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RESEARCH ARTICLE

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Abandoned pastures cannot spontaneously recover the attributes of old-growth savannas

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Abstract

1. Active restoration strategies have been recommended to recover Neotropical savannas in abandoned lands, but no studies have investigated the trajectories and speeds of spontaneous recovery for these systems. Research into the dynamics of degraded savannas is urgently needed to guide restoration decision making.
2. We analysed the dynamics of secondary savannas in the Brazilian Cerrado by sampling 29 abandoned pastures (time since abandonment ranging from 3 to 25 years) and applying the space-for-time substitution method. We modelled the temporal changes in plant community attributes and estimated the time (years) required for these attributes to match those of two reference ecosystems (three replicates each), old-growth savanna and a forest-type savanna, which had encroached following fire suppression (encroached savanna). We also analysed the plant community composition of the study sites.
3. Our models showed that tree canopy cover, richness and density rapidly increased with time since pasture abandonment, easily surpassing the values of the old-growth savanna (28 years) and reaching the values of encroached savanna 49 years after abandonment. The cover and richness of the ground layer increased at a much slower pace. Since the species in this layer, including the exotic grasses, are shade intolerant, they will be eliminated by canopy closure over time.
4. Up to 25 years after abandonment, secondary savannas continued to lack many (37%) old-growth savanna species, mostly from the ground layer (82% of grasses absent). This period was also not sufficient for the secondary savannas to become floristically similar to the encroached savannas, which are dominated by shade-tolerant tree species.
5. *Synthesis and applications*. Despite the reported high natural regeneration of Neotropical savanna vegetation, abandoned pastures will not spontaneously return to an old-growth savanna state. Protected from fire and lacking the native ground layer, the end state of secondary savannas will be a low-diversity forest. If restoration goals include the recovery of old-growth savanna biodiversity and structure, interventions are required to prevent woody encroachment and reintroduce native grasses, forbs and shrubs. However, if the desirable endpoint is a low-diversity forest, passive restoration (non-intervention) and fire protection are appropriate.

KEYWORDS
Cerrado, chronosequence, encroached savanna, natural regeneration, Neotropical savanna, passive restoration, savanna restoration, secondary savanna, vegetation trajectories, woody encroachment

1 | INTRODUCTION

In the last 10 years, practically all countries in the world have made ambitious global commitments involving the restoration of degraded ecosystems (Aronson & Alexander, 2013; Suding et al., 2015), including Neotropical savannas (Strassburg et al., 2017), which are biodiversity hotspots (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Therefore, restoration scientists and practitioners have developed and tested several methods to actively restore these ecosystems (Ferreira, Walter, & Vieira, 2015; Pereira, Laura, & Souza, 2013; Pilon, Buisson, & Durigan, 2017; Silva, Oliveira, Rocha, & Vieira, 2015; Silva & Vieira, 2017). However, active savanna restoration is challenging due to the high cost of controlling exotic grasses (Breed, Lowe, & Mortimer, 2016) and the unavailability of commercial propagules (vegetative material or seeds) of native plants, especially grasses, forbs and shrubs, to replace exotics (Pilon et al., 2017).

An additional challenge to the ecological restoration of savannas is that they are fire-prone ecosystems that depend on fire for maintenance (Veldman, 2016). If savanna restoration does not include re-establishing the historical fire regime, the maintenance of vegetation structure and diversity, as well as the ecological processes that depend on fire, will be jeopardized (Abreu et al., 2017; Durigan & Ratter, 2016; Honda & Durigan, 2016). Without fire, both old-growth and restored savannas tend to become forests, which are possible alternative states in many parts of the world (Bond, Woodward, & Midgley, 2005; Staver, Archibald, & Levin, 2011).

Studies in tropical forests have shown that passive restoration (non-intervention) may produce results similar to those of active restoration over relatively short time frames in abandoned pastures (Meli et al., 2017). Passive restoration can be advantageous because of its low cost (Zahawi, Reid, & Holl, 2014), but some systems do not spontaneously return to their pre-disturbance state and instead transition to undesirable alternative states (Standish et al., 2014; Suding, Gross, & Houseman, 2004). Restoration strategies should, therefore, be selected based on the potential for natural regeneration (Holl & Aide, 2011) and the recovery dynamics of the target system (Suding, Spotswood, Chapple, Beller, & Gross, 2016). If the final ecological state of the regenerating community can be predicted, and if this state is desirable, passive restoration is appropriate (Holl & Aide, 2011; Prach, Marrs, Pysek, & van Diggelen, 2007).

To our knowledge, no studies have investigated the dynamics of Neotropical savannas following conversion to productive land uses and subsequent abandonment, and their potential for natural regeneration has not been evaluated. Consequently, active restoration has been widely recommended for these systems, with high costs and disappointing outcomes. The aim of this study was to generate data to inform which restoration strategy to adopt in these cases. We analysed the temporal trajectories of secondary savannas in the Brazilian Cerrado, by sampling 29 pastures abandoned between 3 and 25 years and applying the space-for-time substitution method. We modelled the temporal changes in richness and structure of the vegetation and estimated the time (years) required for these attributes to reach a pre-disturbance state (old-growth savanna) or a possible alternative state (encroached savanna). We also analysed the plant community composition of the study sites to verify if the abandoned pastures are becoming similar to the reference ecosystems.

2 | MATERIALS AND METHODS

2.1 | Study region

The study region is in the austral limit of the Cerrado ecoregion (sensu Olson et al., 2001), which is the largest representation of the savanna biome in the Americas. The 35 study areas are distributed along 11,747 km^2 in the central-west region of the state of São Paulo, Brazil (ranging from 22°20′ to 22°50′S latitude and from 48°44′ to 50°37′W longitude) at altitudes varying between 445 and 854 m above sea level. The region's climate is characterized by cold and dry winters from April to September and hot and humid summers from October to March. The average annual rainfall in the study region varies between 1,170 and 1,302 mm, but the monthly average may be as low as 22 mm in the driest month of the year (August) and reach 223 mm in the wettest month (January). The average annual temperature varies among sites between 20.2°C and 22.4°C, and it is approximately 16.5°C in the coldest month of the year (July) and may reach 25.2°C in the hottest month (February). The study region was formerly covered by a mosaic of Cerrado (tropical grassy savanna biome) and Atlantic forest (seasonal tropical forest), but the landscape is currently strongly fragmented with a matrix dominated by pasture (Durigan, Siqueira, & Franco, 2007).

2.2 | Study areas

Three types of study sites were sampled: secondary savannas (abandoned pastures), old-growth savannas and encroached savannas (Figure S1).

To build a chronosequence, we selected 29 secondary savannas resulting from the conversion of old-growth savannas into pastures for several decades and subsequent pasture abandonment. The size of the abandoned pastures varied between 0.37 and 114 ha (26 ± 33 ha, on average). Pasture formation in the study region commonly involves the almost complete elimination of native trees (shade trees may be kept) and the planting of exotic grasses (Klink & Machado, 2005; Pivello, Carvalho, Lopes, Peccinini, & Rosso, 1999; Williams & Baruch, 2000), especially *Urochloa decumbens* (Stapf) R.D. Webster and *Urochloa humidicola* (Rendle) Morrone & Zuloaga. Most of the pastures selected for this study had been abandoned by landowners for conservation purposes, once Brazilian environmental law (by law no. 4.771 from 1965 until 2012 and law no. 12.651 from 2012 on) requires that 20% of the total area of a private rural property must be covered by native vegetation (preserved or restored). The time since livestock removal from the pastures varied between 3 and 25 years, according to the landowners or people responsible for the study areas. Despite the importance of fire for the maintenance of secondary savannas (Veldman, 2016), these pastures had been protected from fire since their abandonment because burning is illegal in Brazil (Durigan & Ratter, 2016). All areas presented a flat relief and relatively homogeneous soils (M. G. B. Cava, unpublished data) that are acidic (pH ranging from 3.7 to 4.8), sandy (total sand content ranging from 765 to 934 g/kg), with low fertility (degree of base saturation [V%] ranging from 8 to 47).

The historical vegetation of the study region was characterized by sparse trees scattered over a continuous grass layer (old-growth savanna) (Borgonovi & Chiarini, 1965), but recent studies have shown that fire suppression results in rapid woody encroachment (Durigan & Ratter, 2006), resulting in a forest-type vegetation (encroached savanna). We, therefore, selected these two types of natural vegetation as the possible final ecological states of regenerating savanna and treated them as reference ecosystems. We selected three sites with well-conserved old-growth savanna and three sites covered by encroached savanna, which has resulted from anthropogenic suppression of natural fires (Abreu et al., 2017; Durigan & Ratter, 2016). These sites are located within the protected natural areas of the Santa Bárbara Ecological Station (Estação Ecológica de Santa Bárbara) (22°48′59″S, 49°14′12″W; 2,712 ha) and the Assis Ecological Station (Estação Ecológica de Assis) (22°34′19.72″S, 50°24′39.98″W; 1,760.64 ha).

2.3 | Vegetation sampling

We sampled the vegetation in 50 × 20-m (1,000-m²) randomly established plots (one plot per site) in secondary savannas (n = 29) and the reference ecosystems (n = 6), avoiding the edges and the riparian zones. We counted and identified all trees with a diameter at breast height (dbh) greater than 5 cm in each plot to determine tree density and richness, and we established a 50 × 1-m (50-m²) subplot along the central longitudinal axis of each study plot in which we identified all plants smaller than 5 cm dbh (young trees, shrubs, subshrubs, lianas, palms, forbs and grasses) to determine the richness of the ground layer. If a species could not be identified in the field, we collected plant material for later identification with the assistance of specialists and herbarium consultations. Finally, we quantified the canopy cover (ground area covered by the projection of the tree canopy), total ground cover (all native plants on the ground), native grass cover (ground area covered exclusively by native grasses) and exotic grass cover (ground area covered exclusively by exotic grasses) within each 50 × 20-m plot using line-intercept sampling (Canfield, 1941). Using 50-m-long tape measures, we established three lines (at the centre and both sides) in each plot. Cover components were quantified separately as the average of the three lines, and their cover was expressed as the percentage of the total length of the line.

2.4 | Data Analysis

2.4.1 | Vegetation attributes

To analyse the trajectory of the regenerating secondary savannas, we determined the following plant community attributes for each site: canopy cover (%), total ground cover (%), native grass cover (%), exotic grass cover (%), tree density (individuals ha^{-1}, dbh ≥5 cm), tree species richness (per 1,000 m², dbh≥5 cm) and species richness of the ground layer (per 50 m²).

2.4.2 | Comparison between reference ecosystems

To analyse the differences in species richness and community structure between old-growth savanna and encroached savanna, we performed one-way analysis of variance after ensuring that the assumptions were not violated. Graphical analyses including plotting residuals against predicted values to verify homogeneity of variances and constructing box plots to verify normality (Quinn & Keough, 2002).

2.4.3 | Trajectory modelling of regenerating secondary savannas

To investigate the temporal trajectories of regenerating secondary savannas in abandoned pastures, we modelled the data using linear models, considering the measured attributes as the response variables and the time since pasture abandonment (years) as the predictor variable. We built models for all measured attributes and chose the best-fit model based on the highest r^2 value (Zar, 1999).

2.4.4 | Predictive analyses using the fitted models

Using the fitted models, we performed a predictive analysis of the time required (years) for each attribute of the regenerating community to equal the values of the reference ecosystems (old-growth savanna and encroached savanna).

2.4.5 | Species composition

All identified species were categorized by life-form: tree, shrub, subshrub, palm, liana, forb and grass. We used this information to determine the partitioning of the species from the reference ecosystems and the secondary savannas among these groups.

To assess the similarity in plant species composition among the secondary, old-growth and encroached savannas, we performed an ordination based on the presence/absence matrix of species per site using non-metric multidimensional scaling (NMDS) with scores built

TABLE 1 Characteristics of old-growth savanna and encroached savanna (mean and standard error, *SE*) and the estimated time (years) required for regenerating secondary savannas to reach these values based on chronosequence models. Except for exotic grass cover, all measured variables of the reference ecosystems were significantly different based on one-way analysis of variance. The values of r^2 presented are related to the chronosequence linear models (Figure 2)

		Old-growth savanna (n = 3)		Encroached savanna (n = 3)	
Vegetation attribute	r^2	M ± *SE*	Time (years)	M ± *SE*	Time (years)
Canopy cover (%)	.67	76.66 ± 2.60	24	98.33 ± 1.20	31
Total ground cover (%)	.40	39.66 ± 12.05	47	2.66 ± 3.78	4
Native grass cover (%)	.53	23.00 ± 4.58	49	1.66 ± 1.67	9
Exotic grass cover (%)	.53	0	36	0	36
Tree density (individuals per hectare)	.56	890 ± 180	28	1,587 ± 117	49
Tree richness (per 1,000 m²)	.60	14 ± 2	17	26 ± 3	30
Richness of the ground layer (per 50 m²)	.26	71 ± 4	49	35 ± 1	19

from Bray–Curtis dissimilarity index values (Clarke, 1993). All analyses were performed using R software (R Development Core Team, 2014).

3 | RESULTS

3.1 | Differences between reference ecosystems

Significant differences were observed between old-growth savannas and encroached savannas for all the measured vegetation attributes, except exotic grass cover, because both reference ecosystems were free of invasive species (Table 1). Cover and richness of the ground layer as a whole and the native grasses were higher in old-growth savannas than in encroached savannas: 37% higher total ground cover ($F_{1,4}$ = 25.72, p = .007), more than twice the ground layer species richness ($F_{1,4}$ = 71.57, p = .001) and 12-fold higher native grass cover ($F_{1,4}$ = 19.14, p = .0119) (Table 1). Canopy cover, tree density and richness were higher in the encroached savannas than in the old-growth savannas: 21% higher canopy cover ($F_{1,4}$ = 57.09, p = .002), 697 more trees per hectare ($F_{1,4}$ = 10.5, p = .032) and almost twice the tree species richness ($F_{1,4}$ = 11.68, p = .027) (Table 1).

3.2 | Vegetation trajectories of regenerating secondary savannas

All the modelled attributes of regenerating savannas were significantly related to the time since pasture abandonment and best fitted by linear models with r^2 values between .26 (species richness of the ground layer) and .67 (canopy cover).

Canopy cover (r^2 = .67, $F_{1,27}$ = 53.6, p < .001; Figure 1a), tree density (r^2 = .56, $F_{1,27}$ = 34.05, p < .001; Figure 1d), tree richness (r^2 = .60, $F_{1,27}$ = 38.91, p < .001; Figure 1e), total ground cover (r^2 = .40, $F_{1,27}$ = 18.66, p < .001; Figure 1b), native grass cover (r^2 = .53, $F_{1,27}$ = 30.05, p < .001; Figure 1g) and species richness of the ground layer (r^2 = .26, $F_{1,27}$ = 9.444, p = .001; Figure 1f) increased linearly with the time since pasture abandonment. In contrast, the exotic grass cover (r^2 = .53, $F_{1,27}$ = 30.88, p < .001; Figure 1c) linearly decreased with the time since pasture abandonment.

3.3 | Time required for secondary savannas to approximate the reference ecosystems

The estimated time for the secondary savanna attributes to reach old-growth savanna values varied widely (Table 1, Figure 1). The first attribute to reach an old-growth savanna value was tree richness, which occurred at approximately 17 years after pasture abandonment, followed by canopy cover 7 years later (24 years after pasture abandonment), both of which were within the period covered by the chronosequence. Tree density was estimated to reach the old-growth savanna value 28 years after pasture abandonment, and exotic grass cover tended to disappear (reach the old-growth savanna value) 36 years after pasture abandonment. Cover and species richness of the ground layer were estimated to reach old-growth savanna values after 47 and 49 years, respectively, since pasture abandonment, and native grass cover was estimated to take 49 years to reach the values of old-growth savanna. However, native grass cover was zero in 22 of the 29 pastures studied.

The predicted time for the secondary savanna attributes to reach the encroached savanna values also varied widely (Table 1, Figure 1). The first attribute to reach an encroached savanna value was ground cover, which occurred 4 years after pasture abandonment, followed by native grass cover (9 years) and richness of the ground layer (19 years), all of which were within the period covered by the chronosequence. In the models, tree species richness approximated that of encroached savanna 30 years after pasture abandonment followed by canopy cover 1 year later (31 years). We estimated that exotic grass cover will reach that of the encroached savanna, i.e., disappear, 36 years after pasture abandonment. Lastly, tree density will reach that of the encroached savanna 49 years after pasture abandonment.

3.4 | Composition

We documented a total of 329 species in the 35 sites (Table S1). We recorded 240 species in the secondary savannas (2.9 ha sampled in total). The old-growth and encroached savannas presented 137 and 81 species, respectively, despite only sampling 0.3 ha each. Up

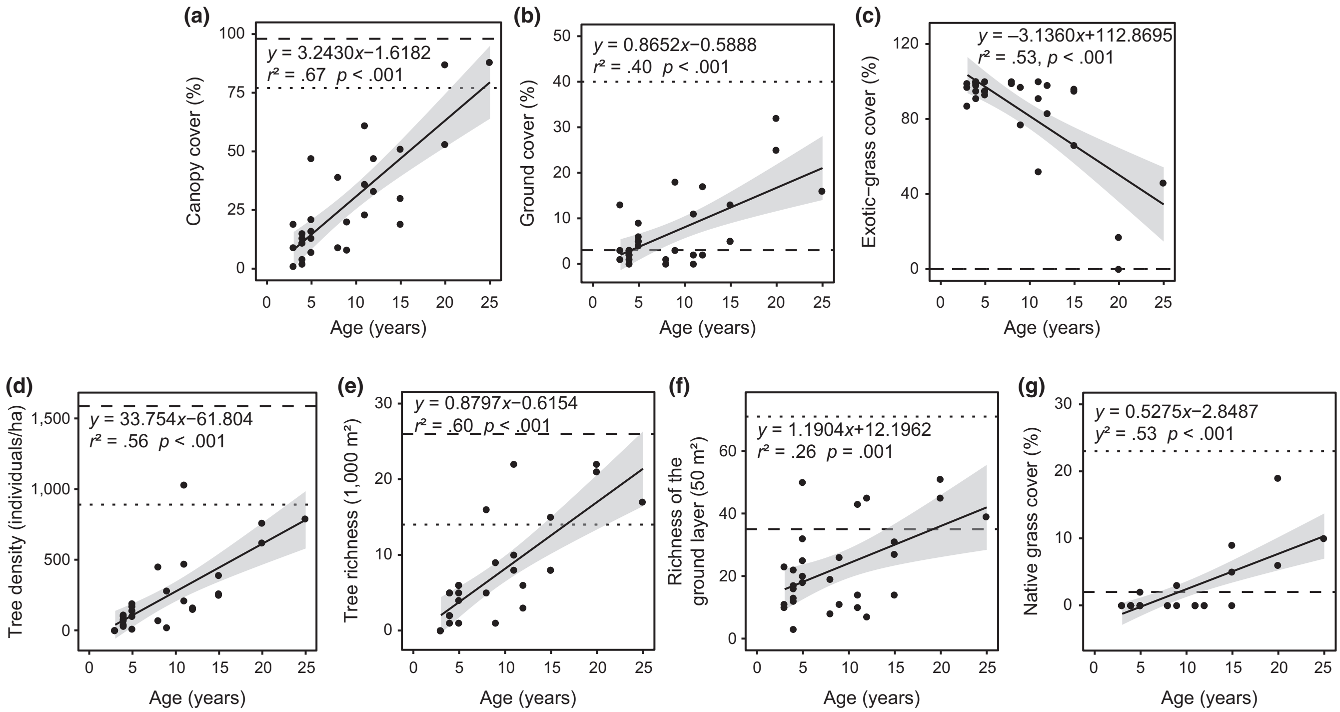

FIGURE 1 Temporal trajectories of the characteristics of regenerating secondary savannas based on a chronosequence (0–25 years): (a) canopy cover, (b) ground cover, (c) exotic grass cover, (d) tree density (dbh ≥5 cm), (e) tree species richness (dbh ≥5 cm), (f) species richness of the ground layer (all plants smaller than 5 cm dbh, including young trees, shrubs, subshrubs, lianas, palms, forbs and grasses) and (g) native grass cover. Dotted horizontal lines represent the means for old-growth savanna, and dashed horizontal lines represent those for encroached savanna (Table 1). The grey areas represent the standard error of the regression analysis

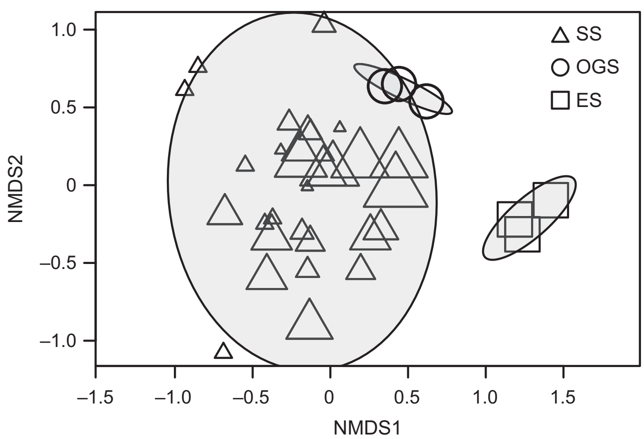

FIGURE 2 Non-metric multidimensional scaling (NMDS) ordination of the species composition of secondary savannas (SS), old-growth savannas (OGS) and encroached savannas (ES) (stress = 0.11). Ellipses represent 95% confidence intervals for the standard deviation. For the secondary savannas (SS), the size of triangles is proportional to the time since pasture abandonment (0–25 years)

to 25 years after pasture abandonment, the species composition of the secondary savannas was more similar to that of the old-growth savannas than the encroached savannas (Figure 2). We verified that 37% of the old-growth savanna species (51 species) and 56% of the encroached savanna species (46 species) were not recorded in the secondary savannas, and partitioning the species into functional groups (see Figure S2) showed that a high proportion of the species from the old-growth savannas, especially grasses, did not recover in the abandoned pastures. Of 17 grass species recorded in old-growth savannas, only three recovered in the abandoned pastures (Table S1).

4 | DISCUSSION

4.1 | The remarkable differences between reference ecosystems

In this study, we considered two different types of reference ecosystems (old-growth savanna and encroached savanna) as the possible final ecological states of the studied regenerating secondary savannas. The old-growth savanna, which corresponded to the pre-disturbance state, is characterized by sparse trees scattered over a continuous grass stratum (Oliveira-Filho & Ratter, 2002); it presents high plant diversity consisting primarily of non-tree species (grasses, forbs and shrubs) in the ground layer (Filgueiras, 2002). The encroached savanna, which corresponded to the alternative state, presents a forest structure (Oliveira-Filho & Ratter, 2002), resulting from the suppression of the fire-vegetation feedback loop (Veldman, 2016). When the natural fire regime is suppressed, the transformation of old-growth savanna can occur in about three decades, which results in the suppression of ground layer species and thus a drastic decline in plant diversity (Abreu et al., 2017; Durigan & Ratter, 2016). Therefore, old-growth savannas are characterized as ancient, flammable and biodiverse ecosystems, whereas encroached savannas are low-diversity forests resulting from anthropogenic fire suppression (Veldman, 2016).

4.2 | Can abandoned pastures approximate the attributes of reference ecosystems over time?

Our models, which were based on a chronosequence, showed that the species richness and structure of secondary savannas, which resulted from the conversion of old-growth savannas to pastures and their subsequent abandonment, change in a predictable manner over time. After pasture abandonment, the regenerating communities will reach an ecological state similar to an encroached savanna in an estimated 49 years. However, they will not return to the old-growth savanna state because the natural succession leads to a forest structure.

This result was observed because fire was not reintroduced to the regenerating savannas. Studies performed in secondary savannas and old-growth savannas in South America (Abreu et al., 2017; Durigan & Ratter, 2006; Henriques & Hay, 2002; Moreira, 2000; Roitman, Felfili, & Rezende, 2008; San José & Fariñas, 1983), Africa (Brookman-Amissah, Hall, Swaine, & Attakorah, 1980; Strang, 1974; Swaine, Hawthorne, & Orgle, 1992) and Australia (Bowman & Panton, 1995; Woinarski, Risler, & Kean, 2004) showed similar vegetation dynamics to those observed in this study (vegetation thickening) in sites where fire, which is essential to maintaining savanna structure, diversity and functioning, was suppressed (Veldman, 2016).

We showed that most secondary savanna characteristics that increase fast were related to the woody layer (canopy cover, tree density and richness), indicating that a significant portion of the tree species of the Cerrado resist the disturbance caused by the conversion of old-growth savanna to pasture and the subsequent grazing. Considering the limited regeneration of Brazilian savanna tree species from seeds (Salazar, Goldstein, Franco, & Miralles-Wilhelm, 2012) and the establishment filter posed by the exotic grasses in abandoned pastures (Hoffmann & Haridasan, 2008), the tree species in the regenerating savannas likely resulted from the resprouting of subterranean structures that had persisted in the study areas since the conversion of the old-growth savannas to pastures, as observed by Durigan, Contieri, Franco, and Garrido (1998) (more than 80% resprouters).

Exotic grass cover, in turn, decreased linearly over time and was estimated to disappear from secondary savannas within 36 years. This is because the C4 grasses present at the study sites (*U. decumbens* and *U. humidicola*) are shade intolerant (Klink & Joly, 1989; Xavier, Leite, & da Silva-Matos, 2016), and the regenerating systems were estimated to exhibit forest canopy by the end of this period.

We found that the cover and richness of the ground layer slowly increased over time due to the low resilience of the non-tree old-growth savanna species. Up to 25 years after abandonment, secondary savannas continued to lack many old-growth species (51 species or 37%) that were unable to recover in abandoned pastures, and of the missing species, most (78%) were not trees. Native grasses, which corresponded to 12% of the species and 23% of the ground cover in the old-growth savannas, were restricted to 1% of the species and 2% of the ground cover in the abandoned pastures. For every five grass species from old-growth savannas, only one was able to recover in abandoned pastures, and of the 29 pastures surveyed, 22 had no native grass cover. Furthermore, most secondary savannas presented exotic grass cover higher than 80%. There are numerous reports of invasive exotic African grasses in old-growth savannas in South America (Barger, D'Antonio, Ghneim, & Cuevas, 2003; Gorgone-Barbosa et al., 2015; Williams & Baruch, 2000) and Australia (Rossiter, Setterfield, Douglas, & Hutley, 2003; Setterfield, Douglas, Hutley, & Welch, 2005; Setterfield, Rossiter-Rachor, Hutley, Douglas, & Williams, 2010); these species displace and replace native grasses because they are more competitive (D'Antonio & Vitousek, 1992; Filgueiras, 2002; Pivello et al., 1999). Moreover, the slow recovery of the ground layer will be interrupted and the ground layer will recede due to predicted canopy closure since most species in this layer are shade intolerant (Abreu et al., 2017). The length of the chronosequence was not sufficient for the secondary savannas to become floristically similar to encroached savannas (56% of the species were not recorded in pastures), which are dominated by shade-tolerant tree species.

4.3 | The potential of natural regeneration for the restoration of Neotropical savannas in abandoned pastures

Whether natural regeneration can be used to recover Neotropical savannas in abandoned pastures will mainly depend on the restoration goals (including project timelines) and available resources (Holl & Aide, 2011). Our models show that passive restoration (non-intervention) may be effective in abandoned pastures previously occupied by old-growth savannas if the goal is, for example, carbon sequestration or the rapid generation of soil cover to control erosion as well as the acceptability of low-diversity forest (encroached savanna), which will not serve as habitat to endemic savanna fauna (Abreu et al., 2017; Veldman et al., 2015).

However, if the goals include the recovery and maintenance of part of the ecosystem structure, diversity and/or services previously provided by old-growth savanna, active restoration is required, and the cost will depend on the level of intervention (McBride et al., 2010). For example, if the goal is to ensure that rivers and underground waters are recharged (water-related ecosystem services), interventions may only involve tree removal to avoid thickening the secondary savannas (Honda & Durigan, 2016), but if the aim is to recover the highly diverse old-growth savanna ground layer in addition to maintaining the savanna structure (sparse trees scattered over a continuous grass stratum), interventions may include controlling exotic grasses and reintroducing native grasses and shrubs (Ferreira et al., 2015). In the former case (tree removal), interventions may be executed at low cost, but in the latter (exotic grass control and the reintroduction of native species), excessive financial resources would be required (Breed et al., 2016). In this scenario, it is up to restorers and, especially, the public policy makers to define realistic goals to ensure successful restoration (Hobbs, 2007; Hobbs, Hallett, Ehrlich, & Mooney, 2011).

Monitoring natural regeneration until some of the secondary savanna characteristics reach old-growth savanna values and subsequently removing trees to avoid the thickening of the vegetation (Brudvig, 2010) may be the most adequate restoration strategy because it has relatively low costs and at least maintains the old-growth savanna structure and part of its animal and plant diversity, which requires an open habitat to survive (Abreu et al., 2017; Durigan & Ratter, 2016; Murphy, Andersen, & Parr, 2016; Veldman et al., 2015). The reintroduction of fire to secondary Neotropical savannas may be equally effective to avoid vegetation thickening, but further studies are needed to optimize this management practice because exotic grasses change fire behaviour (Gorgone-Barbosa et al., 2015) and may have undesirable effects on secondary savannas.

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AUTHORS' CONTRIBUTIONS

G.D. conceived and designed the research, and M.G.B.C., N.A.L.P. and G.D. collected the data. N.A.L.P. analysed the data, and M.G.B.C., N.A.L.P., M.C.R and G.D. interpreted the results. M.G.B.C. wrote the paper. All authors revised the paper and gave final approval for publication.

DATA ACCESSIBILITY

Data used for this study are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.65jr5 (Cava, Pilon, Ribeiro, & Durigan, 2017).

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