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ECOSYSTEMS

Vegetation patterns and the influence of rainfall after long-term fire suppression on a woody community of a Brazilian savanna

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Abstract: We evaluated the structural and floristic characteristics of a Brazilian savanna fragment occupied by *cerradão* (CD) and *cerrado sensu stricto* (CS) in response to the influence of rainfall and long-term fire suppression. We carried out floristic, phytosociological and remote sensing studies in a *cerrado* fragment located in Corumbataí (SP, Brazil) after 43 years of complete fire suppression. We surveyed 43 plots of 200 m^2 each (17 plots in CS and 26 plots in CD) and all individuals ≥ 0.32 cm diameter measured at 30 cm from the ground were included in the sample. We calculated phytosociological parameters for each species and classified them in three ecological groups, namely savanna, generalist and forest species. The remote sensing analysis used aerial photographs and satellite images from 1962 to 2019 (i.e. 59 years). The structural study of community revealed high predominance of forest and generalist species when compared to savanna species. Non-linear correlation between CD expansion rates and total rainfall within the study period indicated a positive influence of the rainfall (R^2 = 0.42). Thus, our analysis indicated a tendency of a continuous and fast expansion of CD over areas of CS in the long-term absence of fire combined with periods of heavy rain.

Key words: Competition, ecological succession, local extinctions, microclimate, remote sensing.

INTRODUCTION

The Brazilian tropical savanna, also known as *Cerrado*, is composed by different vegetation types, such as *cerrado sensu stricto* (discontinuous tree cover with a herbaceous shade-intolerant vegetation) and *cerradão* (forest vegetation type) (Furley 1999, Ratter et al. 2006). The dynamics and structure of different vegetation physiognomies in *Cerrado* are mainly influenced by climatic and edaphic factors (Eiten 1972, Goodland & Pollard 1973, Puigdefabregasand & Pugnaire 1999, Wiegand et al. 2006, Meyer et al. 2007, Wright 2007). However, other factors play an important role in the vegetation establishment, namely fire occurrence, soil moisture, geomorphologic and topographic components (Solbrig 1996, Pinheiro et al. 2010, Silva & Batalha 2008, Assis et al. 2011, Silva et al. 2013a, Bueno et al. 2018).

Large-scale fire disturbances frequently affect extensive vegetation areas, favoring the establishment of fire-prone plant species and the occurrence of savanna formations with less woody cover (Coutinho 1990, Hutchings 2007). Conversely, fire suppression in plant savanna communities (Miranda et al. 2009) can influence the natural vegetation dynamics by increasing the prevalence of plant formations with greater coverage of woody plants (Coutinho 1990, Crawley 2007). Indeed, the long-term absence of fire can trigger ecological succession tending to an edaphoclimatic climax of greater phytomass (Pinheiro & Durigan 2009) frequently dominated by fire-sensitive forest species (van der Maarel 1988, Hoffmann et al. 2012, Veldman et al. 2015a).

The *Cerrado* biome suffered a large area reduction in the last decades, but ecologically important patches of native vegetation remain in the state of São Paulo (Siqueira & Durigan 2007, Durigan et al. 2007). Some of them have a history of long-term fire suppression, e.g. a savanna remnants located in the district of Emas, Pirassununga (Coutinho 1990) and Assis Ecological Station, located in Assis (Durigan & Ratter 2006, Pinheiro & Durigan 2009).

The existence of savanna remnants with long-term fire suppression give scope for studying the consequences of fire absence on the floristic composition and vegetation structure. Thus, we evaluated the current floristic and structural characteristics of a savanna remnant with ca. 40 years of fire suppression, located in the Corumbataí municipality (SP, Brazil). In this locality, vegetation descriptions dated from the 1960s and 1970s indicate the dominance of open-savanna environments (Camargo & Arens 1967, Piccolo et al. 1971). No information is available on the structural and floristic data in this period.

In addition to the wildfires, periods of intense rainfall in savanna-forest ecotones can greatly influence the expansion of forest formations (Bowman et al. 2001, Banfai & Bowman 2005). Therefore, good conditions for forest expansion over savanna areas involve the combination of rainy periods and fire suppression (Brook & Bowman 2006, Ondei et al. 2017).

We expected that forest and generalist species would benefit from long-term fire suppression and higher water availability (Pinheiro et al. 2010) when compared to savanna species. Therefore, we expected an increase in woody cover, a pattern observed in other regions of Brazil (Durigan & Ratter 2006, Hoffmann et al. 2012). We also expected an encroachment of *cerradão* over areas of *cerrado sensu stricto* during periods of heavy rain, i.e. changes in the structural and floristic composition of the plant community due to the predominance of non-savanna species.

MATERIALS AND METHODS

Study area

The survey occurred in a *cerrado* fragment belonging to *Instituto de Biociências* of UNESP, *campus Rio Claro*. The study area is named *Reserva de Cerrado* "Prof. Karl Arens" and is located on the steep slopes of the Corumbataí municipality (SP, Brazil) (22º14'21.68" S - 47º40'52.85" W and 22º14'41.71" S - 47º41'14.80" W), in the transition between *Depressão Periférica Norte* and *Cuestas Basálticas* (Troppmair 2000). The *cerrado* fragment in Corumbataí has 38.8 ha and has been isolated for many years from other natural plant formations by pastures and sugar cane plantations. The study area has been effectively protected against cattle entrance and wood removal since the land purchase by UNESP in 1962. According to some university employees, fires no longer occurred after the property was purchased.

The climate is tropical humid with a dry (April – September) and wet (October – March) season. According to Köppen, the climate is Cwa (Alvares et al. 2014). The soil was classified as Red-Yellow Latosol, sandy phase, according to the classification adopted by Tauk & Marco (1990). The area has groundwater located 30 m below the surface (Camargo & Arens 1967). The nearest remnants of native vegetation were composed by seasonal forests on the top of hills and slopes and located a few kilometers away from the study area.

Previous descriptions of the vegetation in the study area by Camargo & Arens (1967) and Piccolo et al. (1971) indicate a dominance of open-savanna environments until the early 1970s. These authors did not provide detailed structural and floristic characteristics of the study area nor mentioned the occurrence of non-savanna species. The latter is a coherent information due to the predominance of heliophilous environments, where herbaceous-shrub species have been abundant, as described by these authors.

In our study period, the *cerradão* dominated almost the entire reserve “Prof. Karl Arens” and *cerrado sensu stricto* was restricted to a smaller area. We describe *cerrado sensu stricto* as a vegetation presenting 20 to 30% of woody cover, which varies from 3 to 8 m in height, and *cerradão* as a vegetation that has a forest aspect with a height ranging from 12 to 15 m (Furley 1999, Ratter et al. 2006). *Cerradão* vegetation predominantly occurs in deep, sandy, dystrophic, acid soils, and in regions where the annual rainfall is lower than 1600 mm (Eiten 1972, Coutinho 1990, Solbrig 1996, Pennington et al. 2006, Ratter et al. 2006). Representatives of the herbaceous community in the study area are *Aristida pallens* Cav. (Poaceae), *Solanum aculeatissimum* Jacq. (Solanaceae) and species of the genus *Sida* L. (Malvaceae) and *Cyperus* L. (Cyperaceae).

Experimental design

The structural and floristic data used in this study were obtained from a phytosociological survey concluded by us in 2005, after 43 years without fire in the study area. We installed 43 plots measuring 200 m^2 (10 m x 20 m) along a topo-edaphic gradient. The plots were positioned in a continuous way reaching 860 m in length and encompassed both vegetation physiognomies: *cerrado sensu stricto* located in the lower part of the area (17 plots) and *cerradão* located in the upper part (26 plots). The soil in the upper part of the area was mainly composed by clay and silt, while particles of fine and coarse sand were predominant in the lower part (see Pinheiro et al. 2010). We measured the diameters and heights of all tree-shrub individuals with diameter of ≥ 0.32 cm, measured at 30 cm from the ground.

When the specimens presented flowers and fruits, samples were collected and included in herbarium - *Herbário Rioclarense* (HRCB). The correct spelling of the scientific names, as well as the abbreviations of the authors’ names and the existence of synonymy were checked in floristic lists available in the website reflora.jbrj.gov.br - *Programa Reflora*.

We analyzed aerial and Landsat images to evaluate the expansion or retraction of each vegetation type. Thus, the visual interpretation of aerial photographs and Landsat images was performed using the hierarchical land use and land cover classification system (Anderson et al. 1976). That procedure classifies land use types at different levels of detail, i.e. relates each level of classification to the types of remote sensing data used. Thus, the caption of the *Cerrado* physiognomies map was assigned according to the assumptions made by Pereira et al. (1989) and Spínola et al. (2007), where the *cerrado sensu stricto* and *cerradão* physiognomies were identified based on color (tone), shape and texture of the objects distributed across the studied area.

Thus, the *cerrado sensu stricto*, observed in both aerial and satellite images, presented less intense hue and less roughness when compared to the *cerradão*, which has a more prominent color and texture. For the more accurate determination of each physiognomy in the Landsat Satellite images, we performed another process that resulted in vegetation index images. Vegetation indices have satisfactorily indicated the leaf phytomass by area (Pereira et al. 1989). Thus, the normalized vegetation index (NDVI) was used to delimit the two savanna physiognomies analyzed (Rouse et al. 1973). This index can be expressed by the following equation:

$$NDVI = (NIR - R) / (NIR + R)$$

where: NIR = near infrared (Band 4), R = red (Band 3). This index ranges from -1 to 1, depending on the vegetation density. Negative values represent bare soils, whereas dense forests will present values closer to 1 (Bitencourt et al. 1997). According to the same authors, *cerrado sensu stricto* physiognomies presented NDVI values between 0.2630 and 0.3813, while *cerradão* presented NDVI indices ranging from 0.4406 to 0.5589. Thus, the two *Cerrado* physiognomies could be differentiated and mapped.

The maps showing the areas occupied by *cerradão* and *cerrado sensu stricto* of the study area along 57 years were elaborated based on aerial photographs of 1962 (scale = 1:25000), 1972 (1:25.000), 1978 (1:35.000), 1988 (1:40.000), 1995 (1:25.000) and 2000 (1:30.000), by using a mirror stereoscope. The aerial photographs were taken by the BASE *Aerofotogrametria e Projetos AS* company, except those from 1972 and 1978, which were the responsibility of IBC/GERCA company. Images from the satellites LANDSAT for the years of 2005 (LT5), 2010 (LT5), 2015 (LC8) and 2019 (LC8) were also used in this study and were provided by United States Geological Survey (USGS) (Figure 1).

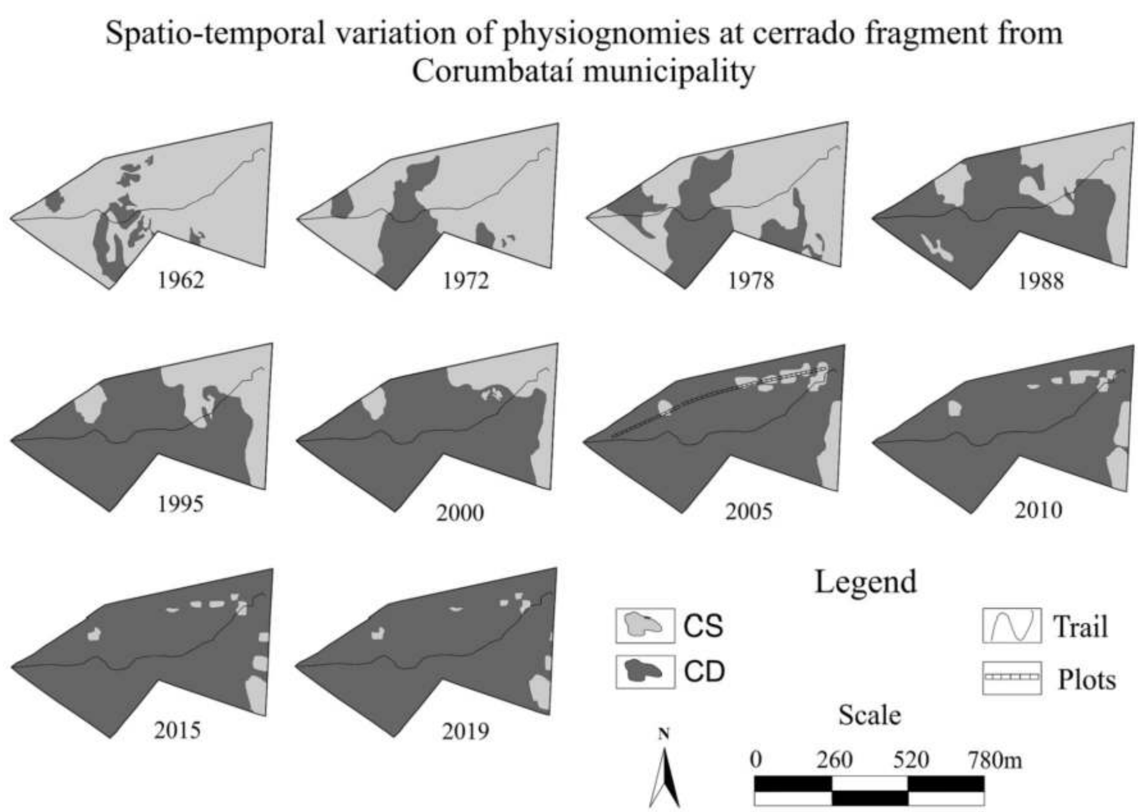

Figure 1. Spatio-temporal variation of *cerradão* (CD) and *cerrado sensu stricto* (CS) physiognomies in a cerrado fragment located in Corumbataí (State of São Paulo, Brazil) along 57 years (1962 to 2019) of fire suppression.

Data analyses

We obtained phytosociological parameters for each species by using the software FITOPAC 2.1 (Shepherd 2009), namely relative density, frequency and dominance. The Importance Value Index (IVI) resulted from the sum of these parameters (Mueller-Dombois & Ellenberg 1974). The values were obtained by following the equations below:

$$DeR = n_i / \Sigma n \times 100$$

$$FeR = F_i / \Sigma AF \times 100$$

$$DoR = BA_i / \Sigma BAt \times 100$$

where: DeR - relative density; ni - number of individuals sampled from species i; n - total number of individuals sampled; FeR - relative frequency; Fi - absolute frequency of species i; AF - absolute frequency of all sampled species; DoR - relative dominance; Bai - basal area of species i; BAt - total basal area; IVI = DeR + FeR + DoR (Damasceno-Junior & Pott 2011).

The frequency of height and diameter classes were presented in histograms to analyze the age structure of the community and recruitment patterns (Newton 2007), following the method used by Spiegel & Stephens (2009).

We have considered the concept *fidelity to communities* (Braun-Blanquet 1979) when analysing the structural and floristic changes in the study area. This concept represents the degree of fidelity of plant species to a particular vegetation physiognomy, directly influenced by the physical-chemical conditions of the habitat and by the species' ability to get resources under competition. This concept is useful to discuss the temporal changes we have observed in our study (Grime 1979, van der Maarel 2005), since it highlights species that have similar performance in the ecosystem, based on a common set of biological attributes (van der Maarel 2005). We classified plant species in three ecological groups, namely forest, generalist and savanna species (Felfili et al. 2006, Andersen et al. 2007, Parr et al. 2012, Villard & Metzger 2014). Savanna and forest species are restricted to specific habitat conditions, depending on fire occurrences and light availability (Hoffmann et al. 2012, Pellegrini et al. 2016). Conversely, generalist species may grow under a wider range of conditions due to their high phenotypic plasticity (Maracahipes et al. 2018). We have assumed that species restricted to specific habitats are better indicators of environmental changes, since they are more susceptible to disturbance (Cáceres & Legendre 2009).

Our classification in three ecological groups was based on species habitats, available on the website of *Flora do Brasil* 2020 - *Programa Reflora* (reflora.jbrj.gov.br/reflora). Data validation and additional information were obtained from other sources (Rizzini 1971, Heringer et al. 1977, Leitão Filho 1992, Mendonça et al. 1998, Castro et al. 1999, Ratter et al. 2000, 2003, 2006, Durigan et al. 2004, IPJBRJ 2010a, b).

We calculated the area (in hectares) occupied by the two vegetation physiognomies along 57 years, and we plotted trend curves of *cerrado sensu stricto* retraction (exponential) and *cerradão* expansion (logarithmic) over the study period (Figure 2). We performed non-linear correlation analysis (Bates & Watts 1988, Mazucheli & Achcar 2002) between total rainfall (independent variable) and expansion rates of *cerradão* (dependent variable) in nine periods (1962-1971, 1972-1977, 1978-1987, 1988-1994, 1995-1999, 2000-2004, 2005-2009, 2010-2014, 2015-2019) – see Pinheiro et al. (2010) for more details. In our study, we assumed that the long-term fire suppression and rainfall were important factors to the encroachment of *cerradão* over areas of *cerrado sensu stricto*.

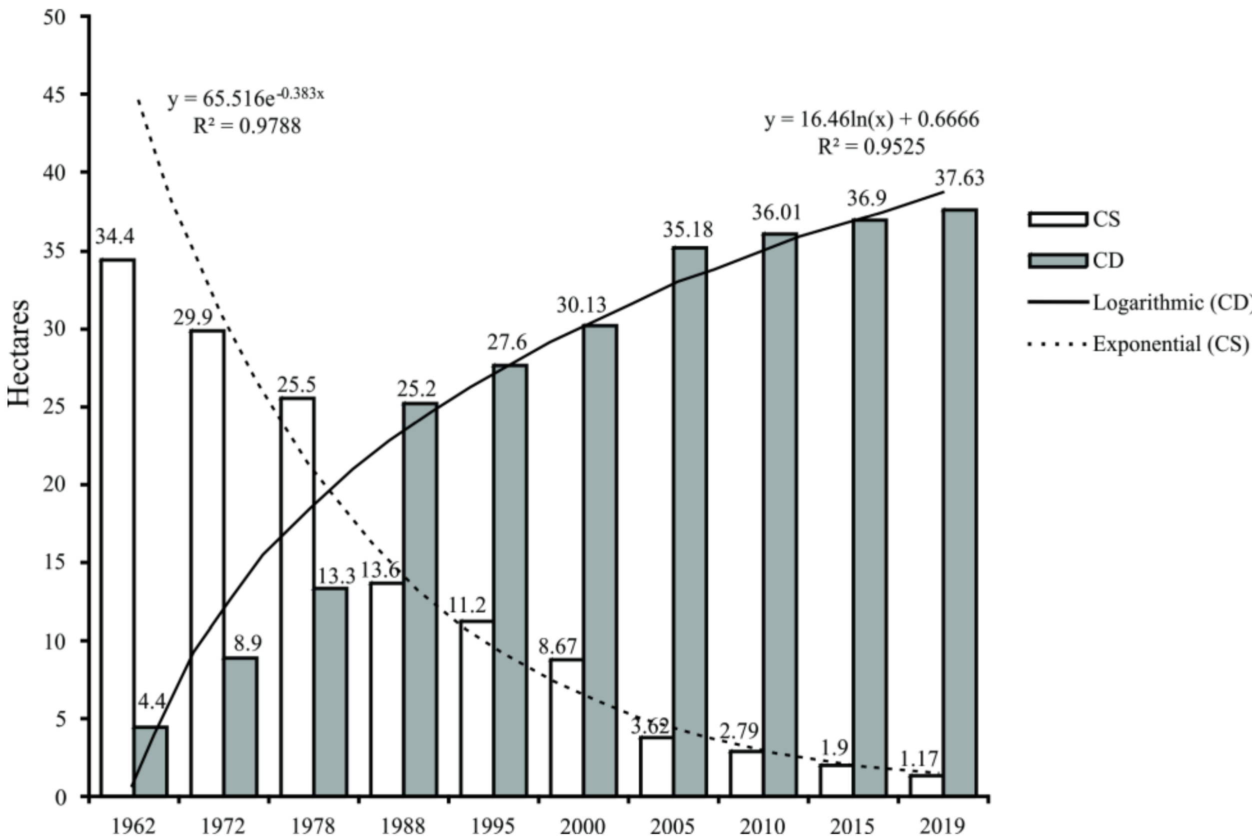

Figure 2. Variation of the area (hectares) occupied by *cerradão* and *cerrado sensu stricto* in a cerrado fragment in *Corumbataí* (State of São Paulo, Brazil) during 57 years of fire suppression.

RESULTS

Composition and structure of vegetation

Our phytosociological survey sampled 11,507 individuals from 103 different species and 43 families (generalists: 66 spp. and 7,951 individuals; savanna: 27 spp. and 456 individuals; forest: 9 spp. and 3,099 individuals) (Table SI – Supplementary Material). The sum of the IVI species of the same ecological group highlighted their importance for the studied community: generalists (IVI = 223), forest species (49) and savanna (28). The five most numerous and important species were *Daphnopsis fasciculata* (IVI= 2,514 individuals), *Amaioua guianensis* (1,452), *Copaifera langsdorffii* (831), *Miconia chartacea* (769) and *Ocotea pulchella* (644). The former species presented greater relative density (21.85) and was classified as a forest species, while the other four species were generalists.

The same species described above represented about 50% of the total number of the sampled individuals, and presented high values for relative frequency, indicating species occurrence in several plots. Other species were also notable for the significant relative frequencies, e.g. *Anadenanthera falcata*, *Myrsine umbellata*, *Schefflera vinosa*, *Siparuna guianensis* and *Virola sebifera*. On the other hand, some species were abundant in few plots, e.g. *Baccharis dracunculifolia*, represented by 44 individuals occurring in four plots, with 40 of them sampled in a single plot of *cerrado sensu stricto.*

Among the savanna species, *Q. grandiflora* presented the highest IVI value, which is far below the values presented by the five most important forest and generalist species (Figure 3). These results highlight the level of importance of forest species and generalists when compared to savanna species in the study area.

More than half of the total sampled species, i.e. 58 species or 56.3% of the total species found in the survey, were represented by populations with up to 10 individuals. Most of the savanna species presented populations with few numbers of individuals, i.e. 21 species or 77.8% of the species belonging to this ecological group sampled, e.g., *Aspidosperma tomentosum*, *Guapira noxia*, *Pouteria ramiflora* and *Stryphnodendron polyphyllum*. These species accounted for only 7.05 of the total IVI, so that the sum of their population resulted in 83 individuals or 0.72% of the individuals sampled in the 43 plots. The most abundant families were Thymelaeaceae (2,514 individuals), Rubiaceae (1,875), Myrtaceae (1,215), Melastomataceae (1,103) and Fabaceae (873), which accounted for 66% of the total specimens sampled. Thymelaeaceae was more abundant due to the large number of individuals of *D. fasciculata*.

Height and diameter averages of sampled individuals were 3.8 m (± 2.3 m) and 3.9 cm (± 4.4), respectively. In our survey, only 2.2% of the individuals presented height ≥ 10 m, and 1.3% presented diameter > 14 cm, once we have included woody individuals with a minimum height of 1.5 m in our samples. Most of the sampled individuals was concentrated in the two first classes of height and diameter: 53.3% and 94.62%, respectively (Figure 4). The contribution of individuals belonging to forest and generalist species to the detriment of savanna species was remarkable. These are important indicators of the competitive advantage of fire-sensitive species after four decades of fire suppression. In the study area, generalist and forest species accounted for 95% and 96.6% of the total individuals included in the first class of height and diameter, respectively. The last six classes of height comprise a little less than 4% of the sampled individuals, i.e. few individuals are taller than 10 m. All classes of height presented individuals, while four classes of diameter did not, specifically classes of diameter > 50cm (Figure 4). The generalist species *Ocotea acutifolia* (13 and 14 m) and *C. langsdorffii* (14.5 m), and forest species *D. fasciculata* (13.5 and 14 m) presented the tallest individuals. With many individuals, *D. fasciculata* also presented the specimens with thick trunks. Forest species *Siphoneugena guilfoyleiana* (individuals with 37.2, 38 and 39 cm), and the generalist species *A. guianensis* (39.5 cm) and *C. langsdorffii* (80.2 cm) also presented the highest values for trunk diameter. These results pointed out the degree of efficiency of this species in occupying the study area. As for the other forest species used as examples, the maximal values for height and diameter of the arboreal *Calyptranthes clusiifolia* and *Rudgea sessilis* were 9 m and 12.7 cm, and 7 m and 14.3 cm, respectively.

Changes in composition and structure of vegetation over 57 - years period

The sequence of images over a 57-year period showed an efficient expansion of *cerradão* in the study area after long-term fire suppression (Figure 1). The *cerradão* encompassed 4.4 ha of the remnant area in 1962 and 37.63 ha in 2019 (Figure 2), representing 97% of the study area The mean annual rates of *cerradão* expansion from the temporal series studied was 0.53 ha (± 0.4). This expansion, according to the non-linear regression analysis (Figure 5), presented a positive correlation with the total rainfall (R^2 = 0.42), suggesting the influence of water availability for the *cerradão* expansion over areas of *cerrado sensu stricto* when wildfires are absent.

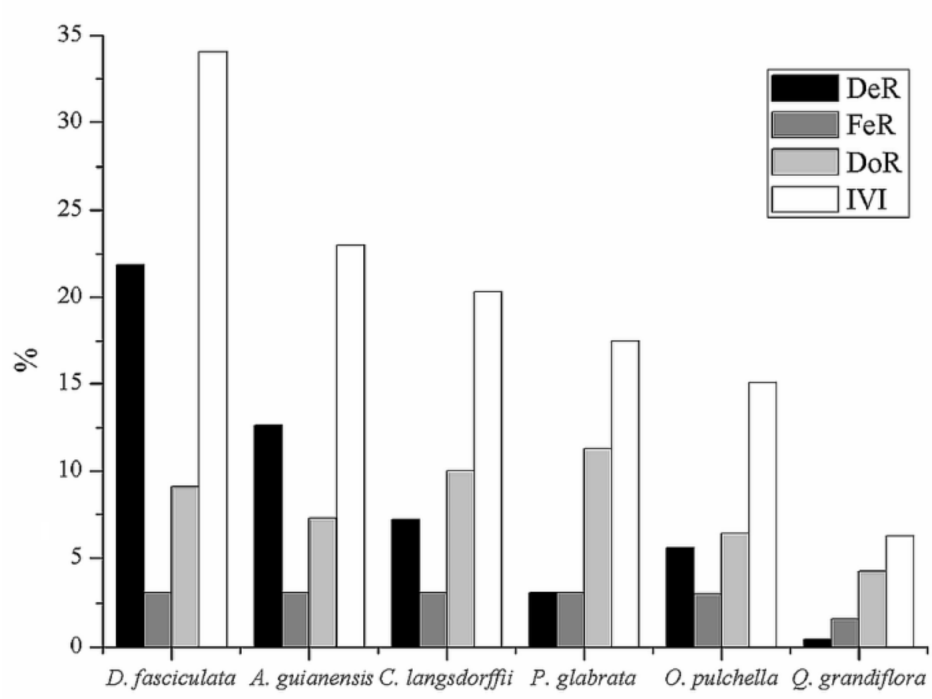

Figure 3. **Phytosociological parameters (relative density - DeR, relative frequency - FeR, relative dominance - DoR, importance value index - IVI) of the five most important species: *Daphnopsis fasciculata*, *Amaioua guianensis*, *Copaifera langsdorffii*, *Pera glabrata*, *Ocotea pulchella.* The savanna species with the highest value for IVI (*Qualea grandiflora*) is also shown for comparison.**

DISCUSSION

Composition and structure patterns

Generalist species accounted for 69.1% of the sampled individuals and played an important role in the vegetation cover increase along the period of fire suppression (Pinheiro et al. 2010). During the first stages of ecological succession, the high richness and abundance of generalist species may have facilitated the colonization by forest species. An explanation for the predominance of the generalists in our study is possibly related to the common phenotypic plasticity within species of this ecological group (Johnson et al. 1996), conferring them a certain advantage in the colonization of new areas (Agrawal 2001), and a greater resistance to environmental variation (Gratani 2014).

The predominance of forest individuals, represented by 26.9% of the sampled specimens indicates a positive effect of fire suppression to forest species, e.g. *D. fasciculata* that accounted for 21.8% of the sampled forest species. On the other hand, fire suppression has negative consequences for fire-prone species, i.e. savanna species. The latter should have occurred in greater number in the study area until the early 1960s (Pinheiro et al. 2010), decreasing over time due to the long-term fire suppression. Indeed, vegetation descriptions of the study area made by Camargo & Arens (1967) and Piccolo et al. (1971) show the dominance of open-savanna environments. The observed successional pattern has similarity with the Relay Floristics principle (Egler 1954), not only for the loss of species groups, but also for the possible influence of invasive forest species during the process (Pulsford et al. 2016).

As expected, we have observed an encroachment of *cerradão* over areas of *cerrado sensu strict*. Our observations corroborate with results related to the expansion of forest formations in other areas of *Cerrado* in Brazil, e.g. central West Brazil (Ratter 1992, Geiger et al. 2011) and in the world, e.g. tropical savannas (Murphy & Bowman 2012, Stevens et al. 2017). An

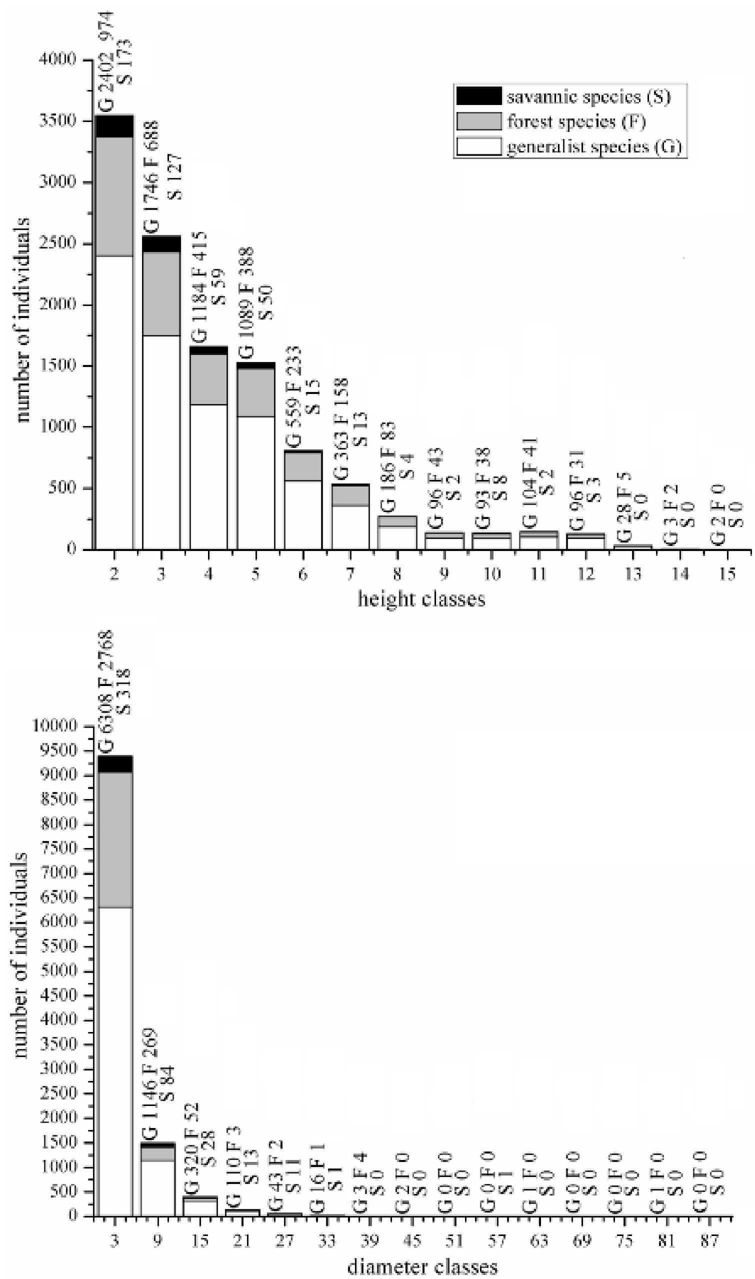

Figure 4. **Number of sampled individuals (ordinates) in different classes of height (in meters) and diameter (in centimeters).**

explanation for the forest expansion during the long-term absence of fire in cerrado fragments considers the vegetation itself as a fire barrier during the ecological succession (Silva et al. 2013b, Rossatto & Rigobelo 2016). Nevertheless, we have also to consider that the forest expansion in savanna areas with long-term fire suppression will depend on other factors, e.g. edaphic nutrients, e.g. Mg, Ca and P (Hoffmann et al. 2009, Pinheiro et al. 2016).

When it comes to the reproduction of plants in the study area, the frequencies of height and diameter classes indicate that population renewal is occurring efficiently. Indeed, the number of individuals in the first classes of height (3,549 sampled individuals, or 31% of the

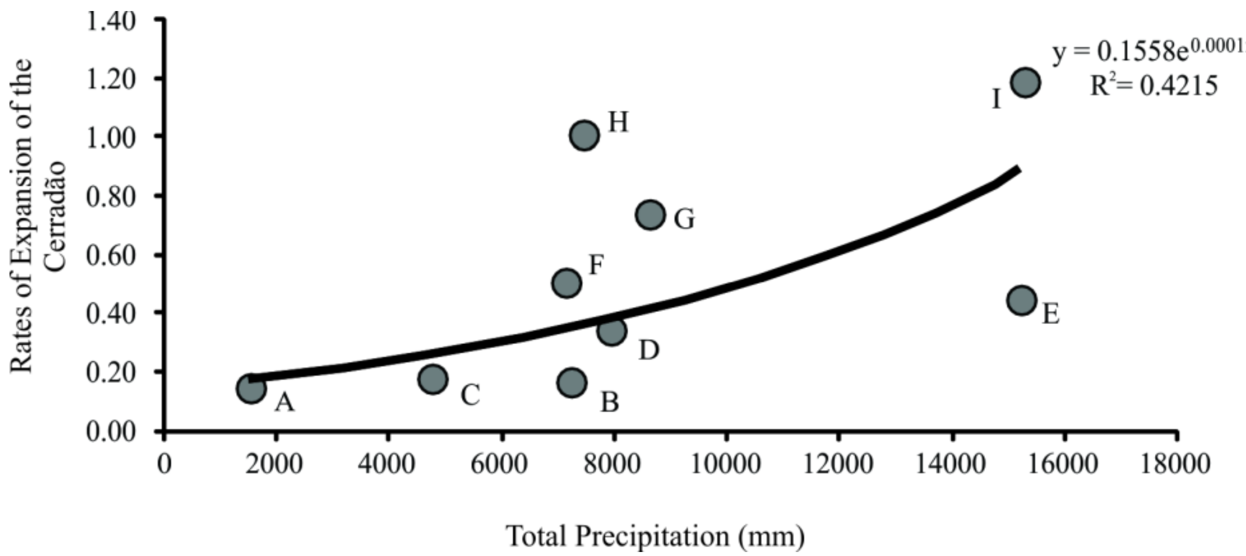

Figure 5. Non-linear correlation between total precipitation (independent variable) and rates of expansion of the *cerradão* (dependent variable) in nine periods: 2015-2019 (A), 2005-2009 (B), 2010-2014 (C), 1988-1994 (D), 1962-1971 (E), 1995-1999 (F), 1972-1977 (G), 2000-2004 (H), 1978-1987 (I).

total of the sampled individuals) and diameter (9,394 sampled individuals, or 81.6% of the total of the sampled individuals) indicates the great competitive advantage that forest and generalist species have presented during four decades of fire suppression. Both ecological groups accounted together for 95.1% (generalists - 67.7%; forest - 27.4%) of the individuals in the first class of height, while accounted for 96.6% (generalists - 67.1%; forest - 29.5%) of the individuals in the first class of diameter.

Factors influencing forest expansion

The results of our work provided important indications on the influence of rainfall for the expansion of forest formations through savanna areas in the long-term absence of fire. Likewise, we provided relevant information about the negative consequences for savanna vegetation under long-term fire suppression.

The effective long-term fire suppression regime and the edaphic water retention capacity due to higher percentage of silt and clay, favored the expansion of the *cerradão* over areas of *cerrado sensu stricto* (Pinheiro et al. 2010). Accordingly, our findings on the structural and floristic data demonstrated an increase of 90.7% (in 2005) of *cerradão* over *cerrado sensu stricto* in little more than four decades (Figure 2). Similarly, Pinheiro & Durigan (2009) showed an increase of 38% of *cerradão* over *cerrado sensu stricto* in another *cerrado* fragment in São Paulo state under long-term fire suppression (44 years). Other important indicator of the *cerradão*'s expansion capacity in the study area is its expansion rate (0.53 ha $year^{-1}$), which is faster than the one found by Couto-Santos et al. (2014; 0.13 ha $year^{-1}$) in a forest-savanna mosaic in the Amazon region. In the latter study, the authors also found a positive influence between forest expansion and precipitation. The Amazon region presented higher annual average rainfall (1,657 mm - average for 98 years) than the Corumbataí region (1,341 mm - average for 30 years; data from *Núcleo de Monitoramento Agroclimático* - NURMA).

The fast expansion rate of the *cerradão* contributed to explain the significant differences between our findings and the first descriptions of the vegetation in the study area (Camargo & Arens 1967, Piccolo et al. 1971). Furthermore, Camargo & Arens (1967) mentioned the presence of some savanna species that we have not reported systematically or opportunistically in our survey, such as *Anacardium nanum* A.St.-Hil. (Anacardiaaceae), *Kielmeyera corymbosa* Mart. & Zucc. (Calophyllaceae) and *Palicourea rigida* Kunth (Rubiaceae). Therefore, the decline of the light intensity due to increased canopy cover along 57 years of fire suppression (Figure 1) may have hindered *cerrado sensu stricto* species (Pinheiro & Durigan 2009, 2012).

In our study, we demonstrated that the total rainfall have influenced the expansion of *cerradão* when fire was absent, explaining 42% of the dependent variable. Other potential independent variables are the water retention capacity of the soil (Pinheiro et al. 2010) and the ability of forest species to increase soil nutrient availability during plant succession in the absence of fire (Silva et al. 2013b).

The decrease of light intensity, imposed by the increase of woody cover in the study area, may have interfered in the growth of seedlings and reproduction of heliophile species. Thus, savanna species adapted to less dense savanna physiognomies must have passed through a setback during the *cerradão* expansion. One of the greatest adversities faced by savanna species in shaded environments is the continuous investment of more resources in the development of the root system when compared to the stalk structure (Franco 2002). As a result, the survival of heliophile species in environments with greater woody cover may be hampered (Durigan & Ratter 2006). Low light intensity compromises species reproduction, including those commonly found in *cerradões,* e.g. *E. gracilipes* and *V. tucanorum* (Barbosa et al. 1999, Ronquim et al. 2003). Thus, the increase of woody cover compromises the establishment of savanna species, which need greater light intensity, and benefits forest and generalist species.

The long-term absence of fire, combined with periods of heavy rain, were essential for the expansion of the *cerradão* and the decline of savanna-plant populations in the *cerrado* fragment in Corumbataí. By carrying on the fire suppression regime, the study area may be totally occupied by the *cerradão* in a few years, with local extinction of savanna species, as a result of the current environmental conditions. Our greatest concern is the negative effects of the long-term fire suppression on the savanna remnants and their biodiversity (Bond & Parr 2010, Veldman et al. 2015b).

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SUPPLEMENTARY MATERIAL

Table SI. Phytosociological parameters of the species sampled in the savannic community of Corumbataí (SP - Brazil). Notations: Individual number (IN); relative density (DeR); relative frequency (FeR); relative dominance (DoR); importance value index (IVI); ecological groups (EG); forest species (F); generalist species, (G); savanna species (S).

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