

Trees and environmental variables influence the natural regeneration of a seasonally dry tropical forest in Central Brazil

Árvores e variáveis ambientais influenciam a regeneração natural de uma floresta estacional decidual no Brasil Central

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Abstract

Seasonally dry tropical forests (SDTFs) have high tree species richness and endemism, whose dynamics and succession depend on natural regeneration (NR). To test whether NR is influenced by the mature stratum and environmental variables, we compared structural and floristic patterns of mature trees [Mt (DBH \geq 5 cm)] with the NR of a SDTF on limestone outcrops in Central Brazil. Additionally, we tested for effects of environmental variables on species abundance in these different strata. Within NR categories [JuvA (total height < 100 cm) and JuvB (total height \geq 100 cm and DBH < 5 cm)], we recorded 597 individuals in 69 angiosperm species. Within NR and Mt we recorded 110 species distributed in 33 families, and 54 were common to both (~50% of total richness). Shannon diversity was 3.83, 3.13 and 3.33 for Mt, JuvA and JuvB, respectively. Besides the high number of exclusive species recorded in Mt (23), JuvA (18) and JuvB (24), comparisons indicated high floristic similarity (51%) between strata. Mt, JuvA and JuvB were influenced by different environmental variables, indicating that species requirements change along the establishment process. This highlights the importance of environmental variability for maintaining tree species diversity in SDTFs, and the importance of this remnant for the conservation of SDTFs in Central Brazil.

Keywords: Cafuringa, Cerrado, dry forest, forest succession, limestone outcrops, sapling.

Resumo

Florestas Estacionais Deciduais (FED) em regiões tropicais possuem elevada riqueza e endemismo de espécies arbóreas, cuja dinâmica e sucessão são dependentes da regeneração natural (RN). A fim de testar se a RN é influenciada pelo estrato adulto e por variáveis ambientais, nós comparamos padrões estruturais e florísticos de árvores adultas [Mt (DBH \geq 5 cm)] com os da RN de uma FED associada a afloramentos calcários no Brasil Central. Adicionalmente, testamos os efeitos de variáveis ambientais sobre a abundância das espécies amostradas nos diferentes estratos. Entre as duas categorias de RN [JuvA (altura total < 100 cm) e JuvB (altura total \geq 100 cm and DBH < 5 cm)], registramos 597 indivíduos pertencentes a 69 espécies de angiospermas. Entre RN e Mt, amostramos 110 espécies distribuídas em 33 famílias. A RN e a Mt apresentaram 54 espécies em comum (~50% da riqueza total). A diversidade de Shannon foi 3,83, 3,13 e 3,33 para Mt, JuvA and JuvB, respectivamente. Apesar do elevado número de espécies exclusivas a Mt (23), JuvA (18) e JuvB (24), os estratos avaliados apresentaram alta similaridade florística (51%). As espécies de Mt, JuvA e JuvB foram influenciadas por diferentes variáveis ambientais, o que indica mudanças de requerimentos ao longo do processo de estabelecimento. Isso ressalta a importância da variabilidade ambiental para a manutenção da diversidade de espécies arbóreas em FEDs, assim como aponta a importância desse remanescente para a conservação das FEDs no Brasil Central.

Palavras-chave: afloramentos calcários, arvoretas, Cafuringa, Cerrado, mata seca, sucessão florestal.

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Introduction

The seasonally dry tropical forests (SDTFs) are one of the most endangered forest types in the world and 54% of their remaining area is located in South America (Miles *et al.*, 2006). Originally, the SDTF covered about 15% of the Brazilian Cerrado (Felfili, 2003), but these forests are heavily degraded by land use (Felfili, 2003; Felfili *et al.*, 2006; Felfili *et al.*, 2007a; Scariot and Sevilha, 2005; Silva *et al.*, 2006). In Central Brazil during the last four decades a large percentage of this forest type was converted into production areas (Felfili, 2003; Klink and Moreira, 2003; Felfili *et al.*, 2006; Silva *et al.*, 2006; Pereira *et al.*, 2011), which has fragmented the natural vegetation and compromises the maintenance of ecosystems and species. This is the case of *Amburana cearensis* (Allemão) A.C. Sm. and *Leucochloron foederale* (Barneby and J.W. Grimes) Barneby and J.W. Grimes, both species occurring in SDTFs and already vulnerable and the latter may be extinct (IUCN, 2013).

In Central Brazil, the SDTFs predominate in the valleys and are surrounded by a savanna formation that covers the plateaus and slopes (Felfili, 2003; Nascimento *et al.*, 2004; Silva

et al., 2006; Felfili *et al.*, 2007a). They generally occur on well-drained soils which are rich in nutrients, and may also occurs on limestone outcrops where they present a different floristic composition (Rizzini, 1997; Ribeiro and Walter, 2008) and considerable endemism similar to ecological refugees (e.g. Chapada dos Veadeiros) (Pereira *et al.*, 1996; Felfili 2003; Fernandes, 2003; Felfili *et al.*, 2006; Vieira and Scariot, 2006; Pereira *et al.*, 2011). The different seasons determine leaf fall and hence variations in canopy opening, which regulate the light index (Vieira and Scariot, 2006; Felfili *et al.*, 2007a; Nascimento *et al.*, 2007).

Species abundance and distribution in SDTFs of Central Brazil are correlated with environmental gradients such as treefall gaps (Oliveira-Filho *et al.*, 1998), soil and topography (Oliveira-Filho *et al.*, 2001; Botrel *et al.*, 2002). Environmental variability in limestone outcrops (Figure 1) can be higher than in deeper and well-drained soils. In these areas, outcrops increase micro-relief variation leading to a higher variability of surfaces, canopy height and substrate characteristics (e.g. capacity of retaining moisture). This microhabitat variability favors species with different requirements,

as those from the Cerrado, Caatinga, Pantanal and dry forests from Bolivia (Rizzini, 1997; Felfili *et al.*, 2007a; Pereira *et al.*, 1996; Pereira *et al.*, 2011). Consequently, climatic seasonality, soil properties and topography may also influence species composition of SDTFs (Eiten, 1994; Pereira *et al.*, 2011).

In tropical forests, the natural regeneration (NR) emerges primarily from seeds and its establishment is dependent of the efficiency of seed dispersion, germination, species interactions and environmental conditions (Dalling *et al.*, 1998a; Dalling *et al.*, 1998b; Guariguata and Pinard, 1998). Additionally, the success of widespread species may be associated with a high population density within saplings and mature trees (Schupp, 1990; Felfili, 1997).

In SDTFs, the NR is highly dependent of the mature stratum and environmental seasonality (Lieberman and Mingguang, 1992; Felfili, 2003; McLaren and McDonald, 2003; Vieira and Scariot, 2006; Vieira *et al.*, 2008). Although resprouting may consist an important regeneration-mechanism (Lieberman and Mingguang, 1992), mostly in degraded areas (Vieira and Scariot, 2006; Vieira *et al.*, 2006), the NR is mainly developed by seeds

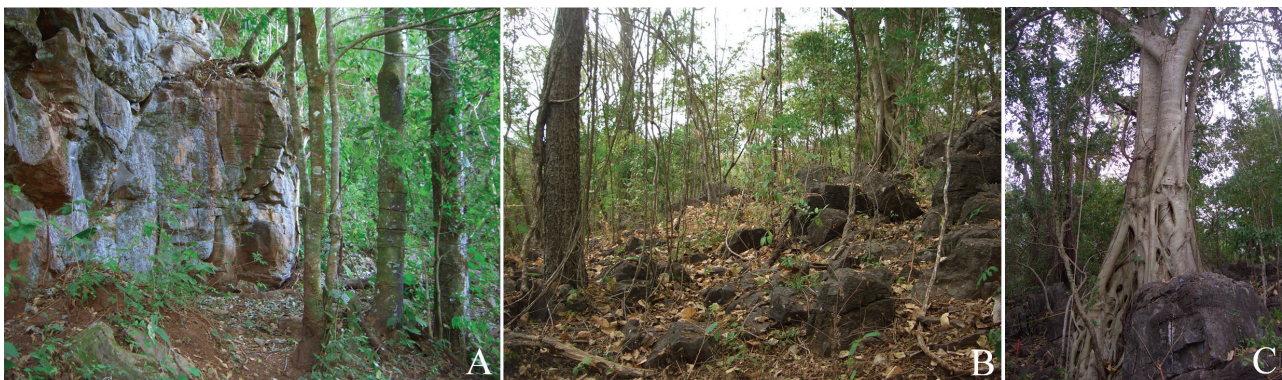


Figure 1. General view of a remnant of seasonally deciduous forest on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. In detail there are the limestone outcrops (A and B) and a tree of *Ficus trigona* L. f. (Moraceae), a typical species of these forests in Central Brazil (C). Pictures: Marra DM (July, 2007).

Figura 1. Aspecto geral de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental de Cafuringa (APAC), Distrito Federal, Brasil. Em detalhe, estão destacados os afloramentos calcários (A e B) e uma árvore de *Ficus pertusa* L. f. (Moraceae), uma típica espécie desse tipo de florestas no Brasil Central (C). Fotos: Marra DM (Julho, 2007).

from wind-dispersed species (Gentry, 1995). Seed banks consist of a strategy of few species and rarely contribute to the NR dynamics (Cabin *et al.*, 2002; Janzen, 2002; Vieira and Scariot 2006). Germination rate is lower during the dry season, whereas seedling survivor and growth tend to be higher in the rainy season (Lieberman and Mingguang, 1992; McLaren and McDonald, 2003). Partial-shading may also positively affect germination, seedling survivor rates and growth (Lieberman and Mingguang, 1992; McLaren and McDonald, 2003). Nevertheless, early establishment may decrease in extreme shading conditions (McLaren and McDonald, 2003; Vieira and Scariot 2006; Vieira *et al.*, 2008).

In SDTFs, the NR also depends on the dynamics of the herbaceous-shrub stratum, which may favor or not the seedling establishment by both regulating light and moisture availability (see review in Vieira and Scariot, 2006). In SDTFs on limestone outcrops (Figure 1), this dependency can be higher than in other types of tropical dry forests. During the rainy season the herbaceous and shrub cover grows densely, whereas in the dry season leaves fall contributing to the formation of a significant litter layer (Pereira *et al.*, 1996; Felfili, 2003; Filgueiras, 2006; Felfili *et al.*, 2007a). During the dry season, this organic layer that covers the soil can be essential for seedling establishment; especially in shallow rocky soils where water stress is higher (Pereira *et al.*, 1996; Felfili, 2003; Vieira and Scariot, 2006; Felfili *et al.*, 2007a).

Although SDTFs are one of the most threatened tropical terrestrial ecosystems, few studies have been conducted on the NR necessary to restore these forests (Felfili, 2003; Vieira and Scariot, 2006; Vieira *et al.*, 2006; Felfili *et al.*, 2007a). Structural and floristic attributes of the NR may (Higuchi *et al.*, 2006; Venturoli *et al.*, 2011) or not (Gonzaga *et al.*, 2013) reflect those patterns of mature trees.

As observed within mature communities (Nascimento *et al.*, 2004; Felfili *et al.*, 2007a; Nascimento *et al.*, 2007; Pereira *et al.*, 2011), the NR of SDTFs can also have distinct floristic composition, which can be attributed both to environmental variations and contact with species from adjacent phytophysionomies of the Cerrado (Gonzaga *et al.*, 2013).

In the NR of tropical rainforests, species abundance and distribution can be influenced by physiographic, edaphic and biotic factors (Garwood, 1989; Schupp, 1990; Guariguata and Pinard, 1998). For the NR of SDTFs, the correlation between species abundance and distribution with environmental variables is poorly studied. In a secondary SDTF in Central Brazil, floristic composition correlated with soil moisture, light availability and geographical gradients (Venturoli *et al.*, 2011). Although regarding a secondary forest, this pattern may suggest that specific species-environmental interactions, already observed in mature communities (Oliveira-Filho *et al.*, 1998; Oliveira-Filho *et al.*, 2001; Botrel *et al.*, 2002; Nascimento *et al.*, 2007), also contribute to shape the floristic composition of the NR.

The information gaps about the regeneration and succession processes, as the incomplete understanding about the species requirements and consequences of human disturbances, constitute barriers that hinder the recovery of degraded areas of SDTFs in Central Brazil (Felfili, 2003; Nappo *et al.*, 2003; Felfili *et al.*, 2006; Vieira and Scariot, 2006; Felfili *et al.*, 2007a; Carvalho and Felfili, 2011a). We aimed to test whether the floristic composition and structural patterns of the NR from a remnant of SDTF on limestone outcrops are influenced by the mature stratum and environmental variables. To address this hypothesis we answered the following questions: (i) *What are structural and floristic similarities between the NR and the mature trees?* (ii) *Do environmental variables influence differently these strata?*

Methods

Study site

We conducted the study in a remnant of a seasonally deciduous forest (SDTF) associated with limestone outcrops (Figure 1), located in the Environmental Protection Area of *Cafuringa* (APAC) (15°30' S, 48°09' W).

The APAC's area was established in 1988, covers an estimated area of 46,510 hectares and the SDTF is one of the forest types that only occurs there within the Federal District (Eiten, 2001; Leite, 2006). The SDTF of APAC covers a depression that has an average altitude of 800 m.a.s.l. The studied remnant is near the beginning of the Rio Maranhão, which is one of the main tributaries of the Rio Tocantins.

The relief of this depression is undulating with many small plains and drainage lines including the Rio do Sal (Novaes-Pinto, 1994; Leite, 2006). The lithology is represented by rocks related to the *Paranoá* and *Canastra* groups, and there are occurrences of Phanerozoic sediments, with a mean age of formation of about 1.0 to 1.2 billion years (Campos, 2006). The soils in these areas are classified as Oxisols and Inceptisols, which are usually very acidic and have low fertility. There are also more fertile soils such as Alfisols, Podzolic, Chernosols and Entisols (Reatto *et al.*, 2006). The Entisols, which are associated with limestone outcrops and covered by SDTFs, have a large variation in depth and texture, high mineral content and water deficit during the dry season (Figure 1) (Eiten 1972, 1994).

The climate type is Tropical (Aw) according to the Köppen classification, with average temperature of the coldest month above 18° C. The average annual rainfall is ~1,500 mm and is concentrated (~80%) from October to April. From May to September is the dry season, when there is almost no rain in driest years (Baptista, 2006; EMBRAPA, 1978).

Vegetation sampling

We carried fieldwork in July 2007. We established plots in undulating terrain with slopes ranging from 12 to 31° and altitudes ranging from 788 to 882 m.a.s.l (Table 1). The forest was mainly surrounded by pasture and remnants of cerrado *sensu stricto*, *campo sujo* and *campo limpo* (Pereira *et al.*, 1996; Felfili *et al.*, 2006).

We sampled mature trees [(Mt) DBH ≥ 5 cm] in 25 non-contiguous plots (20 m x 20 m) (1 ha) distant at least 150 m from each other (Felfili and Rezende, 2003; Felfili *et al.* 2005). We marked the plots over parallel transverse transects disposed from the bottom to the top of three slopes of the Rio do Sal. We measured DBH and total height of all trees. For measuring height we used telescopic pole scaled in cm.

We sampled the NR in subplots set in the bottom left hand corner of the Mt's plots. We defined two size-categories based on the total height: JuvA (plants less than 100 cm height with, at least, a pair of totally expanded/developed leaves) and JuvB (plants taller than 100 cm and DBH < 5.0 cm). We sampled JuvA in 25 subplots of 2 m x 2 m (4 m²) and JuvB in 25 subplots of 5 m x 5 m (25 m²). We measured the total height of JuvA and JuvB with a metal ruler scaled in centimeters. For both MT and NR, we followed the Protocol of Permanent Plots for the Cerrado biome (Felfili *et al.*, 2005).

For both strata we carried out the botanical identification of all recorded stems to the species level by comparing the collected material with specimens at herbaria of the University of Brasília (UnB) and the Brazilian Institute of Geography and Statistics (IBGE). We deposited fertile botanical vouchers in the IBGE herbarium, Brasília, DF (Pereira, 2008). We assigned genera in the families according to the Angiosperm Phylogeny Group III (APGIII, 2009), and checked genera and species' names on the Tropics database at the base of the Missouri Botanic Garden's website (www.mobot.org).

Environmental variables

To test for possible correlations between species abundance and environmental attributes, we took measurements of soil properties, altitude, limestone outcrop coverage and slope. For JuvA and JuvB we also took estimates of the canopy aperture and relative density of the herb-shrub stratum. Environmental variables were measured at the same time as the forest inventory.

For the analysis of soil properties we collected four samples of 0.5 kg of topsoil (0-20 cm depth) at the midpoints between the vertices and the center of each 20 m x 20 m plot. Further, we homogenized these soil samples to form a representative composite sample and analyzed them in an accredited laboratory (Lab. Soloquímica Ltda., Brasília, DF), following the methods recommended by EMBRAPA (1997). We determined the content of: Al³⁺, C, Ca²⁺, H⁺ + Al³⁺ (total acidity), K⁺, Mg²⁺, Na⁺, organic matter, P⁺, pH, clay, sand and silt.

We visually-empirically estimated the percentage of limestone outcrop coverage (Figure 1A and 1B). Our estimates were made by the same person, after a detailed inspection of the plots at the time of soil samples collection. Following the inspection, we classified the plot by its outcrop coverage according *Braun-Blanquet* (Kent and Coker, 1994). We adopted the following four classes of outcrop coverage: 1-25% of the plot's area (nine plots in total), 26-50% (six), 51-75% (two) and 76-100% (eight) of the total plot area (Felfili *et al.*, 2007a; Carvalho *et al.*, 2010) (Table 1). We measured plots' slope by using a clinometer (*Suunto*). For acquiring altitude we used a Global Positioning System (GPS) device (*Garmin eTrex*) (Table 1). Specifically for the NR, we indirectly observed the canopy condition (during the dry season) and classified the plots in relation to light availability in the following categories: (i) under closed canopy (four plots in total), (ii) under partially closed canopy (10);

(iii) in gap or under mostly deciduous canopy (11).

In order to measure the relative density of the herb-shrub stratum, we counted herb and shrub stems. We estimated the relative density of the herb-shrub stratum dividing the density of herbs and shrubs by the density of tree, shrub and herb species. The relative density of the herb-shrub stratum varied from 0-95% within JuvA plots (mean of 66 ± 5 , CI = 95%). Within JuvB plots, the relative density of the herb-shrub stratum also ranged greatly (0-90%), but the mean (34 ± 8) was significantly low (ANOVA, $F = 96.6$, $P < 0.001$).

Data and statistical analysis

Structural and floristic similarities

To address our first question, related to the similarities between the NR and the Mt, we compared structural and floristic attributes of Mt, JuvA and JuvB.

We first described the structure of each stratum by the mean estimate of density (ind.ha⁻¹). For each stratum we evaluated α -diversity by measurements of species richness (S) and Shannon Index (H') (Kent and Coker, 1994; Felfili and Rezende, 2003). We computed species accumulation curves at plot and individual basis (rarefaction method of Hulbert, 1971) to evaluate the floristic coverage of the study and check for species richness differences between strata (Kent and Coker, 1994; Colwell *et al.*, 2004; Carvalho and Felfili, 2011a; Oksanen *et al.*, 2013).

We also assessed phytosociological patterns (Curtis and McIntosh, 1950; Kent and Coker, 1994) of the recorded species. For the Mt, we calculated the Importance Value Index (IVI) by the formula $IVI = DR + FR + DomR$, where DR corresponds to the relative density, FR to the relative frequency and DomR to the relative dominance (relates to basal area). As proposed in other studies with NR in Cerrado (Felfili, 1997; Oliveira and Felfili, 2005; Medeiros *et al.*, 2007; Ribeiro

Table 1. Selected variables used to test for environmental effects on tree species abundance of a seasonally deciduous forest remnant on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. alt- altitude (m.a.s.l.); C- carbon content [C] (g.kg⁻¹); Ca- calcium content [Ca²⁺] (cmolc.dm⁻³); H.Al- total acidity [H⁺ + Al³⁺] (cmolc.dm⁻³); K- potassium content [K⁺] (mg.dm⁻³); Mg- magnesium content [Mg²⁺] (cmolc.dm⁻³); Na- sodium content [Na⁺] (cmolc.dm⁻³); om- organic matter content (g.kg⁻¹); out- limestone outcrop coverage; P- phosphorus content [P⁺] (mg.dm⁻³); pH- pH in water; san- percentage of sand (%); sil- percentage of silt (%); slo- plots' slope (°).

Tabela 1. Variáveis selecionadas para testar o efeito de fatores ambientais na abundância de espécies arbóreas de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental de Cafuringa (APAC), Distrito Federal, Brasil. alt- altitude (m.a.n.m.); C- teor de carbono [C] (g.kg⁻¹); Ca- teor de cálcio [Ca²⁺] (cmolc.dm⁻³); H.Al- acidez total [H⁺ + Al³⁺] (cmolc.dm⁻³); K- teor de potássio [K⁺] (mg.dm⁻³); Mg- teor de magnésio [Mg²⁺] (cmolc.dm⁻³); Na- teor de sódio [Na⁺] (cmolc.dm⁻³); om- teor de matéria orgânica (g.kg⁻¹); out- afloramento calcário; P- teor de fósforo [P⁺] (mg.dm⁻³); pH- pH em água; san- porcentagem de areia (%); sil- porcentagem de silte (%); slo- declividade da parcela (°).

Plot	C	Ca	H.Al	K	Mg	Na	om	P	pH	san	sil	alt	out	slo
p1	21.5	14.6	4.0	0.2	1.5	0.07	59.7	3.0	6.3	32.5	37.5	788	1	13
p2	22.7	14.8	5.0	0.18	2.0	0.06	51.9	2.5	6.0	25.0	42.5	812	2	16
p3	28.7	24.5	4.3	0.14	1.9	0.06	59.3	2.5	6.5	20.0	42.5	841	3	25
p4	23.4	34.0	4.3	0.16	4.1	0.12	92.9	2.5	6.6	22.5	42.5	866	2	18
p5	19.4	12.0	5.8	0.28	3.9	0.05	80.0	3.0	6.1	30.0	37.5	880	1	16
p6	34.7	18.6	4.3	0.21	1.9	0.07	77.1	9.0	6.3	27.5	37.5	814	4	12
p7	33.7	31.2	4.3	0.19	1.9	0.08	97.5	19.0	6.4	25.0	40.0	818	4	8
p8	26.5	25.8	2.7	0.42	1.9	0.11	74.8	178.0	7.1	37.5	30.0	820	4	20
p9	34.5	32.4	2.7	0.31	3.8	0.13	130.7	69.0	7.3	37.5	32.5	818	4	21
p10	24.3	21.0	5.8	0.22	0.6	0.04	51.9	10.0	5.9	30.0	37.5	809	1	13
p11	20.3	34.6	2.7	0.18	4.0	0.15	97.2	180.0	7.2	37.5	30.0	831	2	12
p12	23.3	15.8	2.2	0.47	4.0	0.19	146.9	24.0	7.5	40.0	32.5	813	3	22
p13	25.2	14.2	5.4	0.29	1.9	0.09	82.2	5.0.0	6.5	25.0	32.5	792	1	19
p14	34.9	33.6	4.3	0.31	1.9	0.09	62.4	4.0.0	6.5	22.5	35.0	795	1	28
p15	34.9	22.2	4.3	0.24	1.8	0.13	145.2	5.0	6.8	32.5	37.5	811	2	29
p16	22.3	19.3	2.2	0.18	1.9	0.14	115.6	8.0	7.6	22.5	37.5	835	4	30
p17	30.8	23.6	3.0	0.21	1.9	0.14	91.0	9.0	7.2	22.5	35.0	856	2	25
p18	22.1	10.0	3.4	0.47	1.9	0.07	58.7	5.5	6.6	35.0	32.5	812	1	13
p19*	19.5	18.8	4.6	0.26	3.9	0.04	49.5	3.0	6.3	35.0	30.0	852	1	15
p20	16.1	14.5	3.2	0.32	1.9	0.07	78.8	3.5	6.8	22.5	40.0	882	1	13
p21	14.4	22.7	5.8	0.36	1.7	0.08	72.1	2.0	6.2	25.0	37.5	843	1	26
p22	25.8	26.4	3.7	0.23	1.9	0.15	97.0	18.0	6.6	20.0	42.5	834	2	23
p23	25.7	31.3	3.0	0.19	1.9	0.10	89.8	7.5	6.9	17.5	40.0	832	4	21
p24	30.5	19.7	3.0	0.21	1.9	0.13	81.4	10.5	7.1	20.0	40.0	861	4	21
p25	28.0	18.9	2.4	0.27	3.2	0.13	80.8	2.5	7.4	32.5	37.5	823	4	25

*Plot excluded for analyzing JuvB

and Felfili, 2009; Gonzaga *et al.*, 2013), the Importance Value Index (IVI) for JuvA and JuvB was calculated by the formula $IVI = DR + FR$. We described the size-distribution of each stratum through an assessment of the relative stem-density per height classes (Kent and Coker, 1994; Felfili, 1997; Felfili and Rezende, 2003; Medeiros *et al.*, 2007). In order to make strata comparable, we defined 10 height classes with intervals based on the height amplitude of each stratum. We tested for differences in size-

distribution between strata with Chi-squared tests (Zar, 1996).

We applied hierarchical clustering method (UPGMA) computed from Bray-Curtis distances between plots, which was computed from qualitative (presence/absence) data. Bray-Curtis distance based in qualitative data is equivalent to Sørensen index (Anderson *et al.*, 2011; Oksanen *et al.*, 2013), which is adequate to assess floristic diversity patterns of tree communities (Anderson *et al.*, 2011; Legendre and Legendre, 2012). We performed analyzes in the R (version

3.0.1) software platform (R Core Team 2013). To compute diversity indices and species curves we used the *vegan* package (Oksanen *et al.* 2013). We produced the UPGMA diagram by using the *cluster* package (Maechler, 2013).

Environmental effects on species abundance

We addressed the second question, related to the effects of environmental variables on species abundance, by using Canonical Correspondence Analysis (CCA).

To compose the species abundance matrices, we have excluded the low-abundant species, which do not strongly influence results and tend to increase noise (Ter Braak, 1987; Kent and Coker, 1994; Felfili *et al.*, 2007b). Thus, for JuvA and JuvB, we used species abundance matrices composed by the number of stems per plot (rows) for 17 species (columns), which had five or more stems in the total sample. For Mt we used a matrix composed by the number of stems per plot for 18 species, which had 20 or more stems in the total sample.

Our environmental variables per plot matrices included all the soil variables, estimates of limestone outcrop coverage, altitude and slope. Specifically for the NR, we included the estimates of canopy aperture and relative density of the herb-shrub stratum. The environmental variables were standardized through division of original values by standard deviation of each variable, which gives equal weight to variables in the analysis (Ter Braak, 1987; Kent and Coker, 1994).

In order to reduce the environmental variables to the most important ones, we performed a CCA-based forward selection (Ter Braak, 1987; Blanchet *et al.*, 2008) associated with ANOVAs to test for statistical significance (Legendre and Legendre, 2012; Oksanen *et al.*, 2013). The forward selection or stepwise method allows for excluding variables with high redundancy or low correlation with the ordination axes (Ter Braak, 1987; Legendre and Legendre, 2012). The CCA was also performed in the R (version 3.0.1) software platform (R Core Team 2013).

Results

Structural and floristic similarities

Within Mt we recorded 1,234 stems. The mean stem density was $1,234 \pm 81$ (mean \pm CI95%) and basal area was 26.0 ± 2.0 m².ha⁻¹. We recorded 306 stems in JuvA and the stem density was $30,600 \pm 9,100$ stems.ha⁻¹.

In JuvB, we recorded 291 stems and the stem density was $4,656 \pm 1,316$ stems.ha⁻¹ (Table 2).

The tree community of the studied forest is composed of micro and meso-phanerophytes which form a discontinuous stratum rich in species. Altogether we recorded 110 tree species. In Mt, we recorded one vulnerable and one endangered species, *Machaerium villosum* Vogel and *Cedrela fissilis* Vell., respectively (IUCN 2013). In this stratum species richness was 92 (23 exclusive species), which are distributed in 76 genera and 33 families. The Shannon diversity was 3.83 nats.ind⁻¹ (Table 2).

We recorded 45 and 51 tree species, in JuvA and JuvB, respectively. Together, JuvA and JuvB had 69 species (54 also recorded in Mt). These 69 species are distributed in 57 genera and 29 botanical families. Twenty seven species (39.1% of the total richness) occurred in both, while 18 (26.1%) were exclusive to JuvA and 24 (34.7%) to JuvB. Shannon diversity was 3.13 and 3.36 nats.ind⁻¹ for JuvA and JuvB, respectively (Table 2).

In all studied strata, the species richness curves related to the sampling effort indicated that more than 65% of the total richness was recorded within the first 10 plots (Figure 2A). Although Mt and JuvA still gained novel

species within the last two sampled plots, JuvB had a clear trend of stabilization. Species richness estimated by the rarefaction curves based on recorded individuals also indicated a stabilization of recording rare species with increasing the sampled effort in Mt, JuvA and JuvB (Figure 2B). The curves' asymptote and reduction of confidence intervals also suggested that sampling effort was satisfactory, more evident in Mt.

In Mt, the 15 most important species accounted for the same amount of the IVI as JuvB (~54%) (Figure 3A). Differently from the NR, these 15 more important species did not reach equilibrium among relative density, frequency and dominance. While *Allophylus sericeus* Radlk., *Casearia rupestris* Eichler and *Celtis iguanaea* (Jacq.) Sarg. had higher frequency values, *Anadenanthera colubrina* (Vell.) Brenan, *Ceiba pubiflora* (A. St.-Hil.) K. Schum, *Ficus trigona* L. f. and *Terminalia phaeocarpa* Eichler had higher relative dominance. *Allophylus sericeus*, *A. colubrina*, *C. iguanaea* and *Machaerium brasiliense* Vogel figured within the 15 most important both in the NR and Mt.

The 15 most important species of the NR maintained equilibrium between

Table 2. Summary of the floristic and structural measures of the natural regeneration and mature trees of a seasonally deciduous forest remnant on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. Den- stem density.ha⁻¹; ES- exclusive species; G- basal area (m².ha⁻¹); JuvA- total height < 100 cm; JuvB- total height \geq 100 cm and DAP < 5 cm; H'- Shannon index (nats.ind⁻¹); Mt- DBH \geq 5 cm; S- species richness.

Tabela 2. Variáveis estruturais e florísticas da regeneração natural e estrato maduro de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental de Cafuringa (APAC), Distrito Federal, Brasil. Den- densidade de árvores.ha⁻¹; ES- espécies exclusivas; JuvA- altura total < 100 cm; JuvB- altura total \geq 100 cm e DAP < 5.0 cm; G- área basal (m².ha⁻¹); H'- índice de diversidade de Shannon; Mt- DAP \geq 5 cm; S- riqueza de espécies.

	No. stems	Den	G	S	ES*	H'
Mt**	1,234	1,234 \pm 81	26.0 \pm 2.0	92	23	3.83
JuvA	306	30,600 \pm 9,100		45	18	3.13
JuvB	291	4,656 \pm 1,316		51	24	3.36
Total	1,831	36,490		110		

*For JuvA and JuvB, the values relate to the richness of NR. **Data compiled from Pereira (2008).

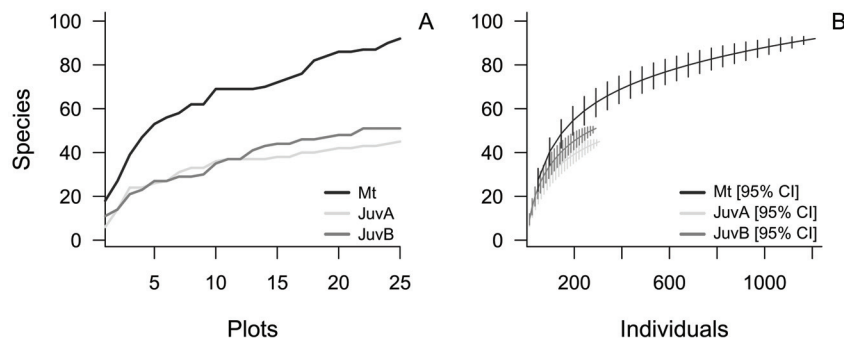


Figure 2. Comparing species richness against the number of plots (A) and individuals (B) (95% confidence interval) sampled from mature trees and the natural regeneration of a remnant of seasonally deciduous forest on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. The plot-based curve was computed using the classical species accumulation method. The individual-based curve was computed using the rarefaction estimator of Hurlbert (1971). JuvA- total height < 100 cm; JuvB- total height \geq 100 cm and DBH < 5.0 cm; Mt- DBH \geq 5 cm.

Figura 2. Curvas de acumulação de espécies em função do número de parcelas (A) e indivíduos (B) (95% intervalo de confiança) amostrados no estrato adulto e na regeneração natural de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental de Cafuringa (APAC), Distrito Federal, Brasil. As curvas de acumulação de espécies em função do número de parcelas amostradas foram computadas a partir do método clássico de acumulação. As curvas de acumulação em função do número de indivíduos amostrados foram computadas por meio do método de rarefação de Hurlbert (1971). JuvA- altura total < 100 cm; JuvB- altura total \geq 100 cm e DAP < 5.0 cm; Mt- DAP \geq 5 cm.

relative density and frequency (Figure 3B and C). *Allophylus sericeus*, *Bauhinia longifolia* D. Dietr. and *C. iguanaea* (Jacq.) Sarg. figured within the five most important species in both JuvA and JuvB. *Allophylus sericeus* and *C. iguanaea* also figured within the 15 most important species of Mt. As with Mt, the 15 most important species of JuvA (~75%) and JuvB (~54%) accounted for a greater proportion of the total IVI.

Within the families recorded in Mt, Fabaceae (IVI value of 61.6), Anacardiaceae (29.9), Malvaceae (26.7), Sapindaceae (19.1) and Apocynaceae (17.6) accounted for 52% of the total IVI and 43% of the total species richness. Within JuvA, Fabaceae (81.3), Myrtaceae (22.5), Ulmaceae (18.0), Sapindaceae (13.6) and Rubiaceae (10.5) accounted for 73% of the total IVI and 51% of the total species richness. Within JuvB, Fabaceae (31.8), Sapindaceae (10.6), Meliaceae (9.9), Ulmaceae and Myrtaceae (7.3) accounted for

33.4% of the total IVI and 53% of the total species richness.

Total height of recorded stems within the NR categories varied from 10 cm (JuvA) to 650 cm (JuvB). Within Mt stems, total height varied from 2 m to 24 m. JuvA and JuvB had a higher proportion of stems within the first two height classes, 34% and 73% respectively, when compared to Mt (17%). While JuvA and Mt had height distributions with a shape tending to a normal distribution, stems from JuvB had a J-reverse pattern (Figure 4). Such differences were confirmed by Chi-squared tests, which indicated that the height distribution of JuvA did not follow both the distribution of JuvB ($\chi^2 = 378.5$, $P < 0.001$) and Mt ($\chi^2 = 118.9$, $P < 0.001$). The height distribution of JuvB did not follow the Mt's distribution ($\chi^2 = 8718.5$, $P < 0.001$) either.

Overall floristic dissimilarity among plots was 0.48 and paired-plots dissimilarity varied from 0.21 (Mt, plots no. 11 and 12) to one (JuvB, plot no. 19) (Figure 5). JuvA and JuvB clustered

together with floristic-distance lower than 0.50. Mt plots mostly formed exclusive clusters, with the exception of plot no. 01, which was paired with plot no. 17 of JuvB (Figure 5).

Environmental effects on species abundance

By applying the CCA-based forward selection, we excluded Al^{3+} , $H^+ + Al^{3+}$ (total acidity), K^+ , Mg^{2+} , Na^+ , organic matter, P^+ , pH and clay within Mt; Al^{3+} , C , Ca^{2+} , K^+ , Mg^{2+} , Na^+ , organic matter, P^+ , pH, clay, limestone outcrop coverage, slope, canopy aperture and relative density of herb-shrub stratum within JuvA; Al^{3+} , C , $H^+ + Al^{3+}$ (total acidity), clay, altitude, slope, canopy aperture and relative density of herb-shrub stratum within JuvB (Table 1 and Table 3).

Overall permutation tests [(Mt, F -ratio = 2.24, $P < 0.001$), (JuvA, F -ratio = 1.80, $P < 0.01$) and (JuvB, F -ratio = 1.78, $P < 0.05$)] of the CCA axes indicated that species are not evenly distributed and that the selected variables were significantly correlated with this variation. In Mt, the first (CCA1) and second (CCA2) canonical axes had a significant correlation with the selected variables and eigenvalues of 0.397 and 0.199, respectively. In JuvA, the eigenvalues of the CCA1 and CCA2 were 0.268 and 0.199, but only the first axis correlated significantly with the selected variables. In JuvB, both CCA1 and CCA2 correlated significantly with the selected variables and had eigenvalues of 0.569 and 0.462, respectively (Table 3).

In Mt, the first two canonical axes captured 54% of the environmental variation among plots, which explained 26% of the species abundance variation. In JuvA, only the CCA1 correlated significantly with the selected variables. This axis captured 33% of environmental variation among plots, which explained a lower proportion (~9%) of the species abundance variation. Compared to Mt, although in JuvB the two canonical axes captured

lower amount of the environmental variation within plots (37%), the selected variables explained a similar proportion of the species abundance variation (21%) (Table 3).

In both NR and Mt, even though the majority of species placed in the middle of the CCA diagrams and did not

show variation in abundance due to the environmental variability within plots, few species correlated significantly. Interestingly, these variables and the influence they had on species abundance varied along the different strata, which may indicate a strong differentiation on the species-environ-

mental relationships along the establishment process. Altitude was significant in Mt and JuvA, while limestone outcrop coverage was significant in Mt and JuvB. C and organic matter were important in defining species abundance in Mt and JuvB. Sand and silt were the only common selected variables within all strata. However, only silt was significant, again in Mt and JuvB (Table 3).

In Mt, five of the seven selected variables had a significant effect on the species abundance. Sand (CCA score = 0.125) and slope (0.661) were more strongly correlated to the CCA1, while C (0.703), altitude (-0.525) and limestone outcrop coverage (0.833) were more strongly correlated to the CCA2. In JuvA, only two variables had a significant effect on species abundance. Both the total acidity (0.325) and altitude (0.845) correlated to the CCA1, the unique significant in this stratum. In JuvB, five of the 10 selected variables had a significant effect on species abundance. Mg, pH and silt correlated both to the CCA1 and CCA2 (Table 3). Organic matter (-0.304) and limestone outcrop-coverage (0.349) correlated more strongly to the CCA2 (Table 3 and Figure 6).

In Mt, sand and slope had a positive effect on the abundance of *Aspidosperma pyriforme* Mart. (CCA score 0.651), *C. fissilis* (1.662), *C. iguanaea* (0.759) and *Urera caracasana* (Jacq.) Gaudich. ex Griseb. (0.775). These variables also had a negative effect on the abundance of *Campomanesia velutina* (Cambess.) O. Berg (-0.703), *C. rupestris* (-0.768), *Diospyros hispida* A. DC. (-0.805) and *Myracrodruon urundeuva* Allemão (-0.675). C content and the limestone outcrop coverage had a positive effect on the abundance of *C. fissilis* (0.696). Altitude affected negatively the abundance of *Aspidosperma subincanum* Mart. (-0.515), *Campomanesia velutina* (Cambess.) O. Berg (-0.872) and *Diospyros hispida* A. DC. (-1.640) (Figure 6A).

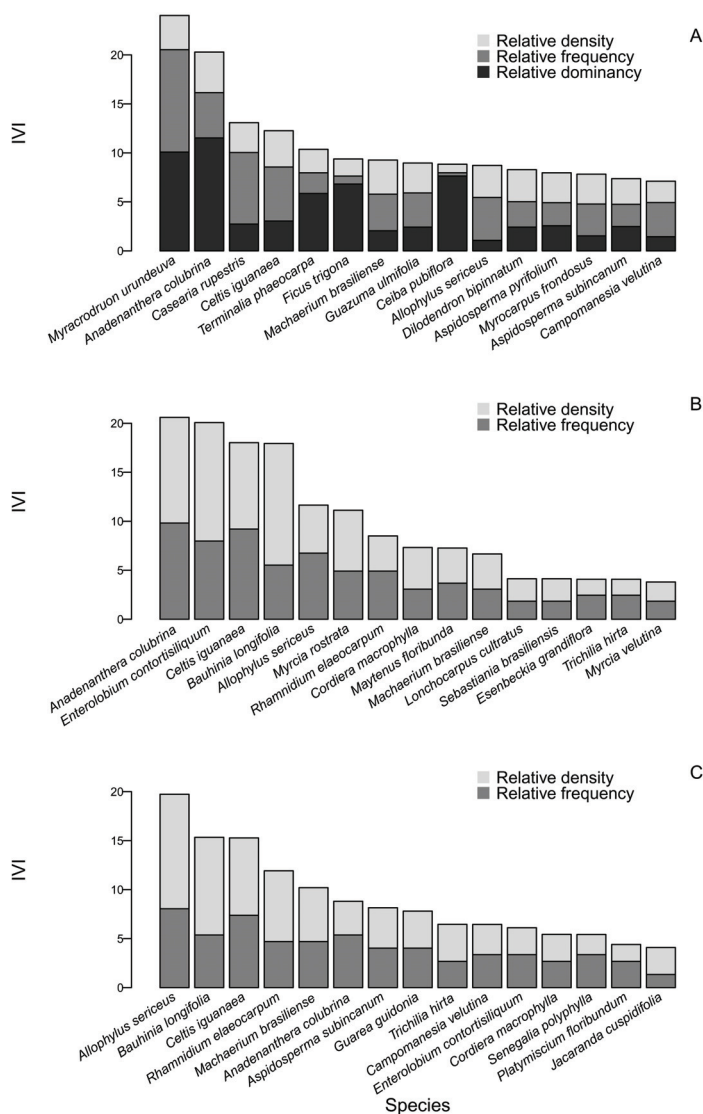


Figure 3. Importance Value Index (IVI) of the 15 most important species from the mature trees (A- DBH ≥ 5 cm) and the natural regeneration (B- total height < 100 cm; C- total height ≥ 100 cm and DBH < 5.0 cm) of a remnant of seasonally deciduous forest on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil.

Figura 3. Índice de Valor de Importância (IVI) das 15 espécies mais importantes encontradas no estrato maduro (A- DAP ≥ 5 cm) e na regeneração natural (B- altura total < 100 cm; C altura total ≥ 100 cm e DAP < 5.0 cm) de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental de Cafuringa (APAC), Distrito Federal, Brasil.

In JuvA, total acidity and altitude had a positive effect on the abundance of *Esenbeckia grandiflora* Mart. (1.144), *Inga vera* Willd. (0.576), *Lonchocarpus cultratus* (Vell.) A.Z. Tozzi e H.C. Lima (2.339) and *Maytenus*

floribunda Reissek (0.540). Nonetheless, these variables also affected negatively *Cordia macrophylla* (K. Schum.) Kuntze (-0.822) and *Erythroxylum vacciniifolium* Mart. (-0.861) (Figure 6B).

In JuvB, all the selected variables correlated strongly with the CCA2. Nonetheless, Mg, pH and silt also correlated to the CCA1 and had a positive effect on the abundance of *A. subincanum* (0.704), *C. velutina* (0.650), *Centrolobium tomentosum* Guillemain ex Benth. (1.905), *Guarea guidonia* (L.) Sleumer (0.908) and *Platymiscium floribundum* Vogel (1.006). These variables had a negative effect on *Enterolobium contortisiliquum* (Vell.) Morong (-0.799), *Rhamnidium elaeocarpum* Reissek (-1.344) and *Sebastiania brasiliensis* Spreng. (-2.119). Regarding the CCA2, Mg, pH and limestone outcrop coverage had a positive effect on the abundance of *C. velutina* (1.429), *C. macrophylla* (1.387), *G. guidonia* (1.122) and *P. floribundum* (1.274). Silt and organic matter had a positive effect on the abundance of *A. subincanum* (-0.579), *C. tomentosum* (-0.579), *Jacaranda cuspidifolia* Mart. (-1.489), *Senegalia polyphylla* (DC.) Britton and Rose (-0.829) and *Trichilia hirta* L. (-0.748) (Figure 6C).

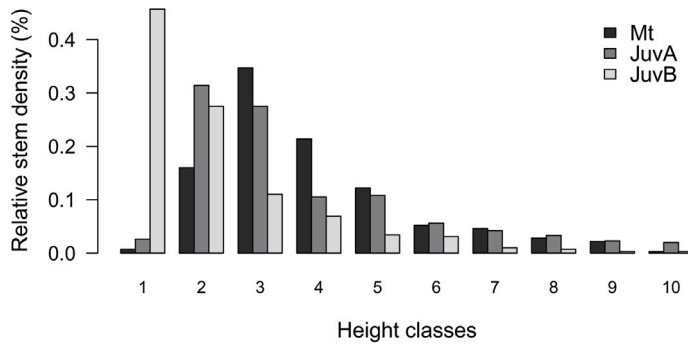


Figure 4. Total height distribution of mature trees and the natural regeneration from a remnant of seasonally deciduous forest on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. JuvA- total height < 100 cm; JuvB- total height ≥ 100 cm and DBH < 5.0 cm; Mt- DBH ≥ 5 cm.

Figura 4. Distribuição da altura total dos indivíduos arbóreos amostrados no estrato maduro e na regeneração natural de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental de Cafuringa (APAC), Distrito Federal, Brasil. JuvA- altura total < 100 cm; JuvB- altura total ≥ 100 cm e DAP < 5.0 cm; Mt- DAP ≥ 5 cm.

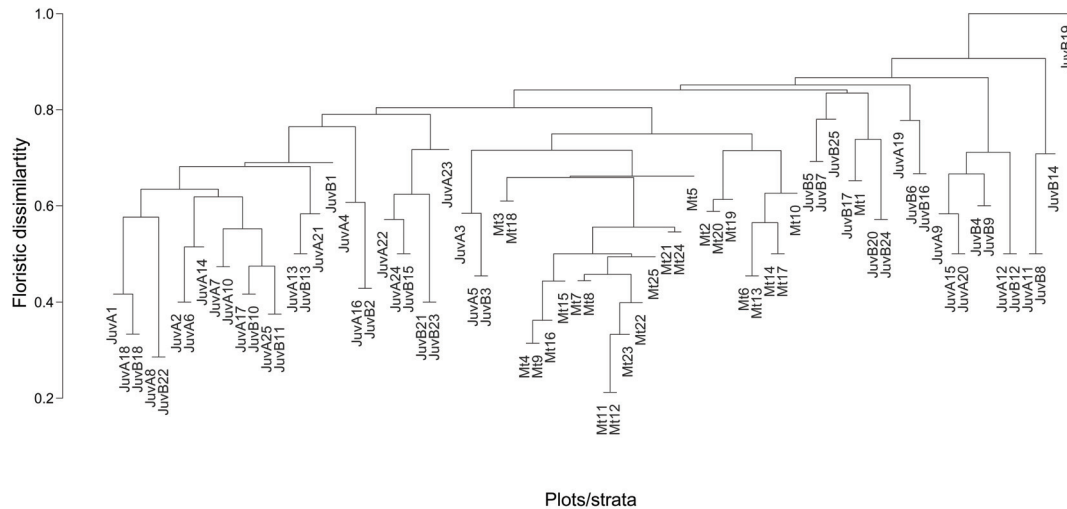


Figure 5. Floristic dissimilarity of pair plots based on Bray Curtis distances computed from presence/absence data of tree species recorded in 25 plots used to sample the mature trees and the natural regeneration of a remnant of seasonally deciduous forest on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. Plots were paired by Hierarchical clustering method (UPGMA). JuvA- total height < 100 cm; JuvB- total height ≥ 100 cm and DBH ≤ 5 cm; Mt- DBH < 5.0 cm.

Figura 5. Dissimilaridade florística entre parcelas definida por índice de Bray-Curtis computado a partir de dados de presença/ausência das espécies arbóreas encontradas em 25 parcelas instaladas para amostrar a regeneração natural e o estrato maduro de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental da Cafuringa (APAC), Distrito Federal, Brasil. As parcelas foram pareadas por meio do método UPGMA, de agrupamento hierárquico. JuvA- altura total < 100 cm; JuvB- altura total ≥ 100 cm e DAP < 5.0 cm; Mt- DAP ≥ 5 cm.

Table 3. Statistics summary of the first two ordination axis computed by Canonical Correspondence Analysis (CCA) related to soil proprieties and environmental variables. The study was carried out in a seasonally deciduous forest remnant on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. alt- altitude (m.a.s.l.); C- carbon content [C] (g.kg⁻¹); Ca- calcium content [Ca²⁺] (cmolc.dm⁻³); CCA1- first CCA axis; CCA2- second CCA axis; H.AI- total acidity [H⁺ + Al³⁺] (cmolc.dm⁻³); JuvA- total height < 100 cm; JuvB- total height ≥ 100 cm and DBH < 5 cm; K- potassium content [K⁺] (mg.dm⁻³); Mg- magnesium content [Mg²⁺] (cmolc.dm⁻³); Mt- DBH ≥ 5 cm; Na- sodium content [Na⁺] (cmolc.dm⁻³); om- organic matter content (g.kg⁻¹); out- limestone outcrop-coverage; P- phosphorus content [P⁻] (mg.dm⁻³); pH- pH in water; san- percentage of sand (%); sil- percentage of silt (%); slo- plots' slope (°).

Tabela 3. Estatística dos dois primeiros eixos da Análise de Correspondência Canônica para teste dos efeitos de variáveis ambientais na abundância de espécies arbóreas da regeneração natural e estrato maduro de um remanescente de Floresta Estacional Decidua associado a afloramentos calcários, localizado na Área de Proteção Ambiental de Cafuringa (APAC), Distrito Federal, Brasil. alt- altitude (m.a.n.m.); C- teor de carbono [C] (g.kg⁻¹); Ca- teor de cálcio [Ca²⁺] (cmolc.dm⁻³); CCA1- primeiro eixo da CCA; CCA2- segundo eixo da CCA; H.AI- acidez total [H⁺ + Al³⁺] (cmolc.dm⁻³); JuvA- altura total < 100 cm; JuvB- altura total ≥ 100 cm e DAP < 5.0 cm; K- teor de potássio [K⁺] (mg.dm⁻³); Mg- teor de magnésio [Mg²⁺] (cmolc.dm⁻³); Mt- DAP ≥ 5 cm; Na- teor de sódio [Na⁺] (cmolc.dm⁻³); om- teor de matéria orgânica (g.kg⁻¹); out- afloramento calcário; P- teor de fósforo [P⁻] (mg.dm⁻³); pH- pH em água; san- porcentagem de areia (%); sil- porcentagem de silte (%); slo- declividade da parcela (°).

Parameters		Eigenvalue		Prop. explained variance	
		CCA1	CCA2	CCA1	CCA2
Mt	env. variables	0.397**	0.199**	0.362	0.182
	species	0.251	0.159	0.173	0.087
	C**	-0.279	0.703		
	Ca	0.316	0.132		
	san*	0.125	0.005		
	Sil	-0.057	-0.053		
	alt**	0.045	-0.525		
	out*	0.272	0.833		
	slo**	0.661	0.052		
JuvA	env. variables	0.268*	0.199	0.334	0.248
	species	0.379	0.351	0.088	0.065
	H.AI*	0.325	0.641		
	san	-0.087	0.637		
	Sil	0.119	-0.131		
	alt**	0.845	-0.482		
JuvB	env. variables	0.569**	0.462**	0.204	0.166
	species	0.481	0.375	0.118	0.096
	Ca	0.319	-0.278		
	K	0.081	0.395		
	Mg*	0.321	0.345		
	Na	0.151	0.171		
	om*	0.051	-0.304		
	P	0.046	0.112		
	pH*	0.254	0.424		
	San	0.126	0.181		
sil*	0.251	-0.351			
out*	-0.021	0.349			

Permutations tests (ANOVA) for the first two CCA axes and constraining variables: *p ≤ 0.05; **p ≤ 0.01.

Discussion

Structural and floristic similarities

We found a high number of common species between Mt and NR. The high floristic similarity between strata and among size categories reveals that species composition and demographic patterns of the NR reflect those observed in the Mt.

When comparing with other SDTFs of Central Brazil, the forest of the APAC had similar or even higher values of stem density and basal area (Silva and Scariot, 2004a; Silva and Scariot, 2004b; Felfili *et al.*, 2007a; Nascimento *et al.*, 2007; Carvalho and Felfili, 2011a; Pereira *et al.*, 2011). Species richness and Shannon diversity were similar or even superior than others SDTF from the Federal District (Ramos, 1989), Goiás (Silva and Scariot, 2003; Silva and Scariot, 2004a; Silva and Scariot, 2004b; Nascimento *et al.*, 2004; Felfili *et al.*, 2007a; Carvalho and Felfili, 2011a; Carvalho and Felfili, 2011b), Minas Gerais (Oliveira-Filho *et al.*, 1998; Werneck *et al.*, 2000), Mato Grosso (Salis *et al.*, 2004) and Mato Grosso do Sul (Daniel and Arruda, 2005).

The NR of the studied forest had stem density, species richness and Shannon diversity similar to a secondary dry forest (Venturoli *et al.*, 2011) and to SDTF fragments (Gonzaga *et al.*, 2013), both within contact of other phytophysionomies of Cerrado in Central Brazil. Compared to the NR in communities of different vegetation types in the Cerrado biome, our study was richer in species than some areas of cerrado *sensu stricto* (Barreira *et al.*, 2002; Medeiros *et al.*, 2007) and poorer than gallery forests (Felfili, 1997; Oliveira and Felfili, 2005; Ribeiro and Felfili, 2009).

The greater exchange between the gallery forest of the Rio do Sal and a stretch of cerrado *sensu stricto*, located in the upper portion of the relief, may contribute to explain the patterns we found on species richness.

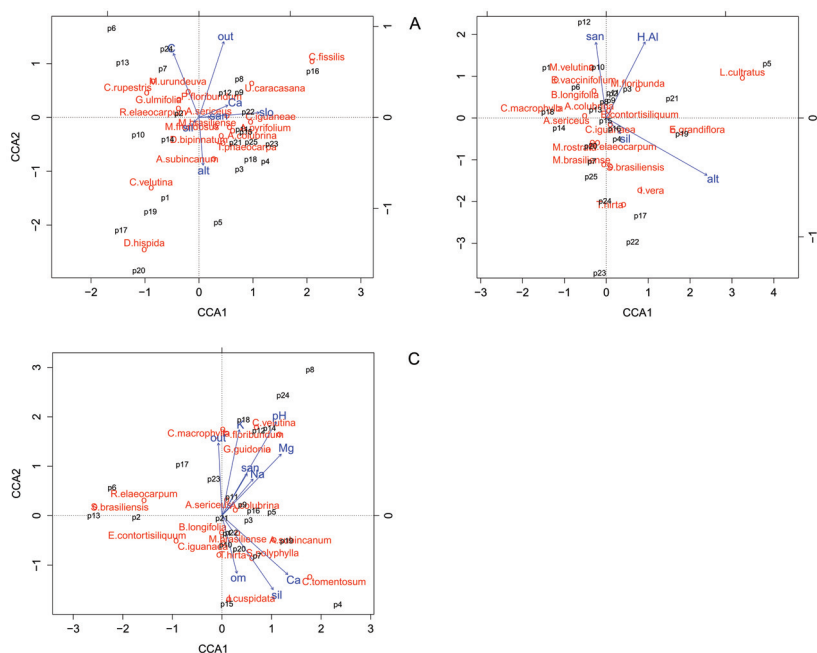


Figure 6. Ordination diagrams computed by Canonical Correspondence Analysis (CCA) with environmental effects related to plots and tree species recorded in 25 plots used to sample the mature trees (A- DBH ≥ 5.0 cm) and the natural regeneration (B- total height < 100 cm; C- total height ≥ 100 cm and DBH ≤ 5 cm) of a seasonally deciduous forest remnant on limestone outcrops, located in the Environmental Protection Area of Cafuringa (APAC), Federal District, Brazil. alt- altitude (m.a.s.l.); C- carbon content [C] (g.kg⁻¹); Ca- calcium content [Ca²⁺] (cmolc.dm⁻³); H.AI- total acidity [H⁺ + Al³⁺] (cmolc.dm⁻³); K- potassium content [K⁺] (mg.dm⁻³); Mg- magnesium content [Mg²⁺] (cmolc.dm⁻³); Na- sodium content [Na⁺] (cmolc.dm⁻³); om- organic matter content (g.kg⁻¹); out- limestone outcrop coverage; P- phosphorus content [P⁺] (mg.dm⁻³); pH- pH in water; san- percentage of sand (%); sil- percentage of silt (%); slo- plots' slope (°).

Figura 6. Diagramas de ordenação computados por meio de Análise de Correspondência Canônica relatando a variação ambiental entre parcelas, assim como seus efeitos sobre a distribuição de espécies arbóreas amostradas no estrato adulto (A- DAP ≥ 5.0 cm) e na regeneração natural (B- altura total < 100 cm; C- altura total ≥ 100 cm e DAP < 5.0 cm) de um remanescente de Floresta Estacional Decidual associado a afloramentos calcários, localizado na Área de Proteção Ambiental da Cafuringa (APAC), Distrito Federal, Brasil. alt- altitude (m.a.n.m.); C- teor de carbono [C] (g.kg⁻¹); Ca- teor de cálcio [Ca²⁺] (cmolc.dm⁻³); H.AI- acidez total [H⁺ + Al³⁺] (cmolc.dm⁻³); K- teor de potássio [K⁺] (mg.dm⁻³); Mg- teor de magnésio [Mg²⁺] (cmolc.dm⁻³); Na- teor de sódio [Na⁺] (cmolc.dm⁻³); om- teor de matéria orgânica (g.kg⁻¹); out- afloramento calcário; P- teor de fósforo [P⁺] (mg.dm⁻³); pH- pH em água; san- porcentagem de areia (%); sil- porcentagem de silte (%); slo- declividade da parcela (°).

Although a larger proportion of species have been recorded within the first 10 plots, novel species were found all over the sampling. This pattern was more evident within JuvA and Mt and corroborates the idea that local environmental variations added to the contact with different vegetation types may influence floristic composition of the NR in SDTFs in Central Brazil (Gonzaga *et al.*, 2013).

The species accumulation curves based on individuals indicated that for a same number of stems, species richness within mature trees is expected to be higher than within the NR categories. These differences between strata may indicate a local declination in the population of species that we recorded in Mt, but did not record in the NR. Additionally, it corroborates that the NR in SDTFs is highly dynamic, thus

depending on temporal and seasonal variations typical of SDTFs (Lieberman and Mingguang, 1992; Felfili, 2003; McLaren and McDonald, 2003, Vieira *et al.*, 2008).

Both in NR and Mt, few species accounted for an expressive proportion of the IVI. Nevertheless, many species were represented by one individual and had low IVI values. This result corroborates the typical pattern of tree communities from other SDTFs of Central Brazil, in which a few abundant and frequent species account for a significant amount of the total IVI, and a large number of species have relatively low density and importance (Nascimento *et al.*, 2004; Felfili *et al.*, 2007a; Carvalho e Felfili, 2011a; Pereira *et al.*, 2011).

Some of the important genera we recorded in NR (e.g. *Allophylus*, *Cordia*, *Bauhinia*, *Platymiscium* and *Rhamnidium*) also had high IVI in Mt, and were recorded in other SDTFs of Central Brazil (Botrel *et al.*, 2002; Nascimento *et al.*, 2004; Felfili *et al.*, 2007a; Pereira *et al.*, 2011). *Senegalia polyphylla* is a widely distributed species which occurs from Mexico to Argentina in different forest types (Oliveira-Filho *et al.*, 2001; Nascimento *et al.*, 2004; Salis *et al.*, 2004; Oliveira and Felfili, 2005; Pinto *et al.*, 2005; Pereira *et al.*, 2011). *Centrolobium tomentosum* is typical from the Atlantic forest but also occurs in the SDTFs of Central Brazil (Rizzini, 1997; Klitgaard, 2013). *Machaerium brasiliense* is also an Atlantic species most common in the southeast of Brazil, Goiás and Mato Grosso, but also associated with dry forests (Sartori and Tozzi, 1998).

The relatively higher importance of Fabaceae both in the NR and Mt is typical of Neotropical dry forests (Gentry, 1995) and this pattern have also been observed within other SDTFs of Central Brazil (Silva and Scariot, 2003; Nascimento *et al.*, 2004; Daniel and Arruda, 2005; Higuchi *et al.*, 2006; Felfili *et al.*, 2007a; Carvalho and Felfili, 2011b).

Trichilia (Meliaceae) (with four species) and *Myrcia* (Myrtaceae) (three species) were the richest genera in NR and also figured within the richest genera in Mt. *Anadenanthera colubrina*, *E. contortisiliquum* and *C. iguanaea* had the highest IVI within JuvA and together accounted for 29% of the total IVI. Within JuvB, *A. sericeus*, *B. longifolia* and *C. iguanaea* occupied the first three positions and together accounted for 25% of the total IVI. *Myracrodruon urundeuva*, *A. colubrina* and *C. rupestris* had the highest IVI within Mt species and together accounted for 28% of the total IVI. The greater capacity of establishment in different environments can explain the success of these important species within strata. Ecological characteristics of these species, such as dispersion syndrome, water stress tolerance and faster growth may be correlated to the high density, frequency and dominance of these species (Nascimento *et al.*, 2004; Felfili *et al.*, 2007a; Pereira *et al.*, 2011; Gonzaga *et al.*, 2013).

The height distribution of Mt and JuvA had a log-normal shape. This pattern diverges from the J-reverse distribution pattern observed in JuvB and many other STDFs from different regions of Central Brazil (Silva and Scariot, 2004a; Nascimento *et al.*, 2004; Daniel and Arruda, 2005; Felfili *et al.*, 2007a). The log-normal shape that we observed in Mt was also reported in other STDFs associated with soils liable to seasonal water stress (Oliveira-Filho *et al.*, 2001; Botrel *et al.*, 2002), in which variations in tree slenderness may be correlated with soil and light gradients (Oliveira-Filho *et al.*, 2001). In JuvA, the lower stem density in the first size classes can also be attributed to the higher mortality within early establishment (from seedlings to saplings) (Schupp, 1990; Lieberman and Mingguang, 1992; Dalling *et al.*, 1998a; McLaren and McDonald, 2003). However, further assumptions regarding these correlations remain to be better investigated.

The floristic-distance among plots (< 0.50) can be considered low (Kent and Coker, 1994; Felfili *et al.*, 2007b). Although JuvA and JuvB were more similar, the low overall floristic-distance suggests a general low variation in β -diversity between strata (Kent and Coker, 1994; Felfili *et al.*, 2007b; Carvalho and Felfili, 2011a). This result correlates to the high equivalence in species richness between the RN and Mt (75%) and to the great number of common species (54), equivalent to 78% of the species richness of the NR (JuvA and JuvB). This result is higher than that reported for different fragments of SDTF in Central Brazil, in which species richness equivalence is closer to 50% (Gonzaga *et al.*, 2013). We suggest that this pattern, added to phytosociological attributes, indicate high species resilience to disturbances, especially of those more abundant and well-distributed all over the forest.

Environmental effects on species abundance

The different strata and size-categories of the NR reacted distinctly to the tested environment variables. This significant and distinct effect indicates that species requirements change from early to late establishment.

The eigenvalues and overall statistical significance of the CCA suggest that, both in NR and Mt, species are not evenly distributed within plots (Ter Braak, 1987; Kent and Coker, 1994; Felfili *et al.*, 2007b). Our results indicate an increasing relationship within species abundance and environmental conditions, from early to late establishment (from JuvA to JuvB). Together with variations in soil properties (Mg, organic matter, pH, silt and total acidity), water availability and the dispersion syndrome of species (Lieberman and Mingguang, 1992; McLaren and McDonald, 2003; Vieira and Scariot, 2006) may be the main factors influencing germination and early establishment (JuvA) in the studied forest. In JuvA, altitude also

had an important influence on defining species abundance. This result correlates to the fact that higher altitude plots were closer to the cerrado *sensu stricto* that remains on the top of the relief. Within a more advanced stage (JuvB), together with the already mentioned soil chemical properties and water availability, the limestone outcrop coverage and organic matter seem to be also important in limiting or favoring species survival. This result corroborates studies with both mature trees in well preserved SDTFs (Felfili *et al.*, 2007a; Pereira 2008; Pereira *et al.*, 2011) and NR in secondary STDFs (Venturoli *et al.*, 2011). Our data captured such relationship and indicate that limestone outcrop coverage and organic matter influence species abundance in the NR.

The weaker relationship between species abundance and environment gradients that we observed in JuvA may also be correlated with the germination of a wide variety of species in different environments and conditions (Vieira and Scariot, 2006; Vieira *et al.*, 2006, 2008). Therefore, a large number of sites with shallow soil, which have a water deficit during drought as well as different levels of deciduousness could also affect the distribution and establishment of species. Probably, as the plants establish and compete into higher levels, more specific relationships are established between plants and the environment. Additionally, for a better understanding of the dynamics of the SDTFs, further research may check for species-abundance and distribution correlations with non-stochastic process, such as seed viability, dispersion and herbivory.

Although the herbaceous-shrub density varied significantly within plots, we did not observe any correlation of this variable with tree species abundance in the NR. We also observed similar pattern for the estimates of canopy aperture, which did not correlate with species abundance, both in JuvA and JuvB. This result may indicate that

the herbaceous-shrub density, besides influencing positively or negatively different species, has an even effect on most by competing for water and nutrients. The influence of the herbaceous-shrub density and light conditions may be enhanced in secondary forests (Venturoli *et al.*, 2011), where the higher light availability may favor herb and shrub species and increase competition.

The higher relationship among species abundance and environmental variation in Mt corroborates other studies which reported an even higher influence of soil (chemical and physical properties) and topography on the distribution of trees (DBH \geq 5 cm) of STDFs (Oliveira-Filho *et al.*, 2001; Botrel *et al.*, 2002; Pereira *et al.*, 2011) and in a valley forest (Pinto *et al.*, 2005) of Central Brazil. The same environmental variability, typical of SDTFs, also contributes to increase species richness and diversity within tree communities (Felfili *et al.*, 2007a; Pereira *et al.*, 2011), which was observed in our study. Mesic microhabitats even during the dry season hold enough water and support more moisture demanding species from other forest types. *Maclura tinctoria* (L.) D. Don ex Steud., *Protium heptaphyllum* (Aubl.) Marchand, *Eugenia florida* DC. and *Copaifera langsdorffii* Desf indicate the existence of these habitats and corroborate other studies which show that SDTFs explain the links between forests of Central Brazil and other South American humid forests (Rizzini, 1997; Oliveira-Filho and Ratter, 1995; Fernandes, 2003; Pereira *et al.*, 2011).

In the Mt stratum, *C. fissilis* and *U. racasana* occurred with higher abundance in plots established in steeper areas and with higher sand content. In our study area, the plots with higher slopes and sand content were set on the bottom of the toposequence, close to the Rio do Sal. *Casearia rupestris* and *M. urundeuva* were more abundant in plots set in less steep areas with higher silt content. *Aspidosperma subincanum*, *C. velutina* and *D. hispida* were

associated to the plots set in higher altitudes, low C content and limestone outcrop coverage. Higher altitude plots were associated to the cerrado *sensu stricto* that remains on the top of the relief. *Cedrela fissilis* (cedro), traditionally used as timber (Felfili, 2003; Pereira *et al.*, 2011), was also more associated with plots set in areas with higher C and limestone outcrop coverage. *Aspidosperma pyrifolium* and *M. urundeuva* are typical species of SDTFs and can be associated to limestone outcrops and soils with water deficit (Felfili *et al.*, 2007a; Pereira *et al.*, 2011).

In JuvA, *E. grandiflora*, *I. vera*, *L. culttratus* and *M. floribunda* were associated with plots established in higher altitudes and with higher total acidity. As we mentioned before, higher altitude plots were closer to the cerrado *sensu stricto* that remains on the top of the relief. Contrary, *C. macrophylla* and *E. vacciniifolium* occurred in higher abundance in those plots set in lower altitude and with more basic pH. In our study area, these are the plots closer to the Rio do Sal, which also had a higher sand content.

Compared to JuvA, in JuvB the species abundance variation was highly correlated to the environmental variation within plots. In the CCA diagrams, JuvB species also formed clusters more closely related to the tested variables, which suggest a more specific relationship among species and the environmental variation among plots. Although highly correlated to the CCA2, Mg, pH and silt were also correlated to the CCA1. These variables had a positive effect on the abundance of *A. subincanum*, *C. velutina*, *C. tomentosum*, *G. guidonia* and *E. contortisiliquum*, which placed them on the right of the diagram. *Rhamnidium elaeocarpum* and *S. brasiliensis* were placed on the left side of the diagram and occurred in higher abundance within plots with lower values of Mg, pH and silt. However, the species-environment associations were better described by the CCA2. *Campomanesia velutina*, *C.*

macrophylla, *G. guidonia* and *P. floribundum* showed preference to the plots with higher values of Mg, pH and limestone outcrop coverage. *Aspidosperma subincanum*, *C. tomentosum*, *J. cuspidifolia*, *S. polyphylla* and *T. hirta* showed clear association to the plots with higher values of silt and organic matter. We recorded *A. colubrina* in all the three strata, but it did not show any correlation with the selected variables. This corroborates the high IVI value of this species and indicates that a more generalist requirement (Nascimento *et al.* 2004; Felfili *et al.* 2007a; Pereira *et al.* 2011; Gonzaga *et al.* 2013) may be associated to the success and widely distribution of *A. colubrina* in the studied forest.

Understanding the biotic and abiotic processes involved in species establishment and forest succession can help the restoration of degraded areas and the definition of conservation priorities (Felfili, 2003; Scariot and Sevilha, 2005; Vieira and Scariot, 2006; Carvalho and Felfili, 2011a; Pereira *et al.*, 2011). Although surrounded by an intense land use, the studied forest had a NR resilient to the surrounding land use and fragmentation, with high tree species richness and diversity comparable to the mature stratum. Moreover, tree species are not evenly distributed, which enhances the importance of the environmental variability, typical of STDFs, in maintaining species richness and floristic composition. This fact contributes to making its protection an important accomplishment, since the seasonal dry forests of the Cafuringa are one of the last remnants of this vegetation type in the Distrito Federal and Central Brazil.

Acknowledgments

We dedicate this study to Prof. Dr. Jeanine Maria Felfili (1957-2009, *in memoriam*). We thank anonymous reviewers who made important contributions, and Ricardo F. Haidar, Gabriel D. Vale, Mariana de Q. Matos, Clarissa G. Fontes, Julianna F. Maroc-

colo, Rafael G. Oliveira and André M. A. Pessoa, who actively participated in the fieldwork. We also thank the University of Brasília, and the National Council for Scientific and Technological Development (CNPq), which provided the first author's scholarship (PIBIC), and scientific support for the latter two authors (Processo 557718/2009-0). Finally, we gratefully acknowledge owners and employees of the farms Santa Sara and Campina Verde (Cafuringa EPA, DF) for their generous hospitality and for the use of their facilities.

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Submitted on July 29, 2013.

Accepted on May 28, 2014.