
FLORISTIC COMPOSITION AND STRUCTURE OF A TROPICAL DRY FOREST AT DIFFERENT SUCCESSIONAL STAGES IN THE ESPINHAÇO MOUNTAINS, SOUTHEASTERN BRAZIL

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SUMMARY

The floristic composition and structure of intermediate and late successional stages of a tropical dry forest (TDF) growing on limestone outcrops, situated in the southern portion of the Espinhaço Mountains, Southeastern Brazil, was studied. In each fragment, three plots of 20×50m were delimited, totaling 0.3ha for each successional stage. In each plot, all trees with a diameter at breast height (DBH) >5cm were sampled and identified. Standard phyto-sociological parameters were calculated and compared between stages. The most representative families in the two successional stages were Fabaceae, Apocynaceae and Malvaceae, but species composition differed between intermediate and late stages: species with highest importance value in the former were *Myracrodruon urundeuva*, *Rauwolfia sellowii* and *Inga platyptera*, whereas *Anadenanthera colubrina*, *Myracrodruon urundeuva* and *Bauhinia brevipes* predomi-

nated in the latter. The main parameters measured varied with the successional stage. In the intermediate stage, the structural parameters were: basal area 17.8m²·ha⁻¹, density 1076 individuals/ha, average height 6.30m, species richness 23, while community indexes were Shannon-Winner biodiversity 1.51 and Pielou evenness 0.48. For the late successional stage, the structural parameters were: basal area 29.3m²·ha⁻¹, density 1226 individuals/ha, average height 7.7m and species richness 38; community indexes were Shannon-Winner's diversity 2.38 and Pielou's evenness 0.64. Due to the marked isolation, this TDF has a unique floristic composition. Results demonstrated important changes in floristic composition and structure along two successional stages, contributing to ecological process understanding. The limited knowledge about this rich ecosystem was expanded and the urgent need for its preservation is reinforced.

Tropical dry forests (TDFs) are characterized by the occurrence of plants that lose at least 50% of their leaves during a prolonged dry season (Sánchez-Azofeifa *et*

al., 2005a, b). These forests originally represented about 42% of tropical forests (Murphy and Lugo, 1986) and are amongst the most threatened ecosystems worldwide (Janzen, 1988; Miles *et al.*, 2006; Portillo-

Quintero and Sánchez-Azofeifa *et al.*, 2010). In spite of their high biodiversity, few ecological studies have been carried out in TDFs as compared to wet forests (Sánchez-Azofeifa, 2005a, b; Quesada *et al.*,

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2009). Thus, urgent research and conservation efforts should be made to avoid massive losses of biodiversity and ecosystem services in these ecosystems. TDFs usually grow on fertile soils and are preferred for agriculture and extensive cattle ranching activities for this reason; it is estimated that 66% of the deciduous forests of Latin America have been lost (Espírito-Santo *et al.*, 2006, 2009; Quesada *et al.*, 2009; Sánchez-Azofeifa *et al.*, 2009).

Brazilian TDFs have a scattered distribution and are encountered within all biomes, but mainly in the Cerrado and Caatinga domains, in northeastern and central Brazil (Nascimento *et al.*, 2004). In terms of structure, these forests usually have lower height, density and basal area than wet forests (Murphy and Lugo, 1986). They are also floristically less complex due to the limited number of plant species adapted to withstand long dry periods (Oliveira-Filho *et al.*, 1998) and have already been considered to be an impoverished Atlantic Rain Forest in Brazil (Rizzini, 1979). The occurrence of epiphytes is rare, but often there are species of the Cactaceae and Bromeliaceae families, adapted to these biophysical conditions and nutritional environments (Felfili, 2001; Felfili *et al.*, 2007). Overall, TDF areas have high biodiversity and a considerable rate of endemism (Pedersoli and Martins, 1972; Coelho *et al.*, 2009). Moreover, many plant species have economic importance for the communities that live in TDF regions, such as *Myracrodruon urundeuva*, *Anadenanthera colubrina* and *Piptadenia* sp. (Meguro *et al.*, 2007).

Brazilian TDFs are usually subdivided into two main types: the first is composed of forests growing on plain soils, also called 'arboreal caatinga'. These forests are associated with crystalline, mesotrophic soils, not associated with watercourses, occurring in interfluvial soils richer in nutrients. The second type comprises forests that develop on limestone outcrops, frequently on steep slopes and shallow soils (Nascimento *et al.*, 2004; Felfili *et al.*, 2007). TDFs on limestone outcrops usually occur as enclaves inside the Cerrado biome and their floristic compositions are influenced by the surrounding vegetation. For this reason, a low similarity in species composition is observed between TDF fragments on limestone outcrops from different regions (Pedralli, 1997; Silva and Sacariot, 2003, 2004a, b; Almeida and Machado, 2007; Meguro *et al.*, 2007).

Several studies have been conducted on the floristics and structure of TDF on limestone outcrops in Brazil (Pedralli, 1997; Silva and Sacariot, 2003, 2004a, b; Nascimento *et al.*, 2004; Almeida and Machado, 2007; Felfili *et al.*, 2007;

Meguro *et al.*, 2007; Santos *et al.*, 2007). However, little is known about the regeneration processes in this ecosystem (Werneck *et al.*, 2000; Vieira *et al.*, 2006; Vieira and Sacariot, 2006; Sampaio *et al.*, 2007). Although some recent studies have addressed this issue for TDFs growing on plain soils (Pezzini, 2008; Madeira *et al.*, 2009), TDFs on limestone outcrops have some peculiar characteristics (e.g., soil, slope) and are affected by different land uses (Oliveira Filho *et al.*, 1998; Werneck *et al.*, 2000; Sampaio *et al.*, 2007). Thus, successional patterns described for TDF on plain soils might not be applied to TDF on limestone outcrops. Only 12% of the papers published on tropical forests and indexed in the ISI platform are dedicated to the TDF, while 88% are dedicated to the rainforests (Quesada *et al.*, 2009). Few studies have been performed about the floristic composition and structure of TDFs in the Espinhaço Range (Almeida and Machado, 2007; Meguro *et al.*, 2007). TDFs on limestone are not mapped and therefore they are legally poorly protected. Due to cement factories, timber extraction and agriculture, coverage areas of TDFs on limestone are increasingly restricted (Silva and Sacariot, 2003). However, information on the ecological succession and natural regeneration of these forests is lacking. The aim of this study was to describe changes in the floristic composition and structure between successional stages of TDF on limestone in Serra do Cipó, at the southern portion of Espinhaço Range, Minas Gerais. To our knowledge, this is the first study concerning successional patterns in a TDF on limestone outcrops in Brazil.

Materials and Methods

Study Area

Sampling carried out in February 2007 in natural fragments of TDF in Serra do Cipó, Minas Gerais, southeastern Brazil. The Serra do Cipó is located in the southern portion of the Espinhaço Range and is dominated by Cerrado and Rupestrian Fields vegetation. The climate is mesothermal (Cwb according the Köppen's classification; Peel *et al.*, 2007), characterized by dry winters and rainy summers, with an annual rainfall average of 1500mm and annual temperature average of 17.4-19.8°C (Giulietti *et al.*, 1987). The Serra do Cipó is located in a high diversity region, and is part of Espinhaço Range Biosphere Reserve. Two forest fragments were chosen: one was considered as at intermediate (43°36'09.3"W, 19°20'24.0"S) and the other one at late (43°36'23.0"W, 19°19'44.6"S) stage of succession. This classification was based on land use history, obtained through interviews with employees from Parque Na-

cional da Serra do Cipó and at local communities. The plots were located at 0.1-0.5km apart while the fragments were 2km apart. The fragment considered as intermediate successional forest has been under protection for the last 15 years, after having been used for cattle raising. The late forest fragment has been protected for at least 30 years (for experimental design, see Nassar *et al.*, 2008). Both fragments were part of the same forest and were separated as a consequence of mining activities, human settlement, timber extraction and cattle grazing. Both have similar soil characteristics.

Sampling

In each fragment, three plots of 20×50m totaling 0.3ha per successional stage were delimited. In each plot, all trees with a diameter at breast height (DBH) >5cm were sampled (Nassar *et al.*, 2008). Also, the height of each individual was visually estimated using a measuring device as reference. Reproductive material was collected from each individual, transported to the laboratory and identified to the lowest possible taxonomic level. Voucher specimens were deposited in the Herbarium of the Departamento de Botânica, Universidade Federal de Minas Gerais (BHCB). The species classification followed the system proposed by the Angiosperm Phylogeny Group (APGII, 2005; Souza and Lorenzi, 2005).

Data analyses

The forest structure variables (height, basal area) were compared between each plot through Kruskal-Wallis tests, using each tree as a replicate. When the tests indicated significant differences between plots ($p < 0.05$), a post-hoc Dunn test was used to detect the source of variation (Zar, 1984). The similarity of the floristic composition was compared among plots through an agglomerative hierarchical cluster analysis using a matrix of Bray-Curtis coefficients. The average linkage with Euclidean distance metric option as the clustering method (Ludwing and Reynolds, 1988) was used.

The following standard phyto-sociological parameters for each successional stage were also calculated: absolute density, relative density, absolute dominance, relative dominance, absolute frequency, relative frequency, importance value index (IVI), and coverage value index (CVI; Kent and Coker, 1992).

The IVI was calculated by the Holdridge complexity index $CHCI = (\text{height} \times \text{density} \times \text{basal area} \times \text{number of species})/1000$. The Shannon-Winner diversi-

TABLE I
PHYTOSOCIOLOGICAL PARAMETERS OF SPECIES IN THE INTERMEDIATE SUCCESSION STAGE FRAGMENT

Species	N	RA	AD	RD	ADo	RDo	AF	RF	IVI	CVI
<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	1	0.13	3.333	0.31	0.445	2.501	33.33	2.56	5.38	2.811
<i>Anadenanthera colubrina</i> (Vell.) Brenan*	1	0.19	3.333	0.31	0.622	3.491	33.33	2.56	6.37	3.801
<i>Annona sylvatica</i> A.St.-Hil.*	3	0.05	10	0.929	0.181	1.014	66.67	5.13	7.07	1.943
<i>Aspidosperma cylindrocarpon</i> Müll.Arg.	2	0.02	6.667	0.619	0.076	0.43	33.33	2.56	3.61	1.049
<i>Aspidosperma multiflorum</i> A. DC.*	4	0.05	13.33	1.238	0.156	0.877	100	7.69	9.81	2.115
<i>Aspidosperma pyriformium</i> Mart.*	8	0.05	26.67	2.477	0.17	0.954	66.67	5.13	8.56	3.431
<i>Aspidosperma subincanum</i> Mart. ex A.DC.	1	0.01	3.333	0.31	0.045	0.251	33.33	2.56	3.12	0.56
<i>Baccharis dracunculifolia</i> DC.	1	0.01	3.333	0.31	0.006	0.034	33.33	2.56	2.91	0.343
<i>Campomanesia guazumifolia</i> (Cambess.) O.Berg*	1	0.03	3.333	0.31	0.109	0.611	33.33	2.56	3.48	0.921
<i>Cassia ferruginea</i> (Schrad.) Schrad. ex DC.*	5	0.04	16.67	1.548	0.128	0.719	66.67	5.13	7.4	2.267
<i>Guazuma ulmifolia</i> Lam.*	7	0.22	23.33	2.167	0.72	4.044	100	7.69	13.9	6.212
<i>Guettarda uruguensis</i> Cham. & Schldl.*	1	0.01	3.333	0.31	0.017	0.097	33.33	2.56	2.97	0.407
<i>Inga platyptera</i> Benth.	30	0.73	100	9.288	2.42	13.59	100	7.69	30.6	22.88
<i>Myracrodruon urundeuva</i> Allemão*	194	2.98	646.7	60.06	9.917	55.71	100	7.69	123	115.8
<i>Peltophorum dubium</i> (Spreng.) Taub.	1	0.01	3.333	0.31	0.019	0.109	33.33	2.56	2.98	0.418
<i>Piptadenia gonoacantha</i> (Mart.) J.F.Macbr.*	1	0.03	3.333	0.31	0.089	0.502	33.33	2.56	3.38	0.811
<i>Platypodium elegans</i> Vogel	1	0.02	3.333	0.31	0.064	0.358	33.33	2.56	3.23	0.668
<i>Pouteria gardneri</i> (Mart. & Miq.) Baehni	2	0.04	6.667	0.619	0.146	0.823	66.67	5.13	6.57	1.442
<i>Rauwolfia sellowii</i> Müll. Arg.	48	0.46	160	14.86	1.528	8.584	100	7.69	31.1	23.44
<i>Stryphnodendron obovatum</i> Benth.	1	0.01	3.333	0.31	0.022	0.125	33.33	2.56	3	0.435
<i>Terminalia argentea</i> (Cambess.) Mart.*	7	0.24	23.33	2.167	0.793	4.457	66.67	5.13	11.8	6.624
<i>Terminalia glabrescens</i> Mart.	2	0.03	6.667	0.619	0.093	0.525	66.67	5.13	6.27	1.144
<i>Vitex polygama</i> Cham.	1	0.01	3.333	0.31	0.034	0.193	33.33	2.56	3.07	0.503
Total	323	5.4	1077	100	17.8	100	1300	100	300	200

N: number of individuals, RA: relative abundance, AD: absolute density, RD: relative density, ADo: absolute dominance, RDo: relative dominance, AF: absolute frequency, RF: relative frequency, IVI: importance value index; CVI: coverage value index.

*Species occurring at intermediate and late succession stages.

ty index (H') and the Pielou evenness index (J') for each successional stage (Magurran, 2004) were also calculated. Data are given as mean \pm SE.

Results and Discussion

In the TDF fragments studied in Serra do Cipó, 691 individuals belonging to 50 species (21 families) were sampled. In the intermediate stage 323 individuals from 23 species (11 families) were found, whereas 368 individuals from 38 species (18 families) were sampled in the late stage. Only 11 species co-occurred in both stages (Tables I, II). The species richness found in this study was similar to other studies of TDF on limestone outcrops (Table III). The same was observed for the floristic composition at the family level. The most representative families in the two successional stages in Serra do Cipó were Fabaceae, Apocynaceae and Malvaceae (Figure 1), which are also the most common families in other studies in TDF on limestone outcrops (Pedralli, 1997; Silva and Sacariot, 2003, 2004a, b; Nascimento, *et al.*, 2004; Almeida and Machado, 2007; Meguro *et al.*, 2007). Other well-represented families in this phytophysiology include Anacardiaceae, Arecaceae, Bignoniaceae, Combretaceae, Euphorbiaceae, Myrtaceae, Rubiaceae and Sapindaceae. Species composition is very simi-

lar to that found in other works, with the occurrence of characteristic species like *Anadenanthera colubrina*, *Annona coriacea*, *Ficus calyptroceras*, *Guazuma ulmifolia*, *Myracrodruon urundeuva*, *Piptadenia gonoacantha* and *Spondias tuberosa*. The two most abundant species in the small diameter classes (5-10cm) in the intermediate succession stage were *Myracrodruon urundeuva* and *Inga platyptera*. In higher diameter classes (≥ 10 cm), *M. urundeuva* and *Rauwolfia sellowii* were the most abundant species (Figure 2). In the late successional stage, the two most abundant species in small diameter classes were *Anadenanthera colubrina* and *M. urundeuva*, whereas *A. colubrina* and *Bauhinia brevipes* predominated in higher diameter classes (Figure 2). The most abundant species in this study are frequently encountered in TDFs, both in plain soils and limestone outcrops (Silva and Scariot, 2003, 2004a, b; Nascimento *et al.*, 2004; Meguro *et al.*, 2007; Madeira *et al.*, 2009). Eleven species (48%) were represented by only one individual in the intermediate succession stage, but the proportion of low-abundance species decreased in late stages (15 species, 39%).

The TDF structure in Serra do Cipó was also similar to other studies conducted in this phytophysiology (Table II). The average tree height was 6.30 \pm 1.62 m and 7.77 \pm 2.93m for the intermediate and

late succession stages, respectively. The basal area ranged from 17.8m²·ha⁻¹ in the intermediate to 29.3m²·ha⁻¹ in the late stages while density ranged from 1076 to 1226 individuals/ha. Oliveira Filho *et al.* (1998) found a close relationship between the floristic composition, topography and soil characteristics in TDFs on limestone outcrops. Nascimento *et al.* (2007), assessing canopy openness in TDFs, showed the highest basal area and tree species richness in fragments with higher canopy openness. Differences in species richness, density and basal area between the studies in TDFs show large variations that may be a consequence of the floristic composition of the surrounding phytophysiology, but mainly to factors related to topography, soil conditions and canopy opening (Table III).

Forest structure changed between plots at different successional stages in the studied TDF. Tree heights were significantly higher in late than in intermediate plots ($X^2= 157.25$; $df= 5$, $p<0.01$; Figure 3), and the same was observed for basal area ($X^2= 29.67$, $GL= 5$, $p<0.01$; Figure 4). This result corroborates other studies conducted in TDF chronosequences (Kalácska *et al.*, 2004; Madeira *et al.*, 2009), which indicated an increase in the forest structural complexity as the succession progresses. Also, Werneck *et al.* (2000) evaluated changes in the floristic composition and

TABLE II
PHYTOSOCIOLOGICAL PARAMETERS OF SPECIES IN THE LATE SUCCESSION STAGE FRAGMENT

Species	N	RA	AD	RD	ADo	RDo	AF	RF	IVI
<i>Albizia</i> sp.	1	3.33	0.27	0.08	0.27	33.3	1.67	2.21	0.54
<i>Anadenanthera colubrina</i> (Vell.) Brenan*	135	450	36.7	10.2	34.6	100	5	76.3	71.3
<i>Annona sylvatica</i> (A. St.-Hil.) Mart.*	4	13.3	1.09	0.09	0.3	33.3	1.67	3.05	1.39
<i>Arrabidaea</i> sp1	6	20	1.63	0.22	0.75	100	5	7.39	2.39
<i>Arrabidaea</i> sp2	1	3.33	0.27	0	0.02	33.3	1.67	1.95	0.29
<i>Aspidosperma multiflorum</i> A.DC.*	1	3.33	0.27	0.1	0.34	33.3	1.67	2.28	0.62
<i>Aspidosperma olivaceum</i> Müll. Arg.	8	26.7	2.17	0.82	2.78	100	5	9.96	4.96
<i>Aspidosperma pyrifolium</i> Mart.*	1	3.33	0.27	0.01	0.02	33.3	1.67	1.96	0.29
<i>Bauhinia acuruana</i> Moric.	1	3.33	0.27	0.01	0.03	33.3	1.67	1.97	0.3
<i>Bauhinia brevipes</i> Vogel	31	103	8.42	1.13	3.81	100	5	17.2	12.2
<i>Bauhinia longifolia</i> (Bong.) D.Dietr.	1	3.33	0.27	0.01	0.04	33.3	1.67	1.98	0.31
<i>Bauhinia rufa</i> (Bong.) Steud.	4	13.3	1.09	0.24	0.81	100	5	6.89	1.89
<i>Bauhinia unguolata</i> L.	1	3.33	0.27	0.01	0.02	33.3	1.67	1.96	0.29
<i>Campomanesia guazumifolia</i> (Cambess.) O. Berg*	2	6.67	0.54	0.04	0.14	33.3	1.67	2.35	0.68
<i>Casearia rupestris</i> Eichler	3	10	0.82	0.08	0.29	33.3	1.67	2.77	1.1
<i>Cassia ferruginea</i> (Schrad.) Schrad. ex DC.*	4	13.3	1.09	0.57	1.92	33.3	1.67	4.68	3.01
<i>Copaifera langsdorffii</i> Desf.	1	3.33	0.27	0.11	0.36	33.3	1.67	2.29	0.63
<i>Dilodendron bipinnatum</i> Radlk.	8	26.7	2.17	1.21	4.09	66.7	3.33	9.6	6.27
<i>Diospyros inconstans</i> Jacq.	2	6.67	0.54	0.08	0.28	33.3	1.67	2.49	0.82
<i>Ficus calyptrocera</i> (Miq.) Miq.	1	3.33	0.27	0.06	0.22	33.3	1.67	2.15	0.49
<i>Galphimia</i> sp1	3	10	0.82	0.02	0.07	33.3	1.67	2.55	0.88
<i>Guazuma ulmifolia</i> Lam.*	10	33.3	2.72	0.53	1.8	66.7	3.33	7.85	4.52
<i>Guettarda uruguensis</i> Cham. & Schldt.*	19	63.3	5.16	0.56	1.88	100	5	12	7.04
<i>Luehea candicans</i> Mart. & Zucc.	1	3.33	0.27	0.21	0.69	33.3	1.67	2.63	0.97
<i>Lithraea molleoides</i> (Vell.) Engl.	1	3.33	0.27	0.1	0.32	33.3	1.67	2.26	0.59
<i>Maclura tinctoria</i> (L.) Steud.	1	3.33	0.27	0.01	0.04	33.3	1.67	1.98	0.31
<i>Mascagni</i> sp1	2	6.67	0.54	0	0.01	33.3	1.67	2.22	0.56
<i>Maytenus robusta</i> Reissek	5	16.7	1.36	0.1	0.32	66.7	3.33	5.02	1.68
<i>Myracrodruon urundeuva</i> Allemão*	68	227	18.5	9.47	32	100	5	55.5	50.5
<i>Picramnia glazioviana</i> Engl.	8	26.7	2.17	0.14	0.47	33.3	1.67	4.31	2.65
<i>Piptadenia gonoacantha</i> (Mart.) J. F. Macbr.*	2	6.67	0.54	0.08	0.27	33.3	1.67	2.48	0.82
<i>Pouteria gardneri</i> (Mart. & Miq.) Baehni*	4	13.3	1.09	0.1	0.33	66.7	3.33	4.75	1.41
<i>Rhamnidium elaeocarpum</i> Reissek	15	50	4.08	2.66	9	100	5	18.1	13.1
<i>Rhamnidium molle</i> Reissek	1	3.33	0.27	0.01	0.03	33.3	1.67	1.97	0.3
<i>Sebastiania brasiliensis</i> Spreng.	2	6.67	0.54	0.03	0.1	33.3	1.67	2.31	0.64
<i>Senna macranthera</i> (Collad.) H. S. Irwin & Barneby	8	26.7	2.17	0.15	0.51	100	5	7.69	2.69
<i>Terminalia argentea</i> (Cambess.) Mart.*	1	3.33	0.27	0.08	0.26	33.3	1.67	2.2	0.53
<i>Trichilia pallida</i> Sw.	1	3.33	0.27	0.24	0.81	33.3	1.67	2.75	1.08
Total	368	1227	100	29.6	100	2000	100	300	200

N: number of individuals, RA: relative abundance, AD: absolute density, RD: relative density, ADo: absolute dominance, RDo: relative dominance, AF: absolute frequency, RF: relative frequency, IVI: importance value index. *Species occurring at intermediate and late succession stages.

TABLE III
MINIMUM DIAMETER, SPECIES RICHNESS, DENSITY, BASAL AREA (G)
AND LOCATIONS OF DIFFERENT STUDIES CARRIED OUT IN SEASONALLY DRY
TROPICAL FOREST FRAGMENTS ON LIMESTONE OUTCROPS (TDFLO) AND
SEASONALLY DRY TROPICAL FOREST FRAGMENT ON PLAIN SOILS (TDFPS)

	Minimum diameter	Species richness	Density (ha)	G (ha)	Location	References
TDFLO	5	23	1076	17.8	Serra do Cipó, MG	Este estudo*
TDFLO	5	38	1226	29.3	Serra do Cipó, MG	Este estudo**
TDFLO	5	39	734	16.73	Iaciara, GO	Felfili <i>et al.</i> , 2007
TDFLO	2.5	29	3300	46.6	Santo Hipólito, MG	Meguro <i>et al.</i> , 2007
TDFLO	5	52	633	19.36	Monte Alegre, GO	Nascimento <i>et al.</i> , 2004
TDFLO	5	44	591	23.17	São Domingos, GO	Scariot and Sevilha, 2000
TDFLO	5	67	1454	20.54	Santa Vitória, MG	Oliveira-Filho <i>et al.</i> , 1998
TDFPS	5	16	762	15.2	Manga, MG	Madeira <i>et al.</i> , 2009*
TDFPS	5	17.3	988	22	Manga, MG	Madeira <i>et al.</i> , 2009**
TDFLO	5	36	536	18.6	São Domingos, GO	Silva and Scariot, 2003
TDFLO	5	48	924	9.9	São Domingos, GO	Silva and Scariot, 2004a
TDFLO	5	51	860	18.6	São Domingos, GO	Silva and Scariot, 2004b
TDFLO	10	114	1771	24	Perdizes, MG	Werneck <i>et al.</i> 2000

*Intermediate succession stage **Late succession stage.

structure of a TDF on limestone outcrops in southeastern Brazil for four years without disturbance; they recorded a significant increase in tree basal area and height classes during this period, indicating that TDFs may show short-time scale alterations on structural parameters. However, in the same study Werneck *et al.* (2000) reported no differences in diversity and evenness in the four years of study. It is reasonable to assume that changes in species composition occur on a longer time-scale. In the present study, Shannon-Winner's diversity index was lower in the intermediate stage (1.52) than in the late stage (2.58) of succession, and

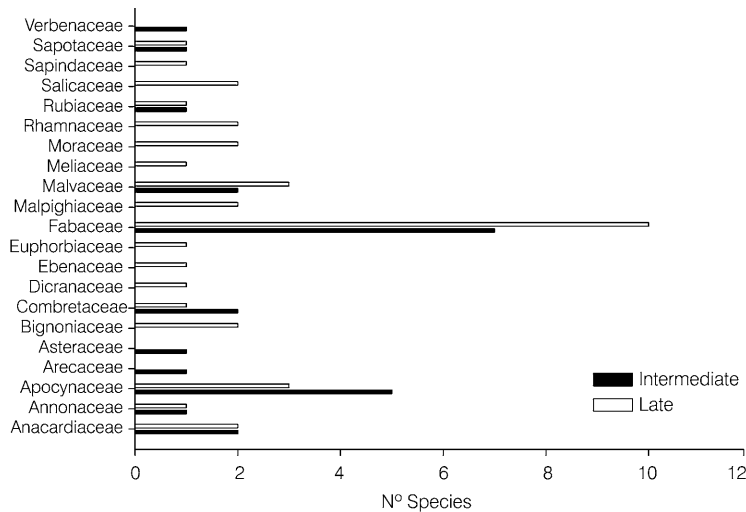


Figure 1. Richness of species per family at intermediate and late stages in fragments of a tropical dry forest on limestone outcrops. Parque Nacional da Serra do Cipó, Brazil.

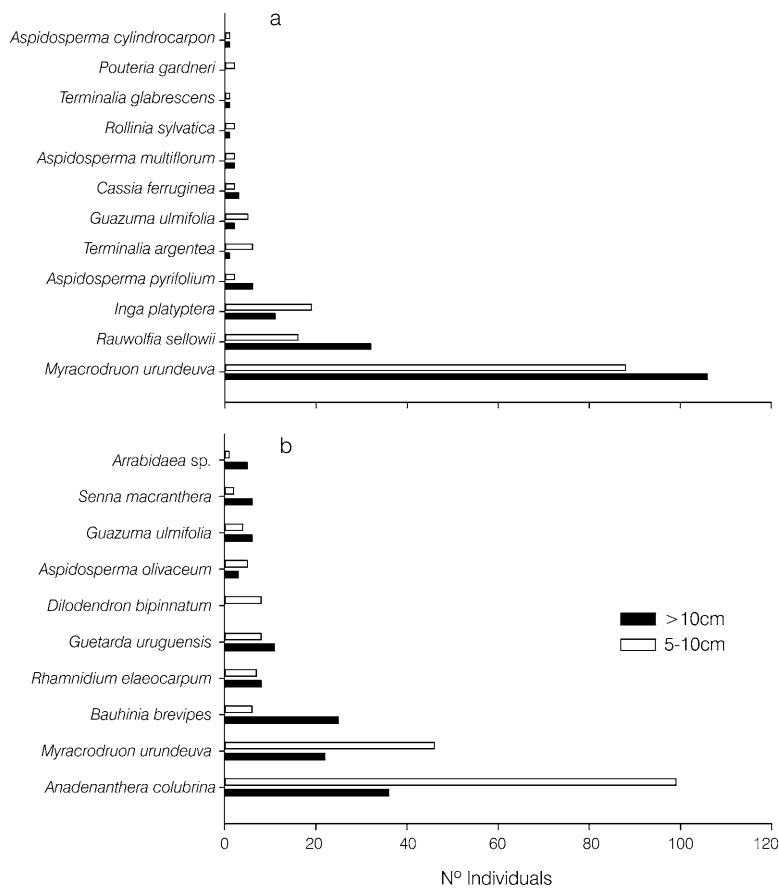


Figure 2. Number of individuals for the ten most abundant species in intermediate (a) and late (b) stages, separated by DBH classes of 5-10cm and >10cm in fragments of a tropical dry forest on limestone outcrops. Parque Nacional da Serra do Cipó, Brazil.

the same was observed for the Pielou's evenness index (0.48 and 0.64, respectively). Similar results were reported by Madeira *et al.* (2009), with greater richness in late successional stages in a TDF in plain soils in the north of Minas Gerais. These authors hypothesized that the successional dynamics

in TDFs would be dominance-controlled. According to this hypothesis, tree diversity would be higher in intermediate stages of succession, due to the competitive exclusion of mid-successional species as the forest matures (Yodzis, 1986). The explanation given by Madeira *et al.* (2009) for such pat-

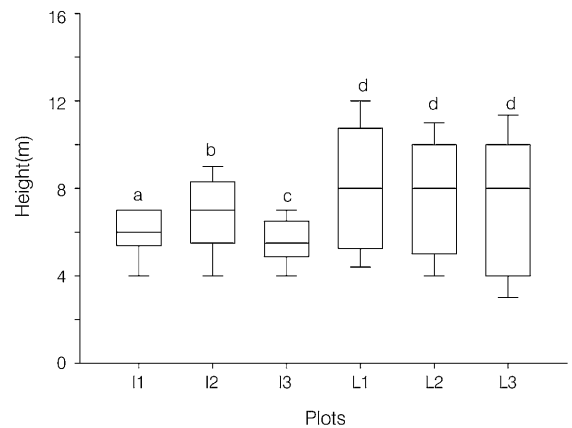


Figure 3. Boxes indicate median, quartiles, maximum and minimum heights of individuals with DBH>5cm in six habitats. Kruskal-Wallis test ($X^2= 157.258$, $df= 5$, $p<0.001$). Different letters indicate statistical differences in the Dunn multiple comparison test, $p<0.05$. Habitats were ranked according to three intermediate (I1, I2, I3) and three late (L1, L2, L3) successional stages in a tropical dry forest fragments on limestone outcrops. Parque Nacional da Serra do Cipó, Brazil.

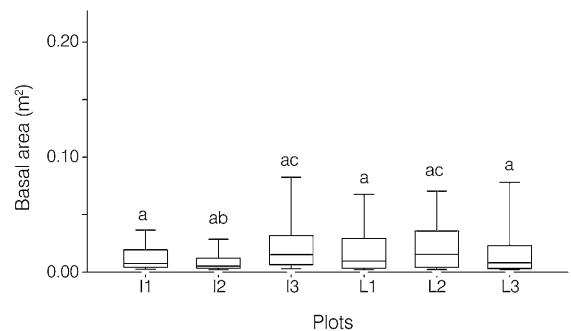


Figure 4. Boxes indicate median, quartiles, maximum and minimum heights of individuals with DBH>5cm in six habitats. Kruskal-Wallis test ($X^2= 29.671$, $df= 5$, $p<0.001$). Different letters indicate statistical differences in the Dunn multiple comparison test ($p<0.05$). Habitats were ranked according to three intermediate (I1, I2, I3) and three late (L1, L2, L3) successional stages in a tropical dry forest fragments on limestone outcrops. Parque Nacional da Serra do Cipó, Brazil.

tern is that the fragment considered here as 'late stage' is probably in the middle of the regeneration process. In this case, a decrease in the number of species would be expected over time in late fragments of TDF in Serra do Cipó.

The agglomerative hierarchical cluster analysis indicated a greater similarity between plots from the same successional stage (Figure 5), indicating a significant change in the floristic composition. This result corroborates the observed by Madeira *et al.* (2009) for a TDF in the north of Minas Gerais, indicating that the successional process in these forests corresponds to the 'relay floristic model' (Egler, 1954). According to model, TDFs would regenerate with a gradual substitution of pioneer species by late species. This pattern contradicts

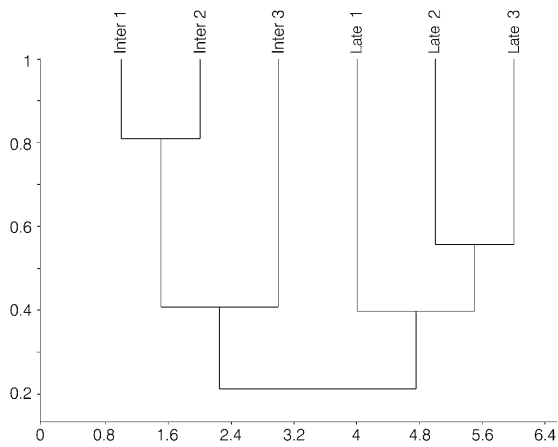


Figure 5. Agglomerative hierarchical cluster analysis from a matrix of Bray-Curtis coefficient between six habitats: three intermediate (Inter 1, Inter 2, Inter 3) and three late (Late 1, Late 2, Late 3) in fragments of a tropical dry forest on limestone outcrops. Parque Nacional da Serra do Cipó, Brazil.

some recent studies in Brazilian TDFs, which described the frequent occurrence of coppicing during succession in these ecosystems. Thus, Vieira *et al.* (2006), Vieira and Sacariot (2006) and Sampaio *et al.* (2007) suggested that TDFs would conform to the 'initial floristic composition model' (Egler, 1954). In this case, late species would re-sprout after clear-cutting in TDFs and would be already present in early and intermediate successional stages.

Indeed, Madeira *et al.* (2009) suggested that the successional pathway that followed after abandonment in TDFs would depend on land-use history. In plain soils, plowing is a common practice to remove plant roots before sowing. In this case, coppicing would not be expected and the forest would regenerate according to the relay floristic model. However, in TDFs growing on limestone outcrops, trees are usually cut for charcoal and wood production without plowing, and regeneration from root suckers would be more common, with a low rate of species substitution during the succession.

Understanding the importance of land-use history for the regeneration dynamics of dry forests and indentifying the different models of succession can point to effective conservation strategies. The present results demonstrated important changes in floristic composition and structure along two successional stages, contributing to ecological process understanding. The limited knowledge about this rich ecosystem has been expanded and the urgent need for its preservation is reinforced.

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REFERENCES

- Almeida HS, Machado ELM (2007) Relações florísticas entre remanescentes de floresta estacional decídua no Brasil. *Rev. Bras. Biociênc.* 5: 648-650.
- APGII (2005) An update of Angiosperm phylogeny group classification for the orders and families of flowering plants: APGII. *Bot. J. Linn. Soc.* 141: 399-436.
- Coelho MS, Almada ED, Fernandes GW, Carneiro MAC, Santos RM, Quintino AV, Sánchez-Azofeifa A (2009) Gall inducing arthropods from a seasonally dry tropical forest in Serra do Cipó, Brazil. *Rev. Bras. Entomol.* 53: 404-414.
- Egler FE (1954) Vegetation science concepts I. Initial floristic composition: a factor in old field vegetation development. *Vegetatio* 4: 412-417.
- Espírito-Santo MM, Fagundes M, Nunes YRF, Fernandes GW, Sánchez-Azofeifa GA, Quesada M (2006) Bases para a conservação e uso sustentável das florestas estacionais decíduas brasileiras: a necessidade de estudos multidisciplinares. *Unimontes Cient.* 8: 12-22.
- Espírito-Santo MM, Sevilha AC, Anaya FC, Barbosa R, Fernandes GW, Sánchez-Azofeifa GA, Scariot A, Noronha SE, Sampaio CA (2009) Sustainability of tropical dry forests: two case studies in southeastern and central Brazil. *Forest Ecol. Manag.* 258: 922-930.
- Felfili JM (2001) As principais fisionomias do Espigão Mestre do São Francisco. In Felfili M, Silva Junior MC (Eds.) *Biogeografia do Bioma Cerrado: Estudo Fitofisionômico da Chapada do Espigão Mestre do São Francisco*. Universidade de Brasília. Brazil. pp. 18-30.
- Felfili JM, Nascimento ART, Fagg CW (2007) Floristic composition and community structure of a seasonally deciduous forest on limestone outcrops in central Brazil. *Rev. Bras. Bot.* 30: 611-621.
- Giulietti AM, Menezes NL, Pirani JR, Meguro M, Wanderley MGL (187) Flora da Serra do Cipó, Minas Gerais: Caracterização e lista das espécies. *Bol. Bot. Univ. São Paulo* 9: 1-151.
- Janzen D (1988) Tropical dry forests: the most endangered major tropical ecosystems. In Wilson EO (Eds.) *Biodiversity*. National Academy Press. Washington, DC, USA. pp 130-137.
- Kalácska M, Sánchez-Azofeifa GA, Calvo-Alvarado JC, Quesada M, Rivard B, Janzen DH (2004) Species composition, similarity and diversity in three successional stages of seasonally dry tropical forest. *Forest Ecol. Manag.* 200: 227-247.
- Kent M, Coker P (1992) *Vegetation Description and Analysis A Practical Approach*. Belhaven. London, UK. 362 pp.
- Ludwig JA, Reynolds JF (1988) *Statistical Ecology: A Primer on Methods and Computing*. Wiley. New York, USA. 337 pp.
- Madeira BG, Espírito-Santo MM, Neto SD, Nunes YRF, Azofeifa AS, Fernandes GW, Quesada M (2009) Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecol.* 291: 291-304.
- Magurran AE (2004) *Measuring Biological Diversity*. Blackwell. Malden, MA, USA. 256 pp.
- Meguro M, Pirani JR, Mello-Silva R, Cordeiro I (2007) Composição florística e estrutura das florestas estacionais decíduas sobre calcário e oeste da Cadeia do Espinhaço, Minas Gerais, Brazil. *Bol. Bot. Univ. São Paulo* 25: 147-171.
- Miles L, Newton AC, Defries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE (2006) A global overview of the conservation status of tropical dry forests. *J. Biogeogr.* 33: 491-505.
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annu. Rev. Ecol. System.* 17: 67-88.
- Nascimento ART, Felfili JM, Meirelles EM (2004) Florística e estrutura da comunidade arbórea de um remanescente de floresta estacional decidual de Encosta, Monte Alegre, GO, Brasil. *Acta Bot. Bras.* 18: 650-669.
- Nascimento ART, Felfili JM, Fagg CW (2007) Canopy openness and LAI estimates in two seasonally deciduous forests on limestone outcrops in Central Brazil using hemispherical photographs. *Árvore* 31: 167-176.
- Nassar J, Rodríguez JP, Sánchez-Azofeifa A, Garvin T, Quesada M (2008) *Manual of Methods: Human, Ecological and Biophysical Dimensions of Tropical Dry Forests*. IVIC. Caracas, Venezuela. 135 pp.
- Oliveira-Filho AT, Curi N, Vilela EA, Carvalho DA (1998) Effects of canopy gaps, topography and soils on the distribution of woody species in a central Brazilian deciduous dry forest. *Biotropica* 30: 362-375.
- Pedersoli JL, Martins JL (1972) A vegetação dos afloramentos de calcário. *Oreades* 5: 27-9.
- Pedralli G (1997) Florestas secas sobre afloramentos de calcário em Minas Gerais: florística e fisionomia. *Bios* 5: 81-88.
- Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci. Disc.* 4: 439-473.
- Pezzini FF (2008) *Fenologia de Comunidades Arbóreas de Mata Seca em Tres Estágios Sucessionais*. Thesis. Universidade Federal de Minas Gerais, Brazil. 130 pp.
- Portillo-Quintero CA, Sánchez-Azofeifa GA (2010) Extent and conservation of tropical dry forests in the Americas. *Biol. Cons.* 143: 144-155.
- Quesada M, Sánchez-Azofeifa GA, Álvarez-Añorve M, Stoner KE, Ávila-Cabadilla L, Calvo-Alvarado J, Castillo A, Espírito-Santo MM, Fagundes M, Fernandes GW, Gamon J, López-Araiza-Mikel M, Lawrence D, Morellato LPC, Powers JS, Neves FS, Rosas-Guerreiro V, Sayago R, Sánchez-Montoya G (2009) Succession and management of tropical dry forests in the Americas: review and new perspectives. *Forest Ecol. Manag.* 258: 1014-1024.
- Rizzini CT (1979) *Tratado de Fitogeografia do Brasil*. HUCITEC. São Paulo, Brazil. 374pp.
- Sampaio AB, Holl KD, Scariot A (2007) Regeneration of seasonal deciduous forest tree species in long used pastures in Central Brazil. *Biotropica* 39: 655-659.

- Sánchez-Azofeifa GA, Kalácska M, Quesada M, Calvo J, Nassar J, Rodríguez JP (2005a) Need for integrated research for sustainable future in tropical dry forest. *Cons. Biol.* 19: 285-286.
- Sánchez-Azofeifa GA, Quesada M, Rodríguez JP, Nassar JM, Stoner KE, Castillo A, Garvin T, Zent EL, Calvo-Alvarado JC, Kalácska M, Fajardo L, Gamon JA, Cuevas-Reyes P (2005b) *Res. Prior. Neotrop. Dry For.* 37: 477-485.
- Sánchez-Azofeifa GA, Quesada M, Cuevas P, Castillo A (2009) Land cover change and conservation in the area of influence of the Chamela-Cuixmala Biosphere Reserve. *Forest Ecol. Manag.* 258: 907-912.
- Santos RM, Vieira FA, Fagundes M, Nunes YRF, Gusmão E (2007) Riqueza e similaridade florística de oito remanescentes florestais no Norte de Minas Gerais, Brasil. *Árvore* 31: 135-144.
- Scariot A, Sevilha AC (2000) Diversidade, estrutura e manejo de florestas decíduas e as estratégias de conservação. In Cavalcanti TB, Walter BMT (Eds.) *Tópicos atuais em Botânica*. Sociedade Botânica de Brasil/Embrapa Recursos Genéticos e Biotecnologia. pp. 183-188.
- Silva LM, Scariot A (2003) Composição florística e estrutura da comunidade arbórea em uma floresta estacional decidual em afloramento calcário (Fazenda São José, São Domingos, GO, Bacia do Rio Paranã). *Acta Bot. Bras.* 17: 305-313.
- Silva LA, Scariot A (2004a) Comunidade arbórea de uma floresta estacional decidual sobre afloramento calcário na bacia do rio Paranã. *Árvore* 28: 61-67.
- Silva LA, Scariot A (2004b) Levantamento da estrutura arbórea em uma floresta estacional decidual sobre afloramento calcário. *Árvore* 28: 69-75.
- Souza VC, Lorenzi H (2005) *Botânica Sistemática: Guia Ilustrado para Identificação das Famílias de Angiospermas da Flora Brasileira*. Baseado em APGII. Instituto Plantarum. Nova Odessa, Brazil. 640 pp.
- Vieira DLM, Scariot A (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restor. Ecol.* 14: 11-20.
- Vieira DLM, Sampaio AB, Scariot A and Holl K (2006) Tropical dry forest regeneration from root suckers in Central Brazil. *J. Trop. Ecol.* 22: 1-5.
- Werneck MS, Franceschinelli EV, Tameirão-Neto E (2000) Mudanças na florística e estrutura de uma floresta decídua durante um período de quatro anos. *Rev. Bras. Bot.* 2: 401-413.
- Yodzis P (1986) Competition, mortality and community structure. In Diamond J, Case TJ (Eds.) *Community Ecology*. Harper and Row. New York, USA. pp 480-491.
- Zar JH (1984) *Biostatistical analysis*. Prentice-Hall. Englewood Cliffs. 929pp.

COMPOSICIÓN Y ESTRUCTURA FLORÍSTICA DE UNA SELVA TROPICAL SECA EN DIFERENTES ESTADIOS SUCESSIONALES EN LA CORDILLERA DEL ESPINAZO, SUDESTE DEL BRASIL

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RESUMEN

Se analizó la estructura y composición florística de fragmentos de selvas tropicales secas (STS) en estadios intermedios y parte sur de la Cordillera del Espinazo, Sudeste de Brasil. En cada fragmento fueron delimitadas tres parcelas de 20×50m, totalizando 0,3ha por estadio sucesional. En cada parcela, todos los individuos con diámetro a altura de pecho (DAP) >5cm fueron registrados. Se calcularon parámetros fitosociológicos y comparados entre estadios. Las familias más representativas en los dos estadios sucesionales fueron Fabaceae, Apocynaceae e Malvaceae, pero la composición de especies difirió entre los estadios intermedios y tardíos: las especies con mayor valor de importancia en el estadio intermedio fueron Myracrodruon urundeuva, Rauwolfia sellowii e Inga platyptera, mientras que Anadenanthera colubrina, Myracrodruon urundeuva y Bauhinia brevipes predominaron en el tardío. Los principales pa-

rámetros medidos variaron entre estadios sucesionales. En el estadio intermedio, los parámetros estructurales fueron: área basal 17,8m²·h⁻¹; densidad 1076 individuos/ha; altura media 6,30m, riqueza de especies 23; mientras los índices de comunidad fueron: diversidad Shannon-Winner 1,51 y equidad Pielou 0,48. Para el estadio tardío de sucesión los parámetros estructurales fueron: área basal 29,3m²·h⁻¹; densidad 1226 individuos/ha; altura media 7,7m; riqueza de especies 38, mientras los índices de comunidad fueron diversidad Shannon-Winner 2,38 y equidad Pielou 0,64. Los resultados mostraron importantes cambios en la composición y estructura florística a lo largo de los estadios sucesionales, contribuyendo al mejor entendimiento de los procesos ecológicos. Se amplió el limitado conocimiento sobre este rico ecosistema y se reforzó la urgente necesidad de conservación del mismo.

COMPOSIÇÃO E ESTRUTURA FLORÍSTICA DE UMA FLORESTA TROPICAL SECA EM DIFERENTES ESTÁGIOS SUCESSIONAIS NA CADEIA DO ESPINHAÇO, SUDESTE DO BRASIL

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RESUMO

Analisaram-se a estrutura e composição florística de fragmentos de florestas tropicais secas (FTS) em estágios intermediários e tardios de sucessão sobre afloramentos calcários, situados na Serra do Cipó, porção sul da Cadeia do Espinhaço, sudeste do Brasil. Em cada fragmento, três parcelas de 20×50m foram delimitadas totalizando 0,3ha por estágio sucessional. Em cada parcela, todas os indivíduos com diâmetro a altura do peito (DAP) >5cm foram amostrados. Parâmetros fitossociológicos foram calculados e comparados entre estágios. As famílias mais representativas nos dois estágios sucessionais foram Fabaceae, Apocynaceae e Malvaceae, mas a composição de espécies diferiram entre os estágios intermediários e tardios: as espécies com maior valor de importância no estágio intermediário foram Myracrodruon urundeuva, Rauwolfia sellowii e Inga platyptera, enquanto Anadenanthera colubrina, Myracrodruon urundeuva e Bauhinia brevipes predominaram no

tardio. Os principais parâmetros mensurados variaram entre estágios sucessionais. No estágio intermediário, os parâmetros estruturais foram: área basal 17,8m²·h⁻¹; densidade 1076 indivíduos/ha; altura média 6,30m, riqueza de espécies 23; enquanto os índices de comunidade foram: diversidade Shannon-Winner 1,51 e equitabilidade Pielou 0,48. Para o estágio tardio de sucessão, os parâmetros estruturais foram: área basal 29,3m²·h⁻¹; densidade 1226 indivíduos/ha; altura média 7,7m; riqueza de espécies 38, enquanto os índices de comunidade foram diversidade Shannon-Winner 2,38 e equitabilidade Pielou 0,64. Os resultados demonstraram importantes mudanças na composição e estrutura florística ao longo dos estágios sucessionais contribuindo para o melhor entendimento de processos ecológicos. Expandimos o limitado conhecimento sobre este rico ecossistema e reforçamos a urgente necessidade de conservação.