REVISTA FORESTAL MESOAMERICANA KURÚ

Changes in forest structure and composition in a successional tropical dry forest of Brazil

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Abstract

We describe changes in forest structure and floristic composition of three successional stages for Mata Seca State Park, in Minas Gerais, Brazil, through the measurement of all trees greater than 5 cm of diameter at breast height (DBH) of 18 permanent plots (6 per stage) for early, intermediate, and late successional stages of a tropical dry forest during a 5-year period. Using this information, we calculated the Importance Value Index (IVI), Holdridge Complexity Index, Jaccard Similarity Coefficient, and Shannon Diversity Index for each stage of succession. The floristic composition and structure of the successional stages expressed by the Holdridge Complexity Index, showed that complexity increases

Resumen

Cambios en la estructura y composición florística de una gradiente sucesional de bosque seco tropical en Brasil

Se describen los cambios en la estructura del bosque y la composición florística de tres estados de sucesión del Parque Estatal Mata Seca, en Minas Gerais, Brasil, a través de la medición de todos los árboles mayores de 5 cm de diámetro a la altura del pecho (DBH), en 18 parcelas permanentes en los estados de sucesión temprano, intermedio y tardío de un bosque seco tropical durante un período de 5 años. Utilizando esta información, calculamos el Índice de Importancia del Valor (IVI), el Índice de Complejidad de Holdridge, el Coeficiente de

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gradually as we advance through the successional stages, while the Shannon Diversity Index indicated that species diversity was higher in the intermediate stage of succession. The Jaccard Similarity Coefficients showed that the intermediate and late successional stages had high similarity, whereas the early successional stage had low similarity with these two successional stages. Mortality rates were higher in the early stage, especially in stems with smaller diameters (5-10 cm). This information contributes to the dissemination of important knowledge for the conservation of the tropical dry forests of Brazil, which are the most threatened ecosystems in this country and, at the same time, the least studied.

Key words: Tropical dry forest, composition, structure, succession, diversity.

Similitud Jaccard y el Índice de Diversidad Shannon para cada etapa de la sucesión. La composición florística y la estructura de los estados de sucesión expresadas por el Índice de Complejidad de Holdridge demostraron que la complejidad aumenta gradualmente a medida que avanzamos a través de los estados sucesionales, mientras que el Índice de Diversidad Shannon indicó que la diversidad de especies era mayor en el estado de sucesión intermedio. Los coeficientes de similitud de Jaccard mostraron que los estados de sucesión intermedio y tardío tenían una alta similitud, mientras que el estado de sucesión temprano tenía baja similitud con estos dos estados de sucesión. Las tasas de mortalidad fueron más altas en el estado temprano, especialmente en tallos con diámetros más pequeños (5-10 cm). Esta información contribuye a la difusión de conocimientos importantes para la conservación de los bosques secos tropicales de Brasil, que son los ecosistemas más amenazados de este país y, al mismo tiempo, los menos estudiados.

Palabras clave: Bosque seco tropical, composición, estructura, sucesión, diversidad.

Introduction

In the Americas, tropical dry forests (TDF) have been the preferred ecosystems for human settlements (Murphy and Lugo, 1986; Sánchez-Azofeifa, Kalácska, Quesada et al., (2005); Calvo-Alvarado, McLennan, Sánchez-Azofeifa y Garvin (2009); Neves, Braga, Espírito-Santos, Do et al., (2010). The economic and human pressure experienced by TDF make these forests one of the most deforested and least protected ecosystems in the Americas (Janzen, 1986; Sánchez-Azofeifa et al., 2005; Neves et al., 2010); Sánchez-Azofeifa and Portillo-Quintero (2011); Calvo-Alvarado, Sánchez-Azofeifa and Portillo-Quintero (2013).

Portillo-Quintero and Sánchez-Azofeifa (2010) found that TDFs of the Americas are located in areas with good to excellent conditions for agricultural and livestock development and, more recently, for the development of large mega - tourism projects. In Brazil, as a result of its high proportion of valuable timber species and fertile soils, TDFs are in high demand for forest exploitation and expansion of agriculture for several crops, which are the main drivers of land cover change (Scariot and Sevilha, 2005;. Anaya, Barbosa and Sampaio (2006); Espírito-Santo, Do, Cássio, Anaya et al,. (2009). Another major threat is the extraction of limestone, as well as the constant pressure on the remaining forest fragments for livestock production and selective logging of tree species (Espírito-Santo et al., 2009). An important cause for the change in forest cover of TDFs is forest fire, which may have a higher occurrence in forest patches immersed in agricultural landscapes (Sánchez-Azofeifa and Portillo-Quintero, 2011).

Due to high rates of deforestation and the restricted and fragmented distribution of remaining TDF areas, these ecosystems are considered the most threatened in Brazil (Espírito-Santo et al., 2009). Only 5,015 km^2 of TDF in Brazil are under protection, representing only 6.2 % of the total area of TDF of Brazil (Portillo-Quintero and Sánchez-Azofeifa, 2010). Among these protected areas is Mata Seca State Park (MSSP). The park is part of a group of federal and state protected areas in the north of the state of Minas Gerais, with 8 units of conservation and 6 units of sustainable use. Most of these units are exposed to several threats, such as (i) poaching, especially for small mammals as a food source, (ii) invasion of the margins of rivers and destruction of riparian forests by fishermen, construction of temporary houses, and crop plantations, (iii) fishing inside lakes, which work as nurseries for fish in the São Francisco river, (iv) invasion of cattle from the surrounding farms, which alter the ecosystem; (v) and uncontrolled anthropogenic fires used to manage grasslands, as well as fires that occur in neighbouring forests (Belem and Carvalho, 2013).

Although the TDFs of the Americas are considered generally less dynamic (Phillips, Nuñez, Timana (1998); Uslar, Mostacedo and Saldias (2004) and less diverse than tropical rain forests (Murphy and Lugo, 1986), TDFs have greater structural and physiological diversity than tropical rain forests (Mooney, Bullock and Medina (1995); Kalácska, Sánchez-Azofeifa, Calvo-Alvarado et al., (2004); Calvo-Alvarado et al., 2013). Another feature of the TDF is that most areas with high species richness are found in the drier areas. For example, there is higher plant diversity in Chamela, Mexico and Quiaca, Bolivia than in sites with higher rainfall such as Guanacaste, Costa Rica (Gentry, 1995; Lobo, Quesada, Stoner et al., 2003; Kalácska et al., 2004). Another significant feature is the high species endemism, which is higher compared to tropical rain forests (Trejo and Dirzo, 2002). Furthermore, Joly (1970) estimated that up to 70 % of all plant species belonged to families that are endemic in the Cerrado region in the dry forest of Brazil (Joly, 1970; Kalácska et al., 2004; Calvo-Alvarado et al., 2013). Madeira, Espírito-Santo, Neto et al., (2009) showed a progressive increase in tree species richness and tree structural traits from early to late successional stage plots in MSSP, as well as important differences in tree species composition and dominance.

Within this framework, our goal is to identify and analyze the structure and floristic composition for three successional stages of MSSP, in Minas Gerais, Brazil and to compare our results with previous studies to determine changes. Also, we analyzed tree mortality and recruitment. These data should contribute to an understanding of the diversity, composition, structure, and recovery of these forests, facilitating the development of natural forest management, biodiversity conservation, land restoration, and payment for environmental services in the tropical dry forests of Brazil.

Materials and methods

Study site

The study was conducted in MSSP (Figure 1), a unit of integrated conservation and protection, which was created after the expropriation of farm land in 2000, and currently managed by the Forestry State Institute (IEF- Instituto Estadual de Florestas). MSSP has an area of 15,466 hectares at an elevation of 452 m.a.s.l and is situated in the São Francisco river valley, in the Minas Gerais, Brazil. The exact location is between coordinates 14°48’36” - 14°56’59” S and 43°55’12” - 44°04’12” W.

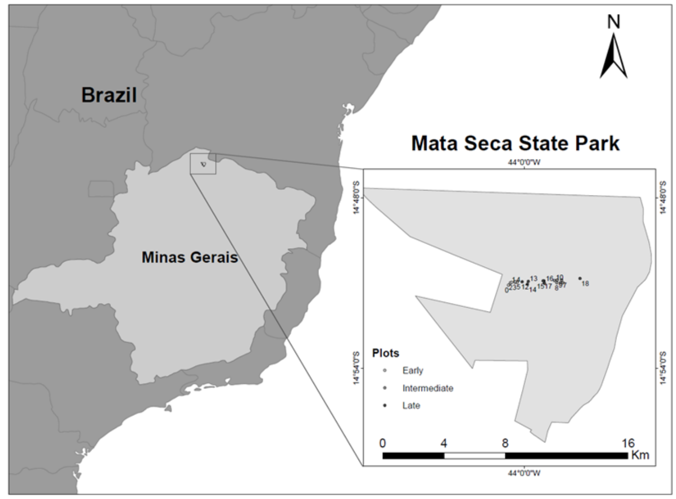

Figure 1. Geographic location of MSSP in the North of Minas Gerais, Brazil

Figure 1. Geographic location of MSSP in the North of Minas Gerais, Brazil

The climate of the region is considered tropical semiarid (Köppen classification) or tropical dry forest (Holdridge classification). The forest is dominated by deciduous trees, which lose almost 90-95 % of their leaf area during the dry season that extends for six months between May and October (Madeira et al. 2009). The average temperature of the study area is 24.4°C with a maximum of 32 °C and a mean annual precipitation of 871 mm (300-1300 mm range), which is concentrated during the rainy season between October and April.

Experimental design

In MSSP, 18 permanent plots (6 plots per successional stage) were established in three successional stages: early, intermediate, and late. These plots were assembled and monitored by the faculty of Biology of Unimontes University and by the University of Alberta, Canada. Each plot has an area of 1.000 m^2 (50 x 20 m), in accordance with the protocols of the Tropi-Dry project (Alvarez, Avila-Cabadilla, Berbara et al., 2008). The plots are located in Fluvisol soils (Da Silva, 2010) that are characterized by being deep and well drained. The early and late successional stages have weak acidity and weak alkalinity, providing a pH range where most nutrients (K, Ca, Mg, N, S, P, and B) are more available (Nunes, Luz, Souza et al., (2013). The intermediate successional stage has a more acidic soil due to higher levels of Al, which is absent in the early and late successional stages, moreover, higher stocks of organic carbon were found in the early and late successional stages (Nunes et al., 2013). Madeira et al., (2009) provided a more detailed description of the characteristics of these soils.

The early successional stage has only one strata of trees and has a very open canopy. This area was pasture land for 20 years and cattle were not removed until 2000. The intermediate successional stage has a strata of trees from 10-12 m high and some emergent trees up to 15 m. The second strata is a dense understory of young trees and abundant lianas. This area was also pasture land for an unknown period and was abandoned in the 1980´s. The late successional stage has a strata of trees 18-20 m high with a closed canopy. The second strata is formed by a scattered understory with low light penetration and low densities of young trees and lianas. There are no records of logging in this area over the last 50 years (Madeira et al., 2009).

In each plot, all individuals with diameters greater than 5 cm DBH (1.3 m) were measured annually. The tree circumferences were recorded in cm using metric tapes. Furthermore, the family and species of each individual were identified with the help of a taxonomist. Each year, the recruitment and mortality of trees were recorded for each plot. The data were collected during February and March each year between 2006 and 2011 (6 years of records).

Data analysis

With data from each successional stage, we proceeded to calculate the diameter in centimwetres for each individual, the basal area per hectare in square meters, and the dominant heights using data from 2006 and 2011. Stem density and number of species per hectare were also calculated to compare differences between stages of succession.

The total number of individuals present in 2006 and 2011 in the 18 plots was used to describe the floristic composition of the plots. We analyzed species composition, and calculated the Importance Value Index (IVI) (Curtis and McIntosh, 1951), the Shannon Diversity Index (H') (Magurran and McGill, 2011) and the Jaccard Similarity Coefficients (Cj) (Magurran and McGill, 2011), and constructed a cluster analysis. The IVI analysis was based on the 10 species with highest values. The structure of our sample plots was described using the density of stems (1 ha), dominant height (m), and the Holdridge Complexity Index (HCI) (Holdridge 1967). For this study we used the modified version of the HCI, because we sampled trees with DBH > 5 cm (Lugo, Gonzalez-Liboy, Cintron and Dugger (1978); Madeira et al., (2009). To determine whether differences existed among the basal areas per successional stage, tree density, and dominant height, we conducted an analyses of variance (ANOVA) and a multiple comparison test (Fisher LSD, α = 0.05). To find significant differences between the Holdridge Complexity Index, we used a multiple comparison test (Dunnett's, α = 0.05). We used the statistical software R 3.01 for the analyses and the creation of figures (R Development Core Team 2013). For the Jaccard cluster analysis we used the Vegan package in R 3.01 (Oksanen, Blanchet, Kindt et al., (2014).

Tree mortality (m), recruitment (r), and annual rates of basal area growth loss (l) and gain (g) were calculated using a logarithmic model (Sheil, Burslem & Alder, 1995; Lieberman and Lieberman, 1987; Carvajal-Vanegas and Calvo-Alvarado, 2013). The mortality and the recruitment per hectare in each successional stage were calculated using the following formulas:

$$m = \frac{\ln N_{06} - \ln N_s}{T} \quad (1)$$

$$r = \frac{\ln N_{11} - \ln N_s}{T} \quad (2)$$

where N06 is the number of individuals present in 2006, NS is the number of individuals surviving in 2011, and for recruitment N11 is the number of individuals surviving in 2011 (Ns) plus the number of individuals recruited during the time period T. The basal area growth loss (l) and gain (g) were calculated using the formulas 3 and 4:

$$l = \frac{\ln \mathrm{BA}_{06} - \ln \mathrm{BA}_{S06}}{T} \quad (3)$$

$$g = \frac{\ln \mathrm{BA}_{11} - \ln \mathrm{BA}_{S06}}{T} \quad (4)$$

where BA06 is the basal area of all living stems in 2006, BAS06 is the basal area of the surviving stems in 2011, BAs11 is the basal area in 2011 of all live stems, and BA11 is the basal area in 2011 plus the basal area of all the recruited stems by 2011.

Results

Floristic composition

The floristic composition analyzed for 2006 and 2011 varied among the three successional stages. By 2006, the early stage had 13 families and 24 species, while in 2011 it increased to 16 families and 36 species. The intermediate stage went from 17 families and 46 species to 18 families and 55 species, while the late stage was the only stage that declined in the number of families from 21 to 19; the number of species, however, increased from 53 to 59 (Figure 2).

For 2011, we found a total of 53 families and 150 tree species within the entire study area (1.8 hectares in total). When analyzing the families that were found in each successional stage (Table 1), Bignoniaceae had the greatest number of individuals and the greatest number of species in the late stage. In the intermediate stage, Bignoniaceae had the greatest number of individuals and 13 species, although Fabaceae had the greatest number of species (17). In the early stage, Anacardiaceae had the greatest number of individuals in only 2 species and Bignoniaceae had the greatest number of species (4).

Importance Value Index for 2011 indicated that the early successional stage had nearly 250 % of the IVI accumulated in the 10 species from Table 2, while the intermediate and late stages had less than 200 % of the IVI in the 10 most common species. This reflects the

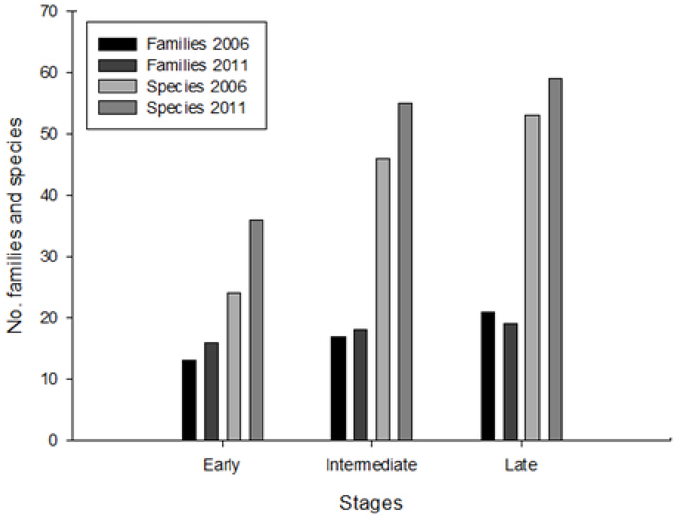

Figure 2. Number of species and families in three successional stages of the tropical dry forest of MSSP, Brazil between the years 2006-2011

Figura 2. Número de especies y familias en tres estados de sucesión del bosque seco tropical del Parque Nacional Mata Seca, Brasil, entre los años 2006-2011.

low diversity of species found in the early stage, where only a few species are the most abundant, dominant, and frequent, while in the more advanced successional stages there was a greater species diversity.

The dominance of tree species showed a change along the successional gradient. This change was more dramatic between the early and intermediate successional stages, and it was much less dramatic between the intermediate and late successional stages, where 5 species with higher IVIs were shared between these successional stages: *Handroanthus reticulatus, Combretum duarteanum, Commiphora leptophloeus, Terminalia fagifolia,* and *Poincianella pluviosa*. Meanwhile, the early successional stage only shared one species with the late stage and none with the intermediate, mostly because this forest is dominated by fast-growing pioneer species that disappear in the more advanced successional stages.

Myracrodruon urundeuva (Anacardiaceae) had the highest ecological weight in the early successional stage with an IVI of 99.06; this species also had the second highest IVI in the late stage (31.57) and it also appeared to a lesser extent in the intermediate stage. *Handroanthus reticulatus* (Bignoniaceae) and *Handroanthus chrysotrichus* (Bignoniaceae) had the highest ecological weight in the intermediate and late stages.

Tree structure and diversity

The structure and diversity of the forest tends to become more complex as we advance in the successional stages and through time. Basal area increased over the 5 years of measurement in all successional stages, increasing from 3.13 to 5.31 (m^2/ha) in the early stage, from 15.19 to 16.55 (m^2/ha) in the intermediate stage, and from 24.55 to 25.34 (m^2/ha) in the late stage (Table 3). The density of stems and the canopy height (Figure 3) increased as well in all stages of succession during the 5 years of measurements.

The calculated Shannon Diversity Index for each successional stage for the year 2011 showed a high diversity of species. In the intermediate stage, a value of 1.3 was obtained and for the late stage a value of 1.2, which are very similar values. The early stage showed a value of 0.9, which was lower than the previous stages. The early successional stage of MSSP had the lowest species diversity index, while the intermediate stage had

Table 1. Families with a composition higher than 5 % (of the sampled individuals) and the number of species per family in three successional stages of MSSP, Brazil.

Cuadro 1. Familias con una composición mayor a 5 % (de los individuos muestreados) y número de especies por familia en tres estados de sucesión en el Parque Nacional Mata Seca en Minas Gerais, Brasil.

Stage	Family	Composition (%)	No. of species
Early	Anacardiaceae	36.8	2
	Apocynaceae	24.3	2
	Bignoniaceae	18.9	4
Intermediate	Bignoniaceae	28.3	13
	Combretaceae	13.6	3
	Euphorbiaceae	9.2	8
	Fabaceae	12.0	17
	Vitaceae	8.8	3
Late	Bignoniaceae	38.1	12
	Combretaceae	18.1	5
	Anacardiaceae	5.9	3

Table 2. Species with the highest Importance Value Index in 2011 in three successional stages of MSSP, Brazil.

Cuadro 2. Especies con los valores más altos del Índice de Valor de Importancia en el 2011 en tres estados de sucesión en el Parque Nacional Mata Seca en Minas Gerais, Brasil.

Early		intermediate		Late	
Species	IVI	Species	IVI	Species	IVI
Myracrodruon urundeuva (Anacardiaceae)	99.06	*Handroanthus reticulatus* (Bignoniaceae)	54.35	*Handroanthus chrysotrichus* (Bignoniaceae)	64.41
Handroanthus ochraceus (Bignoniaceae)	44.21	*Combretum duarteanum* (Combretaceae)	29.68	*Myracrodruon urundeuva* (Anacardiaceae)	31.57
Mimosa hostilis (Fabaceae-Mimosoideae)	24.48	*Commiphora leptophloeus* (Burseraceae)	17.09	*Combretum duarteanum* (Combretaceae)	29.45
Senegalia polyphylla (Fabaceae-Mimosoideae)	19.23	*Terminalia fagifolia* (Combretaceae)	15.73	*Handroanthus reticulatus* (Bignoniaceae)	15.96
Piptadenia oftalmocentra (Fabaceae-Mimosoideae)	10.61	*Pseudopiptadenia contorta* (Fabaceae Mimosoideae)	14.65	*Poincianella pluviosa* (Fabaceae-Caesalpinoideae)	14.03
Prosopis sp (Fabaceae-Mimosoideae)	10.17	*Poincianella pluviosa* (Fabaceae-Caesalpinoideae)	10.77	*Aspidosperma polyneuron* (Apocynaceae)	13.73
Schinopsis brasiliensis (Anacardiaceae)	9.98	*Spondias tuberosa* (Anacardiaceae)	10.14	*Commiphora leptophloeus* (Burseraceae)	12.48
Aspidosperma parvifolium (Apocynaceae)	8.80	*Stillingia saxatilis* (Euphorbiaceae)	9.53	*Terminalia fagifolia* (Combretaceae)	8.54
Senna spectabilis (Fabaceae-Caesalpinoideae)	8.21	*Handroanthus spongiosus* (Bignoniaceae)	8.45	*Cavanillesia arborea* (Malvaceae)	8.23
Platymiscium blanchetii (Fabaceae-Faboideae)	8.02	Patagonula bahiensis (Boraginaceae)	8.40	*Casearia selloana* (Salicaceae)	7.25
Other species	57.23	Other species	121.22	Other species	94.34
Total	300.00		300.00		300.00

the greatest species diversity, even though the late stage had the greatest species richness.

In contrast, the Holdridge Complexity Index (Figure 3), which integrates both dasometric variables (diameter and height) and floristic variables, showed that the early successional stage had a poorly developed structure, even though its HCI increased from 1.0 in 2006 to 9.3 in 2011. The intermediate stage increased in level of complexity by more than 50 units, from 49.3 in 2006 to 102.6 in 2011. The late stage was the most complex forest, increasing from 113.8 in 2006 to 159.3 in 2006; these values exceeded the intermediate stage by 57 units and the early stage by 150 units by 2011.

According to Figure 3, although the late stage appeared to be the most complex, there was no statistical difference with the intermediate stage. Dominant tree height also did not differ between late and intermediate stages ($P<0.050$). Moreover, basal area was significantly different among late, intermediate, and early stages. The early stage also differed from the late and the intermediate stages in canopy height and the Holdridge Complexity Index. The density of stems did not differ statistically among the three successional stages.

By calculating the Jaccard Similarity Coefficient (Cj), we found that the relationship between early and intermediate forest was 0.16, implying that the species shared by both structures were few, and that even fewer species were shared between the early and late stages (0.12). This is in contrast to the relationship obtained between the intermediate and late stages of 0.45, which indicated that both forests shared almost half of their species. The cluster analysis (Figure 4) using Jaccard Similarity Coefficients showed a similar composition of species between the plots of the intermediate and late stages, producing a single cluster. Early plots were separated into another cluster, and differed significantly from the other two stages in terms of species composition.

Mortality and recruitment

The highest mortality occurred in the early successional stage where there were 306 individual trees in 2006, and 202 trees had died by 2011. However, the highest recruitment occurred in the early successional stage with 368 new individual trees. The intermediate stage had 89 dead individuals and 302 recruits, while the late stage had 79 dead individuals and had the lowest number of recruits with 221.

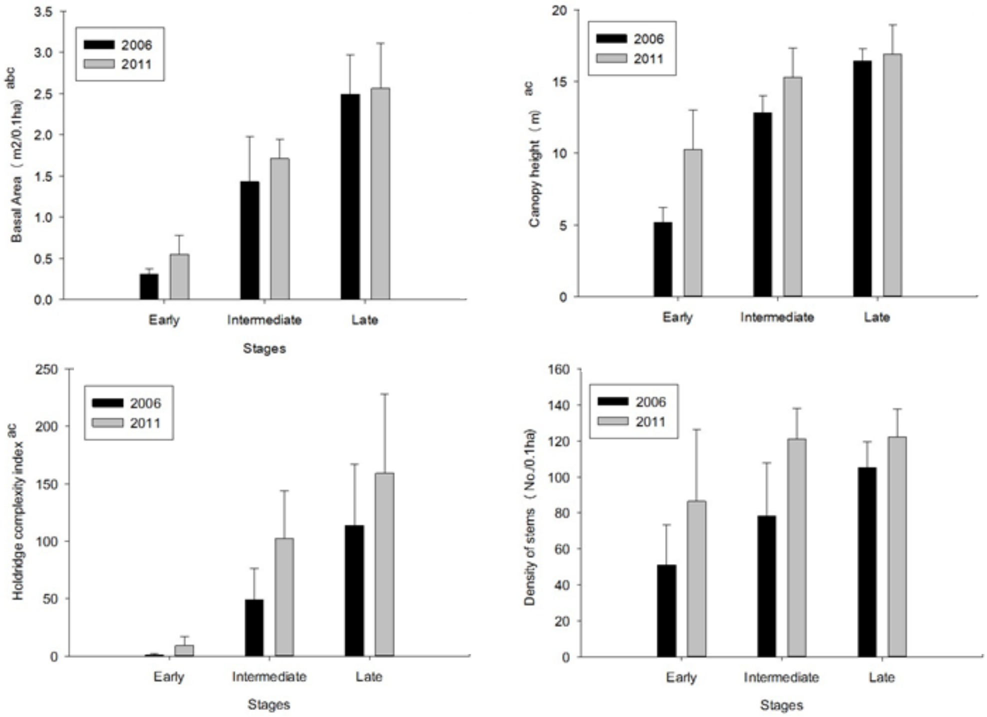

Figure 3. Mean values with standard deviation of the structural characteristics of the stages and the Holdridge Complexity Index. Superscript indicates significant differences using one-way ANOVA. The superscripts indicate significant differences between stages where: a) there is a difference between initial and intermediate stage, b) there is a difference between intermediate and late stage, c) there is a difference between early and late stages.

Figura 3. Valores medios con desviación estándar de las características estructurales de los estados de sucesión y el índice de complejidad de Holdridge. Las letras en superíndice indican diferencias significativas usando una ANDEVA unidireccional. Los superíndices indican diferencias significativas entre las etapas donde: a) hay una diferencia entre el estado temprano y el intermedio, b) hay una diferencia entre el estado intermedio y tardío, c) hay una diferencia entre los estados temprano y tardío.

Mortality rates were significantly higher during the early stage of succession at 9.52 %, in the intermediate stage at 3.61 %, and in the late stage at 2.38 % (Table. 4). The recruitment rate was higher in the early stage where 18.19 % of the total number of individuals in 2011 were new stems, and 13.27 % in the intermediate stage. The late stage had the lowest recruitment percentage with 7.24 %. Mortality increased during the 5 years of measurement (Figure 5). In year 4 (2010), there was an increase in mortality in the early stage; according to information obtained verbally from students who visited those plots that year, a strong wind storm caused falling trees and branches to form canopy gaps in several of the plots in the early and intermediate stages, which would explain the increased mortality for that year.

Figure 6 shows the number of dead stems for size categories in an inverted "J" pattern, where smaller diameter classes had the greatest number of dead stems. Moreover, the mortality in the intermediate and late stages had a very similar pattern. In the size category of 15-20 cm, the curve stabilizes and the number of dead stems in larger diameter categories were reduced to the minimal.

Discussion

The dominance of families and species that comprise tropical dry forests varies between regions. According to Gentry, (1995), continental dry forests are dominated by species of Fabaceae and Bignoniaceae. The Bignoniaceae family was the most dominant in composition and number of species in the late successional stage; in the intermediate stage, Bignoniaceae had the greatest number of individuals, while species of Fabaceae were the most common. In the early stage, Anacardiaceae was the family with the greatest number of individuals and Bignoniaceae was the dominant in number of species. Therefore, Bignoniaceae and Fabaceae deserve special attention for providing the greatest species richness.

Composition and dominance of families that characterized MSSP are similar to results observed in dry forests of Costa Rica, Nicaragua, and elsewhere in Brazil. Gillespie, Grijalva and Farris (2000) found that Fabaceae was the most dominant family in some of the Central American tropical dry forests such as in Guanacaste, Costa Rica (Palo Verde, Santa Rosa) and in Nicaragua (La Flor, Chacocente, Ometepe Island, Masaya National Park, Cosiguina). Coelho, Almada, Quintino et al., (2012) found that species of Fabaceae was the most dominant

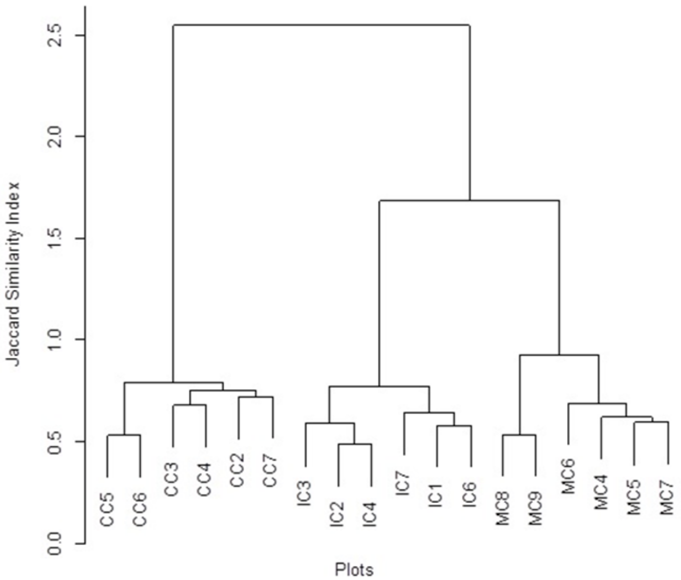

Figure 4. Cluster analysis of Jaccard Similarity Coefficients (similarity in species composition) between the plots of all stages in MSSP in the North of Minas Gerais, Brazil. CC corresponds to the early stage plots, IC the intermediate stage, and M is the late stage forest plots.

Figura 4. Análisis de clusters de los coeficientes de similitud de Jaccard (similaridad en la composición de especies) entre las parcelas de todos los estados en el Parque Nacional Mata Seca en Minas Gerais, Brasil. CC corresponde a las parcelas del estado temprano, IC estado intermedio, y M estado tardío.

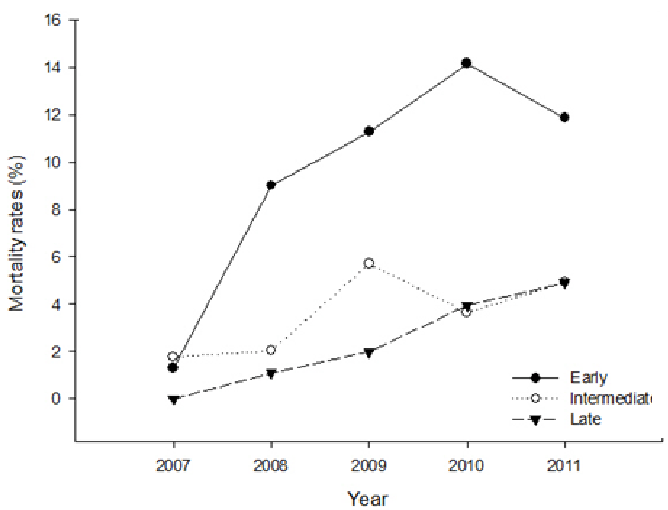

Figure 5. Mortality rates per year between 2006 and 2011 for the three successional stages in MSSP, Minas Gerais, Brazil.

Figura 5. Tasas de mortalidad por año entre 2006 y 2011 para los tres estados de sucesión en el Parque Nacional Mata Seca en Minas Gerais, Brasil.

in a tropical dry forest in southeastern Brazil, moreover Bignoniaceae, Anacardiaceae and Combretaceae were also among the well-represented families.

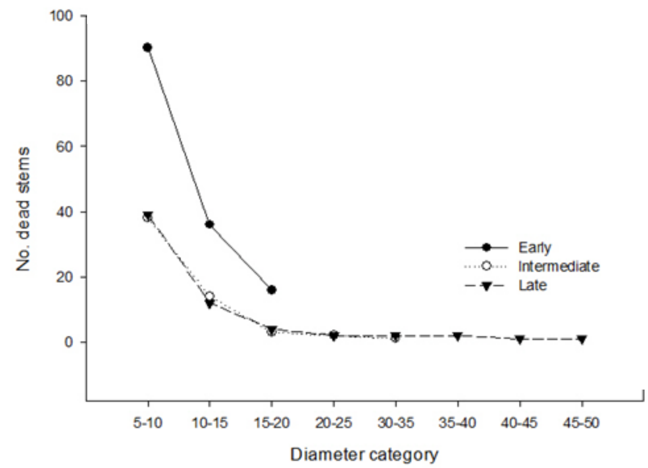

Figure 6. Number of dead stems within the diameter categories found in the three successional stages, MSSP, Minas Gerais, Brazil.

Figura 6. Número de tallos muertos dentro de las categorías de diámetro encontradas en los tres estados de sucesión, en el Parque Nacional Mata Seca en Minas Gerais, Brasil.

For 2011, we found a total of 53 families and 150 tree species in the entire study area (1.8 hectares in total). Kalácska (2004), who used the same methodology for establishing plots for the Tropi-Dry project in the dry forest of Santa Rosa, Costa Rica, found a total of 55 families and 159 species in 2.8 hectares (28 plots from different stages of succession). Quigley and Platt (2003) found a similar number of families and species per hectare in the tropical dry forests of Palo Verde (50 families, 121 species), Chamela (52 families, 137 species) and Guanica (41 families, 103 species).

In the 5-year of sampling period, we perceived some changes in the structure and composition of the successional stages. The number of families and species increased each year in the early stage, and the number of families and species increased in the intermediate stage also but at a lower rate. The number of families in the late stage decreased, indicating that the forest may have been reaching maturity. Madeira et al., (2009) explained that these changes were consistent with the “the relay floristics model” described by Egler (1954), in which a gradual replacement of species is expected over time in forest succession.

The Shannon Diversity Index suggested that by 2011, the most diverse stage was the intermediate successional stage. Kalácska et al., (2004) found similar results using the Shannon Diversity Index in the dry forest of Santa Rosa, Costa Rica, where they found greater diversity in the intermediate stage of succession and lower diversity in the early stage.

Table 3. Average and standard deviation of stem density and basal area in 2006 and 2011 in three successional stages in MSSP, Brazil.

Cuadro 3. Promedio y desviación estándar de densidad de tallos y área basal en el 2006 y 2011 en tres estados de sucesión en el Parque Nacional Mata Seca en Minas Gerais, Brasil.

Year	2006		2011	
Stage	Density of stems (stems ha^{-1})	Basal area (m^2 ha^{-1})	Density of stems (stems ha^{-1})	Basal area (m^2 ha^{-1})
Early	510	3.13 ± 0.06	786	5.31 ± 0.23
Intermediate	782	15.19 ± 0.55	925	16.55 ± 0.24
Late	1053	24.55 ± 0.48	1091	25.34 ± 0.56

Table 4. Percentage mortality and recruitment per year, and the percentage of loss and gain of basal area in three successional stages of MSSP, Minas Gerais, Brasil.

Cuadro 4. Porcentaje de mortalidad y reclutamiento por año, y porcentaje de pérdida y ganancia en área basal en tres estados de sucesión en el Parque Nacional Mata Seca en Minas Gerais, Brasil.

Stage	Mortality (% $year^{-1}$)	Recruitment (% $year^{-1}$)	Loss (% $year^{-1}$)	Gain (% $year^{-1}$)
Early	9.52	18.19	5.84	6.73
Intermediate	3.61	13.27	2.24	7.95
Late	2.38	7.24	1.98	4.39

However, Madeira et al., (2009) obtained different results in MSSP analyzing the same plots with data from 2006, where they concluded that at that time it was the late successional stage that had the greatest diversity. They also concluded that their results were not consistent with the idea of "dominance-controlled communities" (Yodzis, 1986; Begon, Harper and Townsend, 2006; Madeira et al., 2009), which states that early successional stages have low diversity by being colonized by a limited group of pioneer species and that as natural succession progresses, other species invade the area. It is this explanation that describes why the intermediate stages of regeneration are comprised of a large number of species. However, as the forest matures, and the late stage species begin to appear, competition tends to expel species from the early and intermediate successional stages, causing a decline in tree diversity. This model predicts that the intermediate stages will have greater species diversity. Madeira et al., (2009) concluded that a decrease in diversity would be expected during the coming decades in the late successional stage, which was confirmed by our study, where a decrease in the number of families was observed, indicating that the forest was maturing. However, this observation reveals the need for more detailed and longer term studies in different successions of the dry forest.

The early successional stage showed the lowest diversity and greatest dominance by a few tree species. The intermediate stage showed the greatest diversity, but it was also very similar in species composition to the late stage of succession. Madeira et al., (2009) found the same similarity in MSSP, using data from 2006, between the intermediate and the late stages, where they obtained a Morisita-Horn Index of 0.55 (i.e., probability of finding an individual of the same species in a sample of both stages). Moreover, the study also found a greater similarity in species composition between plots of the same stage of succession than from different stages of succession (see figure 4). Furthermore, Madeira et al., (2009) attributed the similarity of the intermediate and late stages of succession by concluding that the sites considered as late forest in these studies (including ours) are more similar in structure and diversity to secondary forests at an advanced stage of succession, given that the recovery time for dry forests in the lowlands can take 150 years (Madeira et al., 2009).

Even though our data suggest that the late stage of succession is the more complex ecosystem, there is no significant difference with the intermediate stage. Following the same protocols as TropiDry, Kalácska et al., (2004) showed that the late stage was the more complex ecosystem in the dry forest of Santa Rosa, Guanacaste, Costa Rica, with a complexity level of 159.0, and that this value exceeded the intermediate stage by more than 90 units. Although, the late stage forest in Santa Rosa has nearly a hundred years old and the intermediate stage around forty (Kalácska et al., 2004) whereas the late stage of MSSP is considered to be around sixty years old, and the intermediate around thirty.

Results in this study demonstrated the species diversity and the complexity of the forest increases through the succession, however there are other factors besides age since abandonment that might influence species density, species richness and rates of recruitment of new species Chazdon, Letcher, van Breugel et al., (2007). It is important to consider for future studies, the landscape context (availability and proximity of seed sources) and the biophysical factors specific to each forest stage or plot (Chazdon et al., 2007; Condit, Ashton, Manokaran et al., 1999).

Mortality and recruitment

It is expected that in more mature forests, mortality and recruitment remain relatively stable over time, given that recruitment depends directly on the mortality rate and is only sufficient to replace the lost biomass (Monge et al., 2002). Therefore, these results reveal that the late successional stage is still going through a dynamic phase of secondary forest succession, where the existing biomass does not reach a point of stability between mortality and recruitment.

Monge et al., (2002) obtained mortality rates of 2.4 % for the Palo Verde dry forest in Costa Rica using measurements from 29 years. Uslar et al., (2004) found that between 1995 and 2002 average mortality rates were 1.98 % for the dry forest of Santa Cruz, Bolivia. However, for pioneer species they reported mortality rates of 100 % and found the highest rates of mortality in pioneer species and understory species (Uslar et al., 2004).

As expected, mortality was higher among trees of smaller diameters, because competition for space is greater due to the higher variety and density of species that occupy or pass through these size categories (Monge et al. ,2002). In contrast, the intermediate and late successional stages tend to have lower rates of mortality, because in more mature forests, mortality stabilizes and the rates decrease with increasing diameters (Condit et al., 1999).

The fact that our study focused on stems higher or equal than 5 cm on DBH helped us perceive the dynamic behaviour of small stems, including changes in abundance, species richness, biomass growth, recruitment and mortality, contrary to studies that focused on diameters greater than 10 cm on DBH (Capers et al., 2005; Chazdon et al., 2007). According to Chazdon et al., (2007) long-term vegetation dynamics studies that include both small and large diametric classes, capture succession events more effectively, making them comparable across regions.

Tropical dry forest succession is still a poorly understood process that deserves additional analysis and monitoring, giving their fragmented and vulnerable status, especially in Brazil. The recovery of these forests is driven by many factors and can last many decades, nevertheless in this study we showed that even in few decades since abandonment, the forest is a highly dynamic and diverse ecosystem, deserving further attention.

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