

FLORISTIC PATTERNS IN UNDERSTOREYS UNDER DIFFERENT DISTURBANCE SEVERITIES IN SEASONAL FORESTS

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PRADO JÚNIOR JA, LOPES SF, VALE VS, ARANTES CS, OLIVEIRA AP & SCHIAVINI I. 2014. Floristic patterns in understoreys under different disturbance severities in seasonal forests. This study evaluated the floristic diversity in the understoreys of 10 seasonal central Brazilian semideciduous tropical forests in different stages of disturbance and tested the hypothesis that increased disturbance severity in a community directly affected the floristic diversity of the understorey. We evaluated phytosociological parameters of species and families as well as the structure of each understorey. Floristic similarity was assessed between understoreys. Results show Celastraceae, Rubiaceae, Myrtaceae, Meliaceae and Siparunaceae as the five most important families. The five most representative species were *Cheiloclinium cognatum*, *Cordia sessilis*, *Siparuna guianensis*, *Trichilia catigua* and *T. clausenii*. The analyses showed greater floristic similarity between understoreys under the same disturbance severity. Increase in density of Rubiaceae and decrease of Meliaceae with increasing disturbance was observed. Density of some species has also been linked to the level of forest disturbance. Evaluating the distribution patterns of understoreys may help in understanding of ecological processes and the responses of vegetation in the face of future disturbances.

Keywords: Conservation, forest ecology, floristic similarity, phytosociology, stratification, Brazil

INTRODUCTION

Seasonal dry forests are among the most fragmented and threatened ecosystems of the world (Miles et al. 2006). They cover 42% of all tropical forests and contain high proportion of endemic species (Kalacska et al. 2004). It is estimated that in South America, this endemism exceeds 73% (Gentry & Emmons 1987). These forests are conditioned to long dry periods (2 to 6 months) and they contain species which exhibit functional phenology and reproductive responses that are very different from species of tropical rainforests (Murphy & Lugo 1986). This complexity in functional structure increases the susceptibility of these forests to disturbance (Miles et al. 2006).

Floristic studies in natural areas affected by human activities are important tools for conservation of these ecosystems. Most of the studies show that floristic similarities between areas are strongly influenced by the distance between them (Condit et al. 2002, McDonald et al. 2005). Moreover, these studies assessed floristic similarities in the plant community as a whole,

neglecting species attributes such as position in the vertical stratum of forests. Evaluation of the distribution patterns of species per stratum can aid in the understanding of responses of forest communities to environmental changes related to disturbance (Poorter et al. 2006).

Compared with rainforests, seasonal dry forests have lower and discontinuous canopy, fewer layers and greater exposition to sunlight in lower strata (Murphy & Lugo 1986). The understorey, in particular, is the stratum that is more sensitive to environmental perturbations such as gap formation (whether natural or manmade) that changes the forest microclimate and increases incidence of light and water stress (Poorter et al. 2006). Thus, differences are expected between floristic patterns in understorey at different stages of preservation.

The objectives of this study were to describe species diversity and floristic similarity between understoreys of 10 seasonal semideciduous forests under different severities of disturbance, and to investigate the influence of disturbance severity

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on patterns of floristic diversity of understoreys based on the following hypothesis: fragments with the same severity of disturbance show greater similarity in their floristic understorey.

MATERIALS AND METHODS

Research areas and stratification

This study used database from previous phytosociological tree community studies (diameter at breast height (dbh) ≥ 5 cm) in 10 areas of seasonal semideciduous forests in Central Brazil, totalling 10 ha (Table 1) (Lopes 2010, Lopes et al. 2012). Lopes et al. 2012 evaluated the structure and floristic diversity of the areas, comparing density, basal area and frequency of community species from the sample plots (25 plots per area). Botanical classification of these studies was based on the Angiosperm Phylogenetic Group (APG 2009). Species sampled from the 10 areas used in this study were classified according to their position in the stratum community as canopy, intermediary stratum (under-canopy) or understorey species, using a non-parametric methodology of quartiles and medians of heights of community and species (Vale et al. 2009, Lopes 2010). For this study, we only used the species classified as understorey species. Since this paper aimed to study tree community with dbh ≥ 5 cm (Felfili et al. 2011), herbaceous and shrubby species that were present in the understorey were not included in the sample. Thus, tested hypothesis are applicable just for tree community in understorey.

Lopes (2010) also classified the areas according to disturbance severity (Table 2) from an impact matrix, in which structural parameters were considered such as abundance of pioneer species, canopy height, presence of large gaps or internal trails and selective logging. Areas under lower disturbance severity (i.e. areas 1 and 4) are forests in advanced succession stages, fragments higher than 70 ha, with lower edge effect, absence of cattle and selective logging (Lopes 2010). These areas present low number of pioneer species ($< 10\%$) and high canopy (> 25 m). Areas under intermediate disturbance (areas 6, 7, 9 and 10), as well as the lower impact areas present high canopy and low number of pioneer species but are small fragments (< 30 ha). Areas highly disturbed (areas 2, 3, 5 and 8) have internal trails and livestock which increase the trampling and grazing in the areas, thus, increasing degradation (Lopes 2010). Areas under higher disturbance severity present large edge effect. They have lower canopies (< 17 m), higher number of pioneer species (25% of trees), many internal trails and presence of cattle and selective logging (Lopes 2010).

Structure and floristic diversity in understoreys

To assess the most representative botanical families in understoreys of seasonal semideciduous tropical forests, we used an adjustment of the index value representing the family importance index (Mori et al. 1983). This index compares the relative parameters of density, dominance and richness of botanical families of each community

Table 1 Location, floristic and structural parameters of tree community (dbh ≥ 5 cm) in 10 areas of seasonal semideciduous forests in central Brazil

Area	Latitude (S)	Longitude (S)	Extension (ha)	S	NI	BA	H'	J'
1	18° 29'	48° 23'	200	78	839	25.5	3.44	0.79
2	18° 43'	49° 56'	40	50	837	15.1	2.92	0.75
3	18° 45'	47° 30'	120	98	798	26.4	3.97	0.87
4	19° 40'	48° 02'	70	90	805	45.8	3.33	0.73
5	18° 40'	48° 24'	18	79	1233	23.5	3.37	0.77
6	18° 56'	48° 12'	30	86	976	26.2	3.71	0.83
7	19° 08'	48° 08'	22	76	945	27.0	3.47	0.81
8	19° 10'	48° 23'	16	98	1292	21.7	3.78	0.82
9	18° 55'	48° 03'	35	103	1144	26.8	3.87	0.84
10	18° 51'	48° 13'	20	88	1063	34.7	3.53	0.79

S = number of species, NI = number of individuals, BA = basal area (m^2), H' = Shannon diversity index and J' = evenness index; structural parameters are equivalent to absolute values per hectare; adapted from Lopes et al. (2012)

Table 2 Classification and description of 10 areas of seasonal semideciduous forests according to severity of disturbance

Area	Disturbance severity	Description
1, 4	Low	Low number of pioneer species, many individuals with high basal area, high canopy, large fragments without internal trails or logging
6, 7, 9, 10	Medium	Low number of pioneer species, few individuals with high basal area, high canopy, small fragments, presence of internal trails with surrounding disturbed matrix
2, 3, 5, 8	High	High number of pioneer species, few individuals with high basal area, low canopy, presence of internal trails with surrounding disturbed matrix

studied. The adjustment consisted of adding the relative frequency to evaluate the distribution of plant families in the 10 study areas. Thus, family importance index per family consisted of the sum of relative density (N_f/N), relative dominance (BA_f/BA), relative frequency (F_f/F) and relative richness (S_f/S) of each family, where N = number of individuals, f = the f th family parameter, BA = basal area, F = number of understoreys occurring and S = number of species.

We evaluated the phytosociology of species for each understorey and also the understoreys as a whole by three parameters: relative density, relative dominance and relative frequency. We used Shannon diversity index (H') and evenness index (J') to estimate diversity of each understorey (Magurran 2004). We assessed the floristic dissimilarity between understoreys using Morisita–Horn similarity index (Magurran 2004). To evaluate how severity of disturbance affect understorey species composition and diversity, areas with the same disturbance severity were combined. Then we calculated the densities of families and species for each of the three categories of disturbance (low, medium and high). We also analysed floristic similarity between the three categories using the Morisita–Horn index (Magurran 2004).

Data analysis

Shannon diversity index between understoreys was compared using a Hutcheson's t-test (Magurran 2004). From values of Morisita–Horn index between understoreys, we performed cluster analysis using the method of grouping the non-weighted averages, calculated using SPSS Statistics (version 17.0, 2008).

To test correlation between geographical distance and floristic similarity in community and in understoreys, we performed the Mantel

test using Pearson (r) correlation index at a significance level of 5% (Legendre 1993). Monte Carlo method with 1000 random permutations was applied to assess the significance of Mantel test (Zar 2010). Geographical distance between areas was calculated using Google Earth (version 6.1, <http://google.com/earth/download/ge/agree.html>). To compare relative density of species between different disturbance severities, we used a non-parametric Kruskal–Wallis test. These analyses were calculated using SPSS Statistics (version 17.0).

RESULTS

A total of 2695 individuals belonging to 65 species and 29 families were evaluated in the understoreys of the 10 study areas. The richest families were Myrtaceae (12 species), Rubiaceae (7), Fabaceae (5), Celastraceae (4) and Meliaceae (4), which represented 49% of total species found in understoreys (Table 3). Rubiaceae (541 individuals), Celastraceae (483) and Siparunaceae (405) had the highest densities and together comprised 53% of individuals. Only Rubiaceae was found in all 10 understoreys while Myrtaceae, Celastraceae, Fabaceae and Meliaceae, in nine. The five families with highest family importance indices were Celastraceae, Rubiaceae, Myrtaceae, Meliaceae and Siparunaceae, which represented over 60% of total importance value families (Table 3).

Of the 65 species sampled in understoreys, 27 were exclusive to one area and 16 were sampled in at least five areas. The other 22 species were sampled in less than five areas. No species were sampled in the all the 10 understoreys. The five species with the highest importance value were *Cheiloclinium cognatum*, *Cordia sessilis*, *Siparuna guianensis*, *Trichilia catigua* and *T. clausenii*, which together comprised 56% of density and 43%

Table 3 Main botanical families (> 90% of total FIV), in descending order of FIV, sampled in 10 understoreys of seasonal semideciduous forest in central Brazil

Family	RD	RDo	RF	RR	FIV (%)
Celastraceae	17.9 (483)	29.8 (5.8)	8.0 (9)	6.2 (4)	15.5
Rubiaceae	20.1 (541)	17.4 (3.4)	8.8 (10)	10.8 (7)	14.3
Myrtaceae	12.0 (323)	11.5 (2.2)	8.0 (9)	18.5 (12)	12.5
Meliaceae	14.0 (378)	13.6 (2.7)	8.0 (9)	6.2 (4)	10.4
Siparunaceae	15.1 (405)	6.8 (1.3)	6.2 (7)	1.5 (1)	7.4
Fabaceae	1.6 (42)	0.8 (0.2)	8.0 (9)	7.7 (5)	4.5
Nyctaginaceae	3.1 (83)	4.0 (0.8)	4.4 (5)	3.1 (2)	3.7
Rutaceae	5.3 (143)	3.4 (0.7)	1.8 (2)	3.1 (2)	3.5
Chrysobalanaceae	2.7 (72)	4.5 (0.9)	4.4 (5)	1.5 (1)	3.4
Cannabaceae	1.2 (33)	1.8 (0.4)	5.3 (6)	3.1 (2)	2.9
Sapotaceae	2.6 (69)	3.2 (0.6)	3.5 (4)	1.5 (1)	2.7
Sapindaceae	0.4 (11)	0.5 (0.1)	3.5 (4)	4.6 (3)	2.3
Malpigiaceae	0.4 (9)	0.6 (0.1)	3.5 (4)	1.5 (1)	1.5
Moraceae	0.3 (9)	0.2 (< 0.1)	3.5 (4)	1.5 (1)	1.4
Primulaceae	0.9 (25)	0.5 (0.1)	2.7 (3)	1.5 (1)	1.4
Erythroxylaceae	0.3 (9)	0.2 (0.0)	1.8 (2)	3.1 (2)	1.3
Piperaceae	0.2 (6)	0.2 (< 0.1)	1.8 (2)	3.1 (2)	1.3
Other families (12)	1.9 (51)	0.9 (1.9)	17.1 (19)	21.2 (14)	9.8

RD = relative density, RDo = relative dominance, RF = relative frequency, RR = relative richness, FIV = family importance value index; numbers in parentheses represent absolute values of each parameter

of total importance value (Appendix). Some species, such as *Coutarea hexandra*, *Trichilia pallida*, *Coussarea hydrangeifolia* and *Myrcia splendens*, although having low densities, occurred in more than five understoreys, indicating its importance in understorey of these seasonal semideciduous forests (Appendix).

Average proportion of species in understoreys was 24% (range 17–28%) compared with average number of species in the communities (all strata) (Table 4). Average proportion of individuals in understoreys, compared with the total number of individuals in that community, was 28%, with highest ratios being obtained from area 4 (44%) and area 1 (38%) and lowest in areas 6 and 7 (20%). Basal area of all understoreys was less than 10% of tree community. Comparisons between Shannon diversity index for each understorey (Hutcheson's t-test, $p < 0.05$) show different results from those obtained for communities (Table 4). For example, the two most conserved areas (1 and 4), which were communities that had lower diversity of tree species, had two of the highest Shannon index results for

their understoreys. Evenness in understorey layer was lower than in communities overall, suggesting that there was less uniformity in ratios between densities of understorey species. Therefore, results suggest that only a few species were responsible for most of total density in understorey.

Floristic similarity between understoreys ranged from 0.01 to 0.93 (Figure 1). Cluster analysis based on Morisita–Horn index show cophenetic correlation of 0.89, forming groups among understoreys with the same disturbance severity (Figure 1). Geographical distance between areas was negatively correlated with floristic similarity in communities (Mantel test, $t = -3.203$, $r = -0.439$). Correlation of floristic similarities between understoreys and geographical distance was lower than with communities (Mantel test, $t = -3.203$, $r = -0.253$).

When areas under the same disturbance severity were grouped, highest floristic similarity (30%) was obtained between intermediate stages and those that were highly disturbed. Similarity between conserved and

Table 4 Comparison of structural parameters and diversity among communities and understoreys of 10 seasonal semideciduous forests in central Brazil

Disturbance level	Area	S		NI		BA		H'		J'	
		Com.	Und.	Com.	Und.	Com.	Und.	Com.	Und.	Com.	Und.
Low	1	78	22 (28)	839	320 (38)	25.5	2.5 (10)	3.44 d, e	2.56 a	0.79	0.83
Low	4	90	25 (28)	805	355 (44)	45.8	3.0 (7)	3.33 f	2.23 a	0.73	0.67
Medium	6	86	16 (19)	976	197 (20)	26.2	1.3 (5)	3.71 c	1.64 b, c, d	0.83	0.59
Medium	7	76	13 (17)	945	209 (22)	27.0	1.2 (4)	3.47 d	1.54 c, d	0.81	0.60
Medium	9	103	22 (21)	1144	234 (20)	26.8	1.3 (5)	3.87 b	1.55 c, d	0.84	0.51
Medium	10	88	17 (19)	1063	265 (25)	34.7	2.8 (8)	3.53 d	1.47 d	0.79	0.50
High	2	50	14 (28)	835	201 (24)	15.1	1.5 (10)	2.92 g	1.94 b, c	0.75	0.73
High	3	98	26 (27)	798	220 (28)	26.4	2.0 (8)	3.97 a	2.59 a	0.87	0.80
High	5	79	17 (22)	1233	357 (29)	23.5	2.4 (10)	3.37 e, f	1.70 b, c, d	0.77	0.60
High	8	98	26 (27)	1292	337 (26)	21.7	1.4 (7)	3.78 b, c	1.90 b	0.82	0.58
Average		84.6	19.8 (23)	993	269.5 (27)	27.3	1.9 (7)	-	-	-	-

Com. = community, Und. = understorey, S = number of species, NI = number of individuals, BA = basal area (m²), H' = Shannon diversity index and J' = evenness index; numbers in parentheses represent percentage between understorey and community parameters; different letters in the same column are significantly different ($p < 0.005$)

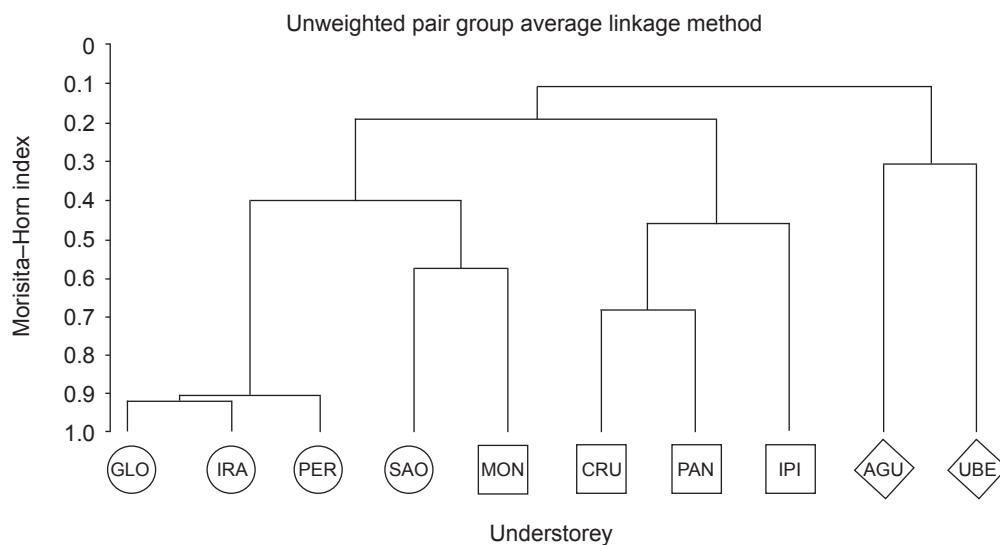


Figure 1 Floristic similarity dendrogram from the Morisita–Horn index, generated by the grouping method group average between understoreys of 10 semideciduous forests in central Brazil; diamonds represent the most conserved sites, circles represent sites of medium disturbance and squares represent the most disturbed sites

intermediate areas was maintained at 13%. It was 16% with most disturbed areas (results not shown). Although the majority of species and families were common to more than one level of disturbance, relative densities of many species differ substantially between different disturbance severities (Tables 5 and 6). The family Rubiaceae, for example, occurred in understoreys at all three stages of disturbances

but its relative density increased significantly in more disturbed area. Moreover, Meliaceae, Rutaceae and Sapotaceae increased in density, mainly in less disturbed stage (Table 5). Siparunaceae showed higher relative density at intermediate stage. *Cordia sessilis*, *Myrciaria glanduliflora*, *Campomanesia velutina* and *Maytenus floribunda* showed higher relative densities in more disturbed area (Table

Table 5 Comparison between relative densities of main families sampled in understoreys of semideciduous forests under different disturbance severities

Family	Disturbance severity			H	p
	Low RD	Medium RD	High RD		
Rubiaceae	3.0 c	12.5 b	36.6 a	74.51	< 0.05
Celastraceae	8.3 a	27.0 a	16.4 a	4.77	0.12
Meliaceae	39.0 a	4.2 b	6.9 b	88.61	< 0.05
Siparunaceae	0.0 b	41.3 a	2.8 b	131.18	< 0.05
Myrtaceae	11.4 a	3.5 b	19.2 a	59.41	< 0.05
Rutaceae	21.2 a	0.0 b	0.0 b	105.42	< 0.05
Sapotaceae	7.0 a	0.1 b	1.9 b	87.16	< 0.05
Nyctaginaceae	1.0 a	3.2 a	4.2 a	1.48	0.90
Chrysobalanaceae	0.1 a	5.5 a	1.9 a	15.56	0.08
Fabaceae	1.6 a	0.7 a	2.2 a	9.08	0.31
Primulaceae	2.8 a	0.0 b	0.5 b	52.20	< 0.05
Cannabaceae	0.4 a	0.3 a	2.4 a	18.61	0.11

Letters indicate the results of median test; RD = relative density, H = critical value of Kruskal–Wallis test, p = probability of Kruskal–Wallis test, bold numbers indicate significant differences; different letters in the same column are significantly different ($p < 0.005$)

Table 6 Comparison between relative densities of main species sampled in understorey of semideciduous forests under different disturbance severities

Species	Disturbance severity			H	p
	Low RD	Medium RD	High RD		
<i>Cheiloclinium cognatum</i>	8.0 a, b	25.2 a	11.2 b	12.51	< 0.05
<i>Siparuna guianensis</i>	0.0 b	41.3 a	2.8 b	131.20	< 0.05
<i>Cordia sessilis</i>	0.3 b	4.2 b	32.6 a	115.54	< 0.05
<i>Trichilia catigua</i>	15.6 a	1.1 b	4.5 b	51.40	< 0.05
<i>Galipea jasminiflora</i>	21.0 a	0.0 b	0.0 b	100.61	< 0.05
<i>Trichilia clausenii</i>	19.3 a	0.0 b	0.0 b	182.44	< 0.05
<i>Myrciaria glanduliflora</i>	0.0 b	1.3 b	8.4 a	18.30	< 0.05
<i>Chrysophyllum gonocarpum</i>	7.0 a	0.1 b	1.9 b	87.15	< 0.05
<i>Campomanesia velutina</i>	0.3 b	0.6 b	7.7 a	69.34	< 0.05
<i>Hirtella gracilipes</i>	0.1 a	5.5 a	1.9 a	15.56	0.08
<i>Maytenus floribunda</i>	0.1 b	1.8 b	4.8 a	25.19	< 0.05
<i>Trichilia elegans</i>	3.6 a	1.0 b	2.0 a, b	25.12	< 0.05
<i>Fareamea hyacinthina</i>	0.0 b	5.6 a	0.6 b	34.00	< 0.05
<i>Eugenia involucreta</i>	4.4 a	0.0 b	1.1 a, b	37.39	< 0.05
<i>Guapira venosa</i>	1.0 a, b	0.0 b	4.2 a	21.75	< 0.05
<i>Eugenia ligustrina</i>	2.5 a	0.3 a	0.6 a	11.27	0.46
<i>Ardisia ambigua</i>	2.8 a	0.0 b	0.5 b	52.20	< 0.05
<i>Coussarea hydrangeifolia</i>	0.3 a	1.5 a	1.4 a	2.32	0.90
<i>Guapira opposita</i>	0.0 a	3.2 a	0.0 a	27.21	0.11
<i>Trichilia pallida</i>	0.6 a	2.1 a	0.4 a	2.71	0.40
<i>Eugenia subterminalis</i>	3.0 a	0.0 b	0.0 b	54.59	< 0.05
<i>Celtis iguanaea</i>	0.4 a	0.3 a	2.2 a	15.52	0.19
<i>Coutarea hexandra</i>	0.9 a	0.2 a	1.2 a	6.82	0.81
<i>Bauhinia unguolata</i>	0.0 a	0.2 a	1.6 a	14.74	0.53

Letters indicate the results of median test; H = critical value of Kruskal–Wallis test, p = probability of Kruskal–Wallis test, bold numbers indicate significant differences; different letters in the same column are significantly different ($p < 0.005$)

6). Higher densities of *Trichilia catigua*, *T. clausenii*, *Galipea jasminiflora* and *Chrysophyllum gonocarpum* were obtained in better preserved area (Table 6).

DISCUSSION

The analysis conducted in understoreys of seasonal semideciduous forests in central Brazil highlighted Celastraceae, Rubiaceae, Myrtaceae, Meliaceae and Siparunaceae as the five most important families, representing more than 60% of the family importance indices for these areas. These five families can be considered typical in the understorey of seasonal semideciduous forests in central Brazil (Oliveira-Filho et al. 2006, Lopes et al. 2012).

Rubiaceae, Myrtaceae and Meliaceae are families that are widely distributed not only in semideciduous forests but also in tropical forests in general (Oliveira-Filho & Fontes 2000). Although they include species of all strata, occurrence of these families is often associated with the understorey (Gentry & Emmons 1987). Celastraceae and Siparunaceae occurred at high density in the understorey and represented 33% of total number of individuals. However, they are not listed among the most representative families in semideciduous forests (Oliveira-Filho & Fontes 2000). Fabaceae (including all subfamilies), which is reported to be the most representative family of semideciduous forests (Oliveira-Filho et al. 2006, Lopes et al. 2012), occurred at low density in this study, indicating that its presence should be associated with the upper strata of these forests. Other families, such as Lauraceae, Annonaceae and Euphorbiaceae which are widely distributed in semideciduous forests (Oliveira-Filho et al. 2006, Lopes et al. 2012), also occurred at low density in understorey.

The majority of floristic lists of central Brazilian seasonal semideciduous forests evaluate representativeness of families according to species richness (Oliveira-Filho & Fontes 2000, Oliveira-Filho et al. 2006, Lopes et al. 2012). This study emphasised the need to include values for density, dominance and frequency of each family and suggested an adaptation of the value of family importance index as appropriate methods to assess representativeness of each family in plant communities.

In this study, the most important species observed in the understoreys included *C.*

gonocarpum, *C. hexandra*, *S. guianensis*, *T. catigua* and *T. elegans*. These species are widely distributed in semideciduous forests of south-eastern South America (Oliveira-Filho et al. 2006). *Cheiloclinium cognatum* has been described as a species common only in semideciduous montane forests of Central Brazil (Oliveira-Filho et al. 2006). *Cordia sessilis*, the second most important species in the understoreys studied, was not classified as very common in semideciduous forests in eastern Brazil (Oliveira-Filho et al. 2006). The genus *Cordia* is usually associated with cerrado (savanna) vegetation in Brazil (Oliveira-Filho & Fontes 2000). The presence of this species in central Brazilian semideciduous forests may be associated with its proximity with cerrado formations as well as the strongly seasonal climate that influences the semideciduous forests of central Brazil (including forests of this study). Our results show high differences between floristic patterns in central Brazilian seasonal forests compared with seasonal forests of eastern Brazil (which are less seasonal) and, thus, the set of species endemic to this region. These results reinforce the importance of developing work on floristic composition and diversity of this region. The understoreys of semideciduous forests in this study had lower species diversity and smaller number of individuals than the rest of the community. Some structural patterns of semideciduous forests such as lower and more irregular canopy when compared with tropical rainforests, favour reduction in number of species in understorey (Gentry & Emmons 1987). Basal area of understorey species was unrepresentative (< 10% of total) of the remainder of community. This is expected since forest biomass is mostly accumulated in canopy (Ozanne et al. 2003).

In the community level, the two most conserved areas (areas 1 and 4) had lower species diversity and fewer individuals than the rest of study areas. However, in the understorey, they had the highest levels of species diversity and the highest ratios between number of individuals in understorey and in the community overall. This result may be related to the higher productivity and differentiation of niches in understorey which increase the ecological importance of understorey vegetation in most conserved areas (Gentry & Emmons 1987, Tabarelli et al. 1999). With exception of areas 1 and 3, evenness was low in the understoreys. This was due to the fact that in the remaining areas, the two most abundant

species corresponded to more than 50% of the total number of individuals.

High number of exclusive species (42%) and low values of floristic similarity between most of the understoreys emphasise the high β diversity (i.e. diversity among areas) found in semideciduous forests (Oliveira-Filho & Fontes 2000, Lopes et al. 2012). In this study, correlation of geographical distance and floristic similarity between communities was higher ($r = 0.439$) than correlation with floristic similarities in understoreys ($r = 0.253$) (Zar 2010), which means that the floristic in understorey were less influenced by the geographical distance. Most floristic patterns are correlated with geoclimate variables and, therefore, the distance between plant communities has strong influence on β diversity (McDonald et al. 2005). In this study, variations in average rainfall, temperature and altitude between the 10 studied areas are subtle (Lopes et al. 2012), increasing similarities between areas. However, to understoreys, other factors such as severity of disturbance, may directly influence the turnover of species and consequently the floristic similarity between them (Kalacska et al. 2004).

Cluster analysis of quantitative floristic similarity confirmed the hypothesis that forests under different disturbance regimes differ in composition and floristic diversity. Therefore, abundance and relative frequency of some families and species may aid in the classification of stages of conservation in forest communities. Human disturbance alters the composition and structure of forests, which is mainly reflected in community of tree species (Turner 2010). Major differences between stages of disturbance were increased density of Rubiaceae and reduction in Meliaceae with increasing disturbance severity. These results are supported by several studies which show a reduction of Rubiaceae during forest regeneration process (Tabarelli et al. 1999, Toniato & Oliveira-Filho 2004) and an increase in abundance of Meliaceae family as indicator of the change in successional stage from an initial successional forest to a mature forest (Toniato & Oliveira-Filho 2004).

Density of Myrtaceae increased in disturbed areas of this study. This family is considered as an indicator of late-successional stages (Tabarelli et al. 1999). Myrtaceae was the family with the highest number of species. Abundance of this family changed according to the disturbance severity.

Campomanesia velutina and *M. glanduliflora*, for example, had high densities in disturbed areas, while densities of species of the genus *Eugenia* (*E. involucrata*, *E. ligustrina* and *E. subterminalis*) had higher density in preserved areas. *Cordia sessilis*, *C. velutina*, *M. floribunda* and *M. glanduliflora* had higher densities in disturbed areas. These species have been reported as representatives of areas that are either disturbed or regenerating (Werneck et al. 2000). Thus, results of this study confirm that high abundance of these species is indicative of the most affected areas. On the other hand, *C. gonocarpum*, *E. involucrata* and *T. catigua* had the highest relative densities in most conserved areas. The same trend was observed by Toniato and Oliveira-Filho (2004) in other areas at advanced stages of succession.

Considering the globally wide distribution of semideciduous forest, with their high proportion of endemic species and different factors that can affect β diversity, it is necessary, even at small spatial scales to establish ecological standards that exceed the regional comparison. Remnants of semideciduous forest are exposed to constant threats, i.e. from fragmentation of habitats to global climate change (Miles et al. 2006). Considering the high phytodiversity and endemism of most species, conservation of these forests should be a priority. As regional and global disturbances directly affect composition and diversity of species, an assessment of the distribution patterns of these natural remnants may help in understanding the ecological processes and responses of vegetation in the face of future disturbances.

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Appendix Understorey species sampled in 10 sites of seasonal semideciduous forest of south-eastern Brazil with their respective botany families and number of individuals per area occurrence

Species	Family	Occurrence										Total
		Site*										
		1	2	3	4	5	6	7	8	9	10	
<i>Cheiloclinium cognatum</i>	Celastraceae	3	-	45	51	79	36	32	1	7	153	407
<i>Siparuna guianensis</i>	Siparunaceae	-	-	14	-	13	97	106	4	131	40	405
<i>Cordia sessilis</i>	Rubiaceae	2	41	25	-	125	15	11	173	9	3	404
<i>Trichilia catigua</i>	Meliaceae	77	40	7	28	3	3	-	-	5	2	165
<i>Galipea jasminiflora</i>	Rutaceae	-	-	-	142	-	-	-	-	-	-	142
<i>Trichilia clausenii</i>	Meliaceae	92	-	-	38	-	-	-	-	-	-	130
<i>Myrciaria glanduliflora</i>	Myrtaceae	-	-	-	-	94	1	2	-	9	-	106
<i>Campomanesia velutina</i>	Myrtaceae	-	31	2	2	8	2	-	45	3	-	93
<i>Hirtella gracilipes</i>	Chrysobalanaceae	-	-	21	1	-	-	36	-	8	6	72
<i>Maytenus floribunda</i>	Celastraceae	-	-	25	1	1	4	-	28	-	12	71
<i>Chrysophyllum gonocarpum</i>	Sapotaceae	30	-	21	17	-	-	-	-	1	-	69
<i>Fareamea hyacinthina</i>	Rubiaceae	-	-	-	-	-	11	2	7	9	29	58
<i>Trichilia elegans</i>	Meliaceae	19	1	20	5	-	2	-	1	-	7	55
<i>Guapira venosa</i>	Nyctaginaceae	6	44	-	1	-	-	-	3	-	-	54
<i>Eugenia involucreta</i>	Myrtaceae	28	-	3	2	-	-	-	9	-	-	42
<i>Coussarea hydrangeifolia</i>	Rubiaceae	-	-	3	2	11	-	11	2	3	-	32
<i>Celtis iguanaea</i>	Cannabaceae	3	22	1	-	1	1	-	-	2	-	30
<i>Guapira opposita</i>	Nyctaginaceae	-	-	-	-	-	-	-	-	29	-	29
<i>Trichilia pallida</i>	Meliaceae	3	-	1	1	3	17	-	1	-	2	28
<i>Eugenia ligustrina</i>	Myrtaceae	-	-	-	17	-	-	-	7	3	-	27
<i>Ardisia ambigua</i>	Myrsinaceae	13	-	6	6	-	-	-	-	-	-	25
<i>Coutarea hexandra</i>	Rubiaceae	-	5	1	6	4	-	-	3	1	1	21
<i>Eugenia subterminalis</i>	Myrtaceae	2	-	-	18	-	-	-	-	-	-	20
<i>Bauhinia unguolata</i>	Fabaceae	-	4	1	-	-	1	-	13	-	1	20
<i>Chomelia pohliana</i>	Rubiaceae	7	-	1	3	-	-	-	-	-	3	14
<i>Byrsonima laxiflora</i>	Malpigiaceae	-	-	8	-	1	-	1	-	2	-	12
<i>Psidium rufum</i>	Myrtaceae	-	-	-	-	-	1	2	5	4	-	12
<i>Myrcia splendens</i>	Myrtaceae	-	1	1	1	4	-	1	3	-	-	11
<i>Rudgea viburnoides</i>	Rubiaceae	-	-	1	-	2	-	3	3	2	-	11
<i>Inga marginata</i>	Fabaceae	10	-	-	-	-	-	-	-	-	-	10
<i>Sorocea bonplandii</i>	Moraceae	-	-	-	2	-	4	-	-	1	2	9
<i>Bauhinia rufa</i>	Fabaceae	-	6	-	-	1	1	-	-	1	-	9
<i>Allophylus racemosus</i>	Sapindaceae	6	-	-	-	-	-	-	1	-	1	8
<i>Symplocos pubescens</i>	Symplocaceae	-	-	-	-	-	-	-	8	-	-	8
<i>Calyptranthes widgreniana</i>	Myrtaceae	4	-	-	3	-	-	-	-	-	-	7
<i>Acalypha gracilis</i>	Euphorbiaceae	6	-	-	-	-	-	-	-	-	1	7
<i>Mollinedia widgrenii</i>	Monimiaceae	-	-	-	4	-	-	-	-	1	1	6
<i>Erythroxylum daphnites</i>	Erythroxylaceae	-	-	-	-	6	-	-	-	-	-	6
<i>Prockia crucis</i>	Salicaceae	-	-	2	-	-	-	-	3	-	-	5
<i>Vochysia tucanorum</i>	Vochysiaceae	-	-	-	-	-	-	-	5	-	-	5
<i>Maytenus robusta</i>	Celastraceae	-	-	4	-	-	-	-	-	-	-	4
<i>Piper amalago</i>	Piperaceae	4	-	-	-	-	-	-	-	-	-	4
<i>Trema micrantha</i>	Cannabaceae	-	2	1	-	-	-	-	-	-	-	3
<i>Lacistema aggregatum</i>	Lacistemataceae	-	-	2	-	-	-	1	-	-	-	3
<i>Ilex cerasifolia</i>	Aquifoliaceae	-	-	3	-	-	-	-	-	-	-	3
<i>Chionanthus trichotomus</i>	Oleaceae	-	-	-	-	-	-	-	3	-	-	3

(continued)

Appendix (continued)

Species	Family	Occurrence										Total
		Site*										
		1	2	3	4	5	6	7	8	9	10	
<i>Erythroxylum deciduum</i>	Erythroxylaceae	-	-	-	-	-	-	-	3	-	-	3
<i>Aloysia virgata</i>	Verbenaceae	2	1	-	-	-	-	-	-	-	-	3
<i>Piper arboreum</i>	Piperaceae	-	-	-	2	-	-	-	-	-	-	2
<i>Myrciaria tenella</i>	Myrtaceae	-	-	-	-	-	-	-	-	2	-	2
<i>Peltophorum dubium</i>	Fabaceae	-	-	-	-	-	1	-	-	-	1	2
<i>Phyllanthus acuminatus</i>	Phyllanthaceae	-	-	-	-	-	-	-	2	-	-	2
<i>Magonia pubescens</i>	Sapindaceae	-	2	-	-	-	-	-	-	-	-	2
<i>Centrolobium tomentosum</i>	Fabaceae	-	-	-	1	-	-	-	-	-	-	1
<i>Porcelia macrocarpa</i>	Annonaceae	-	-	-	1	-	-	-	-	-	-	1
<i>Xylosma prockia</i>	Salicaceae	-	-	1	-	-	-	-	-	-	-	1
<i>Syzygium jambos</i>	Myrtaceae	-	-	-	-	-	-	-	-	1	-	1
<i>Tocoyena formosa</i>	Rubiaceae	-	-	-	-	-	-	-	1	-	-	1
<i>Gomidesia lindeniana</i>	Myrtaceae	-	-	-	-	-	-	1	-	-	-	1
<i>Annona montana</i>	Annonaceae	-	1	-	-	-	-	-	-	-	-	1
<i>Allophylus edulis</i>	Sapindaceae	1	-	-	-	-	-	-	-	-	-	1
<i>Campomanesia guazumifolia</i>	Myrtaceae	-	-	-	-	1	-	-	-	-	-	1
<i>Pilocarpus spicatus</i>	Rutaceae	1	-	-	-	-	-	-	-	-	-	1
<i>Salacia elliptica</i>	Celastraceae	1	-	-	-	-	-	-	-	-	-	1
All species		320	201	220	355	357	197	209	337	234	265	2695

*Numbers represent sites in Table 1; densities of species in each site are reported in Lopes et al. (2012)