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Structure of the understory community in four stretches of *Araucaria* forest in the state of São Paulo, Brazil

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ABSTRACT

We analyzed the structure of the understory community in the Atlantic Forest *sensu lato*, for which phytosociological descriptions of the understory are lacking. We delineated 50 plots of 10 × 20 m each at four sites within an *Araucaria* forest (a subtype of Atlantic Forest), located in the municipalities of Bananal, Campos do Jordão, Itaberá and Barra do Chapéu, all of which are in the state of São Paulo, Brazil. To sample the resident species of the understory, we randomly selected five 1 × 1 m subplots within each plot, resulting in a total sampling area of 250 m^2 at each site. We identified differences among the locations, mostly due to proportional differences in growth forms, in terms of species richness and the importance values within the community. Factors potentially influencing the understory structure include macroclimatic and microclimatic conditions, as well as forest fragmentation, the abundance of deciduous trees in the canopy, the surrounding vegetation and geographic location.

Key words: herb-shrub layer, phytosociology, species richness, mixed rain forest, Atlantic Forest

Introduction

The herb, subshrub, shrub, vine, small tree and epiphyte growth forms account for up to 75% of the vascular species richness in tropical forests (Gentry 1990; 1992). However, most of the published data on the floristic composition, structure and dynamics of Brazilian forests is restricted to the tree layer, and the available data related to the phytogeographic aspects of Atlantic Forest are consequently restricted to those obtained through the analysis of the upper strata of the forest (Meireles *et al.* 2008; Yamamoto 2009; Bertoncello *et al.* 2011; Furlaneti 2011; Souza *et al.* 2012). Therefore, there is a considerable knowledge gap between what is known of the tree layer and what is known of the understory, in terms of composition and structure, in these forests. There is evidence that the understory of the Atlantic Forest creates microclimates, as well as harboring species that are indicators of specific environments, in terms of edaphic and even geographic aspects (Laska 1997; Müller & Waechter 2001).

The species present in the understory can be divided into two components, which compete for the same resources in the early stages of development (Gilliam *et al.* 1994): the resident component and the transient component. The resident species spend their entire lives in the understory, whereas the transient species remain in the understory while young, reaching adulthood in the canopy. The spatial and temporal structure of the forest understory is related not only to abiotic factors, such as light and soil gradients (Meira-Neto and Martins 2003; Rigon *et al.* 2011), but also to biotic factors, such as the successional stage of the forest (Rigon *et al.* 2011) and the influence of canopy species. The findings of Souza *et al.* (2010; 2013) indicate that there are plant-plant interactions between canopy and understory species, primarily related to changes in light regimes, to seed dispersal capacity and to allelopathic processes. The authors suggested that canopy species act as "ecological filters", determining, at least in part, the structure and richness of the tree-shrub community in the understory.

In the particular case of the mixed rain forest known as *Araucaria* forest (a subtype of Atlantic Forest) in Brazil, the few phytosociological studies of the resident community of the understory have been conducted in the southern region, which is considered the core area of distribution of this vegetation type in the country. Specifically, the structure of the herbaceous layer has been evaluated at the Aracuri Ecological Station, in the state of Rio Grande do Sul (Cestaro *et al.* 1986), and in the city of Guarapuava, in the

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state of Paraná (Rigon *et al.* 2011). From the southern state of São Paulo and to the north, the *Araucaria* forest becomes naturally fragmented, present in floristic refugia at high elevations in the Serra do Mar and Serra da Mantiqueira mountain ranges in the states of São Paulo, Minas Gerais and Rio de Janeiro (Klein 1960; IBGE 2012). *Araucaria angustifolia* (Bertol.) Kuntze, known as araucaria, Brazilian pine, Paraná pine and candelabra tree, has been recorded only as far north as the Serra do Caparaó mountain range, near the border between the states of Minas Gerais and Espírito Santo (Leite 2000). For the disjunct fragments of Araucaria forest, there are no data available regarding the structure of the resident community in the understory. To bridge the knowledge gap related to mixed rain forests, data collection has begun in *Araucaria* forests in the state of São Paulo (Souza *et al.* 2012; Ribeiro *et al.* 2012, 2013).

In the present study, we evaluated stretches of forest in the Serra da Bocaina and Serra da Mantiqueira mountain ranges, as well as in the upper basins of the Ribeira and Paranapanema Rivers, all of which are in the state of São Paulo, using the same sampling protocol in all of the areas evaluated. We present the first data for the understory of *Araucaria* forests in southeastern Brazil, describing and comparing the structure of the understory community at four locations considered representative of the geographic distribution of *Araucaria* forest in the state of São Paulo. Our analyses were guided by the following questions: "Are there differences in the composition and diversity of species in the understory of different *Araucaria* forests within the state?"; "What is the relative contribution of each growth form to the species richness of the understory?"; "For the various taxa and growth forms that make up the resident community of the understory, how are the importance values distributed?"; and "Can the phytosociological parameters of the resident community of the understory be used as indicators of the degree of conservation of a given area?"

Material and methods

Study area

The study was conducted in *Araucaria* forests mapped *a priori* as natural areas of mixed rain forest in the 2005 São Paulo State Forest Inventory of Natural Vegetation (Kronka *et al.* 2005). We selected stretches of forest that we considered representative of the range of environments in which the population of *Araucaria angustifolia* occurs within the state of São Paulo, in an area of contiguous forest originating in the core area of *A. angustifolia* occurrence in the state of Paraná to the south, in the upper basins of the Ribeira and Paranapanema Rivers, as well as in disjunct forest fragments in the Serra da Bocaina and Serra da Mantiqueira mountain ranges (Fig. 1). At all four locations, the climate is temperate, without a true dry season (Köppen climate classification Cfb). The geographic coordinates, climatic

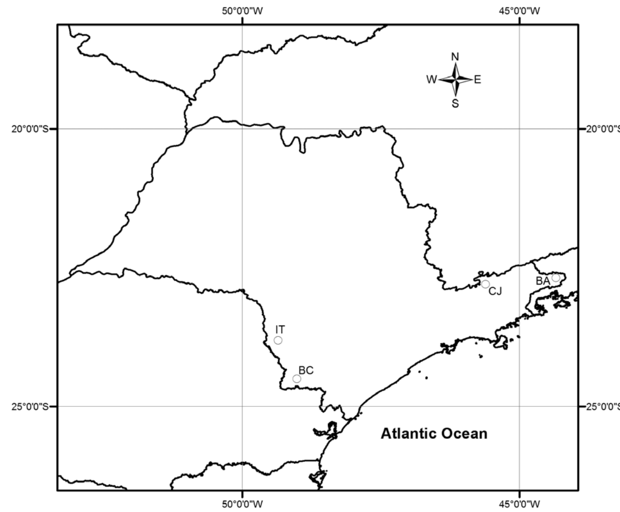

Figure 1. Approximate locations of the stretches of *Araucaria* forest sampled in the state of São Paulo.
CJ – Campos do Jordão; BA – Bananal; IT – Itaberá; BC – Barra do Chapéu.

aspects and edaphic properties of the study locations are summarized in Tab. 1.

Although it would be desirable to evaluate only old growth communities that are protected from human activity, the fact that the selected areas had a history of varying levels of disturbance, highlighting the precarious state of conservation of *Araucaria* forests in the state of São Paulo. In the Serra da Mantiqueira mountain range, the study was conducted in Campos do Jordão State Park, which encompasses 8172 ha and is located within the municipality of Campos do Jordão. In Campos do Jordão State Park, the stretches of native *Araucaria* forest are restricted to valley bottoms, with interfluves occupied by natural grasslands. The sample plots were established along Waterfall trail, which runs along the basin of Galharada creek. Although the study area is within a "conservation unit" (protected area), we observed signs of the presence of cattle from neighboring properties during the field sampling.

In the Serra da Bocaina mountain range, the study was conducted at Bananal Ecological Station, which occupies 884 ha in the eastern portion of the state, in the part of the range known locally as the Serra da Macaca, along the border with the state of Rio de Janeiro. On the basis of information obtained from the staff of this protected area and supplemented by field observations, the Bananal Ecological Station area has been mapped as *Araucaria* forest (Kronka *et al.* 2005). Nevertheless, the stretches studied are in fact secondary forest embedded in a matrix of dense rain forest, which is the predominant vegetation formation in the area. It is possible that the araucarias therein were introduced in the early 1960s, at the time within crop fields and abandoned pasture, set on a hillside with the grade increasing from the bottom to the top. However, the *Araucaria* forest in the region is mentioned in a historical study (Lutz 1926) and

Table 1. Main climatic and edaphic parameters for the four stretches of *Araucaria* forest sampled in the state of São Paulo.

Location	Area (ha)*	Latitude (S)	Longitude (W)	Elevation (m)	Climate	Precipitation (mm) Average (range)**	Temperature (°C) Average (range)**	Frost	Soil
CJ	8.17	22°41'	45°27'	1511	Cfb	1650 (37 to 276)	17 (−4.4 to 27)	Frequent, heavy	LVAd
BC	48	24°28'	49°01'	900	Cfb	1405 (75 to 204)	22 (2 to 30)	Frequent, moderate	LVd
BA	884	22°45'	44°18'	1011	Cfb	1500 (22 to 232)	24 (0 to 38)	Occasional, light	AVAda
IT	180	23°50'	49°08'	705	Cfb	1050 (41 to 165)	20.3 (4 to 32)	Frequent, light	LVd

CJ – Campos do Jordão (protected area); Cfb – Köppen climate classification system designation for a climate that is temperate, without a true dry season; LVAd – *latossolo vermelho-amarelo distrófico* (dystrophic red-yellow oxisol); BC – Barra do Chapéu (private property); LVd – *latossolo vermelho distrófico* (dystrophic red oxisol); BA – Bananal (protected area); AVAda – *argissolo vermelho-amarelo distrófico-álico* (dystrophic-acidic red-yellow ultisol); IT – Itaberá (protected area).
*Overall size of the areas sampled; **Annual average (minimum and maximum monthly averages).
Sources: Modenesi 1988; Ribeiro *et al.* 2013; Seibert *et al.* 1975; Souza *et al.* 2012.

natural populations can still be found in Serra da Bocaina National Park. The record of an individual of *Podocarpus lambertii* (conifer), a species closely associated with *Araucaria* spp. and observed near the study area is an element that indicates the possible natural occurrence of *Araucaria* forest in the past (Backes 2009), although natural populations of *P. lambertii* are currently found in the so-called "Bocaina backwoods".

In the upper basin of the Ribeira river, the study was conducted in the municipality of Barra do Chapéu, on a 48-ha tract of private property. The tract comprises a remnant of *Araucaria* forest that was planted for pasture and has been in natural regeneration for at least 120 years, according to the owner. Despite the small size of the property, the regional landscape is still quite favorable to biodiversity conservation, with about 21% of the municipality covered by native vegetation (Kronka *et al.* 2001).

In the upper basin of the Paranapanema river, the study was developed at the Itaberá Ecological Station, located in the municipality of Itaberá. The protected area preserves a remnant of *Araucaria* forest of approximately 180 ha, surrounded by agricultural crops and urban areas. Unlike the three other study areas, where the topographical conditions (steep mountains) allowed the preservation of extensive fragments in areas unsuitable for agriculture, the upper basin of the Paranapanema river presents a more gentle relief, with hillocks and hills, where agricultural activity is quite intense and there had been considerable extraction of araucaria for timber and pulp production up through the 1960s (Ivanauskas *et al.* 2012). The isolation of the protected area in the current landscape is striking, because the remnant vegetation covers only 7% of the city (Kronka *et al.* 2001).

Data collection

As previously mentioned, the study sample included only plants that complete their life cycle in the understory and have the following growth habits (definitions adapted from Richards 1996): bamboo-like (plant with a stem; well-defined nodes and internodes; and gemmae at ground level); herb (non-woody terrestrial plant); scandent (vine rooted in the ground and resting on other plants as support); subshrub (small plant with a woody, branching base but with herbaceous branches); shrub (woody plant branching from its base); and small tree (woody plant with a well-defined trunk and reaching reproductive maturity in the understory). Juvenile individuals of canopy tree species—defined here as those with a diameter at 1.30 m (breast height) of ≥ 5 cm—were excluded because they do not complete their life cycle in the understory and are therefore classified as a transient species in the understory. Therefore, the scope of the present study was restricted to the resident community of the understory. However, it should be emphasized that vines can be resident or transient, depending on their upper reach in the forest: there are those who complete the life cycle below the canopy and others who need to reach it for reproduction. Due to the difficulty in distinguishing among these two growth habits, especially in juvenile individuals, we chose to include both vine groups in the inventory. Epiphytes were not included in the sample. However, a number of species traditionally described as epiphytes (Waechter 2009), including some of the genera *Asplenium* and *Peperomia*., were recorded as terrestrial species. These are facultative epiphytes, whose occurrence on the forest floor might be related to the fall and subsequent decomposition of a part of the host tree or even to conditions conducive to their establishment on the forest floor.

Data collection was carried out in permanent plots that had been established at four locations for sampling of the tree component (Souza *et al.* 2012; Ribeiro *et al.* 2013). At each location, we established 50 contiguous plots of 10 × 20 m, totaling 1 ha, with the exception of the Bananal location, where the limited size of the stretch of *Araucaria* forest allowed the establishment of only 43 such plots, totaling 0.86 ha. For sampling the understory, we established five 1 × 1 m subplots within each 10 × 20 m plot. The positioning of the subplots was defined by random selection of the coordinates x and y, based on the upper left vertex (origin – 0,0), the 20 m and 10 m sides of the larger plot (x and y axes, respectively) forming a Cartesian axis and serving as a reference (Fig. 2).

We sampled all plants that had rooted within the subplots. For herbs, bamboo-like plants, subshrubs and vines, we annotated species and cover values, estimated with the Braun-Blanquet scale at values from 0 to 5 (Müller-Dombois & Ellenberg 1974). The total plant cover on the soil of this community was obtained by substituting the cover values of the species per subplot with the corresponding percentage, based on the Braun-Blanquet scale score (0 = 0%; 1 = 10%; 2 = 15%; 3 = 25%; 4 = 50%; and 5 = 75%), and then calculating the relative area occupied by the community in the subplot and the corresponding value for the sample as a whole. For shrubs and small trees, we noted the species and recorded the number of woody plants taller than 30 cm with a circumference at breast height < 15 cm.

The floristic survey was complemented by the collection of reproductive material from species observed in the surrounding area, whether or not those species were present in the phytosociological inventory of the subplots. The material was characterized morphologically and identified by means of comparisons with material in the collection of the Dom Bento José Pickel Herbarium of the São Paulo State Forestry Institute (code, SPSF), by consultation with experts and by reference to the literature. The fertile collections were incorporated into the collection of the SPSF. When it was not possible to identify botanical material in the field, the material was collected and observations relevant to the subsequent identification (growth form, size, flower color, aroma of the fruit and the presence of exudates) were recorded.

Data Analysis

The classification of plant families followed the Angiosperm Phylogeny Group III guidelines (APG III 2009). Plants that would not have occurred naturally in the study area if not intentionally or accidentally introduced were considered exotic species (Moro *et al.* 2012). All non-native species were included in the exotic species category, as described by Forzza *et al.* (2012) and Wanderley *et al.* (2011). Native or exotic plants that are common in areas heavily disturbed by human activity were classified as ruderal plants, as defined by Moro *et al.* (2012), and were identified by comparison between the floristic list of our study areas and those of the studies conducted by Leitão-Filho *et al.* (1972), Gavilanes & D'Angieri-Filho (1991), Lorenzi (2000) and Carneiro & Irgang (2005).

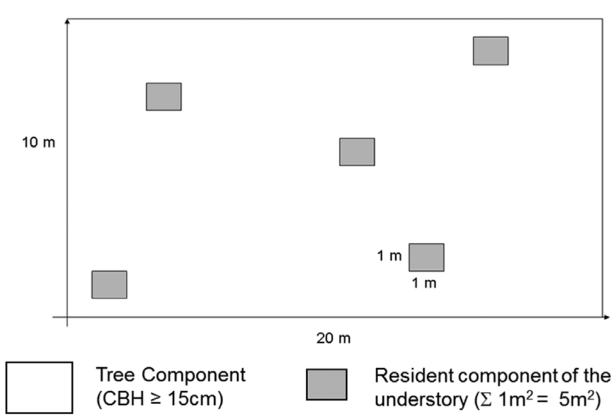

Figure 2. Schematic representation of a 10 × 20 m plot containing five 1 × 1 m subplots used in order to study the resident component of the understory in the four stretches of *Araucaria* forest sampled in the state of São Paulo.
CBH – circumference at breast height.

In order to evaluate the sampling effort and to compare the four locations, in terms of species richness, we obtained species accumulation curves, with data input in random order. We constructed the curve by resampling with 100 bootstrap replications and 95% confidence intervals, using the software EcoSim 7.0 (Gotelli & Entsminger 2004) and EstimateS (Colwell 2009). Because the data comparison involved four locations evaluated under the same sampling design and effort (despite the fact that the Bananal location was 35 m^2 smaller), it was performed in a direct way with the species accumulation curves, comparing the evolution of the curve for the same sample size.

The importance value for the shrubs and small trees was calculated by summing the frequency and relative density, according to the formulas described in Martins (1991). For herbs, vines, subshrubs and bamboo-like plants, the coverage value replaced the relative density in the calculation of the importance values, as proposed by Müller & Waechter (2001). For each spreadsheet, the values of importance of each species were converted to percentages to allow comparisons between species and different growth forms. The Shannon diversity index (Pielou 1969) was calculated according to Müller & Waechter (2001), considering the frequency of species, because that was the phytosociological parameter obtained for the growth forms by evaluating cover or abundance.

Rare species were defined as those registered with a value of one in the vegetation total (for bamboo-like plants, herbs, subshrubs and vines) or with one individual sampled per species (for shrubs and small trees) at each location.

Results

In the floristic survey of the resident community of the understory in the four stretches of *Araucaria* forest evaluated, we recorded 266 species, belonging to 136 genera and 65 families. Of those 266 species, 39 were ferns and lycophyta, whereas 227 were angiosperms. The growth habits and records of the core material are available in the supplementary material and in Polisel *et al.* (in press). A total of 62 species (23.3%) were not identified down to the species level, 28 being identified down to the family level (mostly sterile Poaceae) and 29 being identified down to the genus level. The five remaining morphospecies were indeterminate plants corresponding to sterile material collected during the phytosociological study.

Considering only the records of the phytosociological inventory, we sampled 237 species (Fig. 3, Tab. 2 and 3): 93 in Bananal; 88 in Campos do Jordão; 69 in Barra do Chapéu; and 48 in Itaberá. By analyzing the species accumulation curves, we found that species richness was greatest at the Bananal and Campos do Jordão locations, followed by the Barra do Chapéu and Itaberá locations (Fig. 3), and that the degree of similarity was highest between the Bananal and Campos do Jordão locations. Although the Shannon diversity index showed that the hierarchical relationships were similar among the locations, the level of diversity was highest at the Campos do Jordão location (Tab. 4).

Each location had distinct floristic composition: there were only two species that were recorded in all areas (the ruderal herb *Anemia phyllitidis* and one indeterminate vine); and only a few species (n = 11) were recorded in three of the four locations. Among these widely distributed species, only the herbs *Ichnanthus pallens* and *Borreria palustris* and the shrubs *Psychotria vellosiana* and *Brunfelsia pauciflora* were among the top five species, in terms of the importance value, in the communities in which they were observed (Tab. 2 and 3). The floristic and structural differences among locations were also reflected in the proportional representation of rare species, which was lowest at the locations with the highest species richness (Tab. 4).

Among the 237 species recorded in the phytosociological inventory, three are exotic and were recorded at two locations (Tab. 2 and 3): the herb *Impatiens walleriana*, recorded

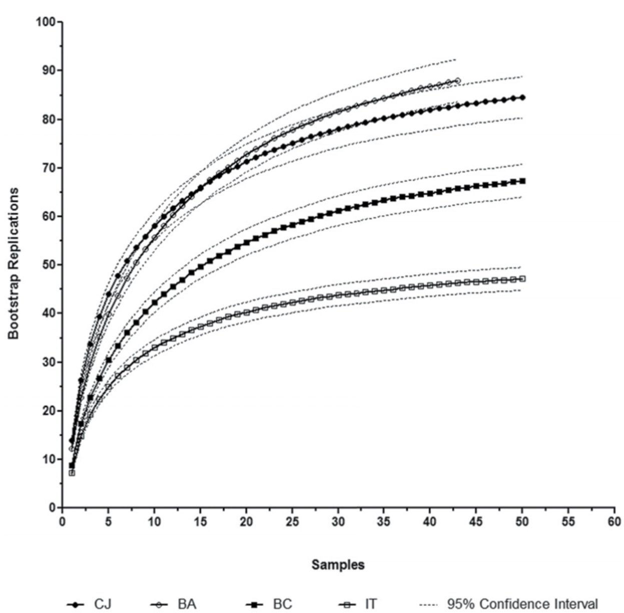

Figure 3. Species accumulation curves generated through the bootstrapping process for the four stretches of *Araucaria* forest sampled in the state of São Paulo. CJ – Campos do Jordão; BA – Bananal; BC – Barra do Chapéu; IT – Itaberá.

in Bananal; the vine *Podranea ricasoliana*, recorded in Campos do Jordão; and the subshrub *Cestrum nocturnum*, also recorded in Campos do Jordão. Ruderal species accounted for 23 of the species recorded at all of the locations combined, and most of those 23 species were recorded in Campos do Jordão and Bananal (Tab. 4). The ruderal herb *Anemia phyllitidis* was recorded at all four locations, whereas the herbs *Emilia sagittata* and *Tripogandra diuretica* were recorded at three of the four locations, the exception being Itaberá (Tab. 2 and 3).

The number of ruderal species was highest (n = 17) in Campos do Jordão: two were shrubs (accounting for 4.7% of the total importance value); 11 were herbs (accounting for 11.9% of the total importance value); two were subshrubs (accounting for 1.8% of the total importance value); and two were vines (accounting for 0.4% of the total importance value). In Barra do Chapéu, the ruderal species (proportion of the total importance value) were one shrub (5.0%), four herbs (12.5%) and one vine (0.3%), compared with two shrubs (1.5%), nine herbs (3.8%), two subshrubs (0.6%) and one vine (0.6%) in Bananal. In Itaberá, the understory community presented indications that the area was more preserved; there were only two ruderal species (both of which were herbs, together accounting for 2.8% of the total importance value).

Discussion

Few studies have described the resident community in the understory of forests in Brazil. Those that have done so have used a variety of methods tailored to specific objectives, as well as including various growth forms in their samples. This study is innovative in describing the community structure of the understory of mixed rain forest in southeastern Brazil, using the same sampling protocol at all of the locations evaluated. The scarcity of data in the literature on the forest understory is even greater for the shrub layer than for the herb layer, because it is common to perform a joint analysis of the floristic composition of the "tree-shrub" community, which includes, in addition to shrubs, the transient community of juvenile individuals of canopy species and adult trees of the upper strata. In some studies, juvenile individuals of tree species have been classified as shrubs (Ribeiro *et al.* 2013).

The first question addressed in the present study refers to the relative contribution of each growth form to the richness and diversity of understory species in *Araucaria* forests. Considering the importance value of each growth form at the various locations, the differences were striking: bamboo-like plants, herbs, subshrubs and vines, collectively, had the highest importance values, ranging from 65.1% (in Barra do Chapéu) to 74.6% (in Itaberá). Analyzed jointly, shrubs and small trees showed importance values ranging from 25.4% (in Itaberá) to 34.9% (in Barra do Chapéu). It is of note, however, that a species considered a shrub at a

Table 2. Relative importance values of bamboo-like, herb, subshrub and vine species in the understory of the four stretches of *Araucaria* forest sampled in the state of São Paulo.

Family	Species	Growth form	IV by location				Total IV
			CJ (%)	BC (%)	BA (%)	IT (%)	(%)
Poaceae	Poaceae sp.2	Herb	-	-	-	18.04	4.51
Poaceae	*Ichnanthus pallens* (Sw.) Munro ex Benth.*	Herb	0.18	7.63	-	2.64	2.61
Rubiaceae	*Borreria palustris* Müll. Arg.	Subshrub	2.04	0.54	7.36	-	2.49
Lamiaceae	*Salvia* sp.2	Subshrub	8.94	-	-	-	2.23
Poaceae	Poaceae sp.5	Herb	-	-	8.53	-	2.13
Poaceae	Poaceae sp.1	Herb	-	-	-	7.54	1.89
Cyperaceae	*Rhynchospora corymbosa* (L.) Britt*	Herb	7.50	-	-	-	1.88
Melastomataceae	*Leandra* sp.1	Subshrub	-	-	7.45	-	1.86
Poaceae	*Chusquea* sp.1	Bamboo-like	-	7.44	-	-	1.86
Poaceae	Poaceae spp.**	Herb	7.03	-	-	-	1.76
Asteraceae	*Mikania lindbergii* Baker	Vine	-	4.23	2.68	-	1.73
Melastomataceae	*Leandra fragilis* Cogn.	Subshrub	-	-	0.49	5.67	1.54
Asteraceae	*Mikania ternata* (Vell.) B.L. Rob.	Vine	3.82	1.91	-	-	1.43
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.	Vine	-	-	-	5.55	1.39
Marantaceae	*Calathea communis* Wand. & S. Vieira	Herb	-	5.25	-	-	1.31
Rubiaceae	*Coccocypselum lanceolatum* (Ruiz & Pav.) Pers.	Herb	-	0.76	4.44	-	1.30
Schizaeaceae	*Anemia phyllitidis* (L.) Sw.*	Herb	0.15	3.95	0.77	0.18	1.26
Rubiaceae	*Coccocypselum condalia* Pers.	Herb	4.93	-	-	-	1.23
Sapindaceae	*Serjania* sp.1	Vine	-	4.31	-	-	1.08
(Indeterminate)	(Indeterminate) sp.3	Herb	-	4.21	-	-	1.05
Celastraceae	*Hippocratea volubilis* L.	Vine	-	-	0.61	3.54	1.04
Rubiaceae	*Psychotria stachyoides* Benth.	Subshrub	0.99	-	0.79	2.29	1.02
Blechnaceae	*Blechnum proliferum* Rosenst.	Herb	-	-	3.85	-	0.96
Melastomataceae	*Pleiochiton blepharodes* (Cogn.) Triana	Subshrub	-	-	3.85	-	0.96
Sapindaceae	*Paullinia rhomboidea* Radlk.	Vine	-	1.88	1.70	0.09	0.92
Sapindaceae	*Paullinia meliifolia* Juss.	Vine	-	0.37	-	3.01	0.85
Poaceae	Poaceae sp.3	Herb	-	-	-	3.28	0.82
Poaceae	Poaceae sp.6	Herb	-	-	3.21	-	0.80
Urticaceae	*Pilea hilariana* Wedd.	Herb	3.13	-	-	-	0.78
Fabaceae-Cercideae	*Phanera microstachya* (Raddi) L.P. Queiroz	Vine	-	0.29	-	2.75	0.76
Sapindaceae	*Urvillea ulmacea* Radlk.	Vine	-	-	-	2.92	0.73
Thelypteridaceae	*Thelypteris tamandarei* (Rosenst.) Ponce	Herb	2.89	-	-	-	0.72
Bignoniaceae	Bignoniaceae sp.2	Vine	-	-	-	2.67	0.67
Asteraceae	*Emilia sagittata* DC.*	Herb	1.56	0.62	0.11	-	0.57
Bignoniaceae	*Anemopaegma* sp.	Vine	0.08	-	-	2.16	0.56
Dryopteridaceae	*Polystichum montevidense* (Spreng.) Rosenst.	Herb	2.22	-	-	-	0.55
Blechnaceae	*Blechnum occidentale* L.	Herb	-	2.08	-	-	0.52
Fabaceae-Faboideae	*Machaerium* sp.	Vine	-	-	2.01	-	0.50
Thelypteridaceae	*Thelypteris mosenii* (C. Chr.) C.F. Reed	Herb	1.92	-	-	-	0.48
Apocynaceae	*Peltastes peltatus* (Vell.) Woodson	Vine	-	1.28	0.22	0.39	0.47
Pteridaceae	*Cheilanthes regularis* Métt.	Herb	1.80	-	-	-	0.45
Bignoniaceae	Bignoniaceae sp.1	Vine	-	1.56	0.22	-	0.44

Continues

Table 2. Continuation.

Family	Species	Growth form	IV by location CJ (%)	BC (%)	BA (%)	IT (%)	Total IV (%)
Commelinaceae	*Tripogandra diuretica* (Mart.) Handlos*	Herb	1.29	0.25	0.22	-	0.44
Sapindaceae	*Serjania* sp.2	Vine	-	-	-	1.58	0.40
Pteridaceae	*Histiopteris incisa* (Thunb.) Sm.	Herb	-	1.42	0.12	-	0.38
Rosaceae	*Rubus rosifolius* Sm. ex Baker*	Subshrub	1.09	-	0.45	-	0.38
Solanaceae	*Solanum* sp.	Subshrub	1.52	-	-	-	0.38
Thelypteridaceae	*Macrothelypteris torresiana* (Gaud.) Ching	Herb	0.63	-	0.82	-	0.36
Poaceae	Poaceae sp.7	Herb	-	1.40	-	-	0.35
Smilacaceae	*Smilax elastica* Griseb.	Vine	-	1.40	-	-	0.35
Rubiaceae	*Galium asperulum* (A. Gray) Rydlb.	Vine	1.40	-	-	-	0.35
Piperaceae	*Peperomia glabella* (Sw.) A. Dietr.	Herb	0.80	0.49	-	-	0.32
Apiaceae	*Hydrocotyle callicephala* Urb.	Herb	-	-	1.28	-	0.32
(Indeterminate)	(Indeterminate) sp.1	Vine	0.08	0.12	0.16	0.90	0.31
Lamiaceae	*Peltodon radicans* Pohl*	Herb	0.53	-	0.72	-	0.31
Commelinaceae	*Dichorisandra pubescens* Mart.	Herb	-	0.42	0.83	-	0.31
Euphorbiaceae	*Fragariopsis scandens* A. St.-Hil.	Vine	1.16	-	-	-	0.29
Piperaceae	*Peperomia rotundifolia* (L.) Kunth	Herb	1.15	-	-	-	0.29
Dioscoreaceae	*Dioscorea laxiflora* Mart. ex Griseb.	Vine	-	0.74	0.11	0.27	0.28
Melastomataceae	*Aciotis* cf. *paludosa* (Mart. ex DC.) Triana	Herb	1.06	-	-	-	0.26
Blechnaceae	*Blechnum* sp.	Herb	0.69	-	-	0.33	0.25
Thelypteridaceae	*Thelypteris amambayensis* (Christ) Ponce	Herb	-	-	0.98	-	0.24
Sapindaceae	*Serjania* cf. *multiflora* Cambess.	Vine	-	-	0.98	-	0.24
Cyperaceae	*Scleria latifolia* Sw.	Herb	-	0.25	0.69	-	0.23
Poaceae	Poaceae sp.4	Herb	-	-	-	0.92	0.23
Malpighiaceae	*Heteropteris intermedia* Griseb.	Vine	-	0.49	0.11	0.27	0.22
Thelypteridaceae	*Thelypteris* sp.2	Herb	-	-	-	0.86	0.21
Asteraceae	*Mikania* sp.1	Vine	-	-	-	0.84	0.21
Pteridaceae	*Pteridium aquilinum* (L.) Kuhn*	Herb	-	-	0.82	-	0.20
Bromeliaceae	Bromeliaceae**	Herb	0.81	-	-	-	0.20
Polypodiaceae	*Pleopeltis pleopeltidis* (Fée) de la Sota	Herb	0.79	-	-	-	0.20
Apocynaceae	*Forsteronia* cf. *pilosa* Müll. Arg.	Vine	-	0.79	-	-	0.20
Campanulaceae	*Siphocampylus fimbriatus* Regel	Subshrub	0.78	-	-	-	0.20
Poaceae	*Chusquea* cf. *ramosissima* Pilg.	Bamboo-like	0.76	-	-	-	0.19
Commelinaceae	*Dichorisandra thyrsiflora* J.C. Mikan	Herb	-	0.66	-	0.09	0.19
Rubiaceae	*Psychotria subtriflora* Müll. Arg.	Subshrub	0.75	-	-	-	0.19
Lamiaceae	*Ocimum carnosum (Spreng.)* Link & Otto ex Benth.*	Subshrub	0.74	-	-	-	0.19
Araceae	*Asterostigma lividum* (Lodd.) Engl.	Herb	0.15	0.49	-	0.09	0.18
Bignoniaceae	*Tanaecium pyramidatum* (Rich.) L.G. Lohmann	Vine	-	-	-	0.71	0.18
Vitaceae	*Cissus striata* Ruiz & Pav.*	Vine	0.15	-	0.56	-	0.18
Cucurbitaceae	Cucurbitaceae sp.2	Vine	0.69	-	-	-	0.17
Apiaceae	*Hydrocotyle leucocephala* Cham. & Schltdl.*	Herb	0.33	-	0.34	-	0.17
Piperaceae	*Peperomia urocarpa* (Fisch. & Meyer)	Herb	-	-	-	0.66	0.16
Orchidaceae	*Habenaria parviflora* Lindl.	Herb	0.54	-	0.11	-	0.16

Continues

Table 2. Continuation.

Family	Species	Growth form	IV by location CJ (%)	BC (%)	BA (%)	IT (%)	Total IV (%)
Poaceae	*Chusquea* sp.3	Bamboo-like	0.08	0.54	-	-	0.15
Balsaminaceae	*Impatiens walleriana* Hook. F.*,***	Herb	-	-	0.59	-	0.15
Pteridaceae	*Cheilanthes radiata* (L.) Fée	Herb	-	-	-	0.54	0.13
Orchidaceae	*Promenaea* cf. *stapelioides* Lindl.	Herb	-	-	-	0.54	0.13
Fabaceae-Faboideae	*Dalbergia frutescens* (Vell.) Briton	Vine	-	-	-	0.54	0.13
(Indeterminate)	(Indeterminate) sp.5	Herb	-	0.54	-	-	0.13
Orchidaceae	*Microchilus* sp.	Herb	-	0.54	-	-	0.13
Cyperaceae	*Pleurostachys stricta* Kunth	Herb	-	0.54	-	-	0.13
Thelypteridaceae	*Thelypteris* sp.1	Herb	-	-	-	0.53	0.13
Rubiaceae	*Manettia gracilis* Cham. & Schltd.	Vine	0.28	0.25	-	-	0.13
Blechnaceae	*Blechnum brasiliense* L.	Herb	-	0.49	-	-	0.12
Acanthaceae	*Mendoncia puberula* (Mart.) Ness	Vine	-	0.49	-	-	0.12
Apocynaceae	*Orthosia urceolata* E. Fourn.	Vine	-	0.17	0.22	0.09	0.12
Oxalidaceae	*Oxalis triangularis* A. St.-Hil.	Herb	-	0.46	-	-	0.12
Caryophyllaceae	*Drymaria cordata* (L.) Willd. ex Schult.	Herb	0.23	-	0.22	-	0.11
Polypodiaceae	*Niphidium crassifolium* (L.) Lellinger	Herb	-	-	0.45	-	0.11
Smilacaceae	*Smilax stenophylla* A. DC.	Vine	-	-	0.45	-	0.11
Sapindaceae	*Serjania multiflora* Cambess.	Vine	0.43	-	-	-	0.11
Cyperaceae	*Pleurostachys* sp.1	Herb	-	-	-	0.42	0.10
Apocynaceae	*Forsteronia pilosa* Müll. Arg.	Vine	-	-	-	0.42	0.10
Loganiaceae	*Strychnos brasiliensis* (Spreng.) Mart.	Vine	-	-	-	0.42	0.10
Lycopodiaceae	*Lycopodiella clavatum* L.	Herb	0.08	-	0.34	-	0.10
Euphorbiaceae	*Dalechampia* cf. *leandrii* Baill.	Vine	0.40	-	-	-	0.10
Acanthaceae	*Staurogyne itatiaiae* (Wawra) Leonard	Subshrub	-	-	0.38	-	0.09
Verbenaceae	*Petrea volubilis* L.	Vine	-	-	-	0.36	0.09
Gleicheniaceae	*Sticherus penninger* (Mart.) Copel	Herb	-	-	0.34	-	0.08
Violaceae	*Anchietea pyrifolia* A. St.-Hill	Vine	-	-	0.34	-	0.08
Sapindaceae	*Paullinia bicorniculata* Somner.	Vine	-	-	0.34	-	0.08
(Indeterminate)	(Indeterminate) sp.2	Herb	-	-	-	0.33	0.08
Onagraceae	*Fuchsia regia* (Vell.) Munz	Vine	0.32	-	-	-	0.08
Poaceae	*Chusquea* sp.2	Bamboo-like	0.30	-	-	-	0.08
Piperaceae	*Peperomia mandioccana* Miq.	Herb	0.30	-	-	-	0.08
Piperaceae	*Peperomia* sp.	Herb	-	0.29	-	-	0.07
Apocynaceae	*Condylocarpon isthmicum* A. DC.	Vine	-	0.29	-	-	0.07
Solanaceae	*Cestrum nocturnum* L.***	Subshrub	0.27	-	-	-	0.07
Polypodiaceae	*Pleopeltis hirsutissima* Raddo	Herb	0.15	-	0.11	-	0.07
Poaceae	Poaceae sp.10	Herb	-	-	0.26	-	0.06
Asteraceae	*Mikania* cf. *capricornis* Baker	Vine	0.25	-	-	-	0.06
Solanaceae	*Solanum brusquense* L.B. Sm. & Downs	Subshrub	0.25	-	-	-	0.06
Poaceae	Poaceae sp.11	Herb	-	0.25	-	-	0.06
Sapindaceae	*Cardiospermum halicacabum* L.*	Vine	-	0.25	-	-	0.06
Menispermaceae	*Cissampelos andromorpha* Eichler	Vine	-	0.25	-	-	0.06

Continues

Table 2. Continuation.

Family	Species	Growth form	IV by location CJ (%)	BC (%)	BA (%)	IT (%)	Total IV (%)
Euphorbiaceae	*Dalechampia triphyla* Lam.	Vine	-	0.25	-	-	0.06
Rubiaceae	*Emmeorhiza umbellata* Nees & Mart.	Vine	-	0.25	-	-	0.06
Malpighiaceae	*Heteropteris martiana* A. Juss	Vine	-	0.25	-	-	0.06
Melastomataceae	*Leandra melastomoides* Triana	Subshrub	-	-	0.25	-	0.06
Malpighiaceae	*Heteropteris* sp.	Vine	-	-	0.25	-	0.06
Melastomataceae	*Leandra* sp.2	Subshrub	-	-	0.24	-	0.06
Blechnaceae	*Blechnum binervatum var. acutum* (Desv.) R.M. Tryon & Stolze	Herb	0.08	-	0.16	-	0.06
Dryopteridaceae	*Elaphoglossum vagans* (Mett.) Hieron	Herb	0.23	-	-	-	0.06
Rubiaceae	*Borreria verticillata* (L.) Mey*	Vine	0.23	-	-	-	0.06
Bromeliaceae	*Bromelia fastuosa* Lindl.	Herb	-	-	0.22	-	0.06
Bromeliaceae	Bromeliaceae sp.3	Herb	-	-	0.22	-	0.06
Marantaceae	Marantaceae sp.	Herb	-	-	0.22	-	0.06
Polypodiaceae	*Serpocaulon fraxinifolium* (Jacq.) A.R.Sw.	Herb	-	-	0.22	-	0.06
Aristolochiaceae	*Aristolochia* cf. *arcuata* Mast.	Vine	-	-	0.22	-	0.06
Cyperaceae	*Pleurostachys* sp.2	Herb	-	0.22	-	-	0.05
Sapindaceae	*Paullinia carpopoda* Cambess.	Vine	-	0.20	-	-	0.05
Begoniaceae	*Begonia cucullata* Willd.*	Herb	0.08	-	0.11	-	0.05
Aspleniaceae	*Asplenium* sp.	Herb	0.18	-	-	-	0.04
Melastomataceae	*Leandra sulfurea* Cogn.	Subshrub	0.18	-	-	-	0.04
Melastomataceae	*Leandra* sp.3	Subshrub	-	0.17	-	-	0.04
Sapindaceae	*Paullinia trigonia* Vell.	Vine	-	-	0.16	-	0.04
Bromeliaceae	*Aechmea distichanta* M.B. Forster	Herb	0.15	-	-	-	0.04
Asteraceae	*Jaegeria hirta* (Lag.) Less*	Herb	0.15	-	-	-	0.04
Bromeliaceae	*Wittrockia* cf. *cyathiformis* (Vell.) Leme	Herb	0.15	-	-	-	0.04
Lythraceae	*Cuphea ingrata* Cham. & Schltdl.	Subshrub	0.15	-	-	-	0.04
Rosaceae	*Rubus urticifolius* Poir.	Subshrub	0.15	-	-	-	0.04
Cucurbitaceae	*Cayaponia* sp.	Vine	0.15	-	-	-	0.04
Asteraceae	*Mikania* cf. *triangularis* Baker	Vine	0.15	-	-	-	0.04
Bignoniaceae	*Podranea ricasoliana* (Tanfani) Sprague***	Vine	0.13	-	-	-	0.03
Bromeliaceae	Bromeliaceae sp.2	Herb	-	0.12	-	-	0.03
(Indeterminate)	(Indeterminate) sp.4	Herb	-	0.12	-	-	0.03
Araceae	*Philodendron* sp.	Herb	-	0.12	-	-	0.03
Poaceae	Poaceae sp.9	Herb	-	0.12	-	-	0.03
Poaceae	*Setaria poiretiana* (Schult) Kunth	Herb	-	0.12	-	-	0.03
Solanaceae	*Solanaceae* sp.2	Subshrub	-	0.12	-	-	0.03
Bignoniaceae	Bignoniaceae sp.3	Vine	-	0.12	-	-	0.03
Alstroemeriaceae	*Bomarea edulis* (Tussac.) Herb	Vine	-	0.12	-	-	0.03
Cucurbitaceae	Cucurbitaceae sp.1	Vine	-	0.12	-	-	0.03
Euphorbiaceae	*Tragia volubilis* L.	Vine	-	0.12	-	-	0.03
Lamiaceae	*Hyptis fasciculata* Benth*	Subshrub	-	-	0.12	-	0.03
Solanaceae	*Solanum* cf. *aculeatissimum* Jacq.	Subshrub	-	-	0.12	-	0.03
Araceae	*Anthurium itanhaense* Engl.	Herb	-	-	0.11	-	0.03

Continues

Table 2. Continuation.

Family	Species	Growth form	IV by location				Total IV
			CJ (%)	BC (%)	BA (%)	IT (%)	(%)
Aspleniaceae	*Asplenium cristatum* Lam.	Herb	-	-	0.11	-	0.03
Marantaceae	*Ctenanthe* sp.	Herb	-	-	0.11	-	0.03
Fabaceae-Faboideae	*Desmodium* cf. *incanum* DC.*	Herb	-	-	0.11	-	0.03
Gesneriaceae	*Nematanthus* cf. *wettsteinii* (Fritsch) H.E. Moore	Herb	-	-	0.11	-	0.03
Poaceae	Poaceae sp.12	Herb	-	-	0.11	-	0.03
Poaceae	Poaceae sp.8	Herb	-	-	0.11	-	0.03
Strelitziaceae	*Strelitzia* sp.	Herb	-	-	0.11	-	0.03
Lentibulariaceae	*Utricularia tricolor* A. St.-Hill	Herb	-	-	0.11	-	0.03
Lauraceae	*Cassytha filiformis* L.	Herb	-	-	0.11	-	0.03
Begoniaceae	*Begonia* sp.1	Vine	-	-	0.11	-	0.03
Begoniaceae	*Begonia* sp.2	Vine	-	-	0.11	-	0.03
Dilleniaceae	*Doliocarpus* cf. *dentatus* (Aubl.) Standl.	Vine	-	-	0.11	-	0.03
Acanthaceae	*Mendoncia velloziana* Mart.	Vine	-	-	0.11	-	0.03
Asteraceae	*Mikania hirsutissima* DC.	Vine	-	-	0.11	-	0.03
Asteraceae	*Mikania* sp.2	Vine	-	-	0.11	-	0.03
Sapindaceae	*Serjania macrostachya* Radlk.	Vine	-	-	0.11	-	0.03
Sapindaceae	*Serjania marginata*Casar.	Vine	-	-	0.11	-	0.03
Aristolochiaceae	*Aristolochia galeata* Mart. & Zucc.	Vine	-	-	-	0.09	0.02
Rubiaceae	*Manettia* sp.	Vine	-	-	-	0.09	0.02
Aspleniaceae	*Asplenium harpeodes* Kunze	Herb	0.08	-	-	-	0.02
Asteraceae	*Erechtites valerianaefolia* (Link. ex Spreng.) DC.*	Herb	0.08	-	-	-	0.02
Apiaceae	*Eryngium elegans* Cham. & Schltdl.*	Herb	0.08	-	-	-	0.02
Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota	Herb	0.08	-	-	-	0.02
Poaceae	*Panicum pilosum* Sw.	Herb	0.08	-	-	-	0.02
Phyllanthaceae	*Phyllanthus roseollus* Müll. Arg.	Herb	0.08	-	-	-	0.02
Plantaginaceae	*Plantago australis* Lam.	Herb	0.08	-	-	-	0.02
Bignoniaceae	*Adenocalymma* sp.	Vine	0.08	-	-	-	0.02
Apocynaceae	*Prestonia calycina* Müll. Arg.	Vine	0.08	-	-	-	0.02
Smilacaceae	*Smilax spicata* Vell.	Vine	0.08	-	-	-	0.02
Araceae	*Philodendron appendiculatum* Naudruz & Mayo	Herb	-	-	0.06	-	0.02
Total for all growth forms			73.27	65.12	66.25	74.58	69.81

CJ – Campos do Jordão (protected area); BC – Barra do Chapéu (private property); BA – Bananal (protected area); IT – Itaberá (protected area).
*Ruderal species; **Morphotype undetermined due to a lack of fertile material; ***Exotic species.

given location could be classified as a different growth form at another location. That was the case for *Psychotria vellosiana* (Rubiaceae), which occurred in Bananal as a small shrub, with the highest importance value in the community, whereas it has been described as a tree of up to 10 m in height in the municipality of Camanducaia, in the Serra da Mantiqueira mountain range (RB Torres, personal communication). In the Phanerogamic Flora of the State of São Paulo (Taylor 2007), the species was described as an herb, shrub or subshrub of 3-6 m in height. This same plasticity was observed for *Cabralea canjerana*, the ecotype of which was sampled as a shrub in the present study (J.A. Pastore, pers. comm.), whereas it is usually described as a tree (Pastore 2003). Another example is *Griselinia ruscifolia*, which was sampled as a small tree in the present study, whereas it was described as a vine (scandent shrub) or shrub by Lorenzi & Souza (2005).

The most important families, in terms of the number of species in the understory of *Araucaria* forests in the state of São Paulo, were Poaceae, Asteraceae and Rubiaceae. Poaceae

Table 3. Relative importance value of shrub and small tree species in the understory of the four stretches of *Araucaria* forest sampled in the state of São Paulo.

Family	Species	Growth form	IV by location				Total IV (%)
			CJ (%)	CJ (%)	CJ (%)	CJ (%)	
Rubiaceae	*Psychotria vellosiana* Benth.	Shrub	0.22	-	25.27	9.71	8.80
Solanaceae	*Brunfelsia pauciflora* (Cham. & Schltdl.) Benth.	Shrub	11.35	2.40	-	1.15	3.72
Solanaceae	*Cestrum* sp.	Shrub	-	12.83	-	-	3.21
Piperaceae	*Piper mollicomum* Kunth	Shrub	-	10.45	1.59	-	3.01
Malvaceae	*Triumfetta semitriloba* Jacq.*	Shrub	-	5.04	1.28	-	1.58
Piperaceae	*Piper aduncum* L.	Shrub	-	-	-	4.76	1.19
Solanaceae	*Cestrum corymbosum* Schltdl.*	Shrub	4.64	-	-	-	1.16
Solanaceae	*Cestrum moriquitense* Kunth.	Small tree	-	-	-	3.92	0.98
Melastomataceae	*Leandra carassana* (DC.) Cogn.	Shrub	2.32	-	-	-	0.58
Griseliniaceae	*Griselinia ruscifolia* (Clos) Taub.	Small tree	2.32	-	-	-	0.58
Celastraceae	*Maytenus glaucescens* Reissek	Small tree	2.32	-	-	-	0.58
Piperaceae	*Piper* cf. *hispidum* Sw.	Shrub	-	-	-	2.29	0.57
Rubiaceae	*Psychotria ruelliifolia* (Cham. & Schltd.) Müll. Arg.	Shrub	-	-	2.25	-	0.56
Rubiaceae	*Palicourea marcgravii* A. St.-Hill	Shrub	-	-	-	2.20	0.55
Euphorbiaceae	*Manihot grahamii* Hook.	Shrub	-	1.96	-	-	0.49
Solanaceae	*Capsicum flexuosum* Sendtn.	Small tree	0.41	0.98	-	-	0.35
Piperaceae	*Piper glabratum Kunth*	Shrub	1.16	-	-	-	0.29
Piperaceae	*Piper gaudichaudianum* Kunth	Shrub	-	0.98	-	-	0.24
Asteraceae	*Eupatorium* sp.1	Shrub	-	-	0.92	-	0.23
Rubiaceae	*Psychotria racemosa* Rich.	Shrub	-	-	-	0.81	0.20
Melastomataceae	*Leandra acutiflora* (Naudin) Cogn.	Shrub	0.75	-	-	-	0.19
Lamiaceae	*Salvia arenaria* A. St.-Hill	Shrub	0.70	-	-	-	0.17
Verbenaceae	Verbenaceae sp.1	Shrub	-	-	-	0.57	0.14
Melastomataceae	*Leandra xanthocoma* (Naudin) Cogn.	Shrub	-	-	0.49	-	0.12
Lamiaceae	*Salvia* sp.1	Shrub	0.47	-	-	-	0.12
Solanaceae	*Solanum guaraniticum* Kunth	Shrub	-	-	0.43	-	0.11
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	Small tree	-	-	0.43	-	0.11
Piperaceae	*Piper crassinervium* Kunth	Shrub	-	-	0.37	-	0.09
Asteraceae	*Baccharis crispa* Spreng.*	Shrub	0.08	-	0.25	-	0.08
Melastomataceae	*Leandra australis* (Cham.) Cogn.	Shrub	-	0.12	-	-	0.03
Solanaceae	*Solanaceae* sp.1	Shrub	-	0.12	-	-	0.03
Asteraceae	*Baccharis singularis* (DC.) Baker	Shrub	-	-	0.12	-	0.03
Urticaceae	*Boehmeria caudata* (Poir.) Bonpl.	Shrub	-	-	0.12	-	0.03
Piperaceae	*Piper strictifolium* D. Monteiro & E.F. Guim.	Shrub	-	-	0.12	-	0.03
Melastomataceae	*Leandra* cf. *fluminensis* Cogn.	Shrub	-	-	0.11	-	0.03
Total for all growth forms			26.73	34.88	33.75	25.42	30.19

IV – importance value; CJ – Campos do Jordão (protected area); BC – Barra do Chapéu (private property); BA – Bananal (protected area); IT – Itaberá (protected area).
*Ruderal species.

Table 4. Summary of the key floristic and phytosociological parameters for the understory community in the four stretches of *Araucaria* forest sampled in the state of São Paulo.

Parameters	Locations			
	CJ (250 m²)	BC (250 m²)	BA (215 m²)	IT (250 m²)
Floristic survey				
Species richness, n	104	95	107	47
Family richness, n	42	36	48	26
Monospecific families, n	23	15	21	18
Exclusive species, n	64	51	57	26
Phytosociological survey				
Species richness, n	88	70	93	47
Ruderal species, n	17	6	14	2
Exotic species, n	2	0	1	0
Shannon diversity index	3.88	3.61	3.80	3.40
Pielou's evenness index	0.86	0.85	0.84	0.88
Shrubs, n of individuals	30	37	559	69
Cover of bamboo-like plants, herbs, vines and subshrubs, %	72	54	20	19
Rare species				
Small trees (one individual sampled per species), n	0	1	0	0
Shrubs (one individual sampled), n	8	3	5	2
Subshrubs (Braun-Blanquet scale score < 1), n	0	0	2	1
Vines (Braun-Blanquet scale score < 1), n	4	6	8	11
Bamboo-like plants (Braun-Blanquet scale score < 1), n	1	0	0	0
Herbs (Braun-Blanquet scale score < 1), n	11	6	18	6
Rare species total, n	24	16	33	20
Proportion of rare species, %	27	23	35	43

CJ – Campos do Jordão (protected area); BC – Barra do Chapéu (private property); BA – Bananal (protected area); IT – Itaberá (protected area).

were also important in previous phytosociological studies of dense rain forest in southern Brazil, although the dominant species varied depending on the site studied (Palma *et al.* 2008; Inácio & Jarenkow 2008).

Regarding the family Rubiaceae, the density of individuals of the genus *Psychotria* was notable in some sections of the areas sampled in Bananal and Itaberá, composing virtually monodominant communities in the understory, as was the case for *Psychotria vellosiana* in secondary vegetation in Bananal. Studies have demonstrated the intense propagation of *Psychotria* species, and the presence of clones might explain its aggregate distribution, given that species of this genus exhibit slow growth and a low seed germination rate (Almeida & Alves 2000; Coelho & Barros 2004; Nery 2010).

Vines were mainly represented by the families Apocynaceae, Asteraceae, Bignoniaceae, Sapindaceae and Rubiaceae. Bignoniaceae has been reported to be highly abundant in rain forests and deciduous forests (Kim 1996). At each of three of the four locations evaluated in the present study, we recorded three species of Bignoniaceae, the exception being the Bananal location, at which we recorded only one. Sapindaceae was absent or showed lower species richness in places where the climate is mild (Campos do Jordão, Bananal and Barra do Chapéu), being well represented only in Itaberá, where the climate is more seasonal. Asteraceae showed the opposite trend, with species recorded only in Campos do Jordão and Barra do Chapéu. The focus of Asteraceae diversity is in the dense rain forests and upland grasslands of southern and southeastern Brazil, the family presenting higher affinity for the lower average monthly temperatures typical of mountainous environments (Kim 1996; Villagra & Romaniuc-Neto 2010). Therefore, climatic conditions are important factors for the floristic differentiation of vines at the scale analyzed. The influence of seasonality on the distribution of vine species was also noted in the analysis of importance value at the locations compared. Of the total importance value, vines accounted for 29.6% in Itaberá, 22.5% in Barra do Chapéu, 12.2% in Campos do Jordão and only 9.8% in Bananal. Therefore, species with the vine growth habit were more common at the location with a more seasonal climate (Itaberá), which can be attributed to their ecological characteristics. Due to the anatomical,

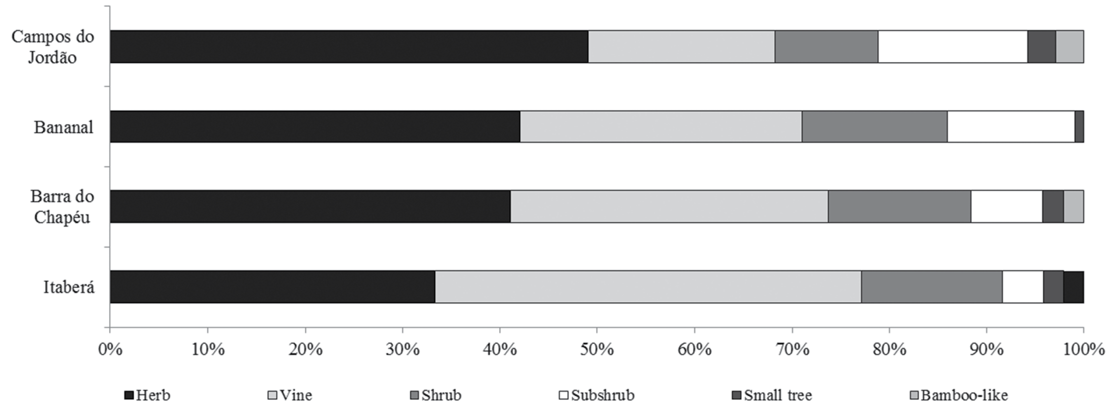

Figure 4. Relative species composition for each growth form in the understory of the four stretches of *Araucaria* forest sampled in the state of São Paulo.

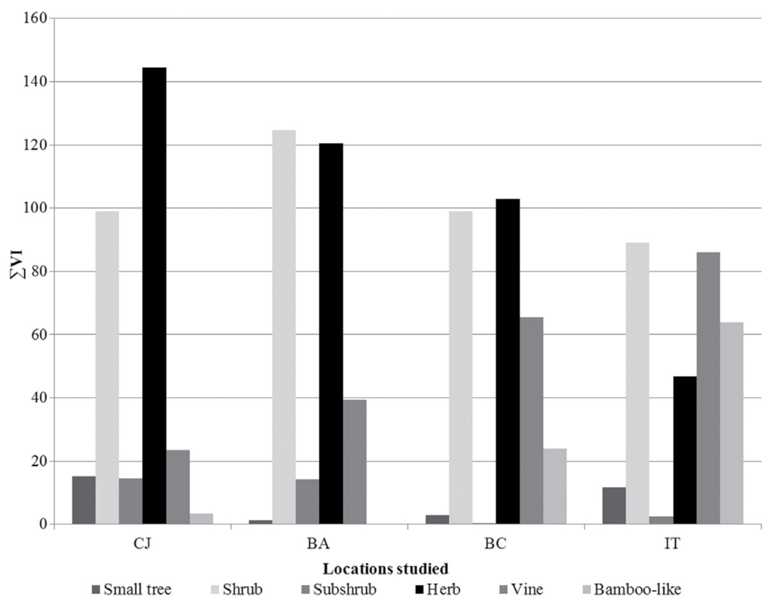

Figure 5. Importance value (IV) of growth forms (sum of the IV of all species in each growth form category) for the four stretches of *Araucaria* forest sampled in the state of São Paulo.
CJ – Campos do Jordão; BA – Bananal; BC – Barra do Chapéu; IT – Itaberá.

ecological and physiological advantages that vines enjoy, at the expense of tree species in regeneration, the recruitment of vines in the forest understory is directly proportional to the seasonality of the local climate (Benítez-Malvido & Martínez-Ramos 2003; Schnitzer 2005).

The major contribution of vines to the community structure of the understory in Itaberá is related to the greater abundance of deciduous trees in the canopy at that location (Ribeiro *et al.* 2013), which results in different conditions of light within the forest, a true environmental mosaic not only for tree regeneration but also for the resident community of the understory (Souza *et al.* 2010; 2013). Given these apparent advantages, Villagra & Romaniuc-Neto (2010) showed that even a small vegetation fragment, such as that evaluated in Itaberá, can harbor the same vine species richness as do large areas of contiguous forest. Therefore, the fragmented landscape is a factor that stimulates the presence of vines, not only at the edges, as described by different authors (Hora & Soares 2002; Benítez-Malvido & Martínez-Ramos 2003), but also in the forest interior. The fragment of *Araucaria* forest in Itaberá also features an extensive edge effect, with an abundance of bamboo-like plants, largely on the perimeter, where the study area borders agricultural land.

In Campos do Jordão, the canopy, which is composed of broadleaf species, is lower and the conditions at the bottom of the valley, in terms of the relative humidity and soil water content, remain constant year round, making it unfavorable for the establishment of vines but quite favorable for many fern species (Prado 1997), which in fact contributed to the high percentage of ground cover at that location. The forest

Table 5. Higher taxa richness and importance value in community understory of in the four stretches of *Araucaria* forest sampled in the state of São Paulo.

Taxa	Private property	Protected areas		
	Barra do Chapéu	Campos do Jordão	Bananal	Itaberá
Family (n of species)	Poaceae (10)	Rubiaceae (9)	Rubiaceae (11)	Rubiaceae (6)
	Piperaceae (6)	Poaceae (8)	Asteraceae (11)	Poaceae (5)
	Solanaceae (6)	Asteraceae (8)	Poaceae (6)	Sapindaceae (5)
	Sapindaceae (5)	Solanaceae (7)	Melastomataceae (6)	Piperaceae (3)
	Asteraceae (5)	Polypodiaceae (7)	Sapindaceae (5)	Bignoniaceae (3)
Genus (n of species)	*Leandra* (5)	*Asplenium* (4)	*Leandra* (5)	*Psychotria* (4)
	Heteropteris (3)	*Campyloneurum* (4)	*Psychotria* (4)	*Paullinia* (3)
	Peperomia (3)	*Psychotria* (4)	*Mikania* (4)	
Family (IV)	Poaceae (17%)	Solanaceae (18%)	Rubiaceae (40%)	Poaceae (32%)
	Solanaceae (16%)	Lamiaceae (11%)	Melastomataceae (12%)	Rubiaceae (15%)
	Piperaceae (12%)	Rubiaceae (10%)	Poaceae (12%)	Piperaceae (8%)
	Sapindaceae (7%)	Poaceae (8%)	Asteraceae (4%)	Sapindaceae (7%)
	Asteraceae (6%)	Cyperaceae (7%)	Blechnaceae (4%)	Melastomataceae (6%)
	Pteridophyta (6%)	Asteraceae (6%)	Sapindaceae (3%)	Cannabaceae (5%)
	Marantaceae (5%)	Thelypteridaceae (5%)	Fabaceae-Faboideae (2%)	Bignoniaceae (5%)
	Urticaceae (4%)	Melastomataceae (4%)	Piperaceae (2%)	Solanaceae (5%)
	Schizaeaceae (3%)	Piperaceae (3%)	Thelypteridaceae (2%)	Celastraceae (3%)
Species (IV)	*Cestrum* sp. (13%)	*Brunfelsia pauciflora* (11%)	*Psychotria vellosiana* (25%)	*Poaceae* sp.2 (18%)
	Piper molliconum (10%)	*Salvia* sp.3 (9%)	*Poaceae* sp.5 (8%)	*Psychotria vellosiana* (10%)
	Ichnanthus pallens (8%)	*Rhynchospora corimbosa* (8%)	*Borreria palustris* (7%)	*Poaceae* sp.1 (7%)
	Chusquea sp. (7%)	*Poaceae* spp.* (7%)	*Leandra* sp.1 (7%)	*Piper aduncum* (5%)
	Calathea communis (5%)	*Coccocypselum condalia* (5%)	*Coccocypselum lanceolatum* (4%)	*Piper* cf. *hispidum* (2%)
	Triumfetta semitriloba (5%)	*Cestrum corymbosum* (5%)	*Blechnum proliferum* (4%)	*Leandra fragilis* (6%)
	Serjania sp. (4%)	*Mikania ternata* (4%)	*Pleiochiton blepharodes* (4%)	*Celtis iguanaea* (5%)
	Mikania lindbergii (4%)	*Pilea hilariana* (3%)	*Poaceae* sp.6 (3%)	*Cestrum moriquitense* (4%)
	(Indeterminate%) sp.3 (4%)	*Thelypteris tamandarei* (3%)	*Mikania lindbergii* (3%)	*Hippocratea volubilis* (3%)
	Anemia phylittidis (4%)	*Griselinia ruscifolia* (2%)	*Psychotria ruelliifolia* (2%)	*Poaceae* sp.3 (3%)

IV – importance value.

fragment evaluated in Campos do Jordão presented more than three times the proportional cover found in Bananal, where the climate is also characterized by the absence of seasonality and low temperatures but whose forest is on a steep slope with shallow soil. The ground cover values for Barra do Chapéu, which were also influenced by the presence of ferns, were intermediate between those observed for Campos do Jordão and Bananal. Ground cover values were lowest for Itaberá, where the climate is more seasonal.

One objective of our study was to look for possible indicators of the degree of conservation of the resident community of the understory. The presence of exotic and ruderal species, *per se*, is an indicator of disturbance caused by human activity. However, the situation worsens when these species come to occupy a prominent place in the community. Among the locations compared, Campos do Jordão should have been the most conserved, being situated in a fully protected area full in the region with the largest number of remnants of *Araucaria* forest in the state of São Paulo. However, the presence of cattle was observed in the area, which contributed to the occurrence of ruderal species with high importance values in the understory community, which is an indicator of degradation not detected in the analysis of the tree component at the same location (Souza *et al.* 2012; Ribeiro *et al.* 2013). Although ruderal species were also observed in great numbers, with high importance values, in the approximately 60-year-old stretch of secondary vegetation in Bananal, the values were not as high as those observed for the more than 100-year-old stretch of forest in regeneration in Barra do Chapéu. In Itaberá, where there was no evidence of timber extraction or cattle grazing, ruderal species showed lower richness and importance values. There, the edge effect and the presence of natural gaps contributed to the abundance of bamboo-like plants.

Conclusions

The understory of the *Araucaria* forest fragments in the state of São Paulo are quite heterogeneous: there were significant differences among the four fragments evaluated, in terms of the proportional representation of growth forms in the resident component of the understory, resulting in low floristic similarity, as well as different levels of richness and diversity. The richness and cover values for vines were higher in areas of high climatic seasonality, whereas the importance of herbs and subshrubs was lower in those same areas. Ruderal and exotic herbs were recorded at all of the locations evaluated, increasing in number in the areas of greatest native species richness. It is recommended that these exotic and ruderal species be recorded in order to analyze the degree of conservation of the understory, because they have proved to be highly sensitive indicators of disturbance caused by human activity, even when such disturbance is not evident in the analysis of the tree component. The presence of exotic and ruderal species was associated with degradation vectors that still exist (cattle in Campos do Jordão), the historical use of the site (secondary vegetation, in Bananal, or planted vegetation, in Barra do Chapéu) or forest fragmentation (the edge effect, in Itaberá).

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