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Savannas after afforestation: Assessment of herbaceous community responses to wildfire versus native tree planting

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Abstract

Afforestation and fire exclusion are pervasive threats to tropical savannas. In Brazil, laws limiting prescribed burning hinder the study of fire in the restoration of Cerrado plant communities. We took advantage of a 2017 wildfire to evaluate the potential for tree cutting and fire to promote the passive restoration of savanna herbaceous plant communities after destruction by exotic tree plantations. We sampled a burned pine plantation (Burned Plantation); a former plantation that was harvested and burned (Harvested & Burned); an unburned former plantation that was harvested, planted with native trees, and treated with herbicide to control invasive grasses (Native Tree Planting); and two old-growth savannas which served as reference communities. Our results confirm that herbaceous plant communities on post-afforestation sites are very different from old-growth savannas. Among post-afforestation sites, Harvested & Burned herbaceous communities were modestly more similar in composition to old-growth savannas, had slightly higher richness of savanna plants (3.8 species per 50-m^2), and supported the greatest cover of native herbaceous plants (56%). These positive trends in herbaceous community recovery would be missed in assessments of tree cover: whereas canopy cover in the Harvested & Burned site was 6% (less than typical of savannas of the Cerrado), the Burned Plantation and Native Tree Planting, supported 34% and 19% cover, respectively. By focusing on savanna herbaceous plants, these results highlight that tree cutting and fire, not simply tree planting and fire exclusion, should receive greater attention in efforts to restore savannas of the Cerrado.

KEYWORDS: Brazil, Cerrado, fire suppression, old-growth grassland, *Pinus*, savanna restoration

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1 INTRODUCTION

Old-growth savannas of the humid tropics and subtropics are threatened by a suite of land-use changes, including agriculture, surface mining, urbanization, tree plantations, and fire exclusion (Bond, 2016; Buisson et al., 2019; Murphy, Andersen & Parr, 2016; Parr, Lehmann, Bond, Hoffmann & Andersen, 2014; Searchinger et al., 2015; Veldman et al., 2015a). Unfortunately, because savanna plant diversity is concentrated in small-statured plants, and savanna biomass is concentrated belowground and in scattered fire-tolerant trees, the conservation values of savannas have been long overlooked relative to forests (Bond & Parr, 2010). Further complicating savanna conservation, old-growth savannas are often misinterpreted as deforested or degraded land rather than ancient ecosystems of high conservation value (Bond, 2016; Murphy et al. 2016; Ratnam et al., 2011). As a consequence of the misinterpretation of savannas as degraded ecosystems, fire suppression and tree planting—typical strategies for forest conservation and restoration, as well as timber production—are commonly misapplied to savannas (Parr et al., 2014; Veldman et al., 2015b).

Conventional approaches to the restoration of degraded tropical forests, which involve dense tree planting and fire exclusion, are ecologically inappropriate for savanna restoration (Buisson et al., 2019; Dalle Laste, Durigan & Andersen, 2019; Pilon, Buisson & Durigan, 2018a). Fire exclusion and afforestation cause fundamental changes to savanna ecosystem functions, vegetation structure, and biodiversity (Abreu et al., 2017; Veldman et al., 2015a; Zaloumis & Bond, 2011). Fire maintains savanna herbaceous plant diversity by limiting tree and shrub densities (Bond & Keeley, 2005; Veldman et al., 2014) and influencing herbaceous community dynamics, including fire-stimulated reproduction and post-fire resprouting (Andrade

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& Miranda, 2014; Lamont & Downes, 2011; Moraes, Carvalho, Franco, Pollock & Figueiredo-Ribeiro, 2016; Pilon, Hoffmann, Abreu & Durigan, 2018b). Fire limits the accumulation of litter and duff, increases nutrient and light availability, and favors fire-adapted over fire-sensitive species (Fidelis, Appezzato-da-Glória, Pillar & Pfadenhauer, 2014; Lamont & Downes, 2011; Pyke, 2017; Veldman et al., 2014). Restoration of savanna plant communities after afforestation and fire exclusion is challenging for a host of reasons, including that many fire-adapted plants are poor colonizers (Buisson et al., 2019; Salazar, Goldstein, Franco & Miralles-Wilhelm, 2012; Zaloumis & Bond, 2011, 2016), but also because research on tropical ecosystem restoration has focused primarily on forests and trees, not savannas and herbaceous plants (Bond & Parr, 2010; Buisson et al., 2019; Overbeck et al., 2015).

Like many savannas globally, old-growth savannas of the South American Cerrado are rapidly disappearing due to agricultural conversion, plantation forestry, and policies that promote fire exclusion (Durigan & Ratter, 2016; Fernandes et al., 2016; Lapola et al., 2014; Sano, Rosa, Brito & Ferreira, 2010; Soterroni et al., 2019; Sano et al., 2019). Cerrado is the second largest biome in Brazil (2 million km^2) and supports the greatest species richness of plants, mammals, amphibians and birds of all savannas globally (Klink & Machado, 2005; Murphy et al., 2016; Ratter, Ribeiro & Bridgewater, 1997). With much of the Cerrado already converted to agriculture, planted pastures, and tree plantations (46%; Strassburg et al., 2017), concern is growing that fire exclusion, afforestation, and misapplied forest restoration practices are a threat to Brazil's remaining old-growth savannas (Durigan & Ratter, 2016; Fernandes et al., 2016; Pilon et al., 2018b). Because fire is illegal on private properties in Brazil, and can only be used in a small number of publically owned protected areas, there is very limited information on how prescribed fire might contribute to savanna conservation and restoration (Damasceno, 2017;

Durigan & Ratter, 2016; Gomes, Miranda & Bustamante, 2018; but see Zanzarini, Zanchetta & Fidelis, 2019). Research from other parts of the world suggests that prescribed fire should be a critical part of savanna plant community restoration (Kelly & Brotons, 2017; Scott, Setterfield, Douglas, Parr & Andersen, 2012; Strahan, Stoddard, Springer & Huffman, 2015; Walker & Silletti, 2006).

In this study, we took advantage of a 2017 wildfire, which burned an area of former old-growth savanna that was converted to plantation forestry in 1965 (Figure 1), to determine the potential for tree cutting and fire to promote the passive restoration (i.e., without the active introduction of propagules) of savanna herbaceous plant communities. Our study compares the herbaceous plant communities of three post-afforestation community types (i.e., Burned Plantation, Harvested & Burned, and Native Tree Planting; Figure 1) in relation to reference plant communities found in old-growth savannas. We expect the results of this study to highlight the severe loss of plant diversity that occurs with the afforestation of old-growth savannas (Zaloumis & Bond, 2011), the importance of focusing on herbaceous plants, not trees, in tropical savanna restoration (Veldman, 2016), and the potential benefits of incorporating fire into tropical savanna restoration practices (Buisson et al., 2019).

2 METHODS

2.1 Study site—This study was carried out in São Paulo State of southeastern Brazil, a region that historically supported a mosaic of savanna (old-growth savannas of the Cerrado biome) and seasonally dry forest (Atlantic Forest). Due to decades of fire exclusion, pasture and agricultural conversion, and exotic tree planting (afforestation), savannas of São Paulo are now extremely rare (Brasil, 2015; Durigan & Ratter, 2006; Durigan, Siqueira, & Franco, 2007). Today, most former savannas of São Paulo are covered by fire-excluded woodlands (*cerradão*), planted pasture, sugarcane, annual crops, and tree plantations of *Pinus* or *Eucalyptus* (Brasil, 2015; Durigan & Ratter, 2006; Durigan, Siqueira, & Franco, 2007). Although there are well-developed state-supported efforts to restore forests of São Paulo, and the Atlantic Forest has garnered international conservation attention, there are few efforts to conserve and restore species-diverse savanna plant communities (São Paulo state law 13,550 from 2009; Durigan & Ratter, 2016).

Our focal study sites were in a public reserve called Mogi-Guaçu Experimental Station (hereafter Mogi-Guaçu; 22º15'29'' S, 47º10'40'' W). Ideally, assessment of herbaceous plant community recovery at Mogi-Guaçu would be informed by comparisons to the historical (pre-afforestation) savanna plant communities. Because there are no old-growth savannas remaining at Mogi-Guaçu or nearby areas, we used old-growth savannas at two additional public reserves in São Paulo state as reference plant communities. These were: Santa Bárbara Ecological Station (Santa Bárbara, 22°49'2.81" S, 49°14'9.46" W, 235 km from Mogi-Guaçu) and Assis State Forest (Assis, 22°34'58" S, 50°25'20" W, 340 km from Mogi-Guaçu, Figure S1).

Mogi-Guaçu has a humid subtropical climate (Köppen Cwa) (Álvares, Stape, Sentelhas, Gonçalves & Sparovek, 2013), with mean annual temperature (MAT) of 21ºC (Secretaria do Meio Ambiente [SMA], 2015). Mean annual precipitation (MAP) is 1,350 mm, with rainfall concentrated in the austral summer (November to March) and a dry season in the winter (May to September). Soils are deep, well-drained oxisols, with low nutrient availability (SMA, 2015). The elevation of Mogi-Guaçu ranges from 600 m to 640 m with flat to gently sloping terrain (<10% slope; SMA, 2015).

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The Santa Bárbara Ecological Station has a humid subtropical climate (Köppen Cfa climate (Álvares et al., 2013), with dry winters and rainy summers. Mean annual precipitation is 1,440 mm, which occurs primarily during the rainy season (October to March), and MAT of 21.1°C (Hoffmann et al., 2019). Santa Barbara also has deep and well-drained oxisols, with low nutrient availability and high aluminum content; the elevation ranges from 600 to 680 m (Secretaria do Meio Ambiente [SMA], 2011).

Assis also has a humid subtropical climate (Köppen Cfa) (Álvares et al., 2013), with annual rainfall of 1,400 mm, mostly during the austral summer (October to March), and MAT of 21.8ºC, (Pinheiro & Durigan, 2009). The soils at Assis State Forest are deep and well-drained oxisols, with low nutrient availability (Juhász, Cursi, Cooper, Oliveira & Rodríguez-Echeverría, 2006). The elevation ranges from 500 to 588 m (Secretaria do Meio Ambiente [SMA], 2007).

Both reference sites (Santa Bárbara and Assis) have a gradient of native vegetation from old-growth savanna to dense woodlands (i.e., encroached savanna) which has resulted from fire exclusion. These sites have served as reference communities for several savanna restoration studies in São Paulo (Abreu et al., 2017; Cava, Pilon, Ribeiro & Durigan, 2018b; Dalle et al., 2019; Pilon et al., 2018a). Although the three sites are distant from one another (Figure S1), all experience the same rainy season, receive similar mean annual precipitation and temperature, occur on deep, well-drained and low-fertility oxisols, and were all historically part of the same, and historically extensive, savanna ecosystem (*cerrados* of São Paulo).

2.2 Study design - Since the 1960s, management of Mogi-Guaçu focused on plantation forestry to produce resin (*Pinus* plantations) and timber (*Pinus* and *Eucalyptus* plantations). Because of fire suppression by managers, the savannas of Mogi-Guaçu that were not converted to tree

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plantations have since transitioned to dense woodlands (*cerradão*). Other vegetation types at Mogi-Guaçu include abandoned pine plantations (no longer used for resin extraction), passive restoration areas (i.e., secondary vegetation forming after clear-cut timber harvests), and native tree plantations.

On 12 September 2017, late in the dry season, a wildfire at Mogi-Guaçu burned an abandoned pine plantation (27-ha; hereafter Burned Plantation) and a passive restoration area that had been harvested in 2008 (25-ha; hereafter Harvested & Burned). The Burned Plantation and the Harvested & Burned sites were adjacent to a native tree planting area that did not burn (27-ha; hereafter Native Tree Planting). The study sites were planted in 1965 (see Figure 1 for details on site history) with two closely related (Gernandt, López, García & Liston, 2005) fire-tolerant pine species, *Pinus elliottii* Engelm and *Pinus caribaea* Morelet, native to savannas of the North American Coastal Plain and the Caribbean, respectively. The Burned Plantation and Harvested & Burned sites were planted with *P. elliottii*, while the Native Tree Planting site was planted with *P. caribaea*. The sites were subsequently managed for resin extraction, which included inter-row roller chopping to control native trees and shrubs. The final resin extraction in the Burned Plantation occurred in 2012, after which there were no other management interventions prior to the 2017 wildfire, which consumed pine litter, top-killed understory plants, and killed approximately 24 percent of overstory pines. The Harvested & Burned area was clear-cut in 2008, subsequently abandoned, and burned in the 2017 wildfire, which was fueled by native and non-native grasses. In the Native Tree Planting site, pine was harvested in 2008 and then remained unmanaged until forest restoration treatments began in 2015. Following protocols to promote woody species (Durigan et al., 2011), management of the Native Tree Planting site relied on natural regeneration of trees and shrubs, supplemented by tree and shrub planting to fill

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areas without woody plants. The trees (~11,000 individuals) and shrubs (~1,000 individuals) were planted 3 m apart in the 27-ha site, resulting in a planting density of 400 trees and 40 shrubs per ha. The tree and shrub planting, implemented by a private company, included 82 species, native to the Cerrado and the Atlantic Forest Biomes. From 2015 until 2017, the company applied herbicide in an attempt to control invasive grasses, which likely also killed native grasses and forbs (Assis, 2017). Apparently, herbicide control of grasses reduced fine fuels to such a degree that the Native Tree Planting area did not burn in the wildfire. As is typical of tree-focused restoration in Brazil, the Native Tree Planting site received no treatments to promote savanna grasses or forbs (e.g., propagule additions, prescribed fire; Buisson et al., 2019).

2.3 Herbaceous Plant Community— On February 2018, 5 months after the fire, in the middle to late rainy season, we sampled the graminoids, forbs, and small-statured shrubs (subshrubs) that formed the herbaceous layer of the post-afforestation sites. At each of the three sites (i.e., Burned Plantation; Harvested and Burned, and Native Tree Planting), we established ten 50 m transects spaced 120 m apart, using systematic random sampling. To establish transects, we randomly selected a point in each site, from which we then created a grid of 10 evenly spaced points, 120 m apart. From each point we selected a random direction (0 to 359°) for each transect. For the old-growth savannas (i.e., the reference sites), we sampled three random 50 m transects at Assis. For the old-growth savannas at Santa Bárbara, we used previously archived data from three 50 m transects (Cava, Pillon, Ribeiro & Durigan, 2018a,b).

Along each 50 m transect, we identified all herbaceous-layer species (graminoids, forbs, and subshrubs) that occurred within 1 m (i.e., 50-m^2 sampled per transect) and estimated herbaceous-layer cover (independent of species) using the line-intercept method (Canfield, 1941). For woody species that were difficult to classify as shrubs or subshrubs, we only counted species described as subshrubs by the Flora do Brasil (2020). We followed Flora do Brasil (2020) for all species identifications. When calculating herbaceous cover, we counted four species of undesirable grasses separately from the rest of the native herbaceous plants. These undesirable grass species included three exotic and one ruderal grass species that can dominate restoration areas and inhibit savanna community recovery. Among these undesirable species, were the exotic grasses *Melinis minutiflora* P.Beauv., *Melinis repens* (Willd.) Zizka and *Urochloa decumbens* (Sapf) R.D.Webster. Of African origin, these species proliferate in degraded areas throughout Brazil and are clearly undesirable for Cerrado restoration (Pilon, Assis & Durigan, 2017; Pivello, Shida & Meirelles, 1999;Wanderley, Shepherd & Giulietti, 2001). We also classified one native ruderal species, *Digitaria insularis* (L.) Fedde, as undesirable. Although *Digitaria insularis* is widely-distributed throughout Americas (Wanderley et al., 2001), Mendonça et al. (2008) do not list it among 12,000 species of the Cerrado Biome, and instead classify the species among the list of "ruderals, invasives and exotics in the Biome". Because *Digitaria insularis* can form dense swards, typically on soils of degraded forests and co-occurring with invasive African grasses (Veldman & Putz, 2011), and has been treated as "weed" (Lorenzi, 2008) or “exotic” by previous plant diversity studies in São Paulo (e.g., Abreu et al., 2017), we counted *Digitaria insularis* grass as undesirable, along with the African grasses.

In addition to data on species presence and cover, at each post-afforestation site, we measured two key variables thought to influence savanna herbaceous plant communities (i.e., tree canopy cover and the O horizon; Hiers, O’Brien, Will & Mitchell, 2007). At four points, spaced 10 m apart, along each transect, we used a spherical densiometer, held at 1.3 m, to estimate tree canopy cover (Lemmon, 1956). At these same four points, we used a ruler to measure O-horizon depth (litter and duff) to mineral soil at the corners and center of a 1 x 1 m subplot (i.e., five O-horizon measurements per point).

2.4 Data Analysis—To assess similarity in herbaceous species composition among post-afforestation sites and old growth-savannas, we first conducted a Principal Coordinates Analysis (PCoA) with Jaccard distance metric. We then calculated the compositional similarity of post-afforestation sites to old-growth savanna (Jaccard's Index, see below) and determined the number of old-growth savanna species per transect. To obtain a mean Jaccard's index of similarity between each post-afforestation transect and the old-growth savannas, we calculated Jaccard's index between each post-afforestation transect and the six transects in old-growth savanna. We then took the arithmetic mean of these six similarity values to obtain a single index of similarity for each transect to the old-growth savannas. For comparisons of old-growth savanna species, we determined the richness of all native taxa that occurred in at least one old-growth savanna transect. Following the compositional analyses, we evaluated vegetation structure among the post-afforestation sites and the old-growth savannas on the basis of tree canopy cover as well as ground cover of native and undesirable grass species. We performed the PCoA and the Jaccard similarity index were with PAST 3 (Hammer, Harper & Ryan, 2001). We produced data graphics in R version 3.6.3 (R Development Core Team 2020).

Because our study lacks replication of the different post-afforestation ecosystem types (10 transects per site but only one site per ecosystem type) we did not perform formal statistical tests. Instead, we plotted the data for each post-afforestation transect and calculated the 95% confidence interval (95% CI) of the mean for each site. As reference values, we also plotted the mean and range for transects in old-growth savannas. When making comparisons among sites in our results, we only discuss trends in which the 95% CI did not overlap between sites. With this approach we are able to explore trends among sites, but must keep in mind the potential for unmeasured factors in each site to influence results. That said, we suggest that there are several reasons why this study, like many other studies of fire in the tropics may offer important insights, despite a lack of replicated treatments (e.g., Brando et al., 2014). Among these reasons, the three study sites are large (24 to 27-ha), immediately adjacent to one another, and share a common management history from 1965 to 2008 (Figure 1). In addition, fire laws in Brazil make it extremely challenging to conduct replicated, large-scale prescribed fires for ecological experiments. In this case, we were able to take advantage of a wildfire to study savanna plant communities on sites that are recovering from afforestation.

3 RESULTS

Herbaceous plant communities of the three post-afforestation sites were all very different from old-growth savannas (Table S1). In the PCoA bi-plot (Figure 2), the plant communities clustered into three groups, with the old-growth savannas clearly separate from all post-afforestation sites, and the burned sites (Burned Plantation and Harvest & Burned) clustered together, distinct from the unburned Native Tree Planting (Figure 2). Axis one explained 15.7% and axis two explained 12.9% of the variation in species composition among transects. Consistent with the PCoA groupings, compositional similarity between post-afforestation sites and old-growth savannas was low (mean Jaccard similarity of 0.02 to 0.04; Figure 3a), equating to mean richness of 2.3 to 3.8 old-growth savanna species per transect (Figure 3b). To interpret such low indices of similarity, it is helpful to note the high beta-diversity among old-growth savanna transects, which

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ranged in similarity from just 0.13 to 0.20, with a mean of 0.16 (Figure 3a). Among post-afforestation sites, Harvested & Burned was more similar in composition to old-growth savannas compared Native Tree Planting (0.04 versus 0.02, respectively; Figure 3a, Table 1), which equated to an additional 1.5 old-growth savanna species per transect (i.e., 3.8 versus 2.3 species per transect in Harvest & Burn and Native Tree Planting, respectively; Figure 3b).

Harvested & Burned had the highest native herbaceous cover (mean 56%), surpassing the values for old-growth savannas in this study (Fig 4a), whereas native cover in Burned Plantation (18%) and Native Tree Planting (14%) were lower than the reference sites (Figure 4a). Both Harvested & Burned (mean 29%) and Native Tree Planting (mean 38%) had more undesirable grass cover than both the Burned Plantation (mean 2%) and old-growth savannas (mean 6%; Figure 4b).

Relative to the large differences in community composition and undesirable grass cover, vegetation structure of post-afforestation sites was more similar to old-growth savannas. Tree canopy cover in Burned Plantation (mean 34%) and Native Tree Planting (mean 19%; Figure 5a) fell within the typical range of old-growth savannas, whereas Harvested & Burn (mean 6%) was lower (Figure 5a). Among post-afforestation sites, Harvested & Burned was the only site with no appreciable O horizon, whereas Native Tree Planting and Burned Plantations had mean accumulations of litter and duff ranging from 0.9 to 3.4 cm, respectively (Figure 5b).

4 DISCUSSION

In this study, we took advantage of a wildfire in Brazil to evaluate the potential for tree cutting and fire to promote the restoration of savannas after afforestation. As expected, the herbaceous

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plant communities of all three post-afforestation sites, regardless of management and fire history, were very different from the old-growth savannas that were destroyed to establish pine plantations five decades ago. Thus, our results are consistent with a growing body of literature that shows that the species-diverse herbaceous plant communities of tropical savannas are unable to rapidly recover after afforestation and fire exclusion (Buisson et al., 2019; Zaloumis & Bond, 2011, 2016). Unfortunately, in the Cerrado of Brazil, most restoration practices focus on dense tree planting, herbicide control of grasses, and fire exclusion, all of which are detrimental to savanna plant communities (Buisson et al., 2019; Dalle et al., 2019; Pilon et al., 2018b). Through comparison of a Harvested & Burned site to a Native Planting Tree site, our results provide an example of how tree harvest followed by wildfire can result in modestly better savanna plant community recovery, compared to tree-promoting management practices.

The herbaceous plant communities of all of our post-afforestation sites contained few species that occur in old-growth savannas. We attribute these differences in composition to species loss due to afforestation (Abreu et al., 2017). Tree planting is known to alter the structure and dynamics old-growth savanna through increased shading, litter accumulation, and root competition, which limit herbaceous community development (Harrington, 2011; Zaloumis & Bond, 2011). In other Brazilian savannas invaded by pines, native herbaceous species were absent (Abreu & Durigan, 2011) or very sparse (Brewer, Souza, Callaway & Durigan, 2018). Similar patterns of species loss and reduced richness of herbaceous plants in abandoned pine plantations versus old-growth savannas are documented in the southern United States (Kirkman, Coffey, Mitchell & Moser, 2004) and southern Africa, even after pine trees have been removed (Zaloumis & Bond, 2011, 2016). Our study is consistent with the idea that secondary communities on post-afforestation sites are qualitatively different ecosystems compared to old-

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growth savannas, even if tree cover is similar (Buisson et al., 2019; Veldman et al., 2015a; Figure 5a).

Because fire is fundamental to the functioning of old-growth savannas, we expected that even one wildfire could be beneficial to the recovery of savanna herbaceous plants after afforestation. Indeed, we found that the Harvested & Burned site had modestly greater compositional similarity to old-growth savannas, greater richness of species in common with old-growth savannas, and greater native herbaceous cover compared to the unburned Native Tree Planting. In Brazilian Cerrado, savannas have higher rates of flowering (Pilon et al., 2018a) and increase in native herbaceous biomass after fire (Oliveras et al., 2013). Although the mechanisms by which fire directly stimulates resprouting, flowering, and seed germination is still not clear (Buisson et al., 2019; Fidelis, Rosalem, Zanzarini, Camargos, 2019), fire does indirectly stimulate herbaceous plants by increasing light availability and soil nutrients (Araújo, Amaral, Bruna & Vasconcelos, 2013) and increases native species richness by reducing exotic grass cover (Martins, Hay, Scaléa & Malaquias, 2017). In sum, our results should be viewed as supportive of the growing recognition that fire is of fundamental importance to the conservation and restoration of savannas in Brazilian Cerrado (Durigan & Ratter, 2016; Fidelis et al., 2019; Maravalhas & Vasconcelos, 2014; Ramos-Neto & Pivello, 2000; Schmidt et al., 2018; Zanzarini et al., 2019).

Our results also suggest that pine harvesting played an important role in promoting savanna plant community restoration. Whereas the Harvested & Burned site had greater compositional similarity to old-growth savannas, more species in common to old-growth savannas and higher native herbaceous cover than the Native Tree Planting, the Burned Plantation did not. We suggest that elimination of pines during harvest permitted herbaceous

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community development through reduced above and belowground competition, and cessation of litter accumulation (Abreu, 2013; Brewer et al., 2018; Cuevas & Zalba, 2010; Harrington, 2011). Indeed, the Harvest & Burned site had lower tree canopy cover and O-horizon depth compared to the Burned Plantation (Figure 4a, Table 1). Our results are consistent with Abreu (2013) and Zanzarini, Zanchetta and Fidelis (2019), who recommend pine tree cutting and burning to restore savanna herbaceous plant communities following afforestation in Brazil.

Colonization of restoration areas by undesirable exotic and ruderal grasses can limit the recovery of species-diverse savanna plant communities; invasive species that are adapted to fire, pose a particular challenge (Durigan, Siqueira, & Franco, 2007; Pivello et al., 1999). Both the Harvested & Burned and the Native Tree Planting had much greater undesirable grass cover compared to the Burned Plantation. Apparently, the open-canopies of the Harvested & Burned and Native Tree Planting offered ample light for undesirable grass establishment after timber harvest (Durigan, Silveira & Melo, 2013; Gimenez, 2005; Klink & Joly, 1989). Our results are similar to those of Damasceno, Souza, Giroldo, Fidelis and Gorgone-Barbosa (2018) whose study sites, following pine harvest, were dominated by exotic grasses. It would seem clear that control of undesirable grass species is needed as part of savanna restoration after the harvesting of afforestation sites (Buisson et al., 2019; Damasceno et al., 2018). We also note that the frequent herbicide used in Native Tree Planting (applied every three months, during the first years after planting) did not eliminate invasive grasses (Figure 5b), but likely killed native herbaceous plants. Similarly, Assis (2017) and Enloe et al. (2013) found decreased native herbaceous cover due to frequent use of herbicide as part of restoration projects.

As afforestation increases in Brazilian Cerrado (Fernandes et al., 2016) it is important for us to evaluate the cost of savanna loss to tree plantations (Parr et al., 2014; Veldman et al.,

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2015b) and to identify ways to restore savannas after plantations are harvested or abandoned (Buisson et al., 2019; Gimenez, 2005). This study contributes to a growing body of evidence that fire and plays a crucial ecological role in maintaining and restoring the old-growth savannas biodiversity of Cerrado (Andrade & Miranda, 2014; Oliveras et al., 2013; Pilon et al., 2018a). Our results are consistent with recent calls for fire to be central to the conservation and restoration of savanna herbaceous plant diversity in Brazil (Andrade & Miranda, 2014; Durigan & Ratter, 2016; Oliveras et al., 2013; Pilon et al., 2018a; Schmidt et al., 2018). We showed that native tree planting (fire exclusion, tree planting, and herbicide usage) does little to restore savanna herbaceous plant communities, and should not be applied if the aim is to restore areas that were historically savanna (Dalle Laste et al., 2019; Durigan & Ratter, 2016; Pilon et al., 2018b). Thus, instead of tree-focused restoration efforts, we recommend that restoration of savannas after afforestation in Brazil, and globally, focus on tree cutting, prescribed fire, and reintroduction of native grasses and forbs.

TABLES

Table 1 Total richness of herbaceous species in old-growth savannas (Assis State Forest and Santa Barbara Ecological Station, São Paulo, Brazil; N=6 50 × 1 m transects) as well as in each of three afforested sites: Burned Plantation, Harvested & Burned, and Native Tree Planting (Mogi-Guaçu, São Paulo, Brazil; N=10, 50 ×1 m transects for each site).

	Native species (total of all transects)	Undesirable grass species (total of all transects)	Old-growth savanna species (total of all transects)	Number of species per transect (mean ± 95% CI)
Old-growth savannas	78	1	78	23 ± 7.2
Burned Plantation	20	2	9	6 ± 1.2
Harvested & Burned	27	4	12	10 ± 1.5
Native Tree Planting	28	4	9	12 ± 1.4

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FIGURES AND LEGENDS

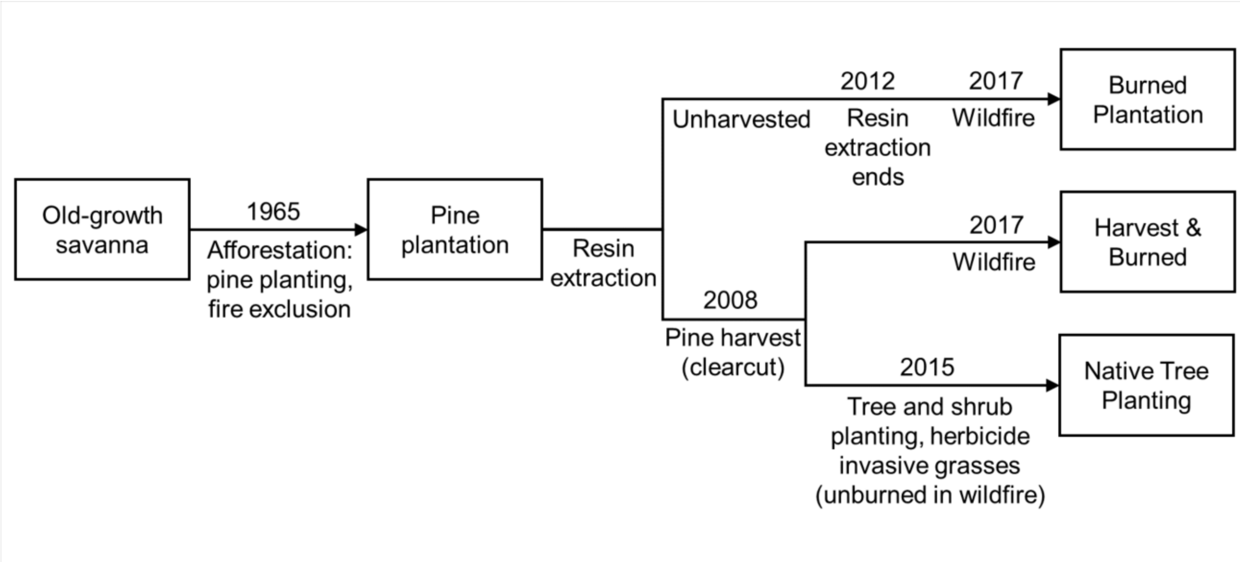

Figure 1 Flow chart of the timing (years) of management interventions that created the three types of post-afforestation sites included in the study (i.e., Burned Plantation, Harvested & Burned, and Native Tree Planting). All post-afforestation sites were historically old-growth savannas.

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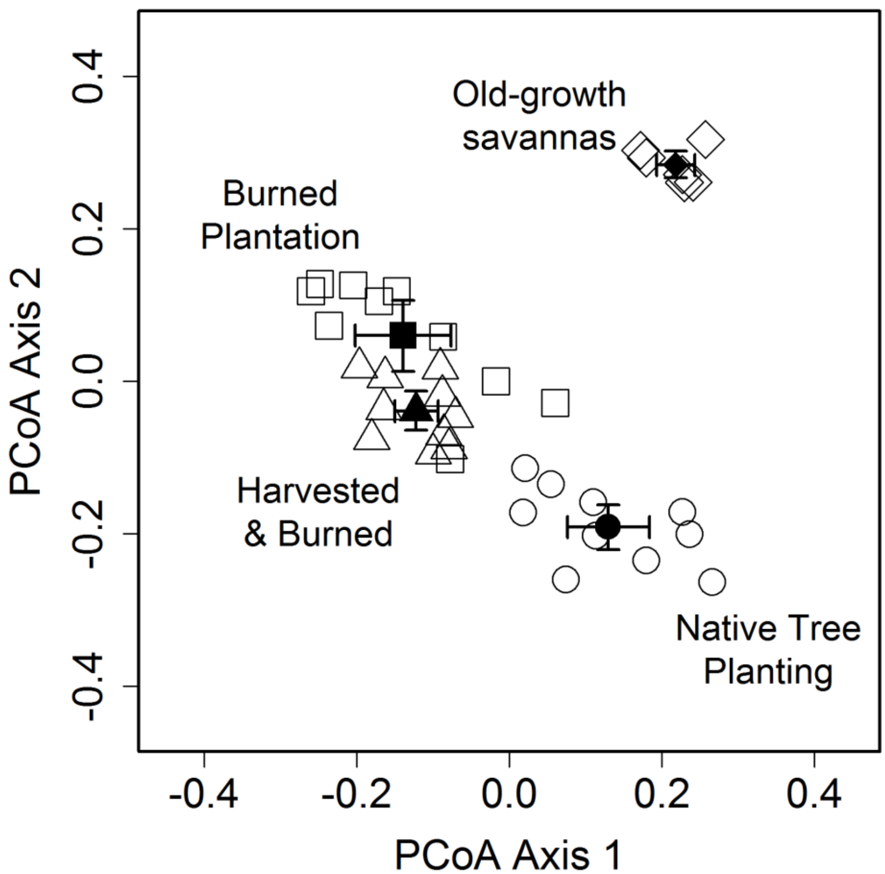

Figure 2 Principal Coordinates Analysis (PCoA) of native herbaceous species in old-growth savannas (*N*=6 transects total) and afforested sites (Burned Plantation, Harvested & Burned, and Native Tree Planting; *N*=10 transects per site). For each site type, open symbols represent transects and filled symbols with bars represent centroids±95% CI.

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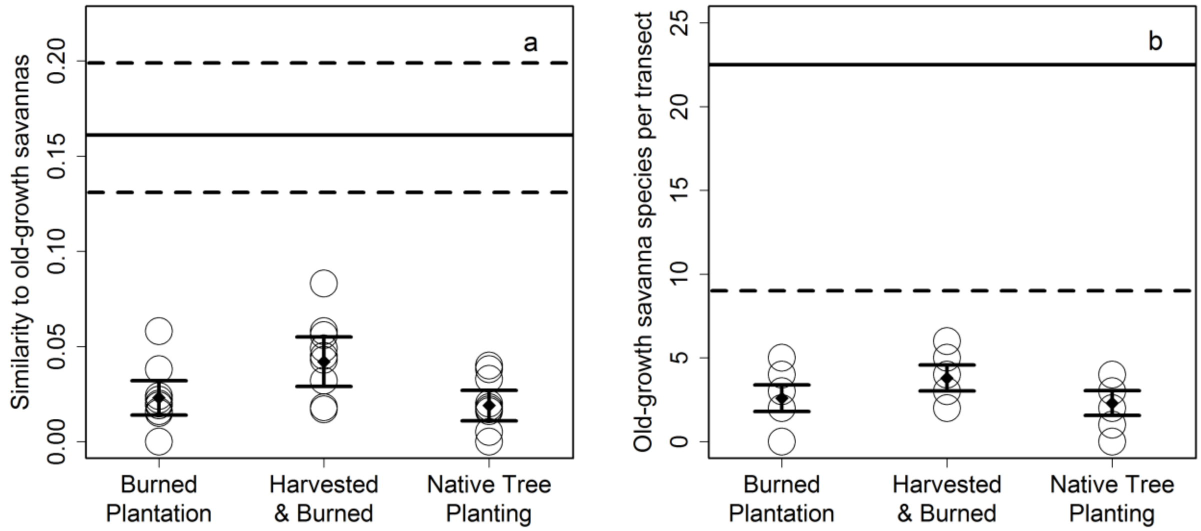

Figure 3 Assessment of compositional similarity of the post-afforestation sites relative to old-growth savannas, based on native herbaceous-layer plant species (i.e., undesirable species were excluded). For post-afforestation sites, open circles represent transects (*N*=10 per site) and black diamonds with bars display the mean±95% CI. Horizontal lines represent the mean (solid), maximum (dashed) and/or minimum (dashed) of old-growth savanna transects (*N*=6) (a) Jaccard similarity between each post-afforestation transect and each of six reference transects in old-growth savannas. Reference values represent the similarity of each of six old-growth savanna transects to the other five reference transects. (b) Richness of native species that occurred in at least one old-growth savanna transect (number of species per 50 × 1 m transect).

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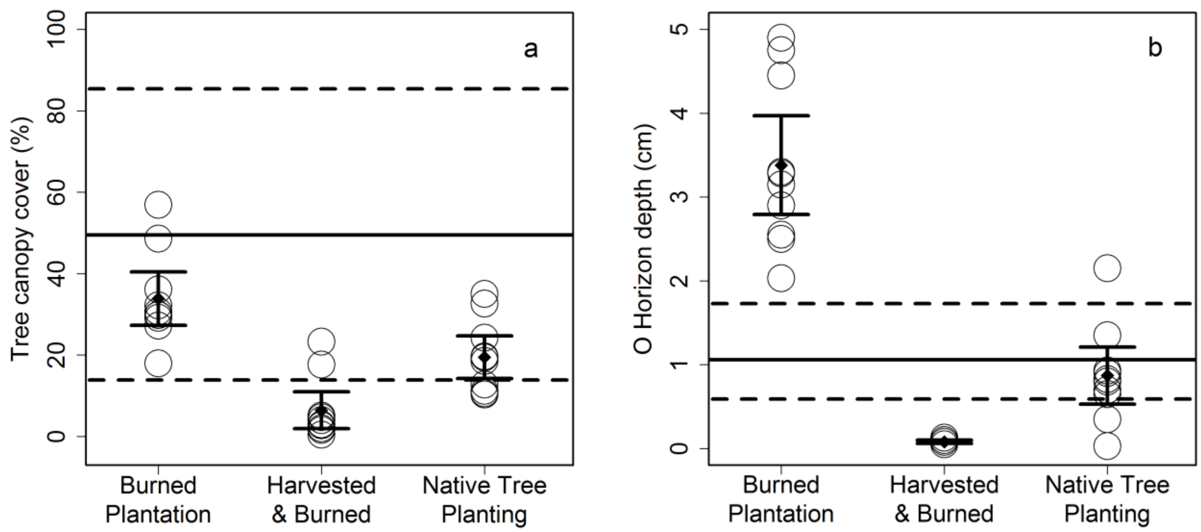

Figure 4 Ground cover of (a) native herbaceous species and (b) undesirable grass species in post-afforestation sites relative to old-growth savannas. For post-afforestation sites, open circles represent transects (*N*=10 per site) and black diamonds with bars display the mean±95% CI. Horizontal lines represent the mean (solid), maximum (dashed) and minimum (dashed) of old-growth savanna transects (*N*=3 for native herbaceous and *N*=6 for undesirable grass cover). Note that the reference values for native herbaceous cover are lower than is typical for cerrado because our old-growth savanna transects had not burned for several years.

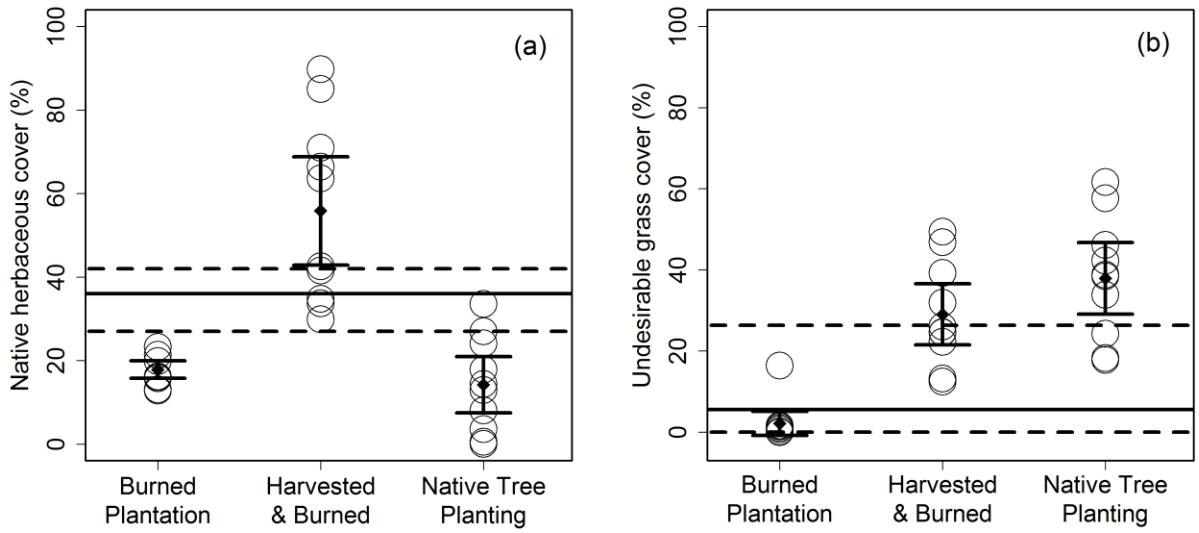

Figure 5 Attributes of vegetation structure and litter accumulation in post-afforestation sites relative to old-growth savannas: (a) tree canopy cover, and (b) O horizon depth (litter + duff). For post-afforestation sites, open circles represent transects (*N*=10 per site) and black diamonds with bars display the mean±95% CI. Horizontal lines represent the mean (solid), maximum (dashed) and minimum (dashed) of old-growth savanna transects (*N*=6)

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DISCLOSURE STATEMENTS

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

Data used for this study will be archived in Dryad Digital Repository.

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SUPPORTING INFORMATION

Content

Figure S1

Table S1

SUPPLEMENTARY INFORMATION

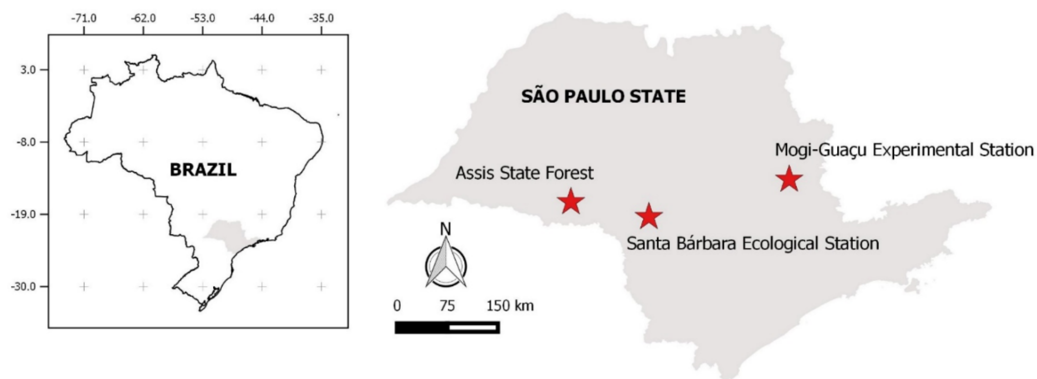

Figure S1 Study locations in São Paulo State, Brazi

Table S1. Herbaceous-layer species recorded in old-growth savannas (Assis State Forest and Santa Bárbara Ecological Station, São Paulo, Brazil; *N*=6, 50 × 1 m transects) and at the three post-afforestation sites: Burned Plantation, Harvested & Burned, and Native Tree Planting (Mogi-Guaçu, São Paulo, Brazil; *N*=10, 50 × 1 m transects for each site).

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Acanthaceae				
Ruellia bulbifera Lindau	X			
Ruellia geminiflora Kunth	X			
Amaranthaceae				
†*Pfaffia* sp.	X			
Anacardiaceae				
Anacardium humile A.St.-Hil.	X	X		
Annonaceae				
Ananas ananassoides (Baker) L.B.Sm.		X		
Apocynaceae				
Mandevilla pohliana (Stadelm.) A.H.Gentry	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Asteraceae				
Acanthospermum australe (Loefl.) Kuntze	X			X
Achyrocline satureioides (Lam.) DC.	X			X
Aspilia clausseniana Baker	X			
Chaptalia integerrima (Vell.) Burkart	X			
Chrysolaena obovata (Less.) Dematt.	X			
Conyza bonariensis (L.) Cronquist				X
Conyza canadensis (L.) Cronquist				X
Emilia sonchifolia (L.) DC. ex Wight				X
Erechtites hieracifolius (L.) Raf. ex DC.		X	X	X
Orthopappus angustifolius (Sw.) Gleason	X		X	
Porophyllum ruderale (Jacq.) Cass.				X
Pterocaulon alopecuroides (Lam.) DC.			X	
Vernonanthura oligolepis (Sch.Bip. ex Baker) H.Rob.	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
†Unknown sp. 1	X			
Bignoniaceae				
Anemopaegma glaucum Mart. ex DC.		X		X
Jacaranda decurrens Cham.	X			
Bromeliaceae				
Ananas ananassoides (Baker) L.B.Sm.	X	X	X	
Bromelia balansae Mez	X			
Chrysobalanaceae				
Licania humilis Cham. & Schltdl.	X			
Commelinaceae				
Commelina erecta L.	X			
Convolvulaceae				
Evolvulus fuscus Meisn.	X			
Evolvulus sericeus Sw.	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Cucurbitaceae				
Melothria campestris (Naudin) H. Schaef. & S.S. Renner	X		X	
Cyperaceae				
Bulbostylis hirtella (Schrad.) Urb.	X			X
Cyperus aggregatus (Willd.) Endl.		X	X	X
Cyperus difformis L.		X		
†*Pycreus* sp.			X	
Rhynchospora exaltata Kunth	X			
Rhynchospora tenuis Link			X	
Scleria gaertneri Raddi		X		X
Scleria scabra Willd.	X			
Euphorbiaceae				
Croton antisyphiliticus Mart.	X			
Croton campestris A.St.-Hil.	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Croton glandulosus L.	X			
Microstachys serrulata (Mart. & Zucc.) Müll.Arg.	X			
Fabaceae				
Andira humilis Mart. ex Benth.	X		X	
Chamaecrista desvauxii (Collad.) Killip	X	X		
Chamaecrista flexuosa (L.) Greene	X			X
Chamaecrista ramosa (Vogel) H.S.Irwin & Barneby	X			
Chamaecrista rotundifolia (Pers.) Greene	X			
†*Crotalaria* sp.				X
Crotalaria micans Link	X	X	X	X
Crotalaria pallida var. *obovata* (G.Don) Polhill	X			
Desmanthus tatuhyensis Hoehne	X			
Eriosema campestre Benth.	X	X	X	
Galactia grewiaefolia (Benth.) Taub.	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Galactia heringeri Burkart			X	
Mimosa dolens Vell.	X			
Mimosa gracilis Benth.		X		X
Mimosa xanthocentra Mart.	X			
Stylosanthes acuminata M.B.Ferreira & Sousa Costa	X		X	
Zornia reticulata Sm.			X	X
Family not determined				
†Unknown sp. 2				X
Lamiaceae				
Gymneia interrupta (Pohl ex Benth.) Harley & J.F.B.Pastore	X			
Hyptis campestris Harley & J.F.B. Pastore	X		X	
Mesosphaerum suaveolens (L.) Kuntze				X
Malpighiaceae				
Aspicarpa pulchella (Griseb.) O'Donell & Lourteig	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Byrsonima subterranea Brade & Markgr.	X			
Camarea hirsuta A.St.-Hil.	X			
Malvaceae				
†*Melochia* sp.			X	
†*Pavonia* sp.	X			
Peltaea polymorpha (A.St.-Hil.) Krapov. & Cristóbal		X		
Sida linifolia Cav.	X			
Waltheria communis A.St.-Hil.			X	X
Menispermaceae				
Cissampelos ovalifolia DC.	X	X	X	X
Myrtaceae				
Psidium australe Cambess.	X			
Psidium grandifolium Mart. ex DC.	X			
Psidium laruotteanum Cambess.	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Phyllanthaceae				
Phyllanthus niruri L.	X			
Poaceae				
Andropogon bicornis L.		X	X	X
Andropogon leucostachyus Kunth	X	X	X	X
Aristida jubata (Arechav.) Herter	X			
Aristida megapotamica Spreng.	X			
Axonopus aureus P. Beauv.	X			
Axonopus compressus (Sw.) P. Beauv.		X	X	X
Axonopus marginatus (Trin.) Chase	X			
Axonopus pellitus (Nees ex Trin.) Hitchc. & Chase	X	X		
Axonopus pressus (Nees ex Steud.) Parodi	X		X	
Axonopus siccus (Nees) Kuhlm.	X			
**Digitaria insularis* (L.) Fedde			X	X

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
†*Digitaria* sp.			X	
Echinolaena inflexa (Poir.) Chase		X	X	X
Elionurus muticus (Spreng.) Kuntze	X			
Eragrostis leucosticta Nees ex Döll	X			
Imperata brasiliensis Trin.			X	X
Loudetiopsis chrysothrix (Nees) Conert	X			
**Melinis minutiflora* P.Beauv.		X	X	X
**Melinis repens* (Willd.) Zizka			X	X
Panicum campestre Nees ex Trin.	X			
Panicum cervicatum Chase			X	
Panicum sellowii Nees				X
Paspalum ammodes Trin.	X			
Paspalum carinatum Humb. & Bonpl. ex Flüggé	X			
Paspalum gardnerianum Nees	X			

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Paspalum hyalinum Nees ex Trin.				X
Paspalum lachneum Nees ex Steud.	X			
Paspalum multicaule Poir.			X	
Paspalum pectinatum Nees ex Trin.	X			
Sporobolus cubensis Hitchc.	X			
Steinchisma laxum (Sw.) Zuloaga				X
Trachypogon spicatus (L.f.) Kuntze	X			
**Urochloa decumbens* (Stapf) R.D.Webster	X	X	X	X
†Unknown sp.3			X	
Polypodiaceae				
Pleopeltis minima (Bory) J. Prado & R.Y. Hirai		X		
Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.	X			
Rubiaceae				
Borreria multiflora (DC.) Bacigalupo & E.L.Cabral			X	

Species	Old-growth savannas	Burned Plantation	Harvested & Burned	Native Tree Planting
Limnosipanea erythraeoides (Cham.) K.Schum.	X			
Mitracarpus hirtus (L.) DC.	X			
Psychotria hoffmannseggiana (Willd. ex Schult.) Müll.Arg.	X			
†*Psychotria* sp.		X		
Richardia scabra L.	X			X
Rubiaceae				
Borreria poaya (A.St.-Hil.) DC.	X			
Coccocypselum lanceolatum (Ruiz & Pav.) Pers.	X			
Sapotaceae				
Pradosia brevipes (Pierre) T.D.Penn.	X	X	X	X
Turneraceae				
Piriqueta aurea (Cambess.) Urb.			X	
Piriqueta rosea (Cambess.) Urb.	X			

* undesirable grass species

†species that could not be identified to species were excluded from the analyses.