area, both located within the state of São Paulo, Brazil. We analyzed 20 plots of 400 $m^2$ each, including only individuals with a circumference at breast height ≥ 15 cm. We employed cluster analysis and ordination (principal component analysis and correspondence analysis), including species data and abiotic data. We evaluated 1051 individuals, belonging to 155 species in 48 families. Of those 155, 18 were threatened species, 33 were endemic species, and 92 (59.4%) were secondary species. The overall Shannon index was 4.524, one of the highest recorded for a dense rainforest in southeastern Brazil. We found that our sample plots fell into three blocks. The first was forest in which there had been human disturbance, showing low species richness, minimal density, and a small relative quantity of biomass. The second was undisturbed mature forest, showing a comparatively larger quantity of biomass. The third was mature forest in which there had been natural intermediate disturbance (dead trees), showing higher species richness and greater density. We identified various groups of species that could be used in monitoring these distinct forest conditions.

**Key words**: Biodiversity, intermediate disturbance, Atlantic Forest, forest monitoring

## Introduction

Although the Atlantic Forest biome originally covered roughly 150 million ha of Brazilian territory, only 11.73% remain. The largest fragments of dense rain forest are located in the Serra do Mar area, distributed throughout the states of Rio de Janeiro, São Paulo and Paraná (Ribeiro *et al.* 2009). The Atlantic Forest biome comprises the dense rain forest and related ecosystems—including open rain forest, *Araucaria* forest, mangrove, *restinga* (coastal woodland) and sand dune vegetation—and has garnered international attention because of its strategic importance, being one of the eight so-called "biodiversity hotspots" (Myers *et al.* 2000), as well as because of its high level of species endemism (Mittermeier 2005) and large number of endangered species (Brasil 2008). The dense rain forest is one of the world's most threatened ecosystems.

To preserve the diversity of biomes worldwide, there are specially protected areas (Dudley 2008), known in Brazil as conservation units (Brasil 2000). The state of São Paulo has 9000 ha of protected areas, approximately 40% of which are in the Vale do Ribeira, the location of our study sites. Studies on biodiversity can effectively promote conservation of these areas, because knowledge of protected species is a prerequisite for efficient management. Such studies can facilitate the development of management plans for these conservation units, as well as of monitoring programs for the ecosystems and species involved.

Several studies have been conducted in order to profile the biodiversity and ecological processes in protected areas of the Atlantic Forest biome in the various states within the southeastern region of Brazil, such as the works of Oliveira *et al.* (2001) and Mamede *et al.* (2004) at Juréia-Itatins Ecological Station (São Paulo); Kurtz & Araújo (2000) at

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Paraíso State Ecological Station (Rio de Janeiro); Moreno *et al.* (2003) at Desengano State Park (Rio de Janeiro); Sztutman & Rodrigues (2004) at Campina do Encantado State Park (São Paulo); Peixoto *et al.* (2004) at Serra da Capoeira Grande Environmentally Protected Area (Rio de Janeiro); Aidar *et al.* (2001), Guilherme *et al.* (2004) and Zipparro *et al.* (2005) at Alto Ribeira Touristic State Park (São Paulo); Guedes-Bruni *et al.* (2006) at Poço das Antas Biological Reserve (Rio de Janeiro); Catharino *et al.* (2006) at Morro Grande Forest Reserve (São Paulo); and Assis *et al.* (2011) and Rochelle *et al.* (2011) at Serra do Mar State Park – Picinguaba base (São Paulo). All of those studies registered high woody species richness and a high Shannon diversity index (H' = 2.88-4.75), demonstrating the importance of the conservation units (Brasil, 2000) in protecting the plant species of the Atlantic Forest biome.

The study sites are located within the Jacupiranga Complex of conservation units (Estado de São Paulo 2008b). This Complex resulted from the redefinition of the boundaries of the former Jacupiranga State Park and now comprises fourteen conservation units, with a total of 243,855.78 ha: three state parks, four environmentally protected areas, five sustainable development reserves and two extractive reserves.

There have been no systematic surveys of woody species diversity in the conservation units within the Jacupiranga Complex. However, the protected areas of Brazil, including our study sites, have been suffering the same problems seen in other countries, such as ecosystem degradation, encroachment and invalidation of the legal instrument of their creation (Terborg 2002). To avoid these problems and guarantee conservation effectiveness, the Brazilian National System of Conservation Units (Brasil 2000) requires that each conservation unit create its management plan within the first five years after its creation. The management plans are important instruments of planning and administration that direct management actions, establish research priorities, set forth restrictions and lay down guidelines for direct and indirect use of protected areas. Even though the importance of having a management plan is recognized by managers and government officials, those plans have yet to be devised for the Jacupiranga Complex, which was created in 2008.

The aim of this study was to investigate woody species richness and structure in the Jacupiranga Complex, especially within the Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area; analyzing the maturity of the plant community and discussing the conservation status of this forest, thereby facilitating the development of management plans for those two preserves. An additional objective was to collect preliminary data for the monitoring of terrestrial ecosystems in these protected areas, under the assumption that there are differences among the fragments of dense rain forest in the studied areas, and that these differences are related to physical features of the environment, as well as to natural or human disturbances.

# Material and methods

### *Study site*

This study was conducted in the Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area, both part of the Jacupiranga Complex (Estado de São Paulo 2008), formerly known as Jacupiranga State Park (Lino 2009). The Caverna do Diabo State Park comprises 40,219.66 ha and the Quilombos do Médio Ribeira Environmentally Protected Area comprises 64,625.04 ha. These two preserves encompass an area stretching from 24°20'S to 24°46'S and from 48°03'W to 48°40'W and are distributed throughout the region in which the cities of Barra do Turvo, Cajati, Eldorado and Iporanga are located. The Jacupiranga Complex is located within the so-called "crystalline complex", which has various lithologies, including the Turvo-Cajati formation, the Costeiro granite belt, the Setuvas assemblage, the (Neoproterozoic) Açungui group, and post-tectonic granites (Almeida *et al.* 1981). The landscape is one of rolling hills (Ponçano *et al.* 1981). The vegetation is comprised of dense rain forest of various subtypes according to the altitude (Veloso *et al.* 1991; Brasil 1992): submontane, montane and high montane.

### *Data collection*

We conducted a phytosociological survey in a dense rain forest (Fig. 1), using the plot method (Mueller Dumbois & Ellemberg 1974).

We placed 20 plots of 400 m$^2$ each (Fig. 1) in the proximities of the following trails: Caverna (plots 1 and 2); Araçá (plots 3 to 11); and Bugio (plots 12 to 20). The Caverna trail grants access from the visitor center to the Diabo Cave and is approximately 150 m long. This trail further divides into two new trails, Araçá to the right, and Bugio to the left (Fig. 1). We placed 9 plots along each of the main trails (Araçá and Bugio), because they circle a group of hills that vary in orientation of sun exposure. On the Araçá trail, declivity, rockiness and the amount of incident light on soil are visibly greater, and the predominant exposure is east by northeast. On the Bugio trail, declivity, rockiness and the amount of incident light on soil are visibly lesser, and the predominant exposure is west by southwest. We placed only two plots on the Caverna trail, because of its short length.

We sampled all woody individuals with a circumference at breast height ≥ 15 cm, collected botanical material for identification and registered their height and circumference at breast height. Data were collected from 2005 to 2009.

In all plots, we analyzed the physical features of the environment (abiotic factors), such as: rockiness, declivity, litter, human disturbance, canopy cover, and altitude. Rockiness was categorized on a four-point scale: 0 = no exposed rock within the plot; 1 = exposed rock in ≤ 10% of the plot; 2 = exposed rock in 11-30% of the plot; and 3 = exposed rock in > 30% of the plot.

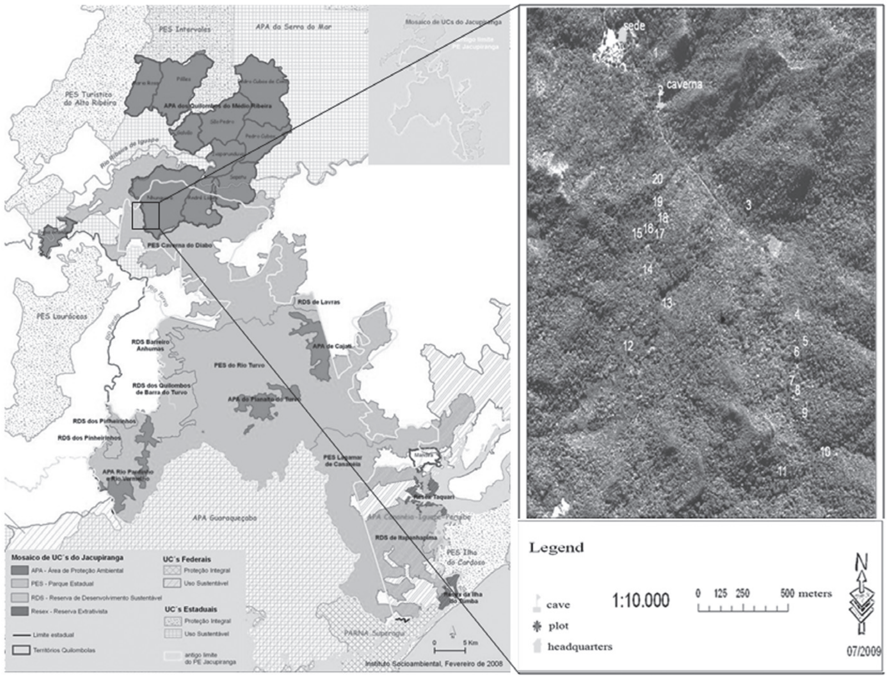


**Figure 1.** A- Map of the Jacupiranga Complex. B- Aerial image of the Jacupiranga Complex (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W) and of the plots sampled in the present study.
*The *quilombolas* are members of the *quilombos*, communities established by freed slaves.
Source (A): Instituto Socioambiental, 2008.

Human disturbance was quantified by assessing the following indicators: the presence of trash/garbage; evidence of fire; felled trees; and evidence of domesticated animals. Human disturbance was categorized as follows: 0 = no impact; 1 = positive for one indicator to a low degree; 2 = positive for two or more indicators to a low degree; and 3 = positive for two or more indicators to a moderate degree or for one indicator to a high degree. Litter was also categorized on a four-point scale, based on the depth of the litter layer: 0 = completely decomposed; 1 = 1-3 cm; 2 = 3-6 cm; and 3 = > 6 cm. To obtain the litter layer thickness values, we randomly measured 10 points within the plot and calculated the mean.

Declivity was categorized as follows: 0 = flat or gently sloping terrain (0-10°); 1 = moderately steep terrain (11-20°); 2 = steep terrain (21-44°); 3 = very steep terrain (≥ 45°). Altitude was measured directly with an altimeter. To quantify canopy cover, we used a densiometer and calculated the percentage of canopy cover.

### *Data analysis*

We identified all species with the use of dichotomous keys and literature on the taxa; through comparison with specimens on file at recognized herbaria (those of the University of São Paulo Luiz de Queiroz Graduate School of Agriculture, the São Paulo State University at Campinas and the São Paulo State Botanical Institute); and with the aid of specialists. Species identification followed the Angiosperm Phylogeny Group II guidelines (APG II 2003; Souza & Lorenzi 2005). Voucher specimens were deposited at the Herbarium of the Federal University of São Carlos at Sorocaba Center for Sustainability Science and Technology. We defined endangered species as those listed as such on the São Paulo State List of Endangered Plant Species (Estado de São Paulo 2008a), the Brazilian National List of Endangered Plant Species (Brasil 2008) and the International Union for Conservation of Nature Red List of Threatened Species (IUCN 2012). We defined species endemic to the Atlantic Forest biome were defined as those having a geographic distribution restricted to the biome and cited as being endemic to Brazil in the 2012 List of Species in the Flora of Brazil (Forzza *et al.* 2012). The species identified were compared with other studies of this nature through SSI = Sorensen similarity index.

All species were categorized in ecological or successional groups according to Budowski (1965): pioneer, early secondary, late secondary and climax. Species classification was based on our own field experience, direct observation and data from the literature, especially the studies of Leitão Filho (1993) and Gandolfi (1995). Species without enough references were deemed "uncategorized". According to Catharino *et al.* (2005), a correct classification of species into functional groups depends upon the knowledge of the species biology and the adaptation of data from classic authors (Budowsky 1965; Denslow 1980; Whitmore 1989). To avoid classification errors and facilitate data analysis, the four groups were united into two—pioneer *sensu lato* (pioneer and early secondary) and non-pioneer *sensu lato* (late secondary and climax)—in agreement with the classification system devised by Whitmore (1989). To identify the development stage of the forest, we analyzed the relative proportion of pioneer and non-pioneer species and individuals, considering a value above 50% as an indicator of a certain successional stage, a procedure also adopted by Dislich *et al.* (2001).

We analyzed the following phytosociological parameters: absolute and relative density; absolute and relative dominance; cover value; and Shannon diversity index (H'). We conducted a cluster analysis with the unweighted pair group method with arithmetic mean and Bray-Curtis similarity, using a matrix of sampling units and total species number.

We also conducted a principal components analysis (PCA), using a matrix of sampling units and number of individuals per species (selecting species with 10 or more individuals). Using this same matrix and adding the data of abiotic factors for each plot, we conducted a correspondence analysis (CA). In this case, the altitude and canopy cover data were grouped in four classes to improve graph visualization. All phytosociological analyses were conducted with the software Fitopac 2.1 (Shepherd 2009).

The cluster analysis indicated three distinct clusters of sampling units, and a similar result was obtained in the CA (the analyses were conducted with the total number of plots, regardless of their location in field). The groups of plots obtained in the CA were compared with Student's t-test (Zar 1996) in terms of phytosociological parameters number of species, total density and biomass (volume and basal area), with the software BioEstat 5.0 (Ayres *et al.* 2007). These groups of plots were also tested in terms of number of dead trees and number of individuals of *Euterpe edulis* (t-test with 5% significance level), due to the large number of dead trees and the small number of individuals of *E. edulis* within the study site.

Because the occurrence of *E. edulis* was greater in the group of plots with the largest number of dead trees, highest density of individuals and greatest species richness, we conducted Pearson's correlation tests between the number of dead trees and number of *E. edulis* individuals; between total density and number of *E. edulis* individuals; and between species richness and number of *E. edulis* individuals. All of those tests were conducted with the software BioEstat 5.0 (Ayres *et al.* 2007).

## Results and discussion

We sampled 1501 individuals belonging to 155 species in 48 families (Tab. 1). Density was 1313.75 ind./ha, and the basal area was 36.45 $m^2$/ha. The Shannon diversity index was 4.524, with an evenness of 0.897. Myrtaceae, Fabaceae (or Leguminosae), Rubiaceae, Meliaceae and Lauraceae were the families with the highest richness and, together with 15 other families (Fig. 2), accounted for 75.36% of the total species and 91.15% of the total individuals. Fabaceae was the family with the greatest number of individuals, followed by Myrtaceae and Rubiaceae. The genera with highest species richness were: *Eugenia* (9), *Myrcia* (7), *Maytenus* (4), *Machaerium* (4), *Nectandra* (4), *Miconia* (4), *Trichilia* (4) and *Zanthoxylum* (4). No exotic species were sampled within the plots.

Our results are in agreement with those of other studies of the Atlantic Forest in southeastern and southern Brazil, in which Myrtaceae and Fabaceae were found to be the families with highest species richness. Rochelle *et al.* (2011) conducted a review of 28 such studies and found that species richness was highest for Myrtaceae in 21 of those studies, whereas it was highest for Fabaceae in four. Most studies conducted in dense rain forest in the state of São Paulo (Melo & Mantovani 1994; Melo *et al.* 2000; Guilherme, 2004; Zipparro *et al.* 2005; Catharino *et al.* 2006) show Myrtaceae as the richest family, usually followed by Fabaceae, Rubiaceae, Lauraceae, Melastomataceae and Euphorbiaceae. Many of the species endemic to the Atlantic Forest (Tab. 1) belong to Myrtaceae. In studies conducted in dense rain forest, the genus *Eugenia* is cited as having the largest number of species (Rochelle *et al.* 2011; Scudeller *et al.* 2001). Oliveira Filho & Fontes (2000) asserted that, in such forests, Myrtaceae is the richest family, the richest genera being *Eugenia*, *Myrcia*, *Miconia* and *Ocotea*.

In the present study, the species with the highest cover values included the pioneers *Anadenanthera colubrina*, *Piptadenia gonoacantha*, *Alchornea triplinervia*, and *Senna multijuga*, as well as the non-pioneers *Ficus enormis*, *Cryptocarya aschersoniana*, *Casearia obliqua*, *Campomanesia guaviroba*, *Myrcia splendens*, *Cabralea canjerana*, *Bathysa australis*, *Chrysophyllum marginatum*, *Eugenia mosenii*, *Guapira opposita*, and *Chrysophyllum* sp. (Tab. 1), collectively accounting for 41.3% of the total cover value (Fig. 3). In a study conducted near the municipality of Ubatuba, in the state of São Paulo, Ramos *et al.* (2011) reported that *B. australis* and *G. opposita* were the species with the largest cover values, whereas Guilherme *et al.* (2004) reported that *B. australis*, *G. opposita* and *A. triplinervia* were among the species with largest cover value at Intervales State Park, also within the state of São Paulo.

In the present study, despite having a relatively large number of individuals (n = 22), *E. edulis* ranked 30th in cover value, because all of those individuals were small in diameter. This contrasts with the results of most studies conducted in dense rain forests, in which *E. edulis* occupied the first positions either in cover value or importance value (Mamede *et al.* 2004; Ramos *et al.* 2011; Guilherme *et al.* 2004). This finding raises concern, because *E. edulis* is an endangered species in Brazil and in the state of São Paulo. Therefore, one would expect that, especially within an area of total conservation, it would be protected.

Dead individuals (treated as a single species) occupied the first position in cover value, emphasizing the intense

**Table 1.** Species sampled within the Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W).

| Species | Individuals n | Collector I.D. | Abbreviation | Ecological group | Endangered status Geographic range-threat level | Exclusive to the AF of Brazil | Cover value |
|---|---|---|---|---|---|---|---|
| Dead individuals | 84 | | | - | | | 13.42 |
| *Anadenanthera colubrina* (Vell.) Brenan | 19 | 1233 | *A col* | P | | No | 7.44 |
| *Ficus enormis* (Miq.) Miq. | 10 | 237 | *F eno* | NP | | No | 7.02 |
| *Piptadenia gonoacantha* (Mart.) J.F.Macbr. | 17 | 703 | *P gono* | P | | No | 6.50 |
| *Alchornea triplinervia* (Spreng.) Müll.Arg | 15 | 655 | *A tri* | P | | No | 6.13 |
| *Cryptocarya aschersoniana* Mez | 9 | 83 | *C asch* | NP | | No | 4.89 |
| *Casearia obliqua* Spreng. | 35 | 190 | *C obli* | NP | | No | 4.63 |
| *Senna multijuga* (Rich.) H.S. Irwin & Barneby | 19 | 289 | *S mult* | P | | No | 4.12 |
| *Campomanesia guaviroba* (DC.) Kiaersk. | 22 | 760 | *C gua* | NP | | No | 4.11 |
| *Myrcia splendens* (Sw.) DC. | 9 | 1236 | *M spl* | NP | | No | 4.03 |
| *Cabralea canjerana* (Vell.) Mart. | 21 | 335 | *C canj* | NP | | No | 3.97 |
| *Bathysa australis* (A. St.-Hil.) Hook. f. ex K. Schum. | 22 | 1499 | *B aus* | NP | | No | 3.93 |
| *Chrysophyllum marginatum* (Hook. & Arn.) Radlk | 20 | 384 | *C marg* | NP | SP-NT | No | 3.51 |
| *Eugenia mosenii* (Kausel) Sobral. | 16 | 05 | *E mos* | NP | | Yes | 3.20 |
| *Guapira opposita* (Vell.) Reitz | 29 | 1430 | *G opp* | NP | | No | 3.09 |
| *Chrysophyllum* sp. | 5 | 346 | *C sp* | NP | | No | 3.00 |
| *Machaerium stipitatum* (DC.) Vogel | 4 | 249 | *M sti* | P | | No | 2.86 |
| *Hieronyma alchorneoides* Allemão | 9 | 1477 | *H alc* | P | | No | 2.81 |
| *Virola bicuhyba* (Schott ex Spreng.) Warb. | 6 | 1467 | *V bic* | NP | | Yes | 2.76 |
| *Annona dolabripetala* Raddi | 12 | 671 | *A dol* | NP | | Yes | 2.64 |
| *Myrcia deflexa* (Poir.) DC. | 11 | 408 | *M defl* | NP | | No | 2.50 |
| *Prockia crucis* L. | 20 | 117 | *P cru* | P | | No | 2.45 |
| *Machaerium* sp.1 | 12 | 216 | *M sp* | - | | No | 2.45 |
| *Dahlstedtia pinnata* (Benth.) Malme | 21 | 323 | *D pin* | NP | | Yes | 2.44 |
| *Coussarea contracta* var. *contracta* | 17 | 371 | *C contr* | NP | | No | 2.41 |
| Indet 1 | 2 | | *In1* | - | | No | 2.37 |
| *Pera glabrata* (Schott) Poepp. ex Baill. | 15 | 743 | *P gla* | P | | No | 2.35 |
| *Guatteria nigrescens* Mart. | 18 | 1333 | *G nig* | NP | | No | 2.26 |
| *Nectandra grandiflora* Nees & C. Mart. ex Nees | 11 | 247 | *N gran* | NP | | No | 2.24 |
| *Euterpe edulis* Mart. | 22 | 860 | *E edu* | NP | BR-EN; SP-VU | No | 2.23 |
| *Tibouchina mutabilis* (Vell.) Cogn. | 9 | 1145 | *T mut* | P | | Yes | 2.09 |
| *Mollinedia uleana* Perkins | 17 | 1260 | *M ule* | NP | | Yes | 1.99 |
| *Pisonia ambigua* Heimerl | 11 | 86 | *P amb* | NP | | No | 1.99 |
| *Coussarea contracta* var. *panicularis* Müll.Arg. | 9 | 35 | *C cont* | NP | | No | 1.99 |
| *Sloanea monosperma* Vell. | 9 | 1221 | *S mon* | NP | | No | 1.96 |
| *Casearia sylvestris* Sw. | 12 | 1234 | *C syl* | P | | No | 1.92 |
| *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. | 17 | 953 | *A edu* | P | | No | 1.90 |
| *Eugenia cuprea* (O. Berg) Mattos | 9 | 112 | *E cup* | NP | | Yes | 1.82 |
| *Gomidesia spectabilis* (DC.) O. Berg (sin. *Myrcia spectabilis* DC.) | 14 | 02 | *G spec* | NP | | Yes | 1.74 |

Continues

**Table 1.** Continuation.

| Species | Individuals n | Collector I.D. | Abbreviation | Ecological group | Endangered status Geographic range-threat level | Exclusive to the AF of Brazil | Cover value |
|---|---|---|---|---|---|---|---|
| *Mollinedia schottiana* (Spreng.) Perkins | 12 | 354 | *M sch* | NP | | Yes | 1.70 |
| *Rudgea jasminoides* (Cham.) Müll.Arg. | 14 | 209 | *R jasm* | NP | | No | 1.61 |
| *Cinnamomum glaziovii* (Mez) Kosterm. | 2 | 680 | *C gla* | NP | | Yes | 1.60 |
| *Cupania oblongifolia* Mart. | 11 | 715 | *C oblo* | NP | | No | 1.57 |
| *Schizolobium parahyba* (Vell.) S.F.Blake | 5 | 917 | *S par* | P | | No | 1.57 |
| *Clusia criuva* Cambess. | 10 | 777 | *C cri* | P | | Yes | 1.57 |
| *Psychotria suterella* Müll.Arg. | 15 | 822 | *P sut* | NP | | No | 1.55 |
| *Nectandra megapotamica* Spreng. Mez | 9 | 870 | *N meg* | NP | | No | 1.52 |
| *Myrocarpus frondosus* Allemao | 4 | 734 | *M fron* | NP | WW-DD, SP-NT | No | 1.44 |
| *Garcinia gardneriana* (Planch. & Triana) Zappi | 9 | 308 | *G gar* | NP | | No | 1.43 |
| *Machaerium scleroxylon* Tul. | 12 | 751 | *M scle* | NP | | No | 1.30 |
| *Eugenia* aff *stictosepala* Kiaersk. | 10 | 280 | *E stic* | NP | | No | 1.29 |
| *Syagrus romanzoffiana* (Cham.) Glassman | 5 | 1238 | *S rom* | NP | | No | 1.17 |
| *Cedrela fissilis* Vell. | 5 | 659 | *C fiss* | NP | WW-EN, SP-NT | No | 1.15 |
| *Prunus sellowii* Koehne | 2 | 1150 | *P sel* | P | | No | 1.13 |
| Indet 2 | 2 | | *In2* | - | | No | 1.10 |
| *Eugenia blastantha* (O.Berg) D.Legrand | 4 | 43 | *E bla* | NP | | No | 0.93 |
| *Hedyosmum tepuiense* Todzia (sin. *Hedyosmum brasiliense* Miq.) | 1 | 1163 | *H tep* | NP | | No | 0.99 |
| *Cryptocarya moschata* Nees & Mart. | 7 | 718 | *C mos* | NP | | No | 0.92 |
| *Inga marginata* Willd. | 8 | 956 | *I mar* | P | | No | 0.91 |
| *Guarea kunthiana* A. Juss. | 4 | 353 | *G kun* | NP | SP-NT | No | 0.90 |
| *Maytenus alaternoides* Reissek | 8 | 359 | *M ala* | NP | | No | 0.90 |
| *Machaerium aculeatum* Raddi | 6 | 271 | *M acu* | P | | No | 0.87 |
| *Eugenia monosperma* Vell. | 4 | 1182 | *E mon* | NP | | Yes | 0.87 |
| *Nectandra leucantha* Nees & Mart. | 4 | 811 | *N leu* | NP | SP-NT | Yes | 0.85 |
| *Sapium glandulosum* (L.) Morong | 7 | 761 | *S gla* | P | | No | 0.84 |
| *Solanum* aff *caavurana* Vell. | 6 | 808 | *S caa* | P | | No | 0.84 |
| *Cestrum axillare* Vell. | 7 | 709 | *C axi* | P | | No | 0.84 |
| *Campomanesia neriiflora* (O.Berg.) Nied. | 5 | 1255 | *C ner* | NP | WW-VU | Yes | 0.79 |
| *Alseis floribunda* Schott | 5 | 1470 | *A flo* | NP | | No | 0.79 |
| *Xylopia brasiliensis* Spreng. | 5 | 142 | *X bra* | NP | | Yes | 0.78 |
| *Eugenia brasiliensis* Lam. | 3 | 179 | *E bra* | NP | | No | 0.78 |
| *Cecropia glaziovii* Snethl. | 5 | 1404 | *C gla* | P | | Yes | 0.77 |
| *Citronella megaphylla* (Miers) R.A. Howard | 7 | 231 | *C meg* | P | | No | 0.76 |
| *Guarea* sp. | 6 | 278 | *G sp* | - | | No | 0.76 |
| *Coutarea hexandra* (Jacq.) K. Schum. | 6 | 894 | *C hex* | NP | | No | 0.74 |
| *Lonchocarpus muehlbergianus* Hassl. | 3 | 1210 | *L mue* | NP | | No | 0.72 |
| *Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & de Boer | 2 | 397 | *S bon* | NP | | No | 0.71 |
| *Pseudobombax grandiflorum* (Cav.) A. Robyns | 3 | 1453 | *P gra* | P | | No | 0.67 |
| *Cordia* aff *sellowiana* Cham | 3 | 319 | *C sel* | P | | No | 0.64 |

Continues

**Table 1.** Continuation.

| Species | Individuals<br>n | Collector<br>I.D. | Abbreviation | Ecological group | Endangered status<br>Geographic range-threat level | Exclusive to the AF of Brazil | Cover value |
|---|---|---|---|---|---|---|---|
| *Quiina glaziovii* Engl. | 4 | 21 | *Q gla* | NP | | No | 0.63 |
| *Zanthoxylum riedelianum* Engl. | 6 | 802 | *Z rie* | P | | No | 0.63 |
| *Sessea brasiliensis* Toledo | 4 | 98 | *S bra* | NP | WW-DD | Yes | 0.62 |
| *Miconia cinnamomifolia* (DC.) Naudin | 5 | 1190 | *M cin* | NP | | Yes | 0.56 |
| *Nectandra oppositifolia* Nees & Mart. | 3 | 754 | *N opp* | P | | No | 0.54 |
| *Parinari excelsa* Sabine | 3 | 390 | *P exc* | NP | | No | 0.53 |
| *Myrcia* sp2 | 4 | 897 | *M sp2* | - | | No | 0.52 |
| *Psychotria mapourioides* DC. | 4 | 700 | *P map* | NP | | No | 0.52 |
| *Pouteria caimito* (Ruiz & Pav.) Radlk. | 4 | 97 | *P cai* | NP | | No | 0.51 |
| *Dalbergia frutescens* (Vell.) Britton | 3 | 904 | *D fru* | NP | | No | 0.50 |
| *Meliosma sellowii* Urb. | 4 | 137 | *M sel* | P | | No | 0.49 |
| *Miconia* cf *brachybotrya* Triana | 3 | 08 | *M bra* | P | | No | 0.49 |
| *Coussapoa microcarpa* (Schott) Rizzini | 1 | 90 | *C mic* | P | | No | 0.49 |
| *Aspidosperma ramiflorum* Müll.Arg. | 2 | 1183 | *A ram* | NP | | No | 0.48 |
| *Bunchosia maritima* (Vell.) J.F. Macbr. (sin. *B. fluminensis* Griseb) | 4 | 706 | *B mar* | NP | | No | 0.48 |
| *Cariniana legalis* (Mart.) Kuntze | 1 | 1162 | *C leg* | NP | WW-VU, SP-NT | No | 0.48 |
| *Strychnos* sp. | 4 | 1458 | *S sp* | - | | No | 0.45 |
| *Guarea macrophylla* subsp. *macrophylla* | 4 | 838 | *G mac* | NP | SP-NT | No | 0.44 |
| *Weinmannia paulliniifolia* Pohl | 1 | 674 | *W pau* | P | | Yes | 0.44 |
| *Marlierea suaveolens* Cambess. | 4 | 99 | *M sua* | NP | SP-VU | Yes | 0.43 |
| *Posoqueria latifolia* (Rudge) Roem. & Schult. | 3 | 422 | *P lat* | NP | | No | 0.43 |
| *Annona sylvatica* A. St.-Hil ( sin - *Rollinia sylvatica* (A. St.-Hil.) Martius) | 4 | 806 | *A syl* | P | | Yes | 0.42 |
| *Miconia cabussu* Hoehne | 4 | 1155 | *M cab* | NP | | Yes | 0.41 |
| *Solanum argenteum* Dunal | 3 | 1192 | *S arg* | P | | No | 0.38 |
| *Trichilia claussenii* C. DC. | 3 | 717 | *T cla* | NP | | No | 0.38 |
| *Lonchocarpus guillemineanus* (Tul.) Malme | 3 | 1172 | *L gui* | P | | No | 0.37 |
| *Coccoloba* sp. | 2 | 1143 | *Co sp* | - | | No | 0.36 |
| *Terminalia triflora* (Griseb) Lillo | 2 | 1219 | *T tri* | - | | No | 0.35 |
| *Zanthoxylum rhoifolium* Lam. | 3 | 668 | *Z rho* | P | | No | 0.34 |
| Solanaceae sp. | 3 | 1454 | *Sol* | - | | No | 0.34 |
| *Ficus obtusifolia* Kunth | 3 | 156 | *F obt* | - | | No | 0.32 |
| *Clethra scabra* Pers. | 3 | 739 | *C sca* | P | | No | 0.32 |
| *Myrcia sosias* D.Legrand | 3 | 660 | *M sos* | NP | | No | 0.31 |
| *Croton* sp. | 2 | 1418 | *Cr sp* | - | | No | 0.31 |
| *Esenbeckia febrifuga* (A. St.-Hil.) A. Juss. ex Mart. | 1 | 09 | *E feb* | NP | | No | 0.31 |
| *Trichilia pallens* C. DC. | 2 | 569 | *T pal* | NP | WW-NT | No | 0.30 |
| *Platymiscium floribundum* Vogel | 2 | 92 | *P flor* | NP | | No | 0.30 |
| *Malouetia cestroides* (Ness) Mull. Arg. | 2 | 1140 | *M ces* | P | | Yes | 0.29 |
| *Luehea* sp. | 1 | 815 | *Lu sp* | - | | No | 0.29 |
| *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult. | 2 | 764 | *M cor* | P | | No | 0.29 |

Continues

**Table 1.** Continuation.

| Species | Individuals n | Collector I.D. | Abbreviation | Ecological group | Endangered status Geographic range-threat level | Exclusive to the AF of Brazil | Cover value |
|---|---|---|---|---|---|---|---|
| *Tetrastylidium grandifolium* (Baill.) Sleumer | 1 | 365 | *T gran* | NP | | Yes | 0.25 |
| Celastraceae sp1 | 2 | 750 | *Cel* | - | | No | 0.24 |
| *Myrsine guianensis* (Aubl.) Kuntze | 2 | 394 | *M gui* | P | | No | 0.24 |
| *Myrceugenia myrcioides* (Cambess.) O.Berg | 2 | 213 | *M myr* | NP | WW-NT | Yes | 0.24 |
| *Ilex theizans* Mart. ex Reissek | 1 | 826 | *I the* | NP | | No | 0.23 |
| *Jacaratia spinosa* (Aubl.) A.DC. | 2 | 307 | *J spi* | P | | No | 0.22 |
| *Eugenia subterminalis* DC. (sin. *E. psidiiflora* O. Berg., *C. pisidiiflorus* (O. Berg) Sobral) | 2 | 344 | *E sub* | NP | | No | 0.22 |
| Rubiacaea sp.1 | 1 | 1283 | *Rub1* | - | | No | 0.22 |
| Myrsinaceae sp | 2 | 232 | *Myrs1* | - | | No | 0.22 |
| *Myrceugenia campestris* (DC.) D.Legrand & Kausel | 2 | 1433 | *M camp* | NP | WW-VU | No | 0.21 |
| *Protium widgrenii* Engl. | 2 | 708 | *P wid* | NP | | No | 0.21 |
| *Myrcia hatschbachii* D. Legrand | 2 | 752 | *M has* | NP | | Yes | 0.21 |
| *Zanthoxylum petiolare* A. St.-Hil. & Tul. | 2 | 663 | *Z pet* | P | SP-VU | Yes | 0.20 |
| *Maytenus officinalis* Mabb (sin. *Maytenus ilicifolia* Mart. *ex* Reissek) | 2 | 1200 | *M off* | NP | SP-EX | No | 0.20 |
| *Actinostemon communis* (Müll. Arg.) Pax | 1 | 297 | *A com* | P | | No | 0.18 |
| *Myrcia* sp1 | 1 | 1472 | *M sp1* | - | | No | 0.13 |
| *Connarus regnellii* G. Schellenb. | 1 | 780 | *C reg* | NP | | Yes | 0.13 |
| *Eugenia pruinosa* D. Legrand | 1 | 70 | *E pru* | NP | | Yes | 0.12 |
| *Trichilia silvatica* C. DC. | 1 | 417 | *T sil* | NP | WW-VU | Yes | 0.12 |
| *Cariniana estrellensis* (Raddi) Kuntze | 1 | 1162 | *C est* | NP | SP-NT | No | 0.11 |
| *Pourouma* sp. | 1 | 277 | *Po sp* | - | | No | 0.11 |
| *Ocotea laxa* (Nees) Mez | 1 | 1186 | *O lax* | NP | | Yes | 0.11 |
| *Maytenus evonymoides* Reissek | 1 | 192 | *M evo* | NP | | No | 0.11 |
| Fabaceae sp.1 | 1 | 351 | *Fab1* | - | | No | 0.11 |
| *Chomelia brasiliana* A. Rich. | 1 | 62 | *C bra* | NP | | No | 0.11 |
| *Marlierea racemosa* (Vell.) Kiaersk. | 1 | 1329 | *M rac* | NP | | No | 0.11 |
| *Miconia* sp. | 1 | 224 | *Mi sp* | - | | Yes | 0.11 |
| *Eugenia stigmatosa* DC. | 1 | 745 | *E sig* | NP | | Yes | 0.10 |
| *Handroanthus serratifolius* (Vahl) S. O. Grose | 1 | 44 | *H serr* | NP | | No | 0.10 |
| *Miconia centrodesma* Naudin | 1 | 1212 | *M cen* | P | | No | 0.10 |
| *Apeiba tibourbou* Aubl. | 1 | 343 | *A tib* | P | | No | 0.10 |
| *Piper* cf *gaudichaudianum* Kunth | 1 | 124 | *P gau* | NP | | No | 0.10 |
| *Maytenus robusta* Reissek | 1 | 285 | *M rob* | NP | | No | 0.10 |
| *Physalis* sp. | 1 | 263 | *Ph sp* | - | | No | 0.10 |
| *Trichilia catigua* A. Juss. | 1 | 534 | *T cat* | NP | | No | 0.10 |
| *Aspidosperma parvifolium* A. DC. | 1 | 87 | *A par* | NP | | No | 0.10 |

AF – Atlantic Forest (biome); P – pioneer; NP – non-pioneer; SP – (state of) São Paulo (Estado de São Paulo 2004); BR – Brazil (Brasil 2008); WW – worldwide (IUCN 2012); EX – extinct; EN – endangered; VU – vulnerable; NT – near threatened; DD – data deficient)

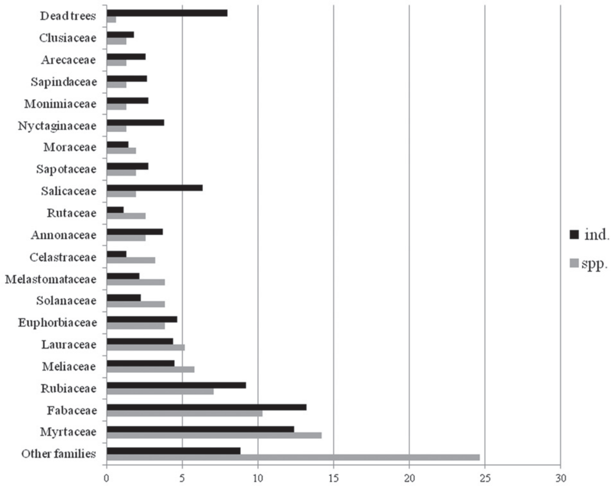


**Figure 2.** Families with highest richness of species and individuals (collectively accounting for 75.64% of the total species and 91.15% of the total individuals) in the Jacupiranga Complex – Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W).


**Figure 3.** Species with greatest cover value (accounting for 41.30% of the total cover value) in the Jacupiranga Complex – Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W).

dynamics of this rain forest. In other studies, dead individuals (when counted/reported) have usually ranked high, although not first, in cover value, being second and sixth in the study conducted by Ramos *et al.* (2011), third in the study conducted by Rochelle *et al.* (2011) and second in the study conducted in a young forest by Aidar *et al.* (2001). The presence of dead individuals and of *E. edulis* individuals seems related, because both occurred mainly in the plots on the Araçá trail (plots 12-20), as will be discussed in detail.

The comparison of our results with those of other studies in protected areas of different subtypes of dense rain forest (Tab. 3) indicated greatest similarity with the Intervales State Park and Alto Ribeira Touristic State Park, followed by the Ilha do Cardoso State Park and Jureia-Itatins Ecological Station, all located within the Ribeira Valley. Geographical distance apparently affected the similarity, because Intervales State Park, Ilha do Cardoso State Park and Jureia-Itatins Ecological Station are the areas closest to the Jacupiranga Complex (Tab. 3). The Intervales State Park and the Alto Ribeira Touristic State Park are located at altitudes similar to that of the Ribeira Valley, which might explain the occurrence of species in common. The lowest similarities were between our sites and coastal areas in the northern parts of the states of São Paulo and Rio de Janeiro, probably influenced by the greater geographical distance.

The species diversity index in the present study was one of the greatest among the areas compared and was similar to that obtained by Rochelle *et al.* (2011) for the Serra do Mar State Park – Picinguaba base (Tab. 3). It was also higher than those recorded for the Juréia-Itatins Ecological Station and Intervales State Park, areas in which species richness is higher than at our site. This can be explained by the fact that the evenness was greater for our study site (0.897) than for those two preserves (0.818 and 0.75, respectively). Therefore, species diversity in the Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area is high and similar to that of other montane and submontane dense rain forests in southeastern Brazil.

We observed 18 threatened species (Tab. 1), of which 12 are listed as endangered in the state of São Paulo (Estado de São Paulo 2007), one (*E. edulis*) is listed as endangered in Brazil (Brasil 2008) and nine are listed as endangered worldwide (IUCN 2012). Most endangered species had a very small number of individuals. This indicates that even within protected areas these species are still at risk of extinction and underscores the importance of these areas, as well as the necessity of monitoring and thorough inspection to ensure the effective conservation of these populations. Few of the floristic and phytosociological surveys conducted in the states of São Paulo and Rio de Janeiro have identified endangered species, except the works of Catharino *et al.* (2006), who reported 31 endangered species (11.9% of the species sampled) at Morro Grande Forest Reserve, and of Ramos *et al.* (2011), who reported 10 endangered species (5.18% of the species sampled) in the municipality of Ubatuba.

Of the 157 species sampled in the present study, 33 are endemic to the Atlantic Forest (Tab. 1). Myrtaceae was the family with the largest number of endemic species. Analyzing the sets of endangered and endemic species (18 and 33, respectively), we observed seven species that belong to both groups, that is, species that occur in a restricted distribution and are endangered. These species require special conservation efforts to ensure maintenance of viable populations, which again underscores the importance of protected areas for the conservation of biodiversity in the Atlantic Forest.

The classification of species into ecological groups resulted in pioneer species accounting for 27.1%, non-pioneer species accounting for 59.4% and uncategorized species accounting for 13.5% (Tab. 4). Of the total number of individuals, 25.9% were of pioneer species, 61.1% were

**Table 2.** Abiotic factors measured in sampling units, Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W).

| Plot | Rockiness | Declivity | Litter | Human disturbance | Cover | Altitude |
|---|---|---|---|---|---|---|
| | Class | Class | Class | Class | % = class | m = class |
| 1 C | 3 | 3 | 3 | 0 | 97.9 = 4 | 472 = 1 |
| 2 C | 1 | 3 | 2 | 0 | 97.9 = 4 | 458 = 1 |
| 3 B | 1 | 1 | 0 | 2 | 87.5 = 1 | 464 = 1 |
| 4 B | 0 | 0 | 1 | 0 | 97.9 = 4 | 528 = 3 |
| 5 B | 2 | 1 | 2 | 1 | 91.6 = 2 | 567 = 4 |
| 6 B | 0 | 3 | 2 | 0 | 91.6 = 2 | 527 = 3 |
| 7 B | 1 | 3 | 1 | 1 | 97.9 = 4 | 550 = 3 |
| 8 B | 1 | 3 | 3 | 2 | 98.75 = 4 | 559 = 4 |
| 9 B | 3 | 3 | 2 | 0 | 98.75 = 4 | 573 = 4 |
| 10 B | 1 | 3 | 1 | 0 | 95.8 = 3 | 569 = 4 |
| 11 B | 1 | 3 | 2 | 0 | 98.75 = 4 | 555 = 4 |
| 12 A | 0 | 1 | 2 | 0 | 96.6 = 4 | 526 = 3 |
| 13 A | 3 | 2 | 2 | 0 | 97.9 = 4 | 563 = 4 |
| 14 A | 0 | 3 | 3 | 0 | 98.75 = 4 | 583 = 4 |
| 15 A | 1 | 3 | 2 | 2 | 98.75 = 4 | 540 = 3 |
| 16 A | 2 | 1 | 1 | 0 | 97.9 = 4 | 544 = 3 |
| 17 A | 1 | 3 | 1 | 0 | 98.75 = 4 | 586 = 4 |
| 18 A | 0 | 3 | 1 | 0 | 96.6 = 4 | 562 = 4 |
| 19 A | 1 | 2 | 1 | 0 | 98.75 = 4 | 539 = 3 |
| 20 A | 2 | 3 | 1 | 0 | 96.6 = 4 | 541 = 3 |

A – on the Araçá trail; B – on the Bugio trail; C – on the Caverna trail

of non-pioneer species and 13% were of uncategorized species. Other studies in dense rain forest have reported that pioneers represent 44-62% of species in disturbed sites and 22-48% of species in preserved or mature sites. Therefore, the proportion of pioneers in our study was relatively low. For non-pioneer species, the reported values range from 49% to 65% for preserved or mature areas. In the dense rain forest evaluated in our study, which can be considered mature or well preserved in comparison with other areas, 59.4% of the species were non-pioneers. The same result was obtained when we used the criterion of the dominant group (50% or more of species), because the ratio of non-pioneer to pioneer species was 2.19 and the ratio of non-pioneer to pioneer individuals was 2.36.

The results of the cluster analysis of species data indicated three clusters of plots (fusion level 0.80), with a cophenetic correlation of 0.832. The first cluster (B) comprised plots 4-11 (all on the Bugio trail) and plot 12 (on the Araçá trail). The second cluster (A) comprised plots 13-20 (all on the Araçá trail), with two subclusters, the first with plots 13, 14, 15, 16 and 19, and the other with plots 17, 18 and 20. The third cluster (C) comprised plots 1 and 2 (on the Caverna trail), together with plot 3 (on the Bugio trail). These results demonstrate that, although the plots on the Araçá trail are different from those on the Bugio trail, plot 12 (on the Araçá trail) is more similar to the cluster B plots and plot 3 (on the Bugio trail) is more similar to the cluster C plots. This might be related to the geographical distribution of the plots (Fig. 1), to the physical features of the environment or to different levels of disturbance in these clusters.

The first two axes of the PCA explained 18.27% and 13.47% of total variation, respectively (Fig. 5). In the first quadrant (positive for both axes), there was a cluster comprising plots 13-16 (all on the Araçá trail), within which we identified the species *E. edulis*, *Guatteria nigrescens*, *Psychotria suterella*, *C. obliqua*, *Cupania oblongifolia*, *F. enormis*, *Clusia criuva*, *Machaerium scleroxylon* and *A. triplinervia*, as well as dead individuals. In the second quadrant (negative for axis 1 and positive for axis 2), there was a cluster comprising plots 4-7 and 9-11 (all on the Bugio trail), together with plot 12 (on the Araçá trail). Within that cluster, we identified the species *Nectandra grandiflora*, *Rudgea jasminoides*, *Coussarea contracta*, *G. opposita*, *Myrcia spectabilis*, *Myrcia deflexa*, *Mollinedia schottiana* and *Mollinedia uleana*. This is agreement with the results of the cluster analysis, in which plot 12 was more similar to the cluster B of plots. In the third

**Table 3.** Comparison between this study (Jacupiranga Complex – Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area, from 24°20'S to 24°46'S and from 48°03'W to 48°40'W) and other studies in protected areas of dense rain forest in two states of southeastern Brazil.

| Study site / Reference | Forest subtype | Method, sample area | Inclusion criterion | Richness n of species | H' | SSI |
|---|---|---|---|---|---|---|
| Juréia-Itatins Ecological Station - SP<br>Oliveira *et al.* (2001) | Submontane | 10 plots, 10 × 20 m (0.2 ha) | DBH ≥ 5 cm (Class IV) | 63 | 3.38 | 0.156 |
| Juréia-Itatins Ecological Station-SP<br>Mamede *et al.* (2004) | Lowland | 50 plots, 10 × 20 m (1 ha) | DBH ≥ 5 cm | 173 | 4.21 | 0.287 |
| Ilha do Cardoso State Park-SP<br>Melo & Mantovani (1994) | Lowland, submontane | 40 plots, 10 × 25 m (1 ha) | CBH ≥ 8 cm | 157 | 3.64 | 0.295 |
| Intervales State Park-SP<br>Guilherme *et al.* (2004) | Submontane | 88 plots, 15 × 15 m (1.98 ha) | DBH ≥ 5 cm | 172 | 3.85 | 0.324 |
| Alto Ribeira Touristic State Park- SP<br>Aidar *et al.* (2001) | Montane | Transect, 20 × 50 m (0.1 ha) | CBH ≥ 15 cm | 87 | - | 0.306 |
| Serra Mar State Park - SP<br>Ramos *et al.* (2011) | Submontane | | | 193 | 3.56-4.05 | 0.236 |
| Serra Mar State Park-SP<br>Rochelle *et al.* 2011 | Submontane | 100 plots, 10 × 10 m (1 ha) | CBH ≥ 15 cm | 206 | 4.48 | 0.216 |
| Serra C.Grande Environmentally Protected Area-RJ<br>Peixoto *et al.* (2005) | Lowland | Quadrant, 200 points | CBH ≥ 15 cm | 44 | 2.42 | 0.080 |
| Paraíso Ecological Station- RJ<br>Kurtz & Araújo (2000) | Submontane | Quadrant, 200 points | DBH ≥ 5 cm | 138 | 4.20 | 0.143 |
| Desengano State Park-RJ<br>Moreno *et al.* (2003) | Lowland, submontane | 10 plots, 30 × 40 m (1.2 ha) | DBH ≥ 10 cm | 210 | 4.21-4.30 | 0.132 |
| Morro Grande Forest Reserve-SP<br>Catharino *et al.* (2006) | Montane | Quadrant, 600 points | DBH ≥ 5 cm | 260 | 4.75 | 0.251 |
| Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area-SP<br>Current study | Submontane | 20 plots, 20 × 20 m (0.8 ha) | CBH ≥ 15 cm | 155 | 4.52 | |

SP – São Paulo; RJ – Rio de Janeiro; DBH – diameter at breast height; CBH – circumference at breast height; H' – Shannon diversity index; E – evenness; SSI – Sørensen similarity index.

quadrant (positive for axis 1 and negative for axis 2), there was a cluster comprising plot 1 (on the Caverna trail), plot 3 (on the Bugio trail), plot 18 and plot 19 (both on the Araçá trail). Within that cluster, we identified the species *P. gonoacantha*, *Allophylus edulis*, *S. multijuga*, *Machaerium aculeatum*, *A. colubrina*, *Casearia sylvestris*, *Annona dolabripetala*, *Dahlstedtia pinnata and Prockia crucis.* Finally, in the fourth quadrant (negative for both axes), there was a cluster comprising only plot 2 (on the Caverna trail) and plot 20 (on the Araçá trail). Within that cluster, we identified the species *C. marginatum* and *Pisonia ambigua.*

The first two axes of the CA explained 16.73% and 15.15% of the total variation, respectively (Fig. 6). The abiotic factors did not strongly influence the ordination of the plots, because most of those factors (rockiness, declivity, canopy cover and altitude) were located in the first quadrant, close to zero. In this quadrant, there was also a cluster (Ba) composed of plots 4-11 (on the Bugio trail), together with plots 12, 18 and 20 (all on the Araçá trail). Within cluster Ba, we identified the species *C. contracta*, *R. jasminoides*, *M. deflexa*, *B. australis*, *M. spectabilis*, *G. opposita*, *M. uleana*, *P. ambigua*, *N. grandiflora*, *A. dolabripetala* and *C. marginatum.* In the third quadrant, there was a cluster (A) comprising plots 13-17 and 19 (all on the Araçá trail), unrelated to the abiotic factors, within which we identified the species *E. edulis*, *C. obliqua*, *A. triplinervia*, *C. oblongifolia*, *Pera glabrata*, *G. nigrescens*, *A. edulis* and *M. scleroxylon*, as well as dead individuals. In the fourth quadrant, there was a cluster with human disturbance (cluster Cb) comprising plots 1 and 2 (on the Caverna trail), as well as plot 3 (on the Bugio trail). Within cluster Cb, we identified the species *S. multijuga*, *P. crucis*, *A. colubrina*, *F. enormis*, *M. aculeatum*, *C. guaviroba* and *C. sylvestris*, all of which, with the exceptions of *F. enormis* and *C. guaviroba*, were pioneers.

**Table 4.** Comparison across studies conducted in protected areas of dense rain forest in southeastern Brazil, in terms of the proportional distribution of species by ecological group.

| Ecological group | Rochelle *et al.* (2011) Disturbed area % species | Rochelle *et al.* (2011) Preserved area % species | Catharino *et al.* (2005) Secondary forest % species | Catharino *et al.* (2005) Mature forest % species | Current study % species | Current study % individuals |
|---|---|---|---|---|---|---|
| Pioneer *sensu lato** | 62 | 22 | 44-54 | 35-48 | 27 | 26 |
| Non-pioneer *sensu lato*** | 18 | 65 | 45-51 | 49-62 | 59 | 61 |
| Uncategorized | 20 | 13 | | | 14 | 13 |

*Pioneer+early secondary; **late secondary+climax.

Because the CA (Fig. 6) indicated three distinct clusters of sampling units (A, Ba and Cb), we compared the phytosociological parameters (number of species, total density, volume and basal area) of these clusters with a t-test.

Total species richness was significantly higher for cluster A, followed by clusters Ba and Cb, with means of 33.3, 29.7 and 18.3, respectively (p-values were 0.8536 for C vs. Ba; 0.8286 for Cb vs. A; and 0.2526 for Ba vs. A). In addition, the plots of cluster A had higher total density than did those of the clusters Ba and Cb, with mean densities of 1820 ind/ha, 1136.6 ind/ha and 950 ind/ha, respectively (p-values were 0.8253 for A vs. Ba; 0.6485 for A vs. Cb; and 0.1844 for Ba vs. Cb). In contrast, the plots of cluster Ba had higher biomass (volume and basal area) than did those of clusters A and Cb, with mean volumes of 36.06 $m^3$, 30.03 $m^3$ and 27.06 $m^3$, respectively (p-values were 0.1834 for A vs. Ba; 0.2009 for Ba vs. C; and 0.0763 for A vs. Cb), and mean basal areas of 1.931 $m^2$, 1.755 $m^2$ and 1.630 $m^2$ for Ba, A and Cb, respectively (p-values were 0.1591 for A vs. Ba; 0.1562 for Ba vs. C; and 0.0724 for A vs. Cb).

The number of dead trees was significantly higher in cluster A, followed by clusters Cb and Ba, in which mortality was quite low, the mean number of dead trees per plot being 11.00, 1.33 and 1.22, respectively (p-values were 0.9889 for A vs. Ba; 0.8768 for A vs. Cb; and 0.0545 for Ba vs. C). Conversely, the occurrence of *E. edulis* individuals of was highest in cluster A, followed by Ba and Cb, the mean number of individuals per plot being 3.0, 0.36 and 0, respectively (p-values were 0.6939 for A vs. Ba; 0.5598 for A vs. Cb; and 0.3177 for Ba vs. Cb).

These results support our field observation that the plots of cluster Cb (comprising plots on the Caverna trail plus plot 3 on the Bugio trail) received more influence from human disturbance than did those of the other clusters (Fig. 1) and therefore exhibited less species richness, density and biomass, probably because they are close to areas of intense traffic (visitor trails and/or houses of traditional peoples). In contrast, the plots of cluster Ba, which had more biomass, are mostly located on the distant and little used Bugio trail. We also observed that cluster Ba exhibited a small number of dead trees in comparison with the other two clusters. Cluster A had less biomass than did cluster Ba but exhibited the highest density, richness and number of dead trees.

Our findings are in agreement with the intermediate disturbance hypothesis (Connel 1978), in which extreme levels of disturbance might explain the loss of richness (intense and frequent disturbances in cluster Cb; and less frequent disturbances in cluster Ba). The large quantity of dead trees found in cluster A might be considered an intermediate disturbance: the opening of clearings might enable the establishment of young and mainly pioneer individuals (Bongers, *et al.* 2009), thereby increasing species richness. In fact, most of the species within cluster Cb (Fig. 6) were pioneers, whereas most of those within cluster Ba were non--pioneers. In a 10-year study carried out in French Guiana, Molino & Sabatier (2001) collected evidence to support the intermediate disturbance hypothesis. However, Bongers *et al.* (2009), in a study of forests in Ghana, found that this hypothesis, although applicable to tropical forests and especially dry forests, explains little of the diversity in humid forests. In our study, it was not possible to determine the influence of intermediate disturbance on the maintenance of diversity in the canopy. However, it is clear that a relationship exists between tree mortality and the diversity of woody species.

The Pearson's correlation tests indicated a correlation between the number of *E. edulis* individuals and species richness (R2=0.5833, p=0.0199), as well as between the number of *E. edulis* individuals and the number of dead trees (R2=0.5585, p=0.0002). However, but a smaller correlation between density and number of *E. edulis* individuals (R2=0.2658, p>0.0001). Therefore, the occurrence of *E. edulis* is related to species richness and adult tree mortality and the consequent formation of clearings. *E. edulis* is a non-pioneer, endangered species that commonly occurs in dense rain forests (Mamede *et al.* 2004; Ramos *et al.* 2011; Guilherme *et al.* 2004). Nakazono *et al.* (2001) observed that young *E. edulis* individuals grew better under intermediate light conditions than under closed canopy or full sunlight, and suggested that this species might benefit from the formation of clearings. Other authors also observed a positive relationship between canopy openness and survival of *E. edulis* seedlings, survival rates being higher in clearings than under closed canopies.

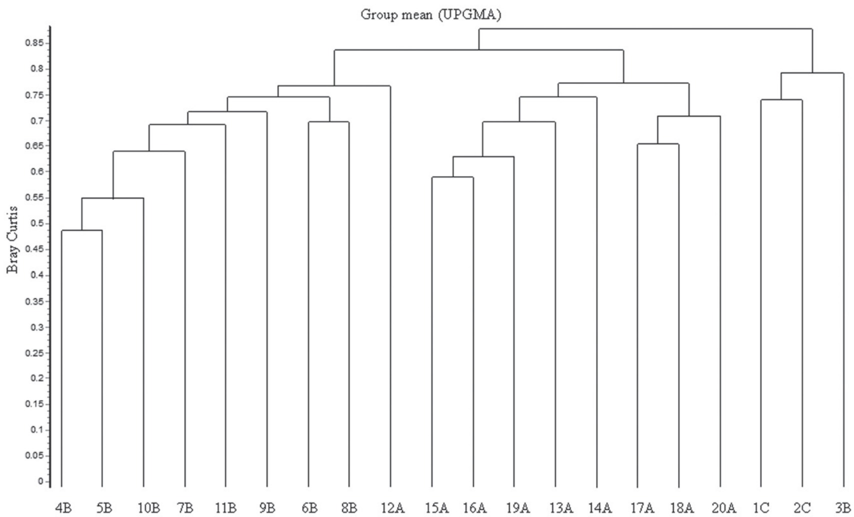


**Figure 4.** Cluster analysis with the unweighted pair group method with arithmetic mean (UPGMA), using a matrix of sampling units and total species number. Jacupiranga Complex – Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W).
A – on the Araçá trail; B – on the Bugio trail; C – on the Caverna trail.

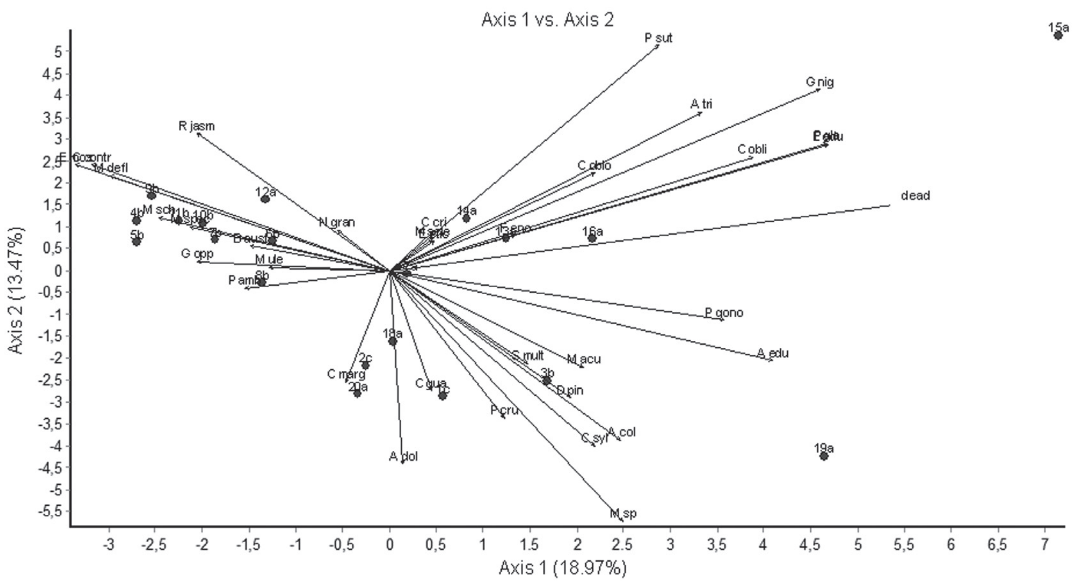


**Figure 5.** Principal components analysis using a matrix of sampling units and number of individuals per species (selecting species with 10 or more individuals). Jacupiranga Complex – Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W).
Dead – dead trees; See Table 1 for other abbreviations.

# Final remarks

The forest fragment under study presents three structurally and floristically distinct conditions: one in which there is low biomass, low density and low species richness, with signs of human disturbance; another in which there is an intermediate quantity of biomass, higher adult mortality, higher density and higher species richness, with signs of intermediate natural disturbance; and a third in which there is even greater biomass, intermediate species richness and no sign of disturbance. The species *C. contracta*, *R. jasminoides*, *M. deflexa*, *P. ambigua* and *M. uleana* can be used as indicators to monitor the condition of mature forest with little disturbance. The species *E. edulis*, *C. oblongifolia*, *P. glabrata* and *G. nigrescens* can be used as indicators to monitor the condition of mature forest with intermediate natural disturbance. The species *A. colubrina*, *A. edulis*, *C. sylvestris*, *M. aculeatum*, *P. gonoacantha*, *P. crucis* and *S. multijuga* can be used as indicators of the condition of young forest with human disturbance. *E. edulis*, a common species in dense

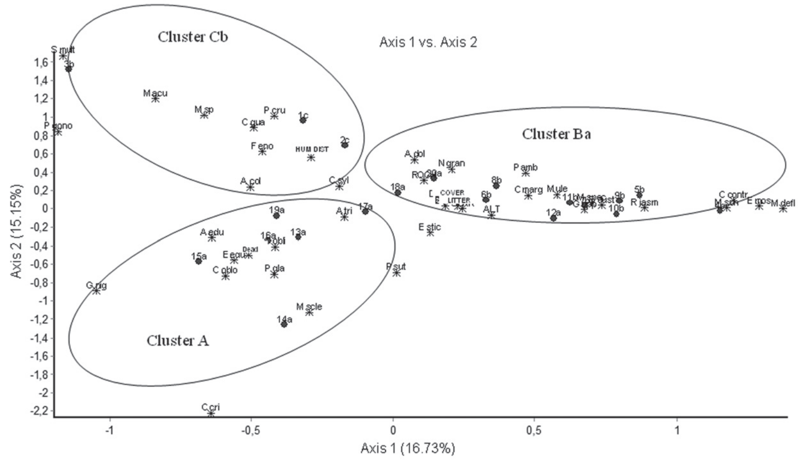


**Figure 6.** Correlation analysis using a matrix of sampling units and number of individuals per species (selecting species with 10 or more individuals), together with abiotic factors. Jacupiranga Complex – Caverna do Diabo State Park and Quilombos do Médio Ribeira Environmentally Protected Area (from 24°20'S to 24°46'S and from 48°03'W to 48°40'W).
ROCK – rockiness; DECL – declivity; HUM DIST – human disturbance; Dead – dead trees; See Table 1 for additional abbreviations.

rain forest studies, exhibited a small number of individuals at our study site and occurred in areas in which there were numerous clearings created by fallen trees.

Due to the redefinition of the boundaries of the former Jacupiranga State Park, our sampling units were located partly within the Caverna do Diabo State Park and partly within the Quilombos do Médio Ribeira Environmentally Protected Area. Because these conservation units have very different land use restrictions, it is important to monitor the conditions of the dense rain forest and analyze the population dynamics of the endangered species in these two preserves. Our data could be used in order to create a baseline for such monitoring.

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