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The enemy lives next door: ecological consequences of woody encroachment in a grassland ecosystem in southern Brazil

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Abstract

The replacement of grasslands by woody plants represents one of the main threats to the biodiversity conservation in open landscapes around the world. This transformation occurs when ecological processes that are essential to avoid the canopy closure are prevented, such as fire. We sampled trees and shrubs and evaluated the effects of fire in an old-growth grassland remnant released from fire for 18 years in Southern Brazil. Our main objective was to analyze whether woody encroachment promotes a biome shift of the grassland ecosystem. We hypothesized if woody encroachment is deterministically structured towards a dominance of forest species and a significant decrease in fire intensity and severity along the encroachment gradient occurs. Then, the woody encroachment does not represent a simple process of woody densification, but a biome shift towards an alternative forest state, that change the ecology of the system in a positive feedback loop and get stability as the woody community expands. We found clear evidences that woody encroachment promotes a biome shift from an open grassland state to an alternative forest state. In this process, our results indicated that woody encroachment was structured deterministically in the multivariate space with the occurrence of indicator species in the early and late stages. Throughout the entire encroachment gradient analyzed, a significant dominance of forest species was found, indicating that Southern Brazilian grasslands have the potential to be converted into forests more rapidly than savannas in the absence of fire. A significant decrease in fire intensity was found as the process of woody encroachment increased, indicating a change in the system behaviour that favoured the occurrence of a positive feedback loop between the canopy cover and the recruitment of shade-tolerant forest species. Simultaneously to fire intensity decrease, we observed that the reversion of the woody encroachment process was significantly reduced as the woody dominance increased. Thus, the woody encroachment mediated by fire suppression can be considered a degradation factor in our study area, since it can shift the system balance to another alternative stable state. By elucidating the ecological consequences behind woody encroachment, we recommend the use of prescribed fires to the conservation of the grasslands landscapes in Southern Brazil.

1. Introduction

Temporal analyses based on satellite images indicated that Araucaria Forest areas are expanding in Southern Brazil, specially in forest-grasslands ecotones where fire has been avoided (OLIVEIRA; PILLAR, 2004). However, it is still unclear whether woody encroachment represent only a process of woody densification or a general biome shift towards a generation of a new alternative forest state. Furthermore, if woody encroachment actually results in a change in the fundamental state of the ecosystem, we still don't know the level of stability of this new state.

To address these issues, we studied an old-growth grassland remnant that was encroached by woody species due to fire suppression for a period of 18 years (from 1999 to 2017). In 2017, this same area was hit by a wildfire, then we analyzed the fire effects over the woody plants community with the objective of to evaluate the fire intensity and severity along the woody encroachment gradient. We hypothesized if woody encroachment is deterministically structured towards a dominance of forest species and a significant decrease in fire intensity and severity along the encroachment gradient occur. Then, the woody encroachment does not represent only a simple process of woody densification, but a biome shift towards an alternative forest state, that change the ecology of the system in a positive feedback loop and get stability as the woody community expands.

2. Material and Methods

2.1. Study area

This study was conducted in Vila Velha State Park (VVSP) located in the municipality of Ponta Grossa, Paraná State, Brazil (latitude: 25° 13' 30" S, longitude: 50° 0' 0" W) (Table 1). The VVSP was created in 1953 (PARANÁ, 1953), in an area of 3,122 ha considered as a remnant of the original vegetation of Campos Gerais region (INSTITUTO AMBIENTAL DO PARANÁ, 2004). The Campos Gerais region comprises areas of old-growth grassland vegetation associated with Araucaria Forest fragments forming mosaics (MAACK, 2012).

2.2. Data collection

2.2.1. Vegetation sampling

We sampled trees and shrubs in five permanent transects measuring 50 m wide per 100 m long (subdivided in 20 plots of 250 m² - 10 x 25 m). The plots were randomly distributed over an area mapped in the VVSP management plan as steppe-savanna transition vegetation (INSTITUTO AMBIENTAL DO PARANÁ, 2004). In this place, we previously assumed that there is a natural tendency of forest expansion over grasslands and that the current vegetation pattern is associated with fire suppression policies, which guided the park management during the past decades. In each plot, tree and shrub data were collected according to the inclusion criterion of DBH equal to or greater than 3 cm.

2.2.2. Assessment of fire intensity and severity

We inferred the intensity of fire by measuring the height of bark-char left on the tree boles after the fire passage. We adopted as standard measure the highest stem-bark char height.

We determined fire severity by calculating the proportion of basal area lost as a result of fire in each plot. For this, one year after fire, trees and shrubs were reassessed according to survival and complete mortality or topkill. Then, the basal area obtained in each plot were compared with the basal area obtained in the first survey. The fire severity ranged from 0 to 1, with 1 being noted for complete mortality or topkill of all woody individuals present in the plot and 0 for complete absence of mortality or topkill of all woody individuals present in the plot.

2.3. Data analyses

2.3.1. Community structure and dominance of forest specialist species along the encroachment gradient

To verify if the woody encroachment was deterministically structured towards a dominance of forest species, we firstly evaluated the floristic-structural relationship among the plots by the construction of a hierarchical cluster dendrogram. Then, the occurrence of multivariate structure among the plots was analyzed by similarity profile test (SIMPROF) (CLARK; SOMERFIELD; GORLEY, 2008). Later, the multivariate structure captured by SIMPROF test was analyzed by a Principal Coordinate Analysis (PCoA) with the adjustment of generalized additive model (GAM) *a posteriori*.

In each cluster identified in the SIMPROF test, we verified the occurrence of indicators woody species through the IndVal analysis (DUFRÊNE; LEGENDRE, 1997). In addition, the species were classified into three distinct functional groups according to the habitat preference: savanna specialists, generalists and forest specialists. To verify the existence of significant associations between the number of individuals in each functional group and the stages of woody encroachment, a chi-square test was applied to a contingency table.

To verify the patterns of change in species richness of each functional group along the woody encroachment gradient, we used a generalized linear model (GLM), in which the absolute and relative species richness was adjusted as a function of the density of woody plants per plot.

2.3.2. Effect of woody encroachment in fire intensity and severity

We analyzed the effect of woody encroachment in fire intensity by a Kruskal-Wallis variance analysis and beta regression models with logit link was applied to model the fire severity as a function of the sum of the basal in each plot.

3. Results

The SIMPROF analysis rejected the null hypothesis ($p < 0.01$) of absence of community structuring associated with the woody encroachment process, indicating the formation of six significantly different floristic-structural groups (Figure 1).

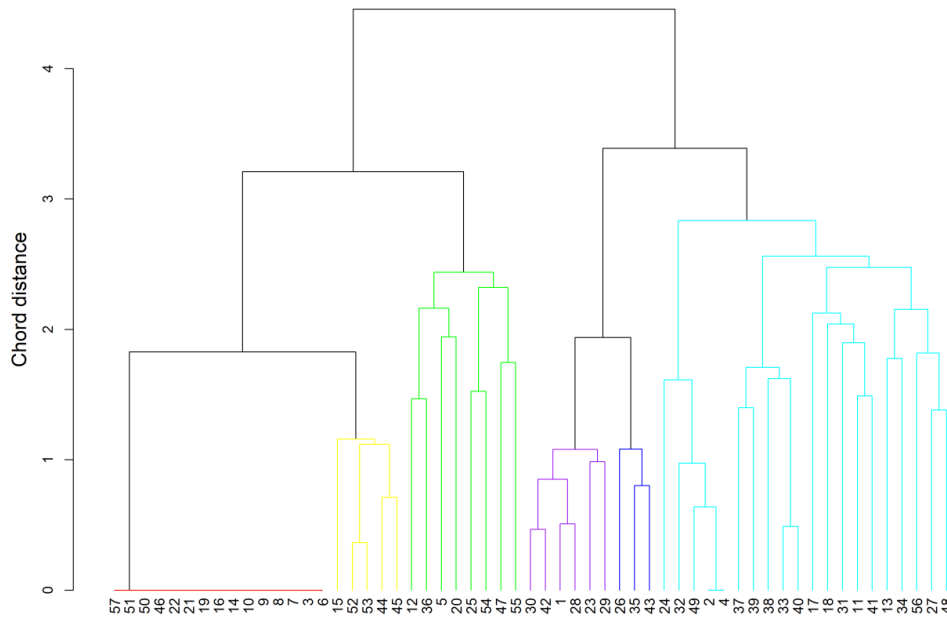


Figure 1 - Similarity profile analysis (SIMPROF)

The ordination produced with the smoothed surface adjusted *a posteriori* by GAM indicated that 55.4% of the floristic-structural variation was explained by the density of woody individuals ($R^2 = 0.502$; $p \leq 0.05$) (Figure 2). Thus, the floristic-structural groups established by the SIMPROF analysis were significantly associated in the multivariate space in response to woody encroachment gradient.

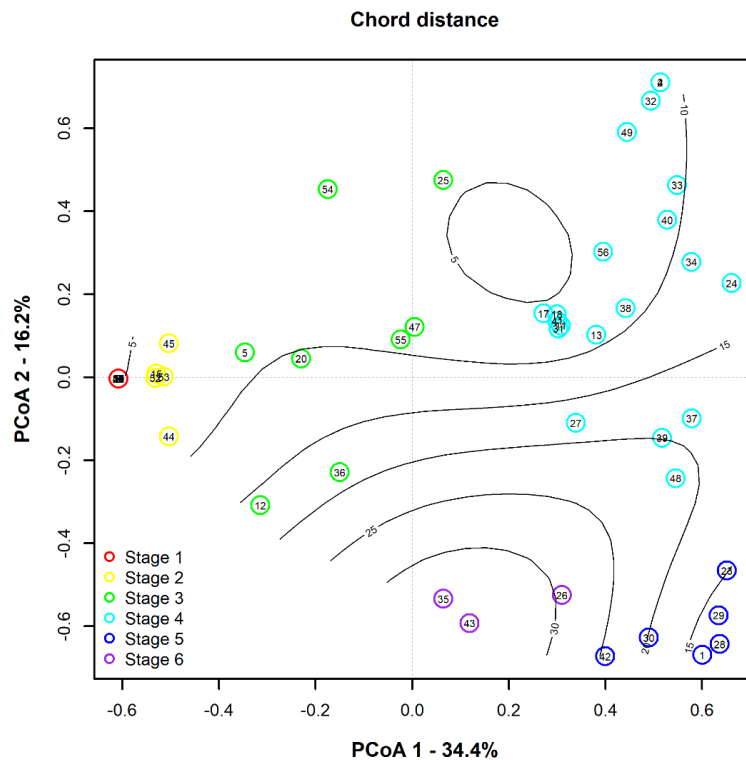


Figure 2 - Principal coordinate analysis with smoothed surface lines of woody abundance per plot adjusted *a posteriori* by GAM

The IndVal analysis recognized the occurrence of typical species in the initial (1 and 2) and advanced (5 and 6) stages of woody encroachment. In early stages 1 and 2, *Clethra scabra* Pers. (IndVal = 38.85%; $p = 0.015$) and *Myrcia splendens* (Sw.) DC. (IndVal = 46.74%; $p = 0.014$) were recognized as indicator species, respectively. In late stages 5 and 6, the indicator species were: *Myrsine umbellata* Mart. (IndVal = 51.84%; $p = 0.010$) and *Miconia sellowiana* Naudin (IndVal = 29.95%; $p = 0.034$), respectively.

We observed significant associations among functional groups and the stages of woody encroachment according to the chi-square test ($\chi^2 = 51.098$; $p = 0.01$; Cramer's V = 0.2072). The analysis of the standardized residuals of chi-square test showed that forest specialist individuals were positively associated with initial and advanced stages of woody encroachment (Figure 3).

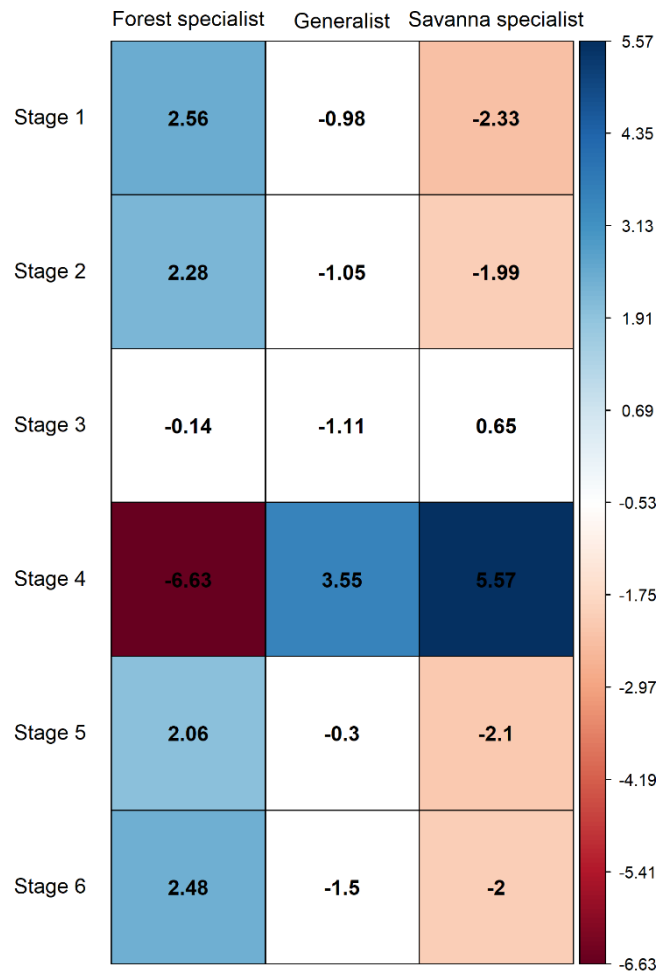


Figure 3 – Pearson's chi-square test (χ^2) between functional groups and stages of woody encroachment

The increase of woody encroachment process resulted in a significant increase in the absolute richness of savanna specialist ($F = 5.45$; $R^2 = 0.23$; $p < 0.01$; Deviance explained = 12.74%) and forest specialist species ($F = 33.72$; $R^2 = 0.34$; $p < 0.01$; Deviance explained = 40.84%). The same pattern was not observed for generalist species ($F = 0.21$; $R^2 = 0.002$; $p = 0.65$; Deviance explained = 0.86%), which showed constant species richness along the woody encroachment gradient (Figure 4A). Proportionally, the species richness of all functional groups maintained constant along the woody encroachment gradient, with forest specialist species being responsible for leading the encroachment process from early to advanced stages (Figure 4B).

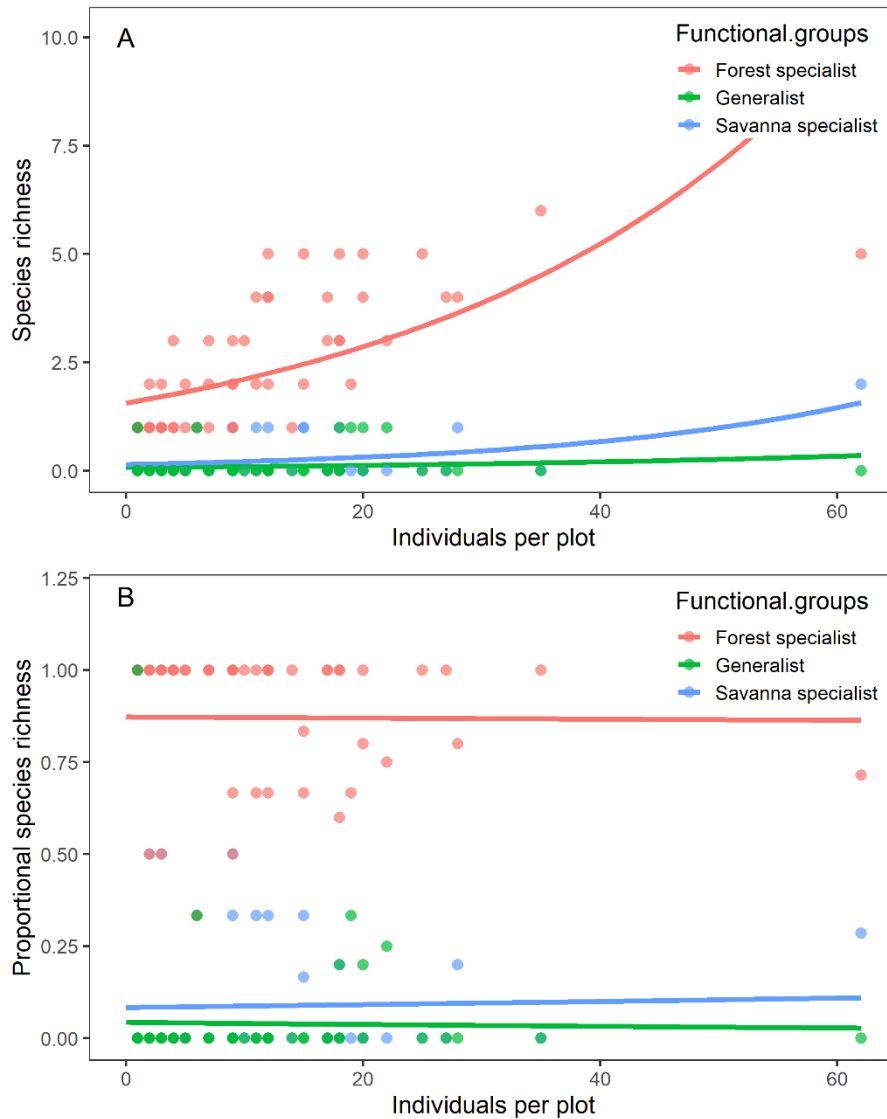


Figure 4 - Changes in absolute (a) and relative (b) species richness of the functional groups along the gradient of woody encroachment

The fireline intensity showed a significant reduction along the woody encroachment gradient (Kruskal-Wallis $\chi^2 = 18.37$; $df = 5$; $p = 0.0002$). The Dunn *post-hoc* test of multiple comparison showed that stage 6 (0.81 ± 0.79 m) had a significantly lower carbonization height than the other stages of encroachment, with the exception of stage 5 (0.93 ± 0.73 m). Stage 5, in turn, showed a significantly lower carbonization height than stages 1 (1.12 ± 0.74 m) and 2 (1.20 ± 0.85 m). The other stages of invasion did not show significant differences among them in relation to the stem-bark char height (Figure 5).

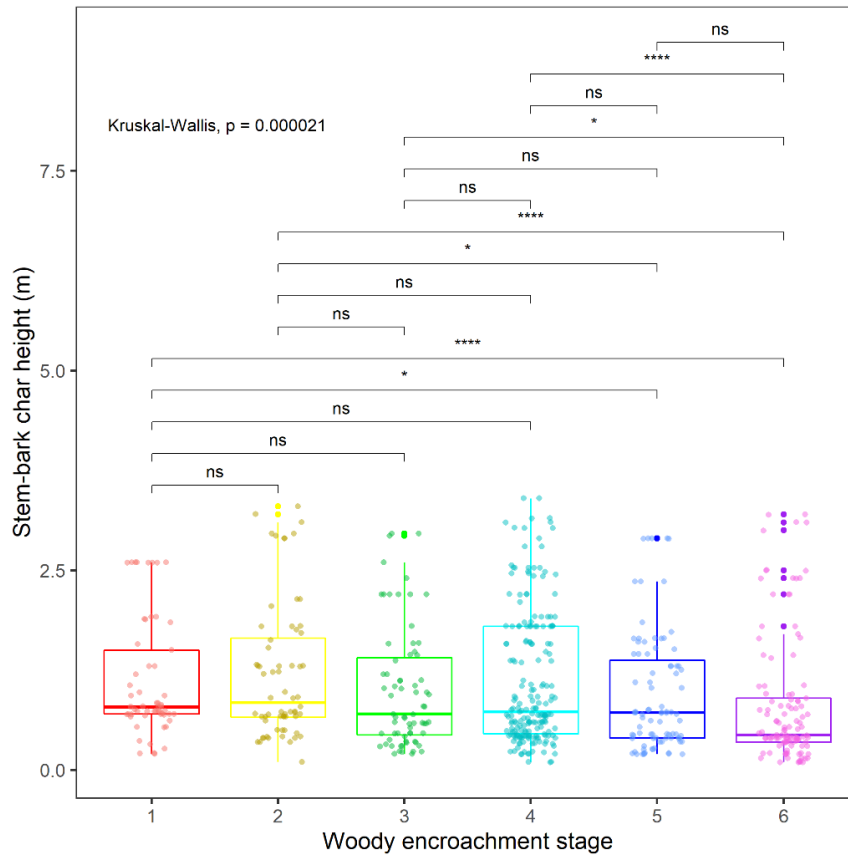


Figure 5 – Kruskal-Wallis's test and Dunn post-hoc test of multiple comparison of the height of stem-bark char and woody encroachment stages

Fire severity significantly decreased as the woody encroachment process advanced ($p = 0.0001$). The fitted GLM model showed that 39% of the variability in fire severity was explained by the increase in basal area per hectare (Figure 6). The value of basal area per hectare needed to reach the fire severity threshold corresponding to 0, i.e., complete absence of mortality and/or topkill, was estimated at $32.3 \text{ m}^2 \cdot \text{ha}^{-1}$.

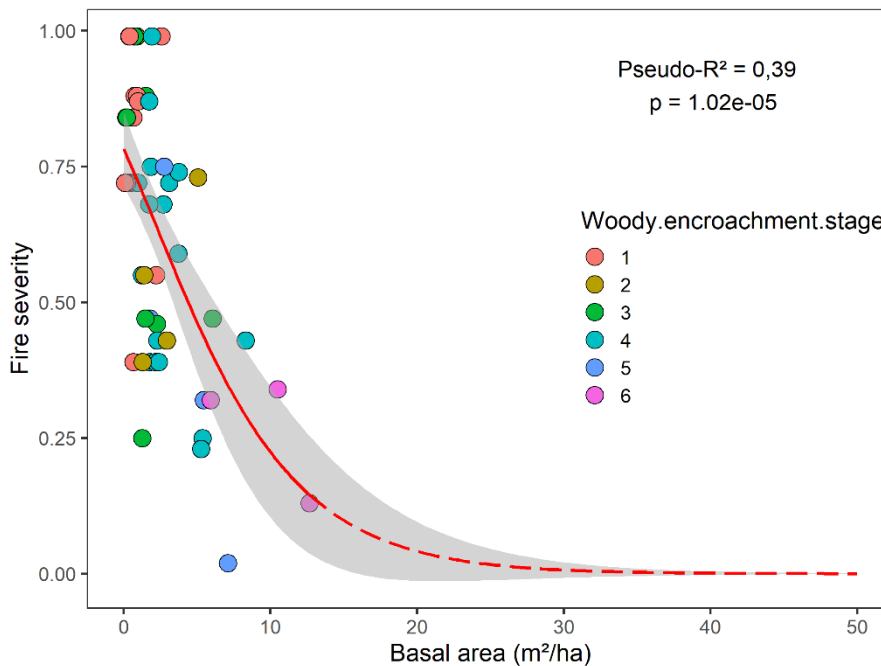


Figure 6 – Beta regression between fire severity and basal area of plots

4. Discussion and concluding remarks

Our results support the assumption that subtropical highland grasslands of the Atlantic Forest Biome are ecosystems that depend of fire for their maintenance (OVERBECK et al., 2018). Studies carried out in the region have shown that in the absence of fire, the remnants of grassland vegetation are likely to be invaded and replaced by woody species (*e.g.* OLIVEIRA; PILLAR, 2004; SÜHS; GIEHL; PERONI, 2020).

Although the woody encroachment has been extensively documented worldwide, few studies explored if this phenomenon exclusively represents a process of woody densification that does not interfere in the flammability of the system, or if it is associated with a change in the fundamental state of the ecosystem towards an alternative forest state. Specifically, the flammability of Southern Brazilian grassland ecosystems is of particular interest for their conservation, because it allows the occurrence of periodic fires, which are capable of sustaining vegetation in an open state, since the climate could otherwise way, promote the forest (BEHLING; PILLAR, 2007). On the other hand, the shading provided by canopy closing of woody species is a critical factor for the survival of light-demanding grassland vegetation (PARR; GRAY; BOND, 2012). Here, we observed that the flammability was negatively affected by the progress of woody encroachment, indicating a change in the behavior of the system.

In the process of state transition between grassland and forest ecosystems, the increase in canopy cover, provided by the woody encroachment, results not only in the reduction of herbaceous biomass, but also in lower air temperature, higher relative humidity, lower wind speed and higher moisture content of the combustible material (HOFFMANN et al., 2012b). Furthermore, as the density of trees and shrubs increases, the fuel bed becomes increasingly dominated by leaf litter, which is less flammable than grasses (PRIOR et al., 2017). Thus, grass loss in response to canopy closure indicates the transition from a fire-maintained state to a fire-independent state (HOFFMANN et al., 2012a). Identifying the transition from one state to another provides a basis for understanding how fire governs the distribution of different types of vegetation under the same climatic conditions. Hoffmann et al. (2012a) indicated that when an ecosystem reaches sufficient canopy cover to suppress fire and exclude grasses, a fire suppression threshold is reached. In order to find an analogous threshold for our study system, we analyzed fire severity along a gradient of basal area per hectare and found that the ability of fire to reverse the invasion process is significantly reduced as the woody encroachment progresses until reaching the threshold of 32.3 m².ha⁻¹, which is when the forest state reaches stability and becomes independent from fire.

Understanding the consequences of woody encroachment is important because grassland ecosystems are undergoing widespread degradation worldwide (HOEKSTRA et al., 2005). In Southern Brazil, the practice of cattle grazing and the preservation of the endemic biodiversity of the highland grasslands fundamentally depend on the maintenance of the ecosystem in an open state, which makes woody encroachment a prominent concern for both the local economy and biodiversity conservation (OVERBECK et al. al., 2007; SÜHS; GIEHL; PERONI, 2018, 2020). In this way, the integration of the woody invasion process into a coherent strategy for the management of natural resources can help the management and restoration of grassland ecosystems. Therefore, we recommend the use of prescribed fires to the conservation of the grasslands landscapes in Southern Brazil.

5. References

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