Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

The influence of fire and cattle grazing on Araucaria population structure in forest-grasslands mosaics

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ARTICLE INFO

Keywords: Land use Subtropical highland grasslands Araucaria forest Management Conservation Protected areas

ABSTRACT

Disturbances caused by land management via fire and cattle grazing can alter the population structure of keystone species that change the output of vegetation dynamics. Adult araucaria trees (Araucaria angustifolia) can facilitate the establishment of other woody plants and, thus, influence the expansion of forests over grasslands in the highlands of southern Brazil. Here we aimed to check araucaria population structure under two types of management - with or without fire and grazing- and in three habitat types: forests, shrublands and grasslands. We sampled araucaria populations in 40 transects (100×4 m), half of each located in the forest, and the other half, in variable extensions of shrublands or grasslands. Of the 40 transects, 18 were under management with fire and grazing and 22 in a protected area where the two disturbances are prevented (São Joaquim National Park). Overall, we sampled 339 araucaria seedlings, 59 saplings, 44 juveniles and 128 adults. Population structure differed both among habitats, between types of management, and between the same habitats but under distinct types of management. Population density was 1.4 times higher in areas with fire and grazing than without such disturbances, which was caused mostly by a larger number of seedlings. Under fire and grazing, we found 1.4 times more adults in forests, 5.7 times more seedlings in shrublands and 5.3 times more seedlings in the grassland than in the same habitat but without disturbances. Our results indicate that araucarias reach and germinate under all conditions but rarely surpass the seedling stage in grasslands and shrublands where fire and grazing is used. Consequently, fire and grazing disturbances should slow down forest expansion over shrublands and grasslands. In contrast, when disturbances are barred, araucarias can grow large enough to trigger their facilitative effect and then gear up the pace of forest expansion.

1. Introduction

Climate is the main driver of broad global vegetation patterns, such as the distribution of forests or open vegetation. However, in certain regions such as the Brazilian Cerrado or in African savannas, disturbance by fire or grazing by large herbivores controls vegetation structure and dynamics, determining the occurrence of open, non-forested vegetation (Bond and Keeley, 2005; Fidelis, 2020; Schmidt and Eloy, 2020). In the highlands of southern Brazil, subtropical grasslands coexist with mixed forests in mosaics, in most cases forming abrupt boundaries (Klein, 1984; Rambo, 1956). Although the distribution of forests and grasslands remained under dynamic stability for the past 70,000 years, an expansion of forests over grasslands has initiated ~5000 years BP, highly influenced by pre-Columbian people (Bitencourt and Krauspenhar, 2006; Reis et al., 2014) and reducing the area occupied by grasslands (Behling, 1995; Behling and Pillar, 2007). Along with forests and grasslands, shrublands, which can be considered as an intermediate stage in this transition (Carlucci et al., 2016; Guido et al., 2017; Oliveira and Pillar, 2004) can also be present. In this landscape, climate and environmental conditions, disturbances and populations of keystone species play roles that are still incompletely understood. Akin to what happens in other systems, the direction of vegetation transitions can be influenced by the frequency of disturbances, such as fire or large herbivores, or changes in environmental conditions (Bond and Parr, 2010).

Forest-grassland dynamics can also be influenced by keystone species and their population dynamics'. During the recent expansion of

Editor: Dr. Gerhard Overbeck

https://doi.org/10.1016/j.flora.2021.151853

Received 28 October 2020; Received in revised form 28 April 2021; Accepted 15 May 2021 Available online 26 May 2021 0367-2530/© 2021 Elsevier GmbH. All rights reserved.







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forests over grasslands, the conifer tree species Araucaria angustifolia (Bertol.) Kuntze (hereafter "araucaria") played an important role in vegetation dynamics. Araucaria is a long-living, abundant and dominant species (Souza, 2020; Souza et al., 2008; Wilson et al., 2019) able to colonize environments with severe weather conditions, such as highlands (Franco et al., 2005). Adult araucaria trees favor the establishment of forests amid open vegetation and forest patch formation by acting as perches (dos Santos et al., 2011; Duarte et al., 2006) and through facilitation, by changing light availability, air temperature and soil fertility (Korndörfer et al., 2015), further modifying environmental conditions. Nearby forest edges, the development of araucaria is greatest and the mortality of its seedlings is lowest (Guglielme and Ganade, 2006). Thus, the expansion of araucarias and forest over grasslands should likely occur at the edges of forests (Carlucci et al., 2011; Oliveira and Pillar, 2004). Towards the forest interior, although often abundant and dominant, the establishment of araucaria is low because of an increase in predation of seeds and seedlings (Brum et al., 2010), and limited light availability (Souza, 2020). Therefore, local scale factors affecting directly or indirectly this keystone species (Bogoni et al., 2020; Pereira and Ganade, 2008) can drive large-scale vegetation patterns and dynamics.

Disturbances such as fire and grazing are important in influencing the dynamics of highland grasslands and araucaria forests in southern Brazil. Because these disturbances have been occurring in these highlands before and during the recent expansion of forests over grasslands (Behling and Pillar, 2007; Jeske-Pieruschka et al., 2013), they are part of the natural dynamics of vegetation, especially for grasslands (Pillar and Vélez, 2010; Overbeck et al., 2007). Out of those, fire is an important driver of the dynamics of grassland-forest mosaics and accountable for abrupt edges between these two habitats (Jeske-Pieruschka et al., 2010). Herbivory by large grazers (herbivores from the extinct megafauna in the past and, currently, cattle) also play an important role in the current dynamics. Grasslands are important source of food for cattle, and extensive livestock is a common activity in the region (Kilca et al., 2020; Nabinger et al., 2000). Some of the disturbance caused by cattle are grazing and trampling on grasslands and adjacent forests. By consuming and/or trampling on seedlings and saplings (Duarte et al., 2006; Jeske-Pieruschka et al., 2010), cattle can affect the survival of seedlings in grasslands and also forest understory (Carlucci et al., 2016). Such behavior can lead to an increase in light availability inside the forest (Pedó et al., 2010). Anthropogenic fire is another disturbance promoted in highland grasslands, aiming at the resprouting of grassland vegetation for feeding the cattle (Sühs et al., 2020). As a side-effect, fire often kills woody plant seedlings, and along with grazing, can also overrode the facilitative effect provided by araucaria trees (Sühs et al., 2018). Consequently, fire and grazing are disturbances with seemingly wide-ranging effects on all different types of vegetation.

The use of fire in the management of grasslands, both in private and protected areas, is still controversial in South America (Mistry et al., 2018). Fire is frequently seen as a bad thing (Fidelis, 2020) and grazing systems where fire is (or should be) used are still undervalued by environmental agencies and protected area managers (Eloy et al., 2018; Overbeck et al., 2018, 2007). These policies averse to fire are adopted by several countries - including Brazil - to prevent fire in fire-prone ecosystems (Mistry et al., 2018), especially in protected areas. Thus, the effects of these management practices are little known in the landscape across different habitats and in biodiversity. Yet, banning fire and grazing in highland grasslands increases the risk of catastrophic fires following the accumulation of flammable biomass. Catastrophic fires have devastating effects on biodiversity (Behling and Pillar, 2007; Berlinck and Batista, 2020), human well-being and landscape cultural values (Sühs et al., 2018; Sühs et al., 2020). When fire and grazing are banned, tussocks and shrubs tend to replace small herbs and grasses (Boldrini and Eggers, 1996; Nabinger et al., 2000), leading unburned and non-grazed areas to shrub encroachment over time (Behling and Pillar, 2007; Oliveira and Pillar, 2004; Overbeck et al., 2007; Sühs et al.,

2020). However, the conservation of the grassland-forest dynamics should not be restricted only to these two stable alternative states, but should also aim to keep transient states, such as shrublands, that may act as shelters for fauna (Carlucci et al., 2016).

Fire and grazing are disturbances that are part of and directly influence the functioning dynamics of subtropical grassland-forest system (Overbeck et al., 2007; Pillar, 2003). However, the mechanisms that affect the distribution of araucaria and its population structure and, therefore, its effects on the grassland-forest dynamics, are still poorly understood. Hence, we assessed the hypothesis that disturbances resulting from fire and grazing management reduce the forest's ability to expand over grasslands and shrublands via negative effects on araucaria populations. Specifically, even though araucarias germinate in grasslands, shrublands or forests, fire and grazing should inhibit araucarias from reaching adult stages, by negatively affecting early stages, thus limiting its facilitative effect for forest species. Therefore, we expect to find araucaria plants of the smallest stages in all habitats, but fewer in places where management involves fire and grazing than in the absence of these disturbances. We assessed this hypothesis by contrasting the density of individuals and the population structure of araucaria in forests, shrublands and grasslands. We further checked for differences in population structure resulting from different types of management and associated disturbances, especially changes in the incidence of light.

2. Material and methods

2.1. Study area

The study was conducted in the highlands of southern Brazil, state of Santa Catarina, inside the São Joaquim National Park (SJNP). The SJNP is a protected area (PA) created in 1961 (Law No. 13,273 of April 15, 2016) and covers 49,672.38 hectares of the Atlantic Forest domain (ICMBio, 2019). From 2006 to 2019, approximately 13,500 hectares were expropriated from several owners by the federal environmental agency, through indemnity processes. These regularized areas, along to the vacant areas (about 10,000 hectares), currently comprise about 47% of the total area of the PA. Thus, the SJNP area is composed by several public and private properties. The climate in these highlands is temperate, with no dry season, with a mean annual temperature of 13.3°C. In winter, the occurrence of frost and snows is common, and the average annual rainfall is ca. 1623 mm / year ("INMET - Instituto Nacional de Meteorologia," 2017). According to Köppen-Geiger climate classification, the climate is warm temperate, fully humid with warm summers, belonging to the Cfb type (Kottek et al., 2006).

In the studied sites, the predominant vegetation is composed of highland grasslands ("Campos de altitude") and mixed rainforests (Araucaria forests). In addition, shrublands, locally known as "vassourais", can also be found. Shrublands are a physiognomy highly dominated by shrubs of the genus *Baccharis*, especially *B. uncinella*, that are particularly common when fire and grazing are absent (Dechoum et al., 2018; Guido et al., 2017; Sühs et al., 2020). All the above mentioned vegetational types will hereafter be called "habitats".

Forty 100 m \times 4 m transects (= 400 m²) were set in ecotones between grasslands and forests, totaling a sampled area of 16000 m² (1.6 ha). Out of the 40 transects, 18 were installed in private areas where the traditional land management is employed, after the authorization of the landowner. Traditional management consists in burning grasslands ca. every 2 years for grassland resprouting for cattle feeding (ca. 4 animals for every 10 hectares) (Sühs et al., 2020). Therefore, it involves disturbances resulting from the burning of the grasslands and grazing and trampling by cattle (hereafter: "fire and grazing") in both grasslands and adjacent forests. The other 22 transects were installed in public protected areas where management aims to prevent these types of disturbances through fire suppression and cattle exclusion (hereafter: "without fire and grazing"). Since the region consists in several private properties, which slightly vary in traditional management practices (*e.g.*

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frequency of burning and number of cattle per hectare; Sühs et al., 2020), two transects were placed in each property. Similarly, two transects were placed in former private properties which are now public protected areas that belong to SJNP and are managed with the exclusion of fire and grazing.

Transects were set perpendicularly to the grassland-forest ecotone and centered at the edge of the forest. Transects were at least 100 m apart from each other and were only set if there was an adult araucaria tree located at the edge of the forest, to reduce the effects of seed or dispersal limitation to recruitment outcomes. Transects consisted of 50 m x 4 m inside the forest and 50 m x 4 m outside the forest. Transects inside the forest were covered with forests all along (i.e., there was no return to open habitats once going towards the forest interior in any transect). Outside the forest, extent of grasslands and shrublands varied across transects. We classified habitat as shrubland when Baccharis spp. covered more than half of the width of the transect for any length > 1 m, which was registered using a stretched tape line along the transect. Outside forests, total grassland coverage was \sim 80% and in three of the 40 transects we found only grassland (under traditional management). While shrubland covered only $\sim 20\%$ the extent of transects outside forests, two transect halves outside forests had only shrubland (both located in the protected area).

2.2. Data collection

2.2.1. Araucaria populations

In the transects, active search was conducted to register all araucaria individuals, from different ontogenetic stages. The classification of ontogenetic stages was performed based on height and reproductive structures (modified from Souza, 2020; Souza et al., 2008). The stages were classified into: seedling (up to 1 m), sapling (from 1 m to 3.5 m), juvenile (from 3.5 to 6 m and unformed crown) and adult (above 6 m with formed crown and / or visible reproductive structure).

2.2.2. Canopy openness

To understand part of the environmental differences between habitats and types of management, we obtained photographs of the canopy every 10 m along each transect. With the photographs, we calculated the canopy openness as an indicator of the availability of light in the different habitats and types of management and, thus, assist in the analysis and understanding of population structure data (Souza et al., 2008). To measure canopy openness, we used a Canon 80D camera with a canon EF-S 18-135 mm USM lens. Camera was set in manual exposure, ISO 100, aperture 5.6, at 18 mm. This setting provides a consistent zoom with an angle of view of approximately 75° across the diagonal. The lens was pointed directly upwards at approximately 30 cm from the ground, held free, every 10 meters along the 100 m transect. Photographs were obtained in RGB color with a resolution of 6000×4000 pixels. All photographs were corrected for geometric lens distortion using the freely available image editor program RawTherapee (V5.7, http://rawtherapee.com), using the correspondent camera and lenses profile. Images were then imported in R platform and resized to a resolution of 1200×800 pixels to improve computational time. RGB images were transformed using the green leaf algorithm (GLA) (Chianucci et al., 2014) to improve contrast between white and dark pixels. Images were binarized using a threshold of 0.5 and the percentage of white pixels was computed for each image. The percentage of white pixels was used as a proxy for canopy openness (Chianucci, 2020). This canopy openness measurement was obtained through a restricted view photographic method (i.e. with non-hemispherical lenses), therefore we did not recommend comparing these results with those obtained with other methods.

2.3. Data analysis

We used a two-way analysis of variance (Anova) to compare the

percentage of canopy openness as a function of habitats (forest, shrubland and grassland), types of management (with and without fire and grazing) and to assess the interaction between habitat and type of management. Given that we had one to five photographs for each of the three habitats in every transect, canopy openness was averaged by habitat and transect (N = 98). Transects were used as a blocking variable to account for variation unrelated to habitats, management types, or both. We checked that we met the assumptions of normality and homoscedasticity based on visual inspection of model residuals.

Population structure was contrasted in terms of the number of individuals at each stage of development. Such counts were pooled for each stage across transects. Chi-square tests (χ^2) were then used to contrast pooled counts by stage between the three habitat types and between the two management types. Additional χ^2 tests were used to contrast the same habitats under different managements (*e.g.*, forest under the management with fire and grazing vs. forest under the management without fire and grazing). P-values for χ^2 tests were calculated based on permutations to reduce problems related to parametric versions of the test. In a complementary way, to improve visual comparisons of population structure given the overall differences in area sampled in grassland and shrubland, we calculated araucaria density and extrapolated it to a standardized size (1 ha). Such extrapolated density was used in population structure barplots.

3. Results

3.1. Canopy openness

Canopy openness was much lower in forests than grasslands and shrublands (Anova, F _{2, 54} = 785.6; P < 0.001), as the vegetation is much taller in the forest than in grasslands and shrublands (Fig. 1). All habitats showed some decrease in canopy openness from the management with fire and grazing to the management without it (Anova, F _{1, 54} = 14.6; P < 0.001). There was also an interaction between habitat and management types (Anova, F _{2, 54} = 4.2; P = 0.021). The significance of the interaction suggests the habitats differ in light availability and that the availability of light in the same habitats is further affected by the type of management, in a combination that can explain the population



Fig. 1. Canopy openness by habitat and type of management. w/ FG: management with fire and grazing; wo/ FG: management without fire and grazing.

differences of araucaria described below.

3.2. Population structure and habitats

We identified differences in population structure among all three habitats ('global' test: contrasting all habitats using counts per ontogenetic stage, $\chi^2 = 87.6$; P <0.001). This result is related to differences between the ontogenetic stages, mainly indicated by the higher density of seedlings in shrublands and adults in forests (Fig. 2). The population structure in the forest differed from the population structure in shrublands ($\chi^2 = 43.1$; P <0.001) and in grasslands ($\chi^2 = 52.7$; P <0.001), but the population structure in shrublands and grasslands did not differ (χ^2 = 6; P = 0.06). The difference between habitats may be related to the decrease in the total densities of individuals in the forest-shrublandgrassland gradient. In the forest, 428 individuals were sampled $(75.1\% \text{ of the sample; area sampled in the forest} = 8000 \text{ m}^2)$, resulting in a density of 535 ind./ha. In the shrublands, 70 individuals (12.3%; sampled area = 1645.2 m^2) were sampled, resulting in a density of 425 ind./ha. In grasslands, 72 individuals (12.6%; sampled area = 6354.8 m^2) were sampled, resulting in a density of 113 ind./ha.

3.3. Population structure and management types

Population structure differed between the two types of management (test based on counting individuals per ontogenetic stage, $\chi^2 = 19.1$; P <0.001), mainly due to the greater number of seedlings found in areas with fire and grazing (Fig. 3). In addition, the difference between types of management may be related to an increase in the total density of individuals in areas with fire and grazing (Fig. 2), since the density of individuals per area was ca. 1.4 times higher in areas with fire and grazing (417 ind./ha, 300 individuals sampled in 7200 m²) than in areas without fire and grazing (307 ind./ha, 270 individuals sampled in 8800 m²).

3.4. Population structure within habitats in different types of management

The population structure in the forest differed between the types of management ($\chi^2 = 11.3$; P <0.008). The density in the forest in areas with grazing and fire was 1.2 times higher for seedlings (283 ind./ha, 102 individuals sampled in 3600 m²) than in areas without fire and grazing (243 ind./ha, 107 individuals sampled in 4400 m²) and 1.4 times higher for adults (189 ind./ha, 68 individuals sampled in 3600 m²)



Fig. 2. Araucaria population structure among different habitats.



Fig. 3. Araucaria population structure among different types of management.

than in areas without fire and grazing (132 ind./ha, 58 individuals sampled in 4400 m²). In shrublands, the population structure did not differ between the types of management ($\chi^2 = 1.96$; P = 0.23). The density in shrublands was 5.7 times higher for seedlings in areas with grazing and fire (1144 ind./ha, 35 individuals sampled in 306 m²) than in areas without fire and grazing (202 ind./ha, 27 individuals sampled in 1339.2 m²). In grasslands, the population structure did not differ between the types of management (test based on the count of individuals per stage, $\chi^2 = 2.2$; P = 0.51). The density in grasslands was 5.3 times higher for seedlings in areas with grazing and fire (176 ind./ha, 58 individuals sampled in 3294 m²) than in areas without these disturbances (33 ind./ha, 10 individuals sampled in 3060.8 m²) (Fig. 4).

4. Discussion

Araucaria angustifolia population structure differs between management types and habitats. Whereas araucaria plants were found under most conditions and on different ontogenetic stages along grasslandforest transitions, large differences exist in population structure among habitats, between types of management, and on the same habitats under distinct management. Specifically, population structure differed in the distribution of stages and in plant density among areas either with or without fire and grazing. Araucaria seedlings and saplings occurred in all habitats but were more abundant under management with fire and grazing. Even though this pattern seems to contradict our hypothesis, araucarias rarely reach juvenile or adult stages under such management, thus limiting their role as facilitator for both other woody species - which occurs as far as known only for large, adult individuals and forest expansion. Our results also point out shrublands as a regeneration spot for araucarias, especially where disturbances are prevented, with potential consequences for regional vegetation dynamics. We therefore corroborate the hypothesis that disturbances resulting from the management with fire and grazing reduces the pace of forest growth over shrublands and grasslands. In turn, preventing such disturbances is likely to have the exact opposite effect in these habitats while disturbances in forests apparently are positive for araucaria populations.

Highlands of southern Brazil are characterized by mosaics of forests, shrublands and grasslands (Rambo, 1956). The understanding of mechanisms by how the resulting mosaics are kept or what drives their dynamics is either limited or recent (Blanco et al., 2014; Sühs et al., 2020). Grasslands and forests have normally sharp boundaries, but shrublands tend to occur in between these two habitats and the extent of



Fig. 4. Araucaria population structure within habitats in different types of management. Statistical tests reported in the main text contrast only the same habitats under distinct management.

shrublands grows quickly as fire and grazing are prevented (Blanco et al., 2014; Sühs et al., 2020), and together with windstorms and tornadoes, disturbances have been suggested as key in shaping Araucaria forests, grasslands and associated habitats (Souza, 2020). Across such landscapes, the distribution and density of araucaria stages differed between forest and the other two habitats, with forests showing the highest overall araucaria densities. Shrublands and grasslands, in turn, were similar in population structure, at least in the proportion of plants falling in each ontogenetic stage (Fig. 2), even though population and seedling density seem highest in shrublands. Because we showed that araucarias colonize shrublands, this habitat is likely to conduct vegetation dynamics to forests, especially if disturbances can be prevented for the time need for araucarias grow into adults. Hence the ongoing shrub encroachment of grasslands (Sühs et al., 2020) is likely to result in the development of forests, especially shrublands close to forest edges. In turn, shrublands can turn back into grasslands if burned, especially in their early ages (2-3 years) (Sühs et al., 2020). Managing lands with fire every two years, as commonly carried out in the region (Sühs et al., 2020), is therefore efficient to both limit shrub encroachment and kill araucaria seedlings and saplings found in shrublands, explaining why they are unlikely to grow into adults under a management with fire and grazing and why vegetation mosaics are mostly stable.

Disturbances caused by fire and grazing can alter vegetation structure and habitat features leading to differences in araucaria populations structure among areas with and without fire and grazing. In areas with fire and grazing, both canopy openness and araucaria densities were greater, with more seedlings and adults. A closed canopy can hamper araucaria plants of growing into later stages while fire and grazing can affect araucaria population structure by killing young and juvenile plants (Souza, 2020). Our results corroborate this idea because araucaria seedlings were unable to reach later ontogenetic stages in grasslands and shrublands where fire and grazing are promoted. In such conditions, forests – where fires do not usually enter into – also had more adults likely because of additional disturbances caused by cattle in this habitat in the past, likely through reduction of understory density (Carlucci et al., 2016), which allowed more light to reach into the forest. In addition, in grasslands and shrublands, fire and grazing also limit araucaria facilitation potential to increase the establishment of forest species (Sühs et al., 2018). Therefore, changes promoted by fire and grazing to both habitats and a keystone population structure have further consequences on forest-grassland dynamics.

In southern Brazil, highland vegetation mosaics are part of a cultural landscape that has been shaped by pre-Columbian people (Bitencourt and Krauspenhar, 2006; Reis et al., 2014; Robinson et al., 2018). Pre-Columbian people fostered the expansion of Araucaria forests and, especially in the last 1.5 ka BP, likely increased fire frequency in such landscapes (Behling et al., 2004; Bitencourt and Krauspenhar, 2006; Kern, 1998; Lauterjung et al., 2018; Robinson et al., 2018). In the last few centuries, ranchers replaced most pre-Columbian people in the region, but learned to use fire to promote resprouting of grasses in grasslands and improve pasture quality (Andrade et al., 2016; Nabinger et al., 2000; Overbeck et al., 2007; Sühs et al., 2020). In an interesting but unplanned experiment, the establishment of a protected area has shifted management into a ban to fire and grazing. Banning both disturbances is causing shrublands to replace grasslands at a fast speed (Sühs et al., 2020). Whereas fire maintains grasslands and its unique diversity, such disturbance slows the pace of forest expansion over grasslands (Overbeck et al., 2007; Pillar, 2003). Here we show that such slow replacement can result also from araucaria seedlings being unable to survive up to latter development stages when they could facilitate woody plants establishment and promote forest expansion. Our results further suggest that araucaria trees have higher success of adults more easily when fire and grazing are prevented, thus fostering facilitative effects, and gearing up forest expansion.

5. Conclusion

Our study demonstrates that disturbances caused by traditional management with fire and grazing alter the population structure of araucaria, with important consequences for its spatial distribution and for the dynamics of forest expansion over grasslands in highlands. Specifically, forest expansion seems to occur more slowly in areas with fire and cattle because araucarias rarely pass the seedling stage in this condition, especially in non-forested habitats. On the other hand, in areas where fire is suppressed and cattle is excluded, as it is the case of protected areas, seedlings establish in more open vegetation such as grasslands and, especially, shrublands, so that the process of forest expansion over grasslands becomes possible. Thus, disturbances caused by the different types of management alter both the distribution of key species and vegetation dynamics.

Funding

This study was financed by The Mohamed bin Zayed Species Conservation Fund (Project 180520070), CNPq/Capes/FAPs/BC-Fundo Newton/PELD n° 15/2016 and FAPESC/2018TR0928. FSR was an undergrad fellow from CNPq – Brazil.

CRediT authorship contribution statement

Rafael Barbizan Sühs: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. Fernando Silva Rosa: Formal analysis, Investigation, Methodology, Writing - review & editing. Jonata Silveira: Investigation, Methodology, Writing - review & editing. Nivaldo Peroni: Conceptualization, Writing - review & editing. Eduardo Luís Hettwer Giehl: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Visualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and Parque Nacional de São Joaquim staff for research permissions. CNPq/Capes/FAPs/BC-Fundo Newton/PELD nº 15/2016 and FAPESC/2018TR0928 for logistic support. CNPq (457451/2012-9) for the productivity fellowship awarded to NP. Gustavo Lemes, João P. Cechinel, Uriel Rover and Nayara Spaniol for field work assistance. Francesco Chianutti for the suggestions on canopy measurements. Marcos B. Carlucci (reviewer) and Gerhard E. Overbeck (reviewer/editor) for valuable comments and suggestions that have helped to improve this manuscript.

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