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Construção de comunidade vegetal em restauração ativa de savana

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Resumo

Ainda existem vários desafios para a restauraçao de savanas, e entender as trajetórias temporais da comunidade em restauração é uma informação crucial para aprimorar técnicas de restauração. Modelos de construção de comunidades em savanas geralmente consideram apenas a regeneração natural após distúrbios naturais, quando espécies conseguem se regenerar por rebrota, e geralmente focam na sucessão entre estrato herbáceo e, arbustivo e arbóreo. Porém, em áreas severamente degradadas, a capacidade de rebrota é perdida, árvores podem demorar bastante tempo para ter influência nas dinâmicas da vegetação, e espécies invasoras podem dificultar a regeneração. Este estudo teve como objetivo investigar trajetórias iniciais de sucessão, identificando grupos funcionais de espécies nativas (arbustos e gramíneas de crescimento rápido e ciclo curto, gramíneas perenes, e árvores nativas) importantes para regeneração, em restauração ativa de savana no Brasil, numa área de pasto abandonado. Nós buscamos responder às perguntas: a proporção relativa final de nativas depende da proporção inicial? A trajetória sucessional depende do grupo funcional dominante inicialmente? Existe uma substituição de espécies?Nós estabelecemos 111 parcelas na área em restauração, abrangendo diferentes composições iniciais de espécies e grupos funcionais, e medimos a cobertura vegetal durante dois anos. No primeiro ano de monitoramento, os arbustos de ciclo curto e crescimento rápido *Lepidaploa aurea*, *Stylosanthes spp.* e o capim anual *Andropogon fastigiatus* estavam entre as seis espécies com maior cobertura vegetal, mas diminuiram 69%, 78% e 100%, respectivamente, nos dois anos seguintes. Parcelas dominadas por essas espécies foram substituídas principalmente por gramíneas perenes nativas (58% das parcelas), mas também por gramíneas invasoras (22% das parcelas). Parcelas dominadas por gramíneas nativas perenes seguiram diferentes trajetórias: 28% continuaram estáveis, 28% foram substituídas pela árvore de crescimento rápido *Tachigali vulgaris*, enquanto 36% foram substituídas por composições sem dominância de um único grupo funcional. 74% das parcelas dominadas por gramíneas invasoras (cobertura ≥ 80%)não teve mudança significativa na cobertura vegetal. Gramíneas invasoras aumentaram consideravelmente, atingindo mesma cobertura de nativas após dois anos.. Ainda, aumentaram cobertura relativa em mais parcelas que nativas (72 x 38 parcelas), chegando à substituir 91% da cobertura de nativas, enquanto a maior substituição de exóticas por nativas foi de 44% da cobertura relativa da parcela. Nosso estudo evidencia a ocorrência de trajetórias sucessionais com substituição de espécies de ciclo de vida curto por espécies perenes. Também ressalta a importância do controle de gramíneas invasoras antes da semeadura, que podem invadir novamente caso o banco de sementes não seja adequadamente eliminado.

Palavras-chave: semeadura direta, substituição de espécies, grupos funcionais gramíneas exóticas invasoras, sucessão, efeito de prioridade

Abstract

There are still many gaps to the restoration of savannas, and understanding community trajectories in areas under restoration is a key information to improve restoration methods. Most assembly models for savannas consider only regeneration after natural disturbances, when species are able to resprout, usually focusing on succession from herbaceous to tree layer. However, in severely disturbed areas, resprouting ability is lost, trees may take a long time to influence on vegetation dynamics, and invasive species may reduce regenerationThis study aimed to track initial successional trajectories, and identify functional groups of native species (fast growing and short-lived shrubs and grasses; perennial grasses; and native trees) relevant to regeneration, in restoration of savanna in Central Brazil on abandoned pasture. We aimed to answer the questions: is final relative proportion determined by initial relative proportion? Is successional trajectory dependent on the initial dominant functional group? Are there species turnover in the successional trajectories? We established 111 plots encompassing a range of different initial compositions of species and functional groups, and measured vegetation cover during two years. In the first year of monitoring, the short-lived and fast-growing shrubs *Lepidaploa aurea, Stylosanthes spp.* and the annual grass *Andropogon fastigiatus* were among the six species with higher vegetation cover, but decreased 69%, 78% and 100%, respectively, in the following two years. Plots dominated by these species were replaced mostly by perennial grasses (in 58% of the plots), but also by invasive grasses (in 22% of the plots). Plots dominated by native perennial grasses followed different trajectories: 28% remained stable; 28% were replaced by *Tachigali vulgaris*, a fast-growing tree; 36% were replaced by a composition of mixed functional groups. 74% of the plots dominated by invasive grasses (cover ≥ 80%) didn’t have significant variation on vegetation cover. Invasive grasses strongly increased cover in the restored area, reaching same cover of native species after two years. They also increased relative cover in more plots than the natives (72 x 38 plots), and were able to replace up to 91% of native cover, whereas native species were not able to replace more than 44% of exotic relative cover in any plot. Our study evidence successional trajectories in restoration of savanna in abandoned pasture, with fast species turnover from short-lived to perennial species. We also highlight the importance of pre-sowing control of invasive grasses, which can reinvade the restored area if seed bank is not adequately eliminated.

Keywords: direct seeding, species turnover, functional group, invasive exotic grass, succession, priority effect

Sumário

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Introduction

Understanding the assembly triggers and trajectories of ecosystem undergoing restoration is essential to improve restoration methods (Suding and Hobbs, 2009). Achieving restoration goals may require implementing different management steps to drive ecosystem into desired assembly trajectories. It may involve recreating physical and chemical conditions, eliminating and controlling invasive species, and planting different functional groups to recreate successional stages, thus reconstructing community structure and biodiversity (Clewell and Aronson, 2007). There is growing consensus that community assembly is not deterministic, and can follow different trajectories, determined by biotic, abiotic, and dispersion filters, and by historical events (Fukami, 2015; Young et al., 2014). Therefore, to understand why a restoration project achieved or not the target goals, it is important to understand community assembly pathways, to access the determinants of success or failure and plan adaptive management.

There is still plenty discussion about savanna trajectories after disturbance. Most studies of succession in savannas focus on the determinants of the balance between trees and grasses. Soil conditions, rainfall seasonality (Lehmann et al., 2011), and frequency and intensity of disturbances, notably fire (Bond and Keeley, 2005; Hoffmann et al., 2012) and grazing (Jacobs et al., 1999), are important factors to the structure of savannas, selecting functional groups with best fitness for each condition. It is well known that savanna species evolved with these disturbances, resulting in adaptations to protect regenerative tissues, such as large belowground organs and thick bark (Simon et al., 2009); (Lawes et al., 2011), thus allowing to resprout after disturbance (Souchie et al., 2017). Eliminating this resprouting potential, as in intensive agriculture, pasture or mining areas, prevents regeneration and diminish savanna resilience, often requiring active restoration (Ferreira et al., 2015); (Ferreira and Vieira, 2017); (Cava et al., 2017). Successional models for savannas do not consider situations in which the bud and seed bank were extinguished (Veldman et al., 2015). Also, species autoecology and vegetation dynamics of herbaceous layer are very unknown in savannas. In short, assembly and succession models must be expanded to include disturbances that eliminate resprouting ability (Cava et al., 2017).

Restoration of grassy biomes faces several challenges. First, natural regeneration tends to be slow in grassy ecosystems, because species are adapted to persist, rather than disperse (Bond and Parr, 2010). As a result, restoring savannas on severely disturbed sites require active restoration and re-introduction of native species. The appropriate method will depend on several factors, like costs limitations and restoration goals. Direct seeding, hay transfer, and topsoil transfer, are considered effective methods for restoring grasslands (Hedberg and Kotowski, 2010; Palma and Laurance, 2015; Ferreira et al., 2015). There are few studies on savanna restoration, but direct seeding is the most common technique (Palma and Laurance, 2015), and has also been used to successfully establish native species in *Cerrado* savannas of Brazil (Silva et al., 2015; Pellizzaro et al., 2017). Advantages of this method include low costs and easy implementation (Grossnickle and Ivetic, 2017; Palma and Laurance, 2015). Mechanization enables introducing seeds in high density (Campos-Filho et al., 2013), a requirement for properly covering the ground with grasses and herbs, what is very expensive using seedlings (Grossnickle and Ivetic, 2017). Moreover, it presents lower anthropic fingerprint, since the resulting community is naturally selected from the large density of individuals sowed initially. For instance, direct seeding allows plants to develop a more natural root system, comparing with seedling planting (Grossnickle and Ivetic, 2017).

Alien invasive species are another important challenge for restoration of grassy biomes worldwide. In Neotropical and Australian savannas, African grasses were introduced for pasture enhancement, and intentionally dispersed in a wide range of areas (Foxcroft et al., 2010; Parsons, 1972) These species evolved with fire and intense herbivory by large mammals, becoming well adapted for grazing, whereas native species of Neotropical Australian savannas are less tolerant to defoliation (Baruch, 1996). Some traits make them very aggressive, displacing natives and leading to alternative stable states (Pivello et al., 1999a; Almeida-Neto et al., 2010; Firn et al., 2010; Veldman et al., 2015). High growth rates enable invasive grasses to establish fast and successfully compete for resources. The high biomass produced increases fire frequency and intensity, creating a fire and invasion cycle, in which fire eliminate native species and propitiates invasion (D'Antonio and Vitousek, 1992). Also, they can alter water balance, increasing water runoff and evapotranspiration, thus reducing water recharge (Baruch, 1996). Native species can also be affected by allelopathy, evidenced in some invasive grasses (Barbosa et al., 2008).

Assembly of grass communities, can be affected by historical events, like order and time of species arrival, known as priority effect (Corbin and D'Antonio, 2004; Fukami, 2015). Assembly trajectories in communities strong determined by priority effects are considered less deterministic, because order and time of arrival are stochastic processes, difficult to predict (Fukami, 2015). However, when restoration in such communities is monitored in the beginning, and order and time of arrival is known, restoration outcome can be predicted by initial composition. In peatlands of Canada dominated by sphagnum moss, species of *Sphagnum* genus are early indicators of restoration success, because areas with more cover of these species remain stable. Conversely, areas with more cover of *Polytrichum strictum* leads to an alternative state dominated by the same species, and areas with bare ground are not colonized by *Sphagnum* species, resulting in restoration failure. Finding initial compositions that leads to restoration success and restoration failure can give a very useful tool for restorers.

Priority effects can also affect the competition between two or more species, and can be used as a tool to give competitive advantage to native species over exotics, even if the native species are not as good competitors as the exotic species (Young et al., 2016).In California grasslands, competition between native species and annual invasive grasses seems to be very contingent on temporal priority. Dominance of invasive grasses is attributed to their rapid growth and resource preemption (Young et al., 2016). However, when native grasses have temporal priority they outcompete invasive grasses (Vaughn and Young, 2015; Young et al., 2016). Priority effects also increase establishment of Californian native grasses over native forbs (Werner et al., 2016). Native species can have temporal priority if are planted before exotic species, if exotic species are controlled in the beginning, or if are pre-germinated (Young et al., 2016).

The objective of this study was to track the community assembly in a large scale restoration experiment of abandoned pasture into *Cerrado* savanna, in central Brazil. In the restored area, invasive grasses were able to reappear from the seed bank, creating patcheswith different proportion of native species and invasive grasses, and dominance of different functional groups (native annual grass, native perennial grasses, native short-lived and fast-growing shrubs, native fast-growing tree, and invasive grasses).. Monitoring this area for two years gave us the opportunity to answer the following questions: (1) is final composition and final proportion of natives and exotic species determined by (a) initial composition, (b) initial native proportion, or (c) initial dominant functional group?, (2) Can temporal dynamics involve successional trajectories, with species turnover, given that in savannas most species are perennial and conservatives? To our knowledge, it is the first experiment to evaluate savanna trajectories in severely degraded areas, based on the dynamics of species and functional traits. We expect to contribute with information for improvement in restoration methods for savannas and understanding of community assembly in this ecosystem.

Methods

Study site

The study was conducted in Chapada dos Veadeiros National Park, a Protected Area located in Goiás state, Brazil (14°7'2.54" S 47°38'30.36" W). The region of Chapada dos Veadeiros is located at 800 to 1650 m of altitude, with 1625 of mean annual precipitation. Topography is characterized by plateaus, mountainous relief and steep terrain (Felfili, 2007). Soils are mostly shallow and predominant types are Cambisol, Litosol and Red-Yellow Latosol (Haridasan, 2007; EMBRAPA 2006). Climate is AW in Köppen classification, characterized by two well defined seasons – one dry and cooler (April to September) and the other, hot and rainy (October to March). Study area present flat terrain, and the prevalent soil is plintosol.

Based on surrounding vegetation, we considered the original vegetation cover in the study site as open to typical savanna, a vegetation type composed of an herbaceous layer, with 10 to 60% of trees and shrubs cover. There is no register of when the area was converted into pasture. It was abandoned for about 20 years and remained stable as exotic pasture before a restoration project was initiated in 2012.

Every year until 2016, a new adjacent area was selected for direct seeding (Fig. 1) of native grasses, shrubs and trees (see the species list at Appendix 1). Each sowing campaign consisted in a large scale experiment (≥ 3 ha) inserted in an adaptive management model (Sampaio et al, in preparation), meaning that the number and type of soil preparation interventions, and seed density and composition varied between years. In all sowing campaigns soil was prepared by harrowing before sowing native species, what enabled to brake soil clods and level the ground. It also eliminated aerial parts and roots of invasive grasses, by trituration and exposition to surface. In 2014, controlled burn was conducted before harrowing the soil.Because harrowing and fire could not eliminate the seed bank, invasive grasses were able to reestablish with more or less intensity, in years following each sowing campaign.

The variation in seed density, species composition, micro-scale soil variation and intensity and type of soil interventions, between each sowing campaing, created patches dominated by invasive grasses, native grasses, native shrubs and trees and intermediary proportions of these groups, with low and high total biomass (Fig 2), with great variation of dominance between and inside each area of planting. The effect of these variables in creating different patches was not the objective of our study. We aimed to understand the short trajectories of these patches, after they were established, from 2015 to 2017.

Experimental design and data collection

In January 2015, 90 1m^2 plots were placed in the sites directed seeded from 2012 to 2014. We visually searched for the highest gradient of functional groups composition, locating plots in areas with different proportions of native grasses, native shrubs, native trees and exotic grasses (Fig. 2). These plots were not manipulated. As a result, plots could also have different biomass and age (1 to 3 years old). In April of the same year, we established more 21 plots, in which we removed (unbury) all the exotic grasses to obtain more plots with dominance of native species, resulting in 111 plots. Plots were not manipulated again until the end of the study.

We measured vegetation cover at species level, with exception of *Aristida spp.* and *Stylosanthes spp.* that were measured at genus level. Cover was repeatedly sampled annually, in January and April, in 2015, 2016 and 2017. We used Point-Intercept Method (Coulloudon et al., 1999; Jonasson, 1988), that allows to have an accurate 3 dimensional representation of the space occupied (vertical occupation and horizontal occupation) by each species in each plot, and also gives a good estimation of plant biomass (Jonasson, 1988) For each permanent plot, we used a $1m^2$ iron frame, subdivided into 100 square cells of 100 cm^2, horizontally positioned at 1.20 m above ground. In each cell, we positioned a 2 m high stick, and verified which species touched the stick and how many contacts it made. We used “number of touchs” as unity of cover. Because cells didn’t have limitation to number of touches, it could easily surpass 100 touches in a single plot (Fig 2).

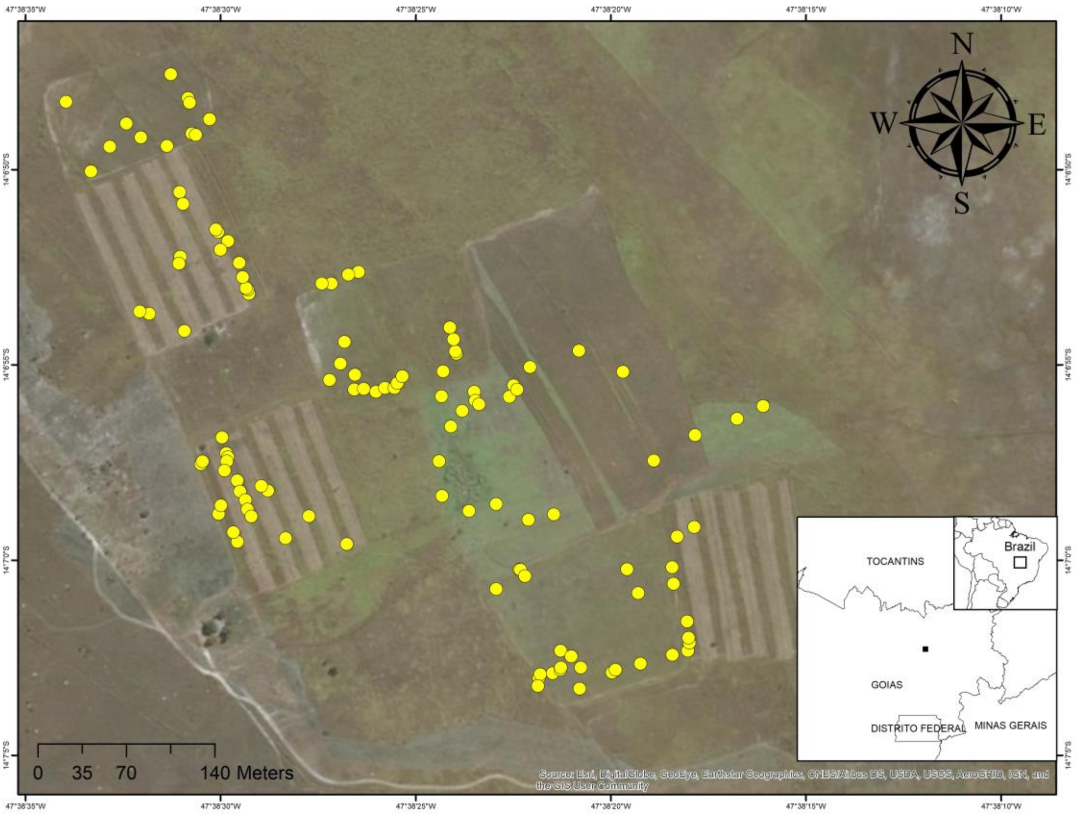

Figure 1. Sowed areas in restoration of *Cerrado* in Chapada dos Veadeiros National Park. Points indicate plot position. Concurrent experiments conducted in the area influenced availables areas for disposing the plots.

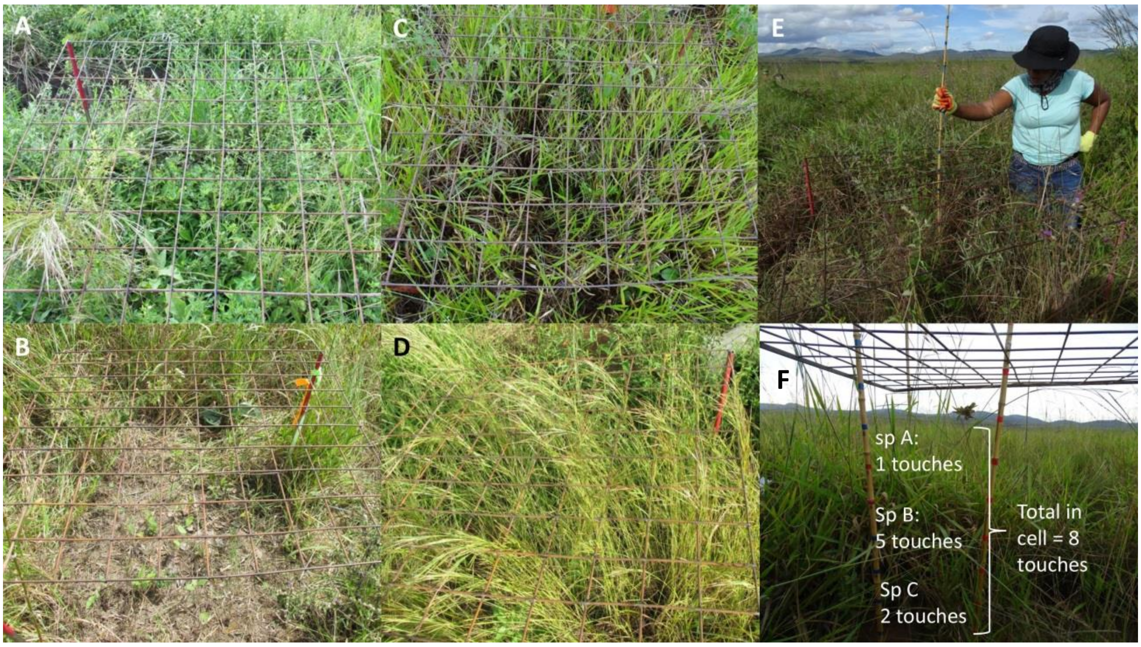

Figure 2. Examples of dominance and coexistence of different functional groups in restoration of *Cerrado* savanna in Chapada dos Veadeiros Natinoal Park – GO – Brazil. A: coexistence of shrub and native grass. B: plot with almost no cover. C: dominance of invasive grass. D: dominance of native grass. E and F: steps for data collection: a stick is placed in each grid cell; observer count number of contacts of each species. More than one touch could be counted in each cell, meaning total cover could surpass 100 touches.

Statistical analysis

We used exploratory graphs to evaluate: (1) total cover in 2017 and variation between 2015 and 2017 of natives and exotic species; (2) success of competition in each plot based on the variation from the initial proportion; and (3) identify the species with best and worst performances, based on the total cover in each year, and the variation between 2015 and 2017.

To group plots based on initial conditions, we segregated them considering dominance of functional groups. First, native species were classified in functional groups based on life form, life cycle and growth rate (see species list by functional group in Annex 2). Invasive grasses found in the study area have important functional differences, and were not grouped. Using a matrix data with functional groups plus invasive species, plots were grouped based on dominance of functional group or invasive species. We used Berger-Parker dominance index (Berger and Parker, 1970), which is a simple measure of the proportional importance of the most abundant species or functional group ($d = C_{max}/C_{tot}$, in which C_{max} = cover of the dominant species and C_{tot} = total cover in the plot). Plots with $d \geq 0.4$ were considered dominated. Plots with $d < 0.4$ were classified as “No dominance”. Plots with cover less than 50 touches were considered empty, and plots with 50 to 200 touches were classified as “Low coverage” (Table 1). All functional groups were dominated by one or two most important species (Table 1). We then compared the transitions of plots between groups in 2015 to groups in 2017. We also observed the final cover of the six species with best performance (*Schizachyrium sanguineum, Trachypogon spicatus, Tachigali vulgaris, Urochloa decumbens, Andropogon. gayanus* and *Urochloa. humidicola*) in function of initial condition.

To analyze temporal variation in species composition, we performed a Non Metric Multidimensional Scaling. Rare species (occurrence < 5%) were excluded from the analysis, because they are of less importance on dynamics studied, but can affect final solution (Poos and Jackson, 2012).

Table 1. Dominant groups found in 2015 and cover proportion of the dominant species found in each functional group (total species cover/total cover in all plots dominated by the functional group).

Functional group	Dominant species	Cover proportion
Native dominance		
Perennial Grass	*S. sanguineum*	40.1%
	T. spicatus	6.6%
Short Life-cycle Shrub	*Stylosanthes spp.*	39.1%
	L. aurea	27.6%
Annual Grass	*A. fastigiatus*	67.3%
Exotic dominance		
A. gayanus	*A. gayanus*	53.9%
U. decumbens	*U. decumbens*	59.5%
M. minutiflora	*M. minutiflora*	55.8%
No dominance		
No dominance	-	-
Low biomass		
Low coverage	*U. decumbens*	39.4%
Empty	-	-

Results

Invasive grass cover and native cover gradually increased in two years, but invasive grasses increased 3.23 more than native cover from 2015 to 2017, resulting in similar cover of invasive grasses and native species in 2017 (Fig. 3). Also, invasive grasses increased cover in 72 plots while natives increased cover in 38 plots out of 111 (72 vs 38 plots; Fig. 3). The proportional increase of natives (restoration success) or invasive grasses (failure) did not correlate with initial proportion of native or invasive grass species (Fig. 4). Only plots dominated by invasive grasses (higher than 80%) remained stable. Plots with more than 20% of natives had both positive and negative variation in proportion (Fig. 4).

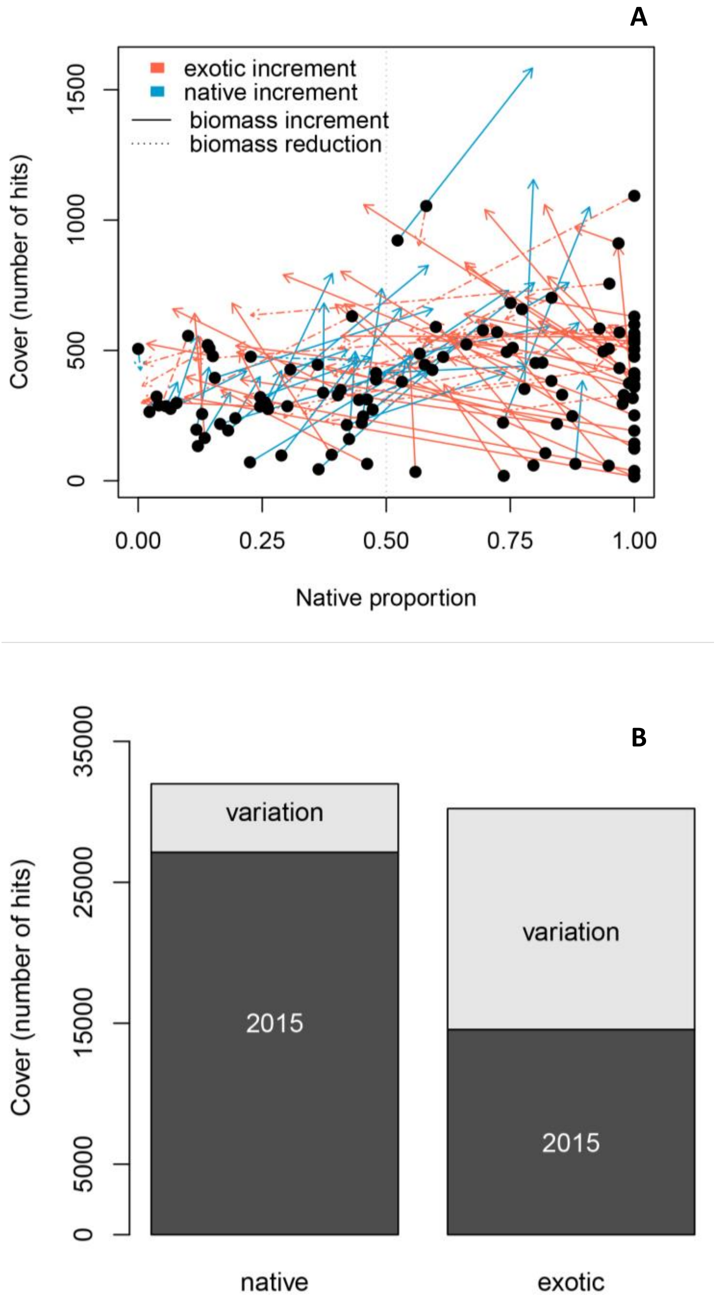

Figure 3. Cover variation of native and alien species in restoration of *Cerrado* savanna in Chapada dos Veadeiros National Park – GO – Brazil. A) Cover and proportion of natives of all plots in 2015. Proportion of natives is relative to total cover (native cover + exotic cover). A value of 0 means that all the plot cover corresponds to invasive grasses. Arrows indicates plot variation form 2015 to 2017. B) Total cover of native and alien species in 2015 and variation between 2015 and 2017.

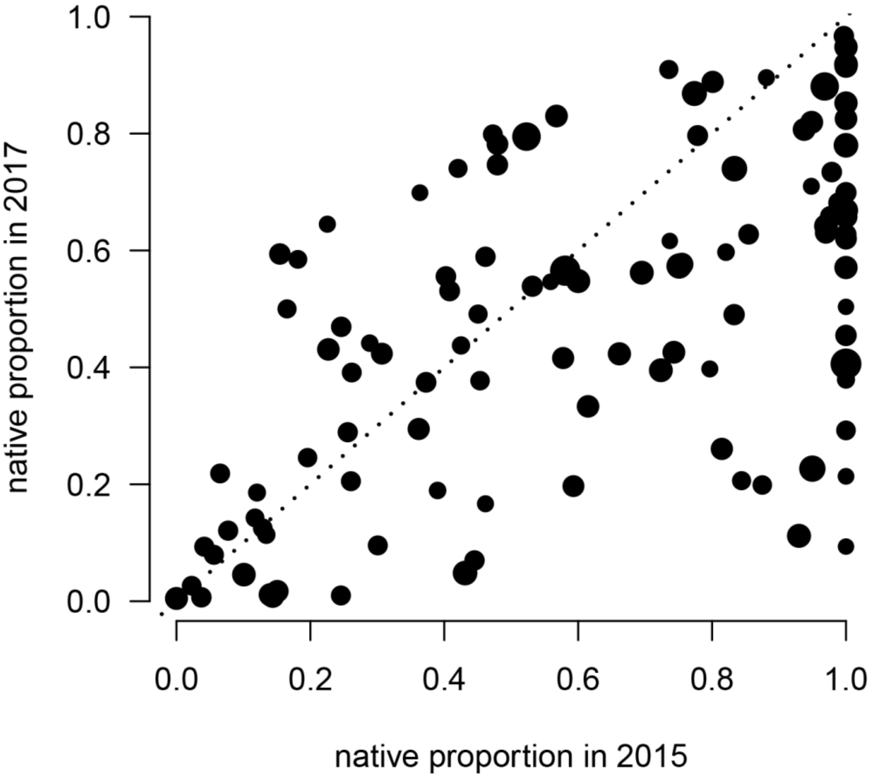

Figure 4. Native proportion in 2017 by native proportion in 2015 in restoration of *Cerrado* savanna in Chapada dos Veadeiros Natinoal Park – GO – Brazil. Dotted line separate plots with increment (above) and reduction (below) of native proportion. Point size represents total cover in 2015 (larger = higher total coverbiomass).

Throughout the plots some species increased cover, others decreased, leading to a species turnover. Short life-cycle shrubs and the annual grass *Andropogon fastigiatus* had high cover in 2015 but strongly decrease along the two years; the shrubs *Stylosanthes spp.* and *Lepidaploa aurea* lived about 3 years and the native grass *A fastigiatus* is an annual grass that did not regenerate after sites increased total cover (Fig. 5). The invasive grasses *Urochloa decumbens* and *Andropogon gayanus*, the native perennial grasses *Schizachyrium sanguineum* and *Trachypogon spicatus*, and the fast growth native tree *Tachigali vulgaris* increased their cover (Fig. 5). Although decreasing in 38 plots, *S. sanguineum* increased in 63 plots, enabling this species to increase the cover and stay in the top species in 2017 (Fig. 5). This native grass, as well as the invasive grasses *U. decumbens* and *A. gayanus,* were the dominant species in all years (Fig. 5). In 2017, they were followed by the native tree *T. vulgaris,* the native grass *T. spicatus,* and the invasive grass *U. humidicola* in the species ranking.

The dominance of functional groups became less apparent in 2017, with 30 plots showing no dominance, 20 more plots than 2015 (Fig. 6A). Perennial grasses occupied most of the plots previously dominated by short-lived shrubs (57%) and annual grasses (60%), but remained stable in 28% of the plots dominated by this functional group (Fig. 6A). *T. spicatus* was the native grass capable of maintaining its dominance, and *S. sanguineum* was capable of invading other plots, mainly those dominated by short-lived shrubs, but also plots dominated by *U. decumbens* (Fig. 6B). In 28% of plots dominated by perennial grasses they were replaced by the fast growing tree *T. vulgaris* and in 36% they lost dominance for other species (Fig. 6). Most plots dominated by *U. decumbens* remained with same composition (43%, fig. 6A), and, where the species dominated in 2015, it reached higher cover than in plots dominated by other functional groups (Fig. 6B) Low coverage plots in 2015 also contributed to dominance of *U. decumbens* in 2017 (Fig. 6), because this species represented the highest proportion of cover in these plots (Table 1). *A. gayanus* in 2017 mostly (50%) came from self-dominated plots. 36% of plots with no dominance remained this way, but 27% became dominated by perennial grasses and 27% became dominated by fast growing tree (Fig 6A).

The NMDS evidenced a compositional change from the short life-cycle species (short-lived shrubs and the annual grass *A. fastigiatus*), towards native and invasive perennial species (Fig. 7). Plots with native perennial grasses also showed a tendency of change toward invasive grasses.

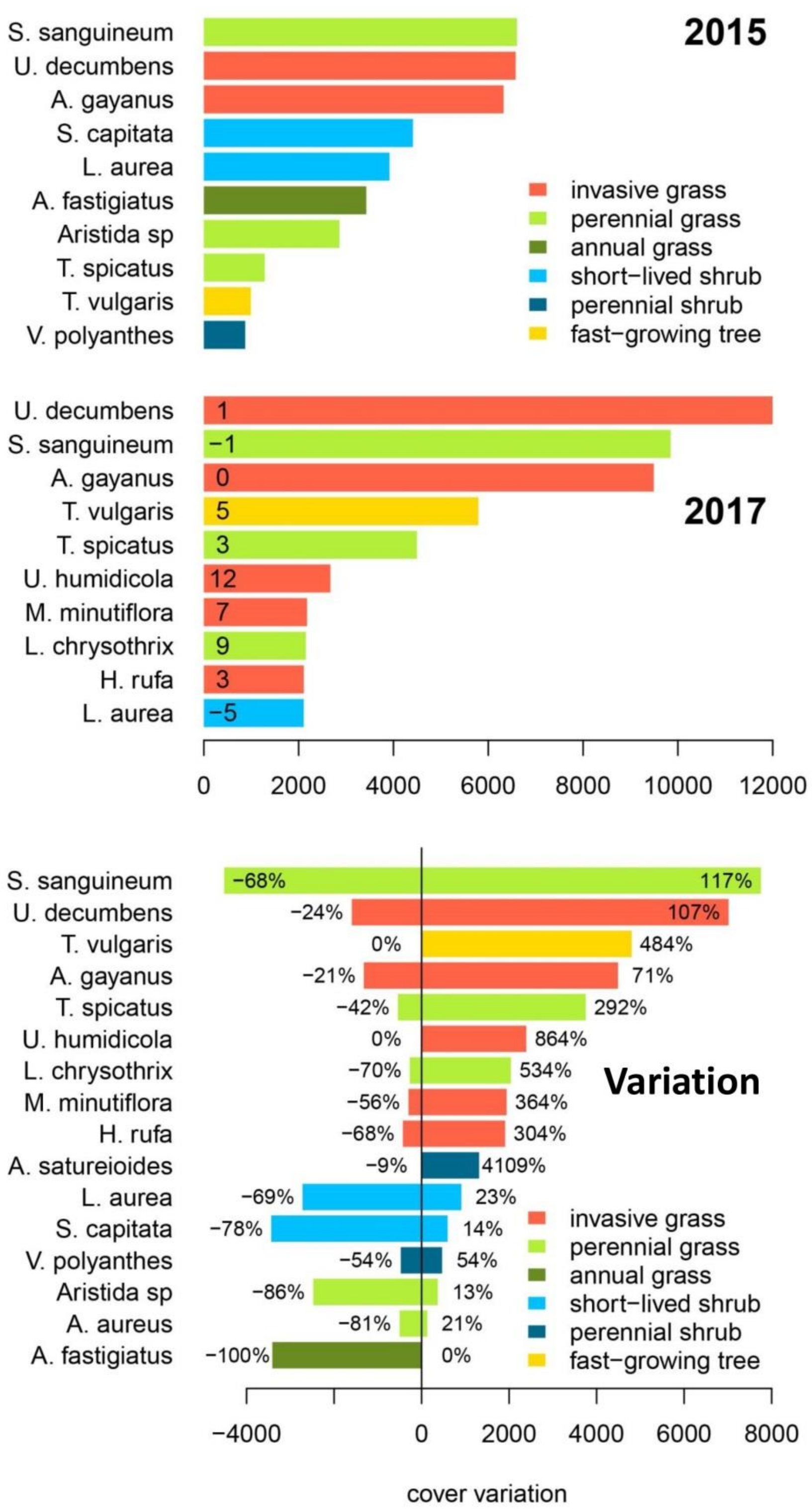

Figure 5. Species ranking based on total cover in 2015 and 2017, and cover variation between these years 2017 in restoration of *Cerrado* savanna in Chapada dos Veadeiros Natinoal Park – GO – Brazil. Numbers in 2017 are variation in position regarding 2015. In variation plot, positive bars are the sum of variation in plots with increase of that species. Negative bars are sum of variation in plots with reduction. Numbers are the percentage variation relative to the initial cover. We present the 10 species with higher increase and the 10 species with higher reduction, sorted by increase.

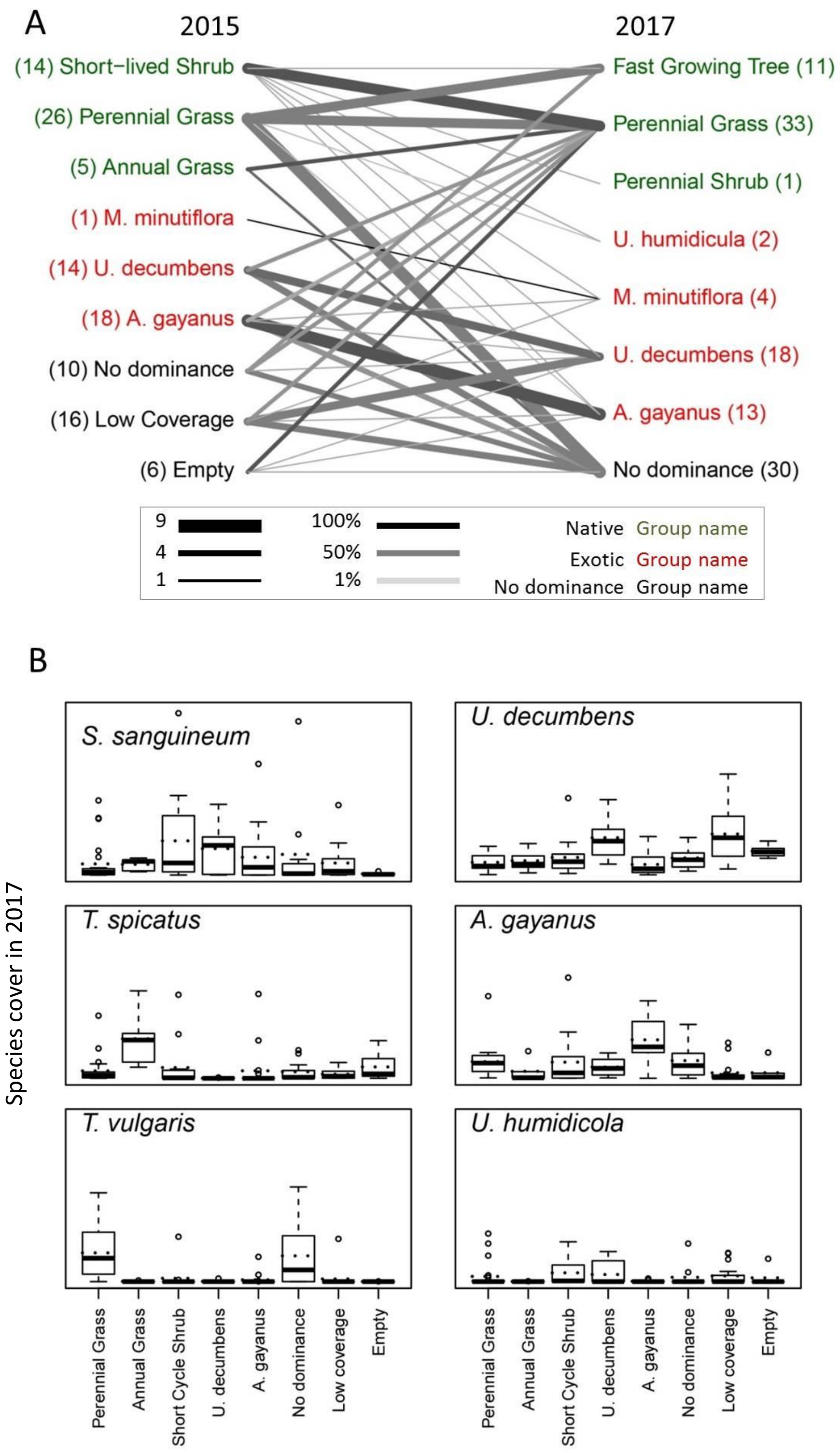

Figura 6. A) Sankey diagram showing change in functional group dominance between 2015 and 2017 in restoration of *Cerrado* savanna in Chapada dos Veadeiros Natinoal Park – GO – Brazil. Amount of change is represented by segment width (number of plots) and grey scale (proportion of plots). Number of plots of each group are in parenthesis. B) Response of species cover in 2017 in function of 2015 functional groups in restoration of *Cerrado* savanna in Chapada dos Veadeiros Natinoal Park – GO – Brazil. The six species selected showed higher total cover in 2017

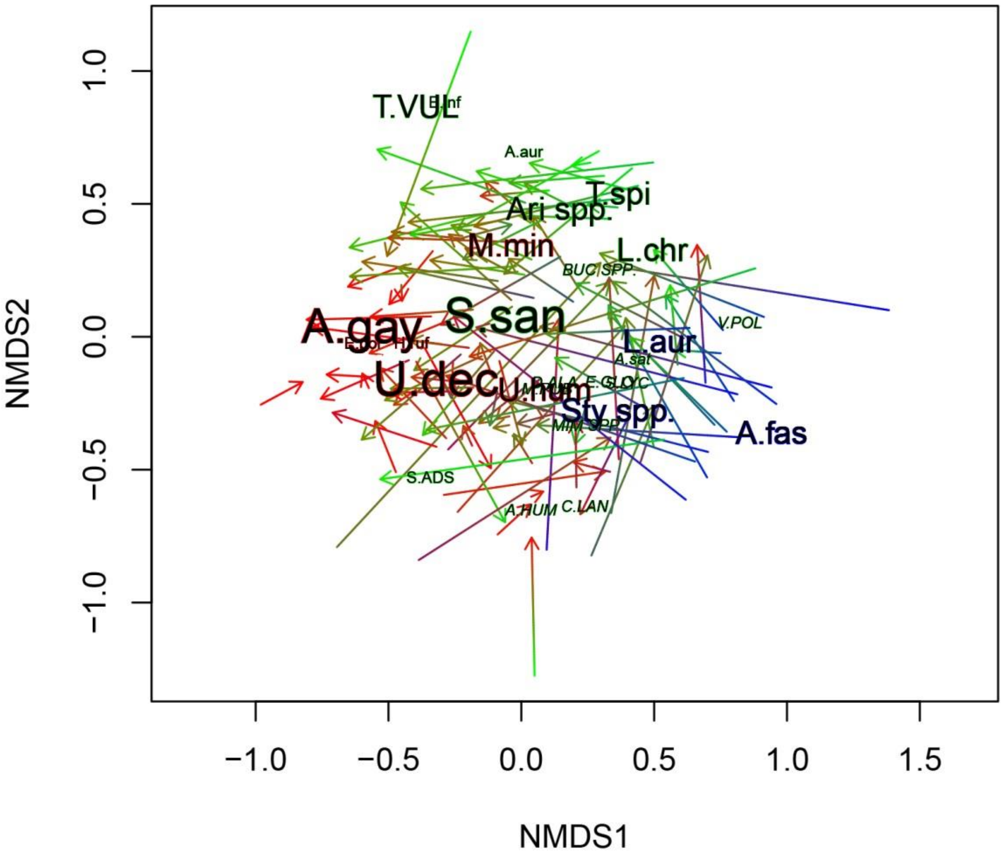

Figure 7. Compositional change of plant community in restoration of *Cerrado* savanna in Chapada dos Veadeiros Natinoal Park – GO – Brazil. Colours indicate the proportion of: annual and short-lived natives (blue), exotic grasses (red) and other natives (green). “Other natives” includes: perennial grasses (plaint text), fast-growing tree (plain text and upper case), and regular/slow-growing trees and shrubs (italic and upper case). For better visualization of most important species, name size is based on total cover from 2015 to 2017. Arrows indicates variation of plots between 2015 and 2017. Bottom is coloured with initial proportion, and top with final proportion.

Discussion

Attempts to reassemble savanna communities by active restoration are very recent and scattered in a few sites (Hedberg and Kotowski, 2010; Kolb et al., 2016). For Brazilian savanna restoration it is known that native species reintroduction is perfectly possible by direct seeding of trees, shrubs and herbs (Pellizzaro et al., 2017; Silva and Vieira, 2017). However, this study found out that there are strong challenges to establish an initial community able to trigger a trajectory of succession and be resistant to invasive grasses re-spreading. But also, we see some paths to follow in order to achieve successful restoration.

Our results evidenced a successional trajectory in the restored area, with fast species turnover. Two short life-cycle shrubs, *L. aurea* and *S. capitata*, rapidly covered the ground in the beginning of the restoration, but they died and left empty space for colonization or expansion of perennial species after two to three years. Native and invasive perennial grasses, as well as the fast growing tree *T. vulgaris*, were able to occupy the available space. It is expected that, as the native tree species grow, canopy cover increases, and achieve a cover of 10 to 70%, typical of open and typical savanna (Ribeiro and Walter, 2008)

The short life cycle plants are a rare functional group in Brazilian savannas, but were an important functional group to rapidly cover the ground, while perennial grasses and trees are growing slow, avoiding soil erosion, modifying microclimate and soil structure. This functional group didn't prevent invasive grasses, that strongly reoccupied the area, but they were important to perennial grasses establishment. *S. sanguineum* showed higher coverage in plots initially dominated by *L.* aurea *Stylosanthes spp.*, and *T. spicatus* presented higher coverage in plots initially dominated *A. fastigiatus.* Subshrubs of genus *Stylosanthes* are used as forage (Miles and Lascano, 1997; Phengsavanh and Ledin, 2003) and can increase soil fertility, what may have contributed to its inefficiency in preventing invasive grasses. In another experiment in the same restored area, *S. capitata* and *S. macrocephala* did not prevent invasive grasses, even when sowed in high density (Alves, 2017). Stylosanthes successfully prevented invasive grasses in restoration of gravel mine in Brazillian savanna (Starr et al., 2013), but in this case the soil was eliminated with mining activity, what created an ambient with hard conditions to the establishment of invasive grasses, and suppressed the seed bank, what reduce considerably the resilience of invasive grasses. The dense seed bank of invasive grasses may also have prevented the priority effect of *L. aurea* and *A. fastigiatus.* The former is considered "pasture invader", sometimes even displacing invasive grasses (Lorenzi, 1991)

In the studied restoration site, *S. sanguineum* and *T. vulgaris* were the best natives substituting the short life-cycle species. *T. vulgaris* is a fast growing tree and this ability permitted this species to overcome the grass cover. All other 21 seeded trees had good establishment, but very poor growth (see (Pellizzaro et al., 2017; Silva and Vieira, 2017). *S. sanguineum* not only occupied space left by the short life-cycle species as was able to invade some plots dominated by invasive grasses. Probably, *S. sanguineum* is more functionally similar to invasive grasses than the other species, enabling this species to compete with them.

Our results showed that the competition was asymmetrical, with invasive species gaining more space than the native species. Invasive grasses were able to hold their dominance in plots with more than 80% of initial proportion and increase their proportion in other plots, totally outcompeting natives in some plots. Asymmetrical competition between invasive and native species is common worldwide (Vilà and Weiner, 2004), and was found between invasive and native grasses in different grassland ecosystems (Bakker and Wilson, 2001; Schwinning et al., 2017; Werner et al., 2015). Exotic grasses can outcompete natives by resource pre-emption or non-resource mediated effects, like allelopathy (Barbosa et al., 2008; Kato-Noguchi et al., 2014).

U. decumbens and *A. gayanus* have some functional traits that make them aggressive invasors. *U. decumbens* was introduced in Brazil as forage (Lorenzi, 1991; Parsons, 1972). It is a very aggressive competitor, becoming a strong invader in Cerrado savannas (Pivello et al., 1999b). *U. decumbens* has allelopathy properties capable of displacing *M. minutiflora*, which is also a strong invasive grass in America (D'Antonio et al., 2017; Pivello et al., 1999b). Native tree species of Australia (Sun and Dickson, 1996) and Cerrado savanna (Pereira et al., 2013) can germinate and grow better in absence of *Urochloa* species, what suggests that these invasive grasses strongly compete for nutrients belowground. In fertilized areas, when P and K are provided, *U. decumbens* shows high productivity, allocating a lot of biomass on the leaves (EMBRAPA, 1980; Rao et al., 1996). However, they are also well adapted to acid and low-fertile soils of *Cerrado*, which has low P and Ca, but high levels of Al (EMBRAPA, 1984; Rao et al., 1996). *A. gayanus* was also introduced intentionally to be used as forage (Boddey et al., 2004) becoming an invasive grass. It has high dispersal ability; one tussock can produce about 12000 caryopses in a year (Bowden, 1964). These traits give these species hierarchical competitiveness, enabling them to invade and be successful in plots where they were not before.

Contrary to our hypothesis, initial proportion was not a good predictor of restoration success, as final proportion was very heterogeneous and little affected by initial proportion, except in the case of high dominance of invasive grasses. At species level, initial proportion was only relevant for *U. decumbens* and *A. gayanus*. These species had higher cover where they dominated two years earlier, indicating that establishing first gave them advantage in the competition, and thus priority effects may have benefited these species. There is evidence that exotic plant species can be more benefited by priority effects than native species (Dickson et al., 2012). In California grasslands, alien annual grasses can outcompete natives because they germinate first and have priority on resource consumption (H. Deering and Young, 2006; Young et al., 2016). *U. decumbens* and *A. gayanus* grow quickly and produce high biomass, what may have given them advantage on establishment. However, both species were successful even were they did not dominate initially, and competitive hierarchy may play a role in the final result (Fukami, 2015; Young et al., 2001). Priority effects only happen if species have similar niches and competitive capacities (Fukami, 2015). In our study, differences in competitive ability between these exotic grasses and native species may have diminished advantage of first establishment for native species. In experiment with old field plant species, success of invasive species didn't reduce when they arrived after native species (Stuble and Souza, 2016).

Our study highlights that community assembly in restoration of non-resilient savannas can follow a successional pathway when short life-cycle and perennial species are sowed. We also showed that invasive grasses can be a difficult challenge if not completely eliminated prior to sowing and constantly kept out. Fire and plowing (Donath et al., 2007; Durigan et al., 2013) can be effective methods to eliminate them, but wasn't enough in the studied sites. One alternative to deplete exotic seed bank is to stimulate germination (Carmona, 1992), what can be done with successive plowing operations in the same area. More drastically, topsoil removal can completely eliminate the seed bank (Kiehl et al., 2010). Herbicides are an effective method that can be applied in large scale (Ansley and Castellano, 2006; Bakker et al., 2003), but may not be allowed in protected areas. To restore Brazilian savannas, we recommend completely eliminate invasive grasses seed bank, using fast growing species to prevent soil erosion and modify microhabitat conditions. Perennial grasses with high success of propagation by direct seeding are fundamental do establish long-term cover and trees and perennial shrubs will make their role after a decade.

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Annexes

Annex 1. Sowed species in 2012, 2013 and 2014, separated by life form (shrubs, herbs, trees), in restoration area in Chapada dos Veadeiros National Park.

Nome científico	Nome comum	Família	Ano
Arbustos			
Anacardium humile A. St.-Hil.	Cajuzinho	Anacardiaceae	2013 / 2014
Bauhinia cf dumosa Benth.	Pata-de-vaca	Fabaceae	2013
Vernonanthura polyanthes (Sprengel)	Assa-peixe	Asteraceae	2012 / 2014
Vega & Dematteis Senna alata (L.) Roxb	Fedegosão	Leguminosae	2014
Lepdaploa aurea (Mart. ex DC.) H.Rob.	Amargoso	Asteraceae	2012 / 2014
Subarbustos			
Aldama cf. bracteata (Gardner) E.E.Schill. & Panero	Margarida	Asteraceae	2013
Stylosanthes capitata Vogel	Estilosantes	Fabaceae	2012
Stylosanthes macrocephala M.B.Ferreira & Sousa	Estilosantes	Fabaceae	2012
Ervas			
Achyrocline satureioides (Lam.) DC.	Macela	Asteraceae	2013
Axonopus aureus P. Beauv.	Pé de galinha	Poaceae	2012
Andropogon bicornis L.	Capim vassoura	Poaceae	2012 / 2014
Andropogon fastigiatus Sw.	Andropogon nativo	Poaceae	2014
Andropogon sp.	Capim mulungu	Poaceae	2014
Aristida sp.	-	Poaceae	2012
Aristida gibbosa (Nees)	Capim rabo de burro	Poaceae	2013
Kunth Aristida riparia Trin.	Rabo-de-raposa	Poaceae	2014
Axonopus aureus P. Beauv.	Capim pé-de-galinha	Poaceae	2014
Axonopus barbigerus (Kunth) Hitchc.	Capim colonião	Poaceae	2014
Echinolaena inflexa (Poir.) Chase	Capim flexinha	Poaceae	2012
Loudetiopsis chrysothrix (Nees) Conert	Capim brinco de princesa	Poaceae	2012 / 2014
Trachypogon spicatus (L.f.) Kuntze	Capim fiapo	Poaceae	2012 / 2014
Schizachyrium sanguineum (Retz.) Alston	Capim roxo	Poaceae	2014 / 2014
Arbóreas			
Alibertia edulis (Rich.) A.Rich.	Marmelada	Rubiaceae	2013
Amburana cearensis (Allemão) A.C.Sm.	Imburana	Fabaceae	2013 / 2014
Anadenanthera colubrina (Vell.)	Angico	Fabaceae	2013 / 2014
Brenan Annona crassiflora Mart.	Araticum	Annonaceae	2013
Aspidosperma macrocarpon Mart.	Peroba	Apocynaceae	2013
Aspidosperma tomentosum Mart.	Perobinha	Apocynaceae	2013
Astronium fraxinifolium Schott	Gonçalo-alves	Anacardiaceae	2014
Bowdichia virgilioides Kunth	Sucupira preta	Fabaceae	2013
Buchenavia tetraphylla (Aubl.) R.A.	Mirindiba	Combretaceae	2012 / 2013
Howard Buchenavia tomentosa Eichler	Mirindiba	Combretaceae	2014
Cybistax antisyphilitica (Mart.) Mart.	Ipê verde	Bignoniaceae	2013
Copaifera langsdorffii Desf.	Copaíba	Fabaceae	2013 / 2014

Cordia alliodora (Ruiz & Pav.) Oken	Louro amarelo	Boraginaceae	2014
Dalbergia miscolobium Benth.	Dalbergia	Fabaceae	2013
Dimorphandra mollis Benth.	Faveiro	Fabaceae	2013
Dipteryx alata Vogel	Baru	Fabaceae	2012/2013/2014
Emmotum nitens (Benth.) Miers	Sôbre	Icacinaceae	2013
Morong Eremanthus glomerulatus Less.	Tamboril	Fabaceae	2012 / 2013
Enterolobium contortisiliquum (Vell.)	Candeia	Asteraceae	2012 / 2014
Enterolobium gummiferum (Mart.) J.F.Macbr.	Tamboril	Fabaceae	2013
Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.	Paineira	Malvaceae	2013
Eugenia dysenterica (Mart.) DC.	Cagaita	Myrtaceae	2013
Guazuma ulmifolia Lam.	Mutamba	Malvaceae	2013
Hancornia speciosa Gomes	Mangaba	Apocynaceae	2013
Handroanthus ochraceus (Cham.)	Ipê Amarelo	Bignoniaceae	2013
Mattos Hymenaea stignocarpa Hayne	Jatobá	Fabaceae	2012/2013/2014
Tabebuia aurea (Mart.) Bureau	Caroba	Bignoniaceae	2012 / 2014
Jacaranda brasiliana (Lam.) Pers.	Tingui	Sapindaceae	2012 / 2014
Magonia pubescens A. St. -Hil.	Aroeira	Anacardiaceae	2012 / 2014
Myracrodruon urundeuva Allemão	Vinhático	Fabaceae	2012
Plathymenia reticulata Benth.	Lobeira	Solanaceae	2012 / 2014
Solanum lycocarpum A. St. -Hil.	Ipê-caraíba	Bignoniaceae	2014
Tachigali vulgaris L.G.Silva & H.C.Lima	Carvoeiro	Fabaceae	2012 / 2014
Terminalia argentea Mart.	Capitão	Combretaceae	2012 / 2014
Terminalia fagifolia Mart.	Capitão do mato	Combretaceae	2014
Palmeira			
Syagrus romanzoffiana (Cham.) Glassman	Gueroba	Arecaceae	2012

Annex 2. Species found in study plots, separated by life-form and functional group. Abreviation in parenthesis.

Herbs and Grasses

Perennial
Aristida spp. (Ari spp.)
Echinolaena inflexa (E.inf)
Loudetiopsis chrysothrix (L.chr)
Trachypogon spicatus (T.spi)

Schizachyrium sanguineum (S.san)
Axonopus aureus (A.aur)
Axonopus barbigerus (A.bar)
Setaria parviflora (S.par)

Annual
Andropogon fastigiatus (A.fas)

Shrubs

Short life-cycle
Stylosanthes capitata (Sty spp.)
Stylosanthes macrocephala (Sty spp.)
Lepidaploa aurea (L.aur)

Others
Bauhinia cf dumosa Benth. (B.dum)
Vernonanthura polyanthes (V.pol)
Senna alata (S.ala)

Mimosa spp. (Mim spp.)
Achyrocline satureioides (A.sat)

Trees

Fast-growing
Tachigali vulgaris (T.vul)
Solanum lycocarpum (S.lyc)

Regular / Slow growing
Alibertia edulis (A.edu)
Anadenanthera colubrina (A.col)
Aspidosperma macrocarpon (A.mac)
Astronium fraxinifolium (A.fra)
Buchenavia tetraphylla (B.tet)
Buchenavia tomentosa (B.tom)
Cybistax antisyphilitica (C.ant)
Copaifera langsdorffii (C.lan)
Dalbergia miscolobium (D.mis)
Dipteryx alata (D.ala)
Eremanthus glomerulatus (E.glo)
Enterolobium contortisiliquum (E.con)
Enterolobium gummiferum (E.gum)
Eugenia dysenterica (E.dys)
Handroanthus ochraceus (H.och)
Hymenaea stignocarpa (H.sti)
Jacaranda brasiliana (J.bra)
Myracrodruon urundeuva (M.uru)
Tabebuia aurea (T.aur)
Terminalia argentea (T.arg)
Terminalia fagifolia (T.fag)

Invasive grasses

Urochloa decumbens (U.dec)
Urochloa humidicola (U.hum)
Andropogon gayanus (A.gay)
Melinis minutiflora (M.min)
Megathyrsus maximus (M.max)
Hyparrhenia rufa (H.hyp)