UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Tese de Doutorado

Grazing and Fire Strategies for Conservation, Restoration, and Ecological Awareness in the South Brazilian Grasslands

Filipe Ferreira da Silveira

Porto Alegre, 16 de Junho de 2026

Grazing and Fire Strategies for Conservation, Restoration, and Ecological Awareness in the Pampa Grasslands

Filipe Ferreira da Silveira

Tese apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como um dos pré-requisitos para a obtenção do título de doutor em Botânica – Área de concentração em Ecologia Vegetal.

Orientação: Prof. Dr. Gerhard Ernst Overbeck

Co-orientação: Prof. Dr. Guilherme Dubal dos Santos Seger

Porto Alegre, 16 de Junho de 2026

FILIPE FERREIRA DA SILVEIRA

Grazing and Fire Strategies for Conservation, Restoration, and Ecological Awareness in the South Brazilian Grasslands

Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul (UFRGS) como requisito parcial para obtenção do título de Mestre em Botânica.

Aprovado em: Porto Alegre, 16 de junho de 2026.

ORIENTADOR:

Dr. Gerhard Ernst Overbeck
Universidade Federal do Rio Grande do Sul (UFRGS)

COORIENTADOR:

Dr. Guilherme Dubal dos Santos Seger
Universidade Federal do Rio Grande do Sul (UFRGS)

BANCA EXAMINADORA:

Dr. João André Jarenkow
Universidade Federal do Rio Grande do Sul (UFRGS)

Dra. Russel Teresinha Dutra da Rosa
Universidade Federal do Rio Grande do Sul (UFRGS)

Dra. Anaclara Guido
Universidad de la República

CIP - Catalogação na Publicação

da Silveira, Filipe Ferreira
Grazing and Fire Strategies for Conservation, Restoration, and Ecological Awareness in the South Brazilian Grasslands / Filipe Ferreira da Silveira. -- 2026.
174 f.
Orientadora: Gerhard Ernst Overbeck.

Coorientadora: Guilherme Dubal dos Santos Seger.

Tese (Doutorado) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Programa de Pós-Graduação em Botânica, Porto Alegre, BR-RS, 2026.

1. manejo de campo. 2. fogo. 3. pastejo. 4. restauração. I. Overbeck, Gerhard Ernst, orient. II. Seger, Guilherme Dubal dos Santos, coorient. III. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

Agradecimentos

Meus sinceros agradecimentos ao Prof. Dr. Gerhard Overbeck, não apenas pela estrutura e suporte acadêmico, mas pela paciência e pela confiança que sempre demonstrou. Gerhard possui o dom raro de semear o amor pelo Pampa em nossos corações, tornando o trabalho de campo muito mais significativo. Agradeço igualmente ao Prof. Dr. Guilherme Dubal dos Santos Seger por ser um porto seguro nas análises de dados e revisões. O rigor técnico e a generosidade pedagógica de vocês foram os pilares para a consolidação das minhas habilidades e o sucesso deste trabalho.

Hoje, minhas expectativas superam em muito o que eu vislumbrava para mim há vinte anos. Meu maior sonho era, simplesmente, cursar Ciências Biológicas na UFRGS. Vindo da escola pública, enfrentei diversos percalços pelo caminho e, ao concluir a graduação, cheguei a duvidar da minha capacidade de seguir para um mestrado. Hoje, finalizo minha tese de doutorado. Embora meu ciclo acadêmico se encerre aqui, pelo menos por enquanto, ele se prolonga na escola pública onde atuo como vice-diretor e professor. Lá, sigo empenhado em mostrar a cada aluno e aluna que, embora o caminho seja árduo, ocupar esses espaços é um sonho possível.

Agradeço imensamente aos amigos e colegas que me acompanharam nas coletas de dados nestes últimos cinco anos. As expedições de campo, apesar dos percalços, tornaram-se mais leves graças à parceria de vocês. Espero que mantenham sempre essa resiliência e alegria. Meu muito obrigado a Ana Porto, Pedro Thomas, Francieli Peter, William Piovesani, Mateus Schenkel, Bruno Soares, Rafael Barboza, Luciana Menezes, Victória Meotti, Lívia Irigoyen, Diego Abade, Graziela Minervini, Lua Cezimbra e Helena Streit. Agradeço também às minhas orientadas em iniciação científica Lucina Bittencourt e Sheron Ferreira, pelo auxílio mútuo em nossa formação acadêmica e humana. Um agradecimento especial à Sheron, meu orgulho e irmã de sangue e alma, por caminhar ao meu lado.

Agradeço aos órgãos de fomento que possibilitaram a subsistência e o financiamento do presente estudo: CAPES, CNPq, PPG Botânica UFRGS, Instituto Humanize e o Programa de bolsas FUNBIO.

Por fim, agradeço aos meus familiares que, mesmo sem compreenderem a fundo as minúcias da minha atuação na universidade, orgulham-se da trajetória que construí e da pessoa que me tornei. Agradeço, especialmente, ao meu companheiro Jonathan Nunes, pelo suporte psicológico e afeto que, há 14 anos, me fortalecem e me sustentam em cada etapa da minha jornada. Obrigado por vocês todos fazerem parte da minha história.

Sumário

Resumo Geral 2

General Abstract 3

General Introduction 4

General Objective 9

Specific Objectives 9

References 10

Capítulo I 1

Southern Brazilian grassland diversity: anti-disturbance regimes are not ideal and grazing maintains plant diversity 3

Capítulo II 1

Should I burn or should I graze: initial effects in the restoration of abandoned subtropical grasslands 3

Capítulo III 1

Burned to Grow, Too Grazed to Stay: Deciphering the Control of Woody Encroachment in Native Grasslands 3

Capítulo IV 1

Resumo Geral

O bioma Pampa constitui um ecossistema campestre de elevada diversidade biológica e relevância ecológica, responsável por múltiplos serviços ecossistêmicos, como conservação da biodiversidade, regulação climática e manutenção de solos e recursos hídricos. Inserido na região dos *Campos do Río de la Plata*, este sistema apresenta uma longa história evolutiva, sendo moldado por condições paleoambientais e pela atuação de grandes herbívoros e fogo, o que resultou em uma vegetação estruturalmente heterogênea e dependente de perturbações. Nesse contexto, o fogo e o pastejo desempenham papel central na manutenção da diversidade e da identidade ecológica dos campos nativos, atuando como processos reguladores da dinâmica da vegetação. Entretanto, a exclusão dessas perturbações, tem promovido mudanças estruturais profundas no ecossistema. A ausência de manejo favorece a dominância de gramíneas cespitosas, o acúmulo de biomassa senescente e o avanço de espécies lenhosas, resultando na redução da diversidade herbácea e na descaracterização da fisionomia campestre. Diante desse cenário, esta tese tem como objetivo geral avaliar o papel de diferentes regimes de manejo na dinâmica e na conservação dos campos nativos, integrando abordagens ecológicas de longo prazo com estratégias aplicadas de restauração e sugerindo a reflexão relacionada à educação ambiental. A tese está estruturada em quatro capítulos complementares. No primeiro capítulo, são analisados os efeitos de diferentes regimes de pastejo (contínuo, diferido e exclusão) sobre a composição, diversidade e estrutura da vegetação ao longo de 12 anos de monitoramento. Os resultados demonstram que a exclusão do pastejo não constitui uma estratégia adequada de conservação, levando à perda de diversidade, enquanto sistemas com pastejo mantêm maior heterogeneidade e riqueza de espécies. No segundo capítulo, são investigados os efeitos da reintrodução do fogo e do pastejo, isolados e combinados, na restauração de áreas campestres abandonadas. Os resultados evidenciam que a herbivoria pírica, resultante da interação entre fogo e pastejo, é a estratégia mais eficaz para promover a recuperação da vegetação, aumentando a riqueza de espécies, reduzindo a biomassa acumulada e restabelecendo a estrutura típica dos campos. No terceiro capítulo, aborda o controle da invasão lenhosa, demonstrando que o fogo atua como agente de impacto inicial na redução da vegetação arbórea-arbustiva, enquanto o pastejo exerce papel fundamental na manutenção desse controle ao limitar o recrutamento e o rebrote de espécies lenhosas. A integração entre esses dois distúrbios emerge, portanto, como a principal estratégia para conter a sucessão florestal e conservar a identidade campestre. Por fim, o quarto capítulo aborda a dimensão social da conservação, destacando a invisibilização dos campos na sociedade e nos currículos escolares. A tese evidencia a existência de uma lacuna na percepção pública sobre o valor ecológico do Pampa, o que compromete sua conservação a longo prazo. Como resposta, propõe-se a utilização da Alfabetização Ecológica como ferramenta para aproximar o conhecimento científico do contexto educacional, promovendo uma "consciência campestre" baseada no reconhecimento, pertencimento e valorização do território. De forma integrada, os resultados demonstram que o Pampa é um ecossistema dependente de perturbação, cuja conservação exige a manutenção de regimes de manejo baseados no fogo e no pastejo. Ao mesmo tempo, evidenciam que a preservação desse bioma não pode ser dissociada da dimensão educativa e cultural, sendo fundamental promover a reconexão da sociedade com os campos nativos. Sendo assim, este estudo contribui para o avanço do conhecimento ecológico aplicado e propõe uma abordagem integrada de conservação, que articula manejo, restauração e educação como pilares para a conservação do Pampa.

General Abstract

The Pampa biome constitutes a grassland ecosystem of high biological diversity and ecological relevance, responsible for providing multiple ecosystem services, including biodiversity conservation, climate regulation, and the maintenance of soils and water resources. Located within the Campos del Río de la Plata region, this system has a long evolutionary history, shaped by paleoenvironmental conditions and by the action of large herbivores and fire, resulting in a structurally heterogeneous vegetation that is dependent on disturbances. In this context, fire and grazing play a central role in maintaining the diversity and ecological identity of native grasslands, acting as key regulators of vegetation dynamics. However, the exclusion of these disturbances has led to profound structural changes in the ecosystem. The absence of management favors the dominance of tussock-forming grasses, the accumulation of senescent biomass, and the encroachment of woody species, resulting in reduced herbaceous diversity and the loss of typical grassland physiognomy. Given this scenario, the overall aim of this thesis is to evaluate the role of different management regimes in the dynamics and conservation of native grasslands, integrating long-term ecological approaches with applied strategies for restoration and environmental education. The thesis is structured into four complementary chapters. The first chapter analyzes the effects of different grazing regimes (continuous, deferred, and exclusion) on vegetation composition, diversity, and structure over 12 years of monitoring. The results demonstrate that grazing exclusion is not an appropriate conservation strategy, leading to biodiversity loss, whereas grazed systems maintain greater heterogeneity and species richness. The second chapter investigates the effects of reintroducing fire and grazing, both independently and in combination, on the restoration of abandoned grassland areas. The findings show that pyric herbivory, resulting from the interaction between fire and grazing, is the most effective strategy for promoting vegetation recovery, increasing species richness, reducing accumulated biomass, and reestablishing the typical structure of grasslands. The third chapter addresses the control of woody encroachment, demonstrating that fire acts as the primary disturbance for the initial reduction of woody vegetation, while grazing plays a fundamental role in maintaining this control by limiting recruitment and resprouting. The integration of these two disturbances thus emerges as the main strategy to contain forest succession and preserve grassland identity. Finally, the fourth chapter explores the social dimension of conservation, highlighting the invisibilization of grasslands in society and in school curricula. The thesis reveals a gap in public perception regarding the ecological value of the Pampa, which compromises its long-term conservation. As a response, Ecological Literacy is proposed as a tool to bridge scientific knowledge and educational contexts, fostering a "grassland consciousness" grounded in recognition, belonging, and appreciation of the territory. Taken together, the results demonstrate that the Pampa is a disturbance-dependent ecosystem whose conservation requires the maintenance of management regimes based on fire and grazing. At the same time, they highlight that the preservation of this biome cannot be dissociated from its educational and cultural dimensions, making it essential to reconnect society with native grasslands. Thus, this study contributes to advancing applied ecological knowledge and proposes an integrated conservation approach that articulates management, restoration, and education as key pillars for the conservation of the Pampa.

General Introduction

The Pampa as a Grassland-Dependent Ecosystem

Grasslands constitute vital multifunctional ecosystems that, in addition to supporting livestock production, play a crucial role in the provision of ecosystem services such as carbon sequestration, soil and water conservation, and biodiversity preservation (Carlier et al., 2009). In the South American context, the Pastizales del Río de la Plata region, shared by Brazil, Argentina, and Uruguay, stands out as an open ecosystem of high complexity, composed of a wide diversity of ecological systems with distinct characteristics (Hasenack et al., 2010). The genesis of this biome dates back to the fragmentation of the Gondwana supercontinent and the stabilization of the Paraná Basin over millions of years (Menegat, 2023). During the Late Quaternary, grassland physiognomies consolidated their predominance in the region, favored by colder and drier glacial climates that restricted forest expansion (Behling et al., 2023).

This paleoenvironmental scenario was profoundly shaped by a herbivorous megafauna (including horses, llamas, glyptodonts, and mastodons) that inhabited the region until approximately 8,500 years ago (da Rosa et al., 2023). The temporal stability of this environment allowed for the arrival and establishment of biotic lineages from neighboring regions, resulting in a pronounced asymmetry in plant exchange (Baez-Lizarazo et al., 2023) and culminating in extraordinary biodiversity, which today exceeds 12,500 recorded species (Overbeck, Bencke, et al., 2023; Andrade, Dröse, et al., 2023). This richness is marked by high levels of endemism, with around 403 exclusive plant species (Andrade, Menezes, et al., 2023). The maintenance of this biota is ensured by a heterogeneous vegetation structure, which provides specific habitats for diverse guilds, such as specialist birds that select different grass strata for nesting (Bencke et al., 2023).

The extinction of the herbivorous megafauna eliminated one of the main natural controls of vegetation which, combined with the transition to a warmer and more humid climate in the Late Holocene, favored the expansion of forest formations (Behling et al., 2023; da Rosa et al., 2023). In the absence of disturbance, such as fire and grazing, large tussock-forming grasses come to dominate the community, competing for light and space with prostrate species (Overbeck, Andrade, et al., 2023). This process results in the accumulation of senescent biomass and increased shrub density, altering the microclimate and creating shaded conditions that facilitate the establishment of woody pioneer species (Andrade, Menezes, et al., 2023; Müller et al., 2023). The accumulation of large amounts

of flammable biomass, resulting from the rapid growth of grasses during the growing season, facilitated the occurrence and increased frequency of natural fires (Behling et al., 2023). While these fire events act as a key mechanism to control woody recruitment by suppressing the survival of seedlings and young saplings, they may be insufficient to halt forest expansion under current favorable climatic conditions. Often mediated by nurse plants or tree nuclei, this successional dynamic promotes the expansion of forest edges over grasslands, reducing the herbaceous biodiversity typical of the biome by converting natural mosaics into stable forest physiognomies (Behling et al., 2023; Müller et al., 2023).

Historically, this forest advance was slowed by the frequent occurrence of fires, often associated with the management practices of Indigenous peoples—such as the Pampeano, Jê, and Guarani groups—who used fire and native animal herding techniques long before European colonization (Golin, 2023). From the seventeenth century onward, the introduction of domestic cattle by the Jesuits filled the ecological niche left by the extinct large herbivores, acting as a key factor in stabilizing grassland physiognomy. The subsequent feralization of these animals, known as *chimarrão* cattle, gave rise to vast cattle ranges (vacarias) that shaped the vegetation dynamics of the biome long before land was fragmented into private properties (Golin, 2023).

From a historical perspective, contemporary extensive livestock grazing on native grasslands is understood as a form of sustainable management, based on the premise that domestic cattle perform the ecological role once carried out by megafauna in maintaining grassland structure (Andrade, Menezes, et al., 2023). Consequently, the preservation of these traditional grazing practices is essential, as the complete exclusion of disturbances would result in the loss of plant diversity and the disappearance of critical habitats for the regional biota (Overbeck, Andrade, et al., 2023). The absence of controlled disturbances, such as fire and grazing, poses a silent threat by promoting the densification of a few tall grass species and the encroachment of shrubs and trees over the grassland (Thomas, Overbeck, et al., 2019; Müller et al., 2023). This process leads to a drastic reduction in the diversity of herbs, prostrate forage species, and geophytes, which lose the competition for light, while also compromising specialist fauna, such as birds that depend on habitat structural heterogeneity for nesting and foraging (Bencke et al., 2023; Overbeck, Bencke, et al., 2023).

Parallel to the process of structural degradation, the Pampa biome faces accelerated suppression due to the direct conversion of land to soybean monocultures and

forestry. This expansion projects the total disappearance of native grasslands on private lands within a critical timeframe of only 64 to 73 years (Saraiva et al., 2025). Such systemic replacement causes biodiversity erosion across multiple dimensions, including functional and phylogenetic, fostering a scenario of biotic homogenization (Staude et al., 2018; Moreira et al., 2020). In this context, specialist species are progressively replaced by generalists and invasive plants, such as capim-annoni (*Eragrostis plana* Nees), which expand aggressively and disrupt native communities (Medeiros et al., 2009; Guido et al., 2023). Finally, the loss of connectivity among grassland remnants hinders gene flow and propagule dispersal, severely reducing the biome's resilience in the face of climate change (Turchetto et al., 2023).

Woody Encroachment and Ecological Restoration

Adding to these external pressures from land conversion, woody encroachment represents a central challenge to the integrity of grassland remnants, being primarily triggered by the exclusion of natural disturbances such as fire and grazing (Sühs et al., 2020). This process is frequently observed in Conservation Units where the adoption of passive protection strategies—often reflecting institutional non-intervention policies—leads to the unintended suppression of ecological processes vital for grassland maintenance. This process alters grassland physiognomy through the dominance of shrubs and tall grasses, which reduce light and space availability for herbaceous flora, resulting in species diversity loss (Thomas, Overbeck, et al., 2019; Andrade, Menezes, et al., 2023). Consequently, ecological restoration in abandoned areas, whether or not they are located within conservation units, requires the active removal of accumulated biomass and woody components, using techniques such as prescribed burning, mowing, or livestock management to reestablish habitat structure (Thomas, Overbeck, et al., 2019; Baggio et al., 2021). If forest succession stabilizes over long periods, the recovery of the original biodiversity becomes a complex and high-cost process, highlighting that the maintenance of traditional management is the most effective strategy to prevent the permanent loss of these ecosystems (Thomas, Schüler, et al., 2019; Müller et al., 2023).

The persistence of these ecological and management challenges is, however, exacerbated by a profound gap between scientific knowledge and social perception. The Pampa suffers from the so-called "Biome Awareness Disparity" (BAD), a consciousness gap that neglects open ecosystems in favor of forest formations (Silveira et al., 2022). This "arboreal precept" distorts conservation policies by prioritizing non-intervention as a default management model, which may be misaligned with the ecological requirements

of disturbance-dependent biomes (Overbeck, Bencke, et al., 2023). It overlooks the fact that the biome harbors more than 12,500 species and holds world records for plant richness at small scales (da Silva Menezes et al., 2018; Overbeck, Bencke, et al., 2023).Therefore, the effectiveness of biological conservation becomes inseparable from cultural appropriation, demanding environmental education that teaches society to recognize the value of what grows close to the ground (Menezes et al., 2022; Overbeck, Bencke, et al., 2023). Only by appreciating natural assets, integrating active management into conservation frameworks, and addressing social and economic aspects will it be possible to consolidate the need to preserve the Pampa for future generations (Overbeck, Bencke, et al., 2023).

Between Rosetas and flechilhas: Spreading Ecological Literacy in Schools

Thus, consolidating the need for preservation requires that scientific knowledge about the grassland-dependent ecosystem be translated into everyday school life as a tool for social transformation. Schools therefore assume a strategic role in mitigating Biome Awareness Disparity (BAD) and botanical imperception, overcoming the forest bias that has historically rendered open formations invisible in curricula and public perception (Silveira et al., 2022). By adopting Ecological Literacy (Lewinsohn et al., 2015) and playful pedagogical practices—such as those developed in the Pampa na Escola project—it becomes possible to transform technical data on biodiversity and management into a "Grassland Consciousness" grounded in emotional connection (Porto et al., 2021). After all, conservation is inseparable from recognition. Only education that integrates the student's concrete reality with an understanding of the biome's ecological dynamics can turn the "look down" into a gesture of belonging and care, ensuring that the appreciation of the Pampa moves from academic consensus to a practice of citizenship and regional sustainability.

This thesis is structured around three complementary perspectives that seek to address the complexity of Pampa conservation through long-term evidence and social intervention practices. From an ecological perspective, the successional effects of exclusion and different grazing regimes (continuous and deferred) are investigated, demonstrating that the absence of disturbance results in biodiversity loss after 12 years of monitoring (Chapter 1). In the technical and management sphere, the research deepens the role of fire and grazing as fundamental controls of vegetation structure, showing how these disturbances ensure the richness of herbaceous species (Chapter 2) and act as essential barriers against woody encroachment and invasion in the grassland environment

(Chapter 3). Finally, from the social and educational perspective, Chapter 4 analyzes the transposition of this scientific knowledge into basic education through the Pampa na Escola project, using Ecological Literacy to mitigate the invisibility of the biome. By integrating these fronts, the overall aim of this thesis is to evaluate the impact of management regimes on the dynamics and integrity of the grassland ecosystem, proposing pedagogical strategies that reconnect society to the appreciation and preservation of the Pampa.

General Objective

The overall aim of this thesis is to evaluate the role of different management regimes in the dynamics and conservation of South Brazilian grasslands, integrating long-term ecological monitoring with reflections on restoration strategies and the social-educational challenges of biome preservation.

Specific Objectives

- Capítulo 1 – To evaluate the long-term effects (12 years) of different grazing management regimes (continuous, deferred, and exclusion) on species composition, diversity, and structural heterogeneity in the Pampa and Highland grasslands
- Capítulo 2 – To investigate the initial effects of reintroducing fire, grazing, and their interaction (pyric herbivory) as tools for restoring vegetation structure and species richness in abandoned subtropical grasslands.
- Capítulo 3 – To analyze the isolated and combined roles of prescribed fire and cattle grazing in controlling woody encroachment, identifying fire as a primary agent for initial biomass reduction (top-kill) and grazing as a factor to suppress resprouting and recruitment.
- Capítulo 4 – To reflect on the social dimension of Pampa conservation, discussing the causes of grassland invisibility in school curricula and inviting a dialogue on how Ecological Literacy can bridge the gap between scientific knowledge and the construction of a "grassland consciousness" in basic education.

References

Andrade, B.O., Dröse, W., Aguiar, C.A. de, Aires, E.T., Alvares, D.J., Barbieri, R.L., et al. (2023) 12,500+ and counting: biodiversity of the Brazilian Pampa. *Frontiers of Biogeography*, 15(2). https://doi.or/10.21425/F5FBG59288

Andrade, B.O., Menezes, L. da S., Boldrini, I.I., Pillar, V.D., & Overbeck, G.E. (2023) Grassland plant community composition and dynamics: disturbance as determinants of grassland diversity. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 177–204. https://doi.org/10.1007/978-3-031-42580-6_8

Baez-Lizarazo, M.R., Köhler, M., & Reginato, M. (2023) A historical perspective on the biogeography of the Pampa Region: imprints of time and origins of its flora. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 101–118. https://doi.org/10.1007/978-3-031-42580-6_5

Baggio, R., Overbeck, G.E., Durigan, G., & Pillar, V.D. (2021) To graze or not to graze: A core question for conservation and sustainable use of grassy ecosystems in Brazil. *Perspectives in Ecology and Conservation.* https://doi.org/10.1016/j.pecon.2021.06.002

Behling, H., Pillar, V.D., & Overbeck, G.E. (2023) Dynamics of south Brazilian grasslands during the late quaternary. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 83–99. https://doi.org/10.1007/978-3-031-42580-6_4

Bencke, G.A., Dias, R.A., & Fontana, C.S. (2023) Birds of the Campos Sulinos. South Brazilian Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 231–287. https://doi.or/10.1007/978-3-031-42580-6_10

Carlier, L., Rotar, I., Vlahova, M., & Vidican, R. (2009) Importance and functions of grasslands. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 37(1), 25–30. https://doi.org/10.15835/nbha3713090

Golin, T. (2023) The Southern Grasslands and the expropriation of Indigenous territories. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 145–174. https://doi.org/10.1007/978-3-031-42580-6_7

Guido, A., Sühs, R.B., Marciniak, B., Bergamin, R.S., & Fidelis, A. (2023) Invasive alien species in the Campos Sulinos: Current status and future trends. South Brazilian

Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer,* 495–527. https://doi.or/10.1007/978-3-031-42580-6_19

Hasenack, H., Weber, E., Boldrini, I.I., & Trevisan, R. (2010) Mapa de sistemas ecológicos da ecorregião das Savanas Uruguaias em escala 1:500.000 ou superior. Porto Alegre: UFRGS.

Lewinsohn, T.M., Attayde, J.L., Fonseca, C.R., Ganade, G., Jorge, L.R., Kollmann, J., et al. (2015) Ecological literacy and beyond: Problem-based learning for future professionals. *Ambio*, 44(2), 154–162. https://doi.or/10.1007/s13280-014-0539-2

Medeiros, R.B. de, Saibro, J.C. de, & Focht, T. (2009) Invasão de capim-annoni (*Eragrostis plana* Nees) no bioma Pampa do Rio Grande do Sul. Campos Sulinos: Conservação e Uso Sustentável da Biodiversidade. 317–330.

Menegat, R. (2023) Geological Memories of South Brazilian Landscapes: From Precambrian Orogenesis to the Quaternary Coastal Plain. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 17–44.

Menezes, L.S., Ely, C. V., Lucas, D.B., Minervini-Silva, G.H., Vélez-Martin, E., Hasenack, H., et al. (2022) Reference values and drivers of diversity for South Brazilian grassland plant communities. *Anais da Academia Brasileira de Ciencias*, 94(1). https://doi.or/10.1590/0001-3765202220201079

Moreira, L.F.B., de Castilhos, H.Z., & Castroviejo-Fisher, S. (2020) Something is not quite right: Effects of two land uses on anuran diversity in subtropical grasslands. *Biotropica*, 52(6), 1286–1297. https://doi.or/10.1111/btp.12836

Müller, S.C., Bergamin, R.S., Duarte, L.S., Peroni, N., Sühs, R.B., & Carlucci, M.B. (2023) Mechanisms and processes shaping patterns of forest-grassland mosaics in southern Brazil. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 417–443. https://doi.org/10.1007/978-3-031-42580-6_16

Overbeck, G.E., Andrade, B.O., Vélez-Martin, E., & Pillar, V.D. (2023) Beyond protected areas: conservation of south Brazilian grasslands. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. Springer, 447–473. https://doi.org/10.1007/978-3-031-42580-6_17

Overbeck, G.E., Bencke, G.A., Müller, S.C., & Pillar, V.D. (2023) The Campos Sulinos:

Introduction to the book. South Brazilian Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 3–13. https://doi.org/10.1007/978-3-031-42580-6_1

Porto, A.B., Rolim, R.G., Silveira, F.F., Overbeck, G.E., Salatino, A. (2021) Consciência campestre: um chamado para o (re)conhecimento aos campos. *Biodiverso*, 1. Available at: https://seer.ufrgs.br/index.php/biodiverso/article/view/113747

da Rosa, Á.A.S., Kerber, L., Pinheiro, F.L., & Manfroi, J. (2023) A look into the past: fossils from the Campos Sulinos Region. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 45–81. https://doi.org/10.1007/978-3-031-42580-6_3

Saraiva, D., Torchelsen, F.P., Overbeck, G.E., Müller, S.C., Hasenack, H., Urruth, L.M., & da Silva, C.R. (2025) Ameaça silenciosa: análise histórica e tendências futuras da supressão dos campos naturais do bioma Pampa pela expansão agrícola. *Bio Diverso,* 5(1).

da Silva Menezes, L., Vogel Ely, C., Lucas, D.B.D.B., Minervini Silva, G.H., Boldrini, I.I., & Overbeck, G.E. (2018) Plant species richness record in Brazilian Pampa grasslands and implications. *Revista Brasileira de Botanica*, 41(4), 817–823. https://doi.or/10.1007/s40415-018-0492-6

Silveira, F.A.O., Ordóñez-Parra, C.A., Moura, L.C., Schmidt, I.B., Andersen, A.N., Bond, W., et al. (2022) Biome Awareness Disparity is BAD for tropical ecosystem conservation and restoration. *Journal of Applied Ecology*, 59(8), 1967–1975.

Staude, I.R., Vélez-Martin, E., Andrade, B.O., Podgaiski, L.R., Boldrini, I.I., Mendonça, M., et al. (2018). Local biodiversity erosion in south Brazilian grasslands under moderate levels of landscape habitat loss. *Journal of Applied Ecology*, 55(3), 1241–1251. https://doi.or/10.1111/1365-2664.13067

Sühs, R.B., Giehl, E.L.H., & Peroni, N. (2020) Preventing traditional management can cause grassland loss within 30 years in southern Brazil. *Scientific Reports*, 10(1), 783. https://doi.or/10.1038/s41598-020-57564-z

Thomas, P.A., Overbeck, G.E., & Müller, S.C. (2019) Restoration of abandoned subtropical highland grasslands in brazil: Mowing produces fast effects, but hay transfer does not. *Acta Botanica Brasilica*, 33(3), 405–411. https://doi.or/10.1590/0102-33062018abb0377

Thomas, P.A., Schüler, J., Boavista, L. da R., Torchelsen, F.P., Overbeck, G.E., & Müller, S.C. (2019) Controlling the invader Urochloa decumbens: Subsidies for ecological restoration in subtropical Campos grassland. *Applied Vegetation Science*, 22(1), 96–104. https://doi.or/10.1111/avsc.12407

Turchetto, C., Segatto, A.L.A., & Freitas, L.B. (2023) Plant microevolutionary processes in the campos sulinos: Why do they matter? South Brazilian Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 205–229. https://doi.or/10.1007/978-3-031-42580-6_9

Capítulo I

Southern Brazilian Grassland Diversity: Anti-Disturbance Regimes Are Not Ideal and Grazing Maintains Plant Diversity

Filipe Ferreira da Silveira, Luciana Silva Menezes, Ana Boeira Porto, Pedro Augusto Thomas, Lidiane da Rosa Boavista, Guilherme Dubal dos Santos Seger, Gerhard Ernst Overbeck

Artigo de qualificação defendido em 03 de maio 2024.
Banca examinadora: Drs. Anaclara Guido (UDELAR, Uruguai), Pedro Tognetti (UBA, Argentina e Pedro Maria Abreu Ferreira (PUCRS)
Manuscrito publicado no periódico Applied Vegetation Science
Submetido em 25 de outubro de 2024
Revisado até 18 de outubro de 2025
Aceito em 23 de outubro de 2025
DOI: **https://doi.org/10.1111/avsc.70049**

Title: Southern Brazilian grassland diversity: anti-disturbance regimes are not ideal and grazing maintains plant diversity

Short title: Management and diversity in South Brazilian grassland

Filipe F. da Silveira[1], Luciana S. Menezes[1], Ana B. Porto[1], Pedro A. Thomas[2], Lidiane da R. Boavista[2], Guilherme D. S. Seger[1], Gerhard E. Overbeck[12].

[1] Graduate Program in Botany, Universidade Federal do Rio Grande do Sul, Brazil.
[2] Graduate Program in Ecology, Universidade Federal do Rio Grande do Sul, Brazil.

Authors and ORCID
Filipe Ferreira da Silveira - 0000-0002-1273-0655
Luciana da Silva Menezes –0000-0002-2961-0190
Lidiane da Rosa Boavista - 0000-0002-1446-790X
Ana Boeira Porto – 0000-0001-7763-013X
Pedro Augusto Thomas – 0000-0001-5629-9222
Guilherme Dubal dos Santos Seger – 0000-0002-0710-3550
Gerhard Ernst Overbeck – 0000-0002-8716-5136

Correspondence
Filipe Ferreira da Silveira, Program of Botany (PPGBot/UFRGS), Universidade Federal do Rio Grande do Sul, RS, Brazil. E-mail: filipesilveferreira@hotmail.com

Funding
FFS was supported by "Bolsas Funbio–Conservando o Futuro" program, awarded by FUNBIO and Instituto Humanize.
Gerhard Ernst Overbeck was supported by CNPq (grant 310345/2018-9).

Acknowledgements
We thank the researchers and staff of the Laboratory of Grassland Vegetation Studies (LEVCamp) - UFRGS for their availability in assisting with expeditions and data collection. We thank Lívia Abib, Lua Cezimbra and Rafael Barbosa for their participation during data collection. For assistance in plant identification, we thank Ilsi Boldrini and Sérgio Bordignon. We acknowledge the constructive comments from the qualification committee to which this article was submitted: Anaclara Guido (UDELAR, Uruguay), Pedro Tognetti (UBA, Argentina), and Pedro Maria Abreu Ferreira (PUCRS, Brazil). This study was partially funded by a research grant from the National Council for Scientific and Technological Development (CNPq) awarded to GEO (477618/2013-8) and by the Coordination for the Improvement of Higher Education Personnel - Brazil (CAPES) - Finance Code 001. GEO acknowledges CNPq productivity grants (310345/2018-9). FFS thanks CAPES for the scholarship (88887.684521/2022-00), was supported by the "Bolsas Funbio–Conserving the Future" program, awarded by FUNBIO and Instituto Humanize. We thank Valério Pillar for helpful comments on an earlier version of the manuscript. This study is part of the LTER/PELD Campos Sulinos, supported by CNPq (CNPq grants PELD 441753/2020-5 and PQ 313315/2022-1 and by FAPERGS grant PELD 21/2551-0000776-1 to Valério De Patta Pillar). We would also like to thank the entire structure provided by the Graduate Program in Botany at the Federal University of Rio Grande do Sul.

Southern Brazilian grassland diversity: anti-disturbance regimes are not ideal and grazing maintains plant diversity

ABSTRACT

Questions: We experimentally test the long-term effects of grazing management regimes on species composition, diversity, and the heterogeneity of grassland vegetation 12 years after implementation of grazing treatments, with a focus on plant life forms.

Location: Seven long-term ecological research sites located in southern Brazil, four in grasslands of the Pampa and three in highland grasslands.

Methods: The experiment was established in 2010 using a randomized block design, with sites serving as replicates. The vegetation at each site was subjected to three management treatments (continuous grazing, deferred grazing simulating rotational grazing, and grazing exclusion) in 0.5-ha experimental plots. In spring-summer of 2021-2022, we estimated the species cover composition for each experimental plot, classifying them according to life-forms, and recorded other variables such as vegetation height. The effects of grazing management on life-form and species cover were examined using Multivariate Analysis of Variance, Redundancy Analysis (RDA), Renyi curve, and Diversity through Hill Numbers.

Results: The results indicate significant effects of grazing treatments on species composition, with grazing exclusion associated with greater average vegetation height. Additionally, grazing impacts diversity profiles and life-form abundance, with notable differences between Pampa and highland grasslands. Overall, continuous and deferred grazing exhibited higher diversity compared to grazing exclusion, with significant variations in diversity among treatments.

Conclusion: Grazing exclusion leads to a loss of grassland diversity, while diversity may not fundamentally differ between sites under continuous or deferred grazing. We demonstrated how different management strategies influence vegetation in the long term, emphasizing the importance of disturbances in maintaining grazing and the need for ongoing research to guide effective management practices.

Key-words: Heterogeneity, Grazing effects, Disturbance legacy, Life-forms, Woody invasion, Grazing exclusion, Diversity patterns, Vegetation composition, Grazing impact.

Introduction

In many regions of the globe where climatic and soil conditions allow for the establishment of trees and the development of forests, grasslands dominate landscapes due to disturbances such as fire and grazing (Veldman et al. 2015). These processes have shaped the species composition of grasslands over evolutionary times and contribute to the maintenance of non-forest vegetation until today (Bond & Keeley, 2005; Bond, 2022). Disturbance regimes can vary in frequency, intensity, and magnitude, and different disturbances, including fire and grazing, can interact (Collins 1987). Among natural disturbances, fire occurs periodically, while grazing can be constant and continuous; however, effects always depend on the specific fire or grazing regime (Bond & Keeley, 2005; Andrade et al. 2023, Ferreira et al. 2020). The relevance of disturbances to maintain grasslands can be observed across a wide spectrum of climatic and edaphic conditions. For example, in the Eurasian steppe, the abandonment of agricultural lands after the dissolution of the Soviet Union resulted in a shift in the disturbance regime, with a reduction in grazing pressure affecting vegetation structure, turning fire the more important disturbance (Freitag et al., 2021). In the tallgrass prairie of Kansas, North America, a study on different grazing intensities suggested that grazing by large herbivores contributed to increased floristic diversity, and both grazing and fire can be considered modulating agents in this system (Hickman et al. 2004).

Importantly, disturbances vary in time and space, promoting vegetation mosaics and environmental heterogeneity, which can be desirable from a conservation perspective (Fuhlendorf et al. 2006). Herbivores, including cattle, can select their forage intentionally when resources are abundant, while the spread of fire is in general less selective at the fine scale, linked to climate, weather, topography and landscape connectivity (Boavista et al 2019; Fidelis, 2020). Today, natural disturbance regimes have often been replaced by human land-management including, in the case of grasslands, grazing by domestic animals which contribute to the maintenance of these ecosystems. The exclusion of a grassland ecosystem from disturbances (Tälle et al. 2016), in contrast, usually leads to changes in the composition of species (Oliveras et al. 2012), resulting in losses of typical plant species of open ecosystems (Ferreira et al. 2020) and, consequently, associated ecosystem services (Sollenberger et al. 2019).

Grasslands under productive climatic conditions, especially those where grazing occurred over evolutionary times, show an increase in species diversity when subjected

to moderate grazing as opposed to high grazing intensities (Cingolani et al. 2005). Therefore, stocking rates and the frequency of grazing events are key variables in shaping the response of pastures to grazing. In subtropical southern Brazil, fire and grazing shape the grasslands and alter plant species dynamics (Quadros et al. 2005). Grasslands under high stocking rates tend to show dominance by prostrate and stoloniferous grass species (Boavista et al. 2019). These life forms exhibit rapid bud burst, highlighting their efficiency in resource acquisition (Cruz et al. 2010). Grazing under moderate pressure tends to allow animals to select the plant species to be consumed (Scimone et al. 2007). Usually, cattle prefer species with high palatability, such as low-fiber grasses and leguminous at the detriment of life forms that have structures making them less palatable species, i.e., with high fiber content, thorns, or toxicity, which are avoided and thus can increase in cover (Overbeck et al. 2007; Scimone et al. 2007; Nabinger et al. 2009). In consequence, species of lower forage value are rejected and thus indirectly favoured, which contributes to environmental heterogeneity (Adler et al. 2001; Morris 2002; Ferreira et al. 2020; Caram et al. 2023). Lastly, ungrazed grasslands tend to become more homogeneous as tall tussock grasses and shrubs become dominant (Ferreira et al. 2020); these grasslands then show low species diversity (Andrade et al. 2016; Guido et al. 2017). In addition to the analysis of species richness or species composition, the evaluation of diversity patterns in space, be it through the analysis of dominance or changes in plant community composition in space, i.e., beta-diversity, is highly informative and widely used as an indicator of environmental heterogeneity (Chase & Myers 2011; Heino et al. 2015; Menezes et al. 2022).

Not only grazing, but also the type of grazing regime defines grazing effects on the plant community. Under continuous grazing, cattle are allowed to freely roam over larger areas, which may lead to differences in grazing pressure depending on attractiveness of the vegetation (Jacobo et al. 2006). This difference can eventually result in the presence of overgrazed patches, but also less grazed patches within a paddock (Caram et al. 2023). Under rotational grazing, cattle graze smaller paddocks over short periods of time, usually with high stocking rates, and the vegetation has a resting period. This leads to more homogeneous grazing, higher grazing efficiency and, ultimately, higher productivity (Boavista et al. 2019). Furthermore, studies indicate that exclusion of cattle from grazed areas for periods that can vary from less than one to several months

100 (grazing deferment) rather quickly lead to the recovery of biomass and sward high
101 (Fedrigo et al. 2022).

102 The South Brazilian Grasslands have historically been grazed by livestock, a key
103 economic activity with cultural significance (Golin 2023). These ecosystems display a
104 notable species richness, particularly in the families Poaceae, Asteraceae, Fabaceae, and
105 Cyperaceae (Overbeck et al. 2007; Boldrini 2009). Furthermore, the South Brazilian
106 Grasslands feature a combination of species with C3 and C4 photosynthetic strategies,
107 ensuring biomass production throughout the year (Overbeck & Pfadenhauer 2007;
108 Andrade, et al. 2019). However, grassland management is often inappropriate, especially
109 due to overgrazing, which leads to losses in plant species diversity and productivity
110 (Fedrigo et al. 2018). Understanding the effects of different management strategies will
111 enable not only an adequate use of grazing resources but also the maintenance of native
112 plant diversity, contributing to conservation and long-term grazing sustainability. For this,
113 detailed knowledge of management effects on diversity patterns is necessary.

114 In this study, we use data from a grazing management experiment established in
115 2010 in the framework of the Long-Term Ecological Research project (LTER/PELD)
116 Campos Sulinos. The experiment is located in seven sites distributed across the South
117 Brazilian Grassland region, with three treatments per site: continuous grazing, deferred
118 grazing, and grazing exclusion. A previous study (Ferreira et al. 2020) evaluated effects
119 of treatments on plant diversity along the first four years of the experiment. Here, we use
120 data collected 12 years after implementation of the treatments to synthesise effects of
121 grazing management on different aspects of diversity, with a specific focus on plant life
122 forms. We hypothesized that: (1) Plant life-form abundances and vegetation composition
123 and structure (average vegetation height, bare soil, and others) will be affected by the
124 grazing regimes. We expect that continuously grazed areas will be dominated by prostrate
125 and stoloniferous species, indicating efficient resource capture. Conversely, in ungrazed
126 areas tussock grasses will be more abundant, exhibiting strategies focused on resource
127 conservation. Lastly, deferred grazing will exhibit a mix of resource capture and
128 conservation, with both tussock and prostrate species coexisting. (2) Richness and
129 vegetation heterogeneity in space will be lower in ungrazed plots than in grazed
130 treatments; among grazed treatments, deferred grazing will be relatively more
131 heterogeneous than continuous grazing. (3) Ungrazed treatments will exhibit the lower

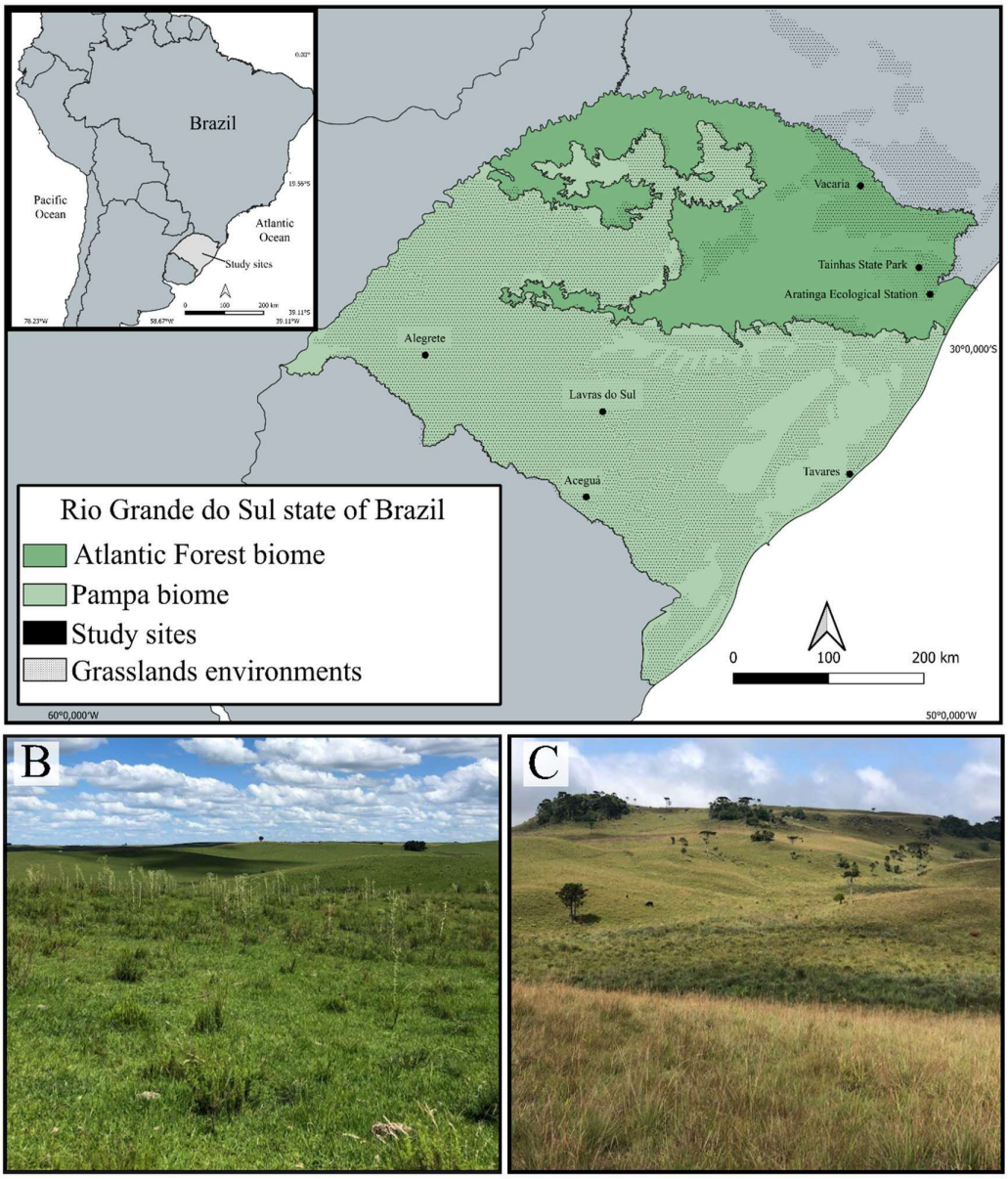
diversity (γ, α, β) compared to the other treatments, indicating a high dominance of a few species, and higher dominance of some life-forms, such as tussock grasses and shrubs.

Methods

Study area

The grazing experiment was carried out in the South Brazilian Grasslands, with replications distributed in two ecoregions: Pampa Grasslands and South Brazilian Highland Grasslands (Overbeck et al. 2022). The South Brazilian Highland grasslands, henceforth Highland Grasslands, form mosaics with Araucaria forests at altitudes of 700-1000 m. In the Pampa, grasslands dominate the landscape and forests are mostly restricted along rivers, and the climate is Cfa with annual precipitation of 1200 –1600mm and mean annual temperature of 13-17 °C (Overbeck et al. 2007; Alvares et al. 2013). The climate in the South Brazilian Highland Grasslands is Koeppen's Cfb, with annual precipitation of 1500 – 2000 mm and a mean annual temperature ranging from 6 –22 ºC.

In the Pampa Grasslands, the experimental sites (Fig.1) are distant from forested areas by at least 1 km, except the Lavras do Sul site. In the Highland Grasslands, the experimental sites are in three municipalities: Vacaria, Jaquirana (Tainhas State Park), São Francisco de Paula (Aratinga Ecological Station). In this region, fire is commonly used as a tool in grazing management to renew the forage in late winter, occurring with a fire return interval ranging from 2 to 3 years at our study sites. The fire history in the Tainhas sampling unit from 2016 to 2023 indicates that the area had at least four fire events with intervals of 1 to 4 years (personal communication from the park manager). Fires often spread to other sites, even to protected areas, as the case for Tainhas State Park and Aratinga Ecological Station.



157 Fig. 1. Location of sampling sites in Rio Grande do Sul state, Brazil (A) and example of
158 a Pampa Grassland site (B: Lavras do Sul) and a Highland Grassland site (C: Tainhas
159 State Park).

Experimental design

The experiment has a randomized block design with three experimental units, one for each treatment, at each of the seven sites: (1) continuous grazing as implemented by the landowner (control), (2) deferred grazing (only periodic cattle access), and (3) grazing exclusion (no cattle grazing). The experimental units are plots of 70 x 70 m (Ferreira, et al. 2020) and the treatments were implemented in 2010 (except Vacaria, which started in 2014) and have been maintained since then. The continuous grazing treatment was maintained under stocking rates between approximately 0.6 and 0.9 animal units per hectare, with some variation across seasons (due to the seasonality in plant biomass production and, in consequence, forage availability). The deferred grazing plot and the grazing exclusion were fenced. In the deferred grazing treatment, cattle periodically had access for a 1- to 2-day grazing event and then was excluded. The interval between events was based on the cumulative thermal sum of 550-degree days (sum of mean temperatures greater than zero °C), which had been 700-degree days until 2016. At each event, vegetation was grazed to an aboveground residual of approximately 1500 Kg of dry plant biomass per hectare. Mostly, the interval of grazing events varied between 22 and 23 days.

Vegetation sampling

Between December 2021 and February 2022, i.e. southern hemisphere late spring and summer, we sampled the grassland vegetation using nine 1 m² (1 x 1 m) subplots per experimental unit. Subplots were systematically located in a 3 x 3 grid with distance of 17 m among units. In each subplot, the cover of all vascular plant species was visually estimated using the Londo decimal scale (Londo 1976). The classification of families and the botanical nomenclature followed APG IV and *Flora do Brasil* (Chase 2016; Jardim Botânico do Rio de Janeiro 2022). To describe vegetation structure, we collected data on total vegetation cover (VC), the average vegetation height (AHV), litter cover (L), the cover of standing dead biomass (SDB), percentage of bare soil (BS), percentage of rock cover (R) and dung cover (M).

Data analysis

Species diversity and composition

Plant communities were characterized by species richness and abundance. We grouped the sampling sites into Pampa grasslands (PG) and Highland grasslands (HG), as regions differ in terms of climate, vegetation (see Andrade et al. 2019), and vegetation management (frequent fires in the HG). For the analyses, we used, for each experimental unit, the mean values of the nine subplots. We used multivariate analysis of variance with permutation test (Pillar & Orlóci 1996; Anderson, 2001), based on Bray-Curtis distances between experimental plots, to compare the grazing treatments regarding the composition (mean cover) of species and life-forms in each experimental plot, as well as the related environmental variables. Regions (Pampa and Highland grasslands) and the permutations were restricted within each site to control the site effects (see Appendix S1). The analysis was implemented using the 'adonis2' function in the Vegan v.2.6.4 package in R statistical environment (Oksanen et al. 2023).

Relations of community composition and environmental descriptors

We used redundancy analysis (RDA; Blanchet et al. 2008) to assess the relations between plant communities and environmental variables, using species cover and, in a second analysis, life-form cover, separately for Pampa and Highland Grasslands, and using log transformation. As environmental variables we used the descriptors of grassland structure: average vegetation height, bare soil, litter, dung, rock, standing dead biomass, and vegetation cover. While some of these variables are related to vegetation composition, they offer a description of the physical structure of the environment. For each RDA, we removed highly collinear environmental variables to avoid variance inflation, and non-significant variables or variables that did not add explanation to the model. In the collinearity test, variables with an inflation factor (vif) greater than 10 were removed individually, repeating the procedure until all variables had values below 10 (see Appendix S2). This process was carried out through the 'vif.cca' function of the Vegan v.2.6.4 package in R (Oksanen et al. 2023). Based on this subset of non-collinear variables, step-by-step (ordistep) variables were selected (Oksanen et al. 2023), using the forward selection procedure.

Diversity and dominance patterns of species and life forms

We built a bar chart of life-forms abundance per treatment using the mean cover of life forms, separately for Pampa Grasslands and Highland Grasslands. The classification of life forms followed Ferreira et al. (2020). Trees and shrubs were grouped as woody species, while non-woody climbers were classified as herbaceous forbs. To illustrate the patterns of diversity and dominance among the different treatments, we built Renyi curves for Pampa and Highland Grasslands, based on absolute cover values through the 'renyi' function of the Vegan v.2.6.4 package (Oksanen et al. 2023) in R (R Core Team, 2024). The higher the order of diversity parameters (q), the greater the weight of dominance. For instance, at q=0, all species carry equal diversity weight regardless of their abundance. Treatments and structural variables (average vegetation height, bare soil, litter, standing dry biomass, and dung cover) were compared using Simpson diversity indices, by a Mixed Generalized Linear Regression Model (GLMM) approaches with inverse Gaussian through the 'glmmPQL' function of the 'MASS' v.7.3.58.2 package (Ripley 2002). The hypothesis test was conducted using the 'glht' function from the "multcomp" v.1.4.23 package (Hothorn et al. 2008). The dependent variables were derived from pairwise comparisons among plots (γ, α and β), with treatments serving as predictor variables. The analysis also incorporated regions (Pampa and Highland grasslands) and sites as random effects.

Within-treatment vegetation heterogeneity

Using the relative species abundance matrix, converted into a richness matrix, and applying Jost's correction, we obtained beta diversity values as the ratio between gamma. (richness per treatment (q=0)) and alpha (richness per plot) diversity (Chao et al. 2014). The data normality was tested using the Shapiro-Wilk Normality Test for all diversity levels (alpha, beta, and gamma). From the Alpha diversity values per experimental plot were obtained by calculating the mean value of all pairwise values from the nine sampling units, we obtained the mean values per plot, through the 'hill_taxa_parti_pairwise' function of the hillR v.0.5.1 package (Li, 2018). We then compared treatments based on these values using Mixed Generalized Linear Regression Model (GLMM) approaches with inverse Gaussian through the 'glmmPQL' function of the 'MASS' v.7.3.58.2 package (Ripley 2002). The analysis code and data are available on Zenodo (Silveira, 2024).

253

254 **RESULTS**

255 *Diversity and composition*

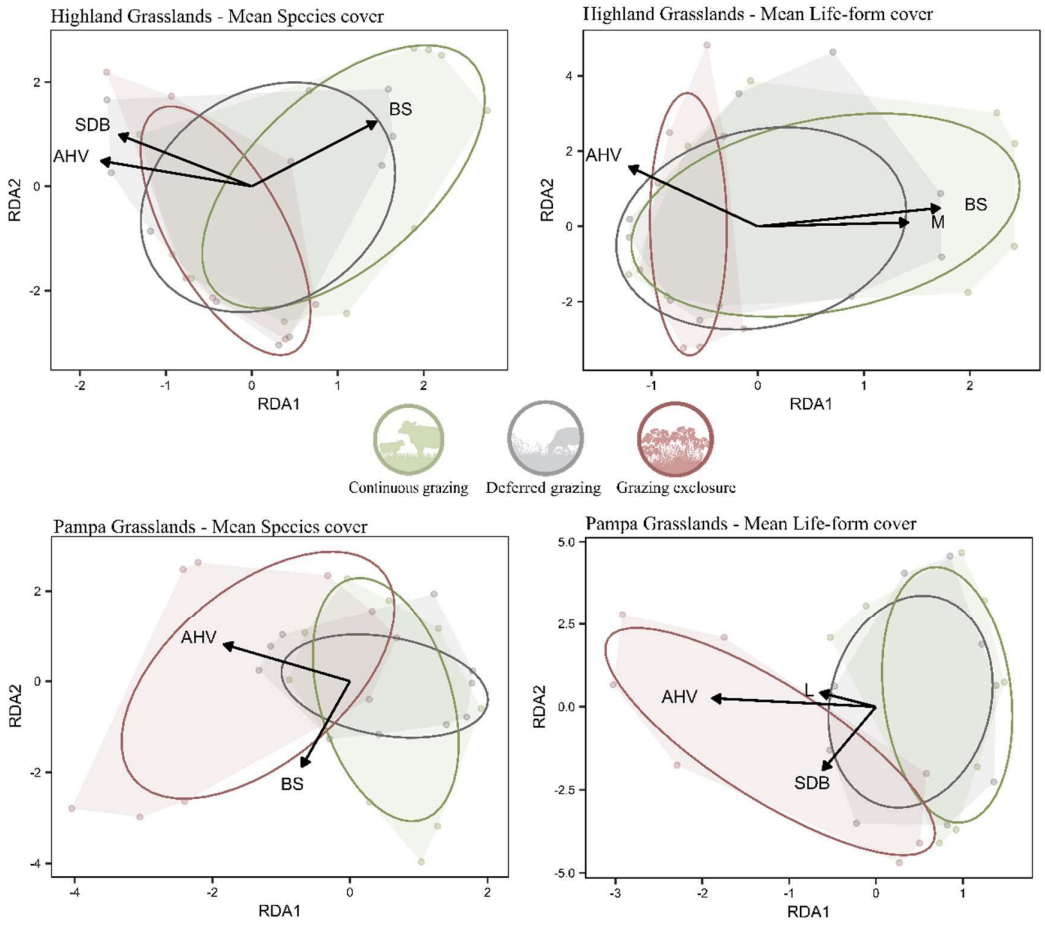
256 We identified 299 species belonging to 48 botanical families (See Appendix S3
257 for complete list, including information on life forms). Mean species richness per plot in
258 each treatment was 18 under continuous grazing, 15 under deferred grazing, and 9 under
259 grazing exclusion. The five most abundant species summed up to 35% (continuous
260 grazing), 40% (deferred grazing) e 38% (grazing exclusion) of relative abundance at the
261 Pampa sites, and to 51% (continuous grazing), 60% (deferred grazing) e 66% (grazing
262 exclusion) at the Highland sites.

263

264 *Relations between community composition and environmental descriptors*

265 The RDA for the Pampa grasslands indicates that grazing exclusion was
266 associated with higher average vegetation height. Standing dead biomass was positively
267 related to the grazing exclusion only when using species cover values (Appendix S2 and
268 Fig. 2). For values of selection of environmental variables see Appendix S2. Using both
269 species and life-form cover, grazing exclusion and the continuous and deferred grazing
270 treatments were significantly different in pairwise comparisons (Appendix S1). In the
271 RDA, Highland Grasslands, the species and life-form composition differed less than in
272 the Pampa, as evidenced by the high overlap in the graph among treatments (Figure 2).
273 All Highland grasslands grazing treatments showed significant differences, except when
274 comparing deferred and continuous grazing based on total species cover (Appendix S1).
275 R^2 adj. values were low, especially in the Pampa (Appendix S4). However, structural
276 variables obtained relatively high values, such as 0.37 and 0.63, demonstrating their
277 significant relevance for explaining the model, suggesting a strong influence of
278 environmental variables on the composition.

279



280

281 Fig. 2 – Redundancy Analysis (RDA) demonstrating the relationship among the grazing
282 regime treatments, based on mean species cover (left), and mean cover of life-forms
283 (right) in the Pampa and Highland sites. The points are the sampling units that define the
284 polygon that comprises all sampling units each treatment Environmental variables:
285 average vegetation height (AHV); bare soil (BS); standing dead biomass (SDB); litter
286 (Lit), dung cover (M).

287

288 The effect of management treatment was significant to both plant community and
289 plant life form abundance, all treatments differed from each other in pairwise comparisons
290 (Appendix S1). All predictor variables significantly contributed to the explanation of
291 species or life-form composition, except SDB for life-form and AHV for species
292 composition. No dispersion effect (by Permutational Analysis of Multivariate Dispersions
293 test) was detected.

294

Diversity and dominance patterns of species and life forms

In the Renyi curve for Pampa Grasslands, the continuous grazing and deferred grazing exhibit the higher values with a slightly difference between them (Fig. 3A). For $q<2$, grazing exclusion exhibits the lowest values; however, starting from order 2, there is a reversal compared to deferred grazing, and this trend continues with increasing q values, indicating that dominant species play a more significant role. In Highland Grasslands (Fig. 3B), the continuous and deferred grazing treatments maintain the same pattern observed in Pampa Grasslands, but with higher values for continuous grazing. However, there is no inversion between deferred grazing and grazing exclusion and the lowest values exhibited by grazing exclusion are consistent from the beginning of the curve.

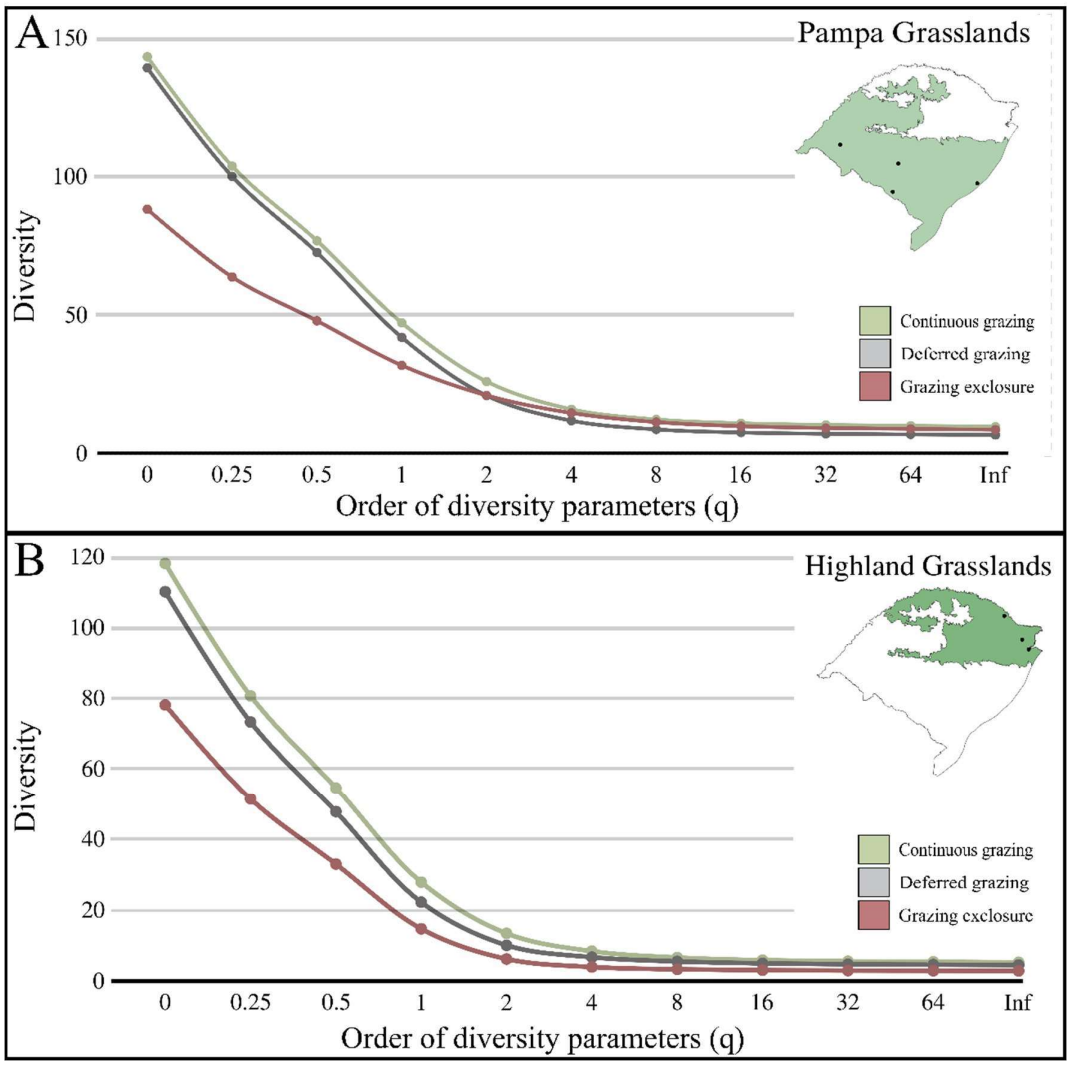


Fig. 3 - Diversity profile (Renyi curves) representing biological diversity for the Highland and Pampa Grasslands according to the continuous grazing, deferred grazing, and grazing exclusion treatments.

Mean life-form relative abundances (Fig. 4) revealed clear differences among treatments, with some differences also between the Pampa and Highland Grasslands sites (Appendix S5). In Highland grasslands, the deferred grazing and grazing exclusion treatments were more similar, with solitary tussocks, rosettes and subshrubs having highest abundances. Continuous grazing always presents the lowest values for these life forms when comparing the treatments. In continuous and deferred grazing, there is a high abundance of rhizomatous and stoloniferous life forms, clearly influenced by grazing. In the Pampa grasslands, solitary tussocks, subshrubs, and rosettes overall have high abundances, with density varying depending on grazing. However, grazing exclusion shows a much higher abundance of ferns, woody species, and herbaceous forbs compared to the other treatments. Continuous and deferred grazing exhibit high values of stoloniferous and rhizomatous species.

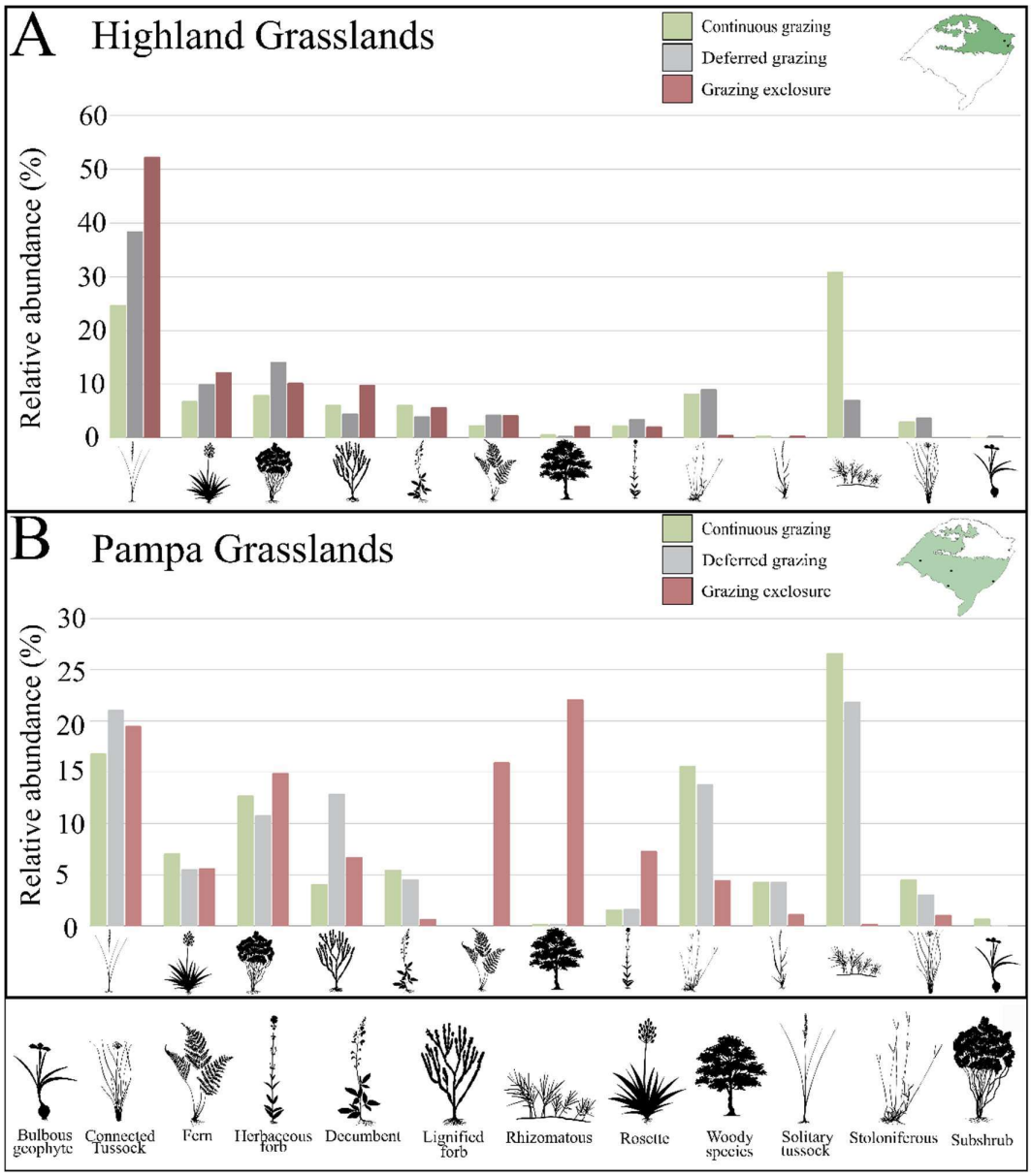


Fig. 4 - Mean life-form relative abundance for the treatments of continuous grazing, deferred grazing, and grazing exclosure in two distinct subsets of sample sites. Upper panel (A) displays Highland Grasslands, while the lower panel (B) depicts Pampa Grasslands.

Within-treatment vegetation heterogeneity

When analyzing species diversity in the paddocks of Pampa and Highland Grasslands, we observed that grazed treatments in Pampa sites exhibited the highest values for total diversity (γ) within the experimental plots and average diversity within each 1m² subplot (α) (Appendix S6). Conversely, grazing exclusion treatments showed the lowest values, both in Pampa and Highland grasslands. In management comparisons, when proven separately in the Pampa and Highland grasslands regions, total diversity and alpha diversity exhibited significant values for all treatments (See Appendix S7). However, when Pampa and Highland grasslands were analyzed together, the grazed treatments did not differ for both gamma and alpha diversity. β diversity within experimental plots differed between continuous grazing and grazing exclusion in all cases, and also between deferred grazing and grazing exclusion for Pampa and Highland grasslands combined data (see Appendix S7).

Discussion

Twelve years after implementation of treatments, our results indicate clear differences in diversity and dominance patterns among treatments. Ferreira et al. (2020), using data from the first four years of the experiment, demonstrated the rapid changes in plant diversity and in vegetation structure after implementation of treatments. Here, we build upon their research and advance our understanding of grassland management effects through an analysis of different aspects of vegetation heterogeneity and diversity in Pampa Grasslands and Highland Grasslands. Taken together, our results indicate that grazing management leads to changes not only in functional composition of the grasslands studied here, but also to changes in diversity patterns, confirming the trends found by Ferreira et al. (2020) in the initial phase of the experiment. We go beyond their study not only by evaluating effects after a longer period, but also by including other diversity descriptors, such as within-experimental plot species diversity, thus presenting a fuller picture of grazing management effects on plant diversity patterns. The analyses based on simple functional groups, in our case, life forms, enabled us to mitigate the interference arising from taxonomic differences among plant communities and the legacy of management practices of the sites. The abundance profiles facilitated the assessment of dominance patterns among life forms influenced by management. The Renyi curve showed a continuity of the results obtained by Ferreira et al. (2020) when we compared grazed treatments with grazing exclusion, for example. Importantly, our results evidenced

clear differences between the two major grassland regions, Pampa and Highland grasslands, in terms of plant community development in the absence of grazing: for some, but not all, of the Pampa sites, we observed early successional processes toward more woody vegetation. In the Highland sites, periodic fires at two of three sites not only prevented these processes by impeding colonization by woody species, but also led to a stronger dominance of tussock grasses.

Our results corroborate the first hypothesis of this study, indicating that the abundance of plant life-forms is indeed influenced by disturbance regimes, consequently shaping vegetation composition and structure, including factors like average vegetation height and bare soil. As anticipated, grazing exclusion increased vegetation height and standing dead biomass cover, but also showed increased bare soil, likely due to shading effects (Andrade et al. 2016; Streit et al. 2022). It is well-documented that the absence of management that involves disturbance and biodmass removal in subtropical grasslands leads to a decline in plant species diversity (Lezama et al. 2014). Increased vegetation height is typical under grazing exclusion, as these environments tend to harbor, after some time, higher cover by tall tussock grasses and of woody species, in other words, life forms specialized in resource accumulation, while less competitive and light-demanding species are excluded (Ferreira et al. 2020; Baggio et al. 2021; Da Silveira et al. 2022). Deferred and continuous grazing shared a considerable number of resource-acquiring species (Baggio et al. 2021). The same attributes that allow these species to be resilient to grazing disturbance are characteristics that make them more palatable to cattle (with fewer fibers, they are better digested) (Andrade et al. 2023). Bare soil and dung cover showed association with grazed environments. In areas where cattle roam freely without fences or restrictions, they exhibit a tendency to choose specific plant species for feeding (Baggio et al. 2018; Boavista et al. 2019). Bare soil associated with grazing exclusion in Highland grasslands is probably indicative of shading (see Appendix S8) (Collins et al. 1995).

Studies from our study region have shown woody species encroachment in the absence of disturbances (Oliveira & Pillar 2004; Müller et al. 2023). Recently, a study conducted in Highland grasslands compared areas managed with fire and grazing to grazing excluded areas and observed that after only one decade grassland transformed into shrubland (Sühs et al. 2020). However, the successful colonization of grassland by woody species depends on various factors such as climate, topography, water availability

in the soil, and propagule availability (Andrade et al. 2023; Müller et al. 2023), which leads to divergent processes at different sites. The Lavras do Sul site (LAV) exhibited a higher richness of woody species (LAV four exclusive species, ACE and ALE one, TAV none (unpublished data)) under grazing exclusion than in deferred grazing in various analyses, especially in the Renyi curve. Most likely, the proximity to a riparian forest, i.e. a propagule source, very close to the experimental site in LAV could be the main factor for this situation. In contrast, the presence of woody species at the other Pampa sites (ACE, ALE, and TAV) was much less pronounced, possibly due to the greater distance from forests. Virtually no woody species – except for subshrubs – were found in Highland grasslands, even under grazing exclusion, what may be explained by the periodic burns at ARA and TAI sites that impede the establishment of shrubs and trees. Here, the fire regime, consequence of unplanned fires, led to similarities between deferred grazing and grazing exclusion treatments, illustrated in the life-form abundance curve (Fig. 4). Fire is commonly used in the region for pasture management (Andrade et al. 2016; Bernardi et al. 2016; Paruelo et al. 2022) and affected the experimental areas several times along the course of the study, even though not applied at the sites itself: as fires often are poorly managed, they easily spread through the landscape and can affect even grasslands in protected areas. This unintentional disturbance blurs the distinction of grazing exclusion and the other treatments, as all treatments suffered from periodic burns at these two sites. In the same region, the VAC site experienced less burning compared to TAI and ARA sites, resulting in higher woody and tussock species cover under grazing exclusion. While it certainly would be interesting to design fire-protected experiments, our results are indicative of the risk that fires may spread periodically when fuel is available. The likelihood of fire occurrences increases under a changing climate with more extreme conditions (e. g., Pivello et al. 2021). This has implications for conservation since at ungrazed sites, such as in some protected areas, prescribed fires can be important to impede catastrophic burns. In fact, management in Aparados da Serra and Serra Geral national parks, both situated in the Highland grassland region, now is using prescribed burns for conservation purposes. Overall, this indicates that when grazing management is abandoned in the region, local factors (landscape context; regional disturbance regimes) will strongly influence successional pathways and shape community dynamics and diversity.

Our second hypothesis posits that richness and vegetation heterogeneity in space would be lower in ungrazed compared to grazed treatments, with deferred grazing being relatively more heterogeneous than continuous grazing. Our findings support this hypothesis, as we observed clear differences in diversity profiles (Renyi curves) among treatments, indicating lower diversity under grazing exclusion at lower orders of diversity (left side of the curve): The legacy of these disturbances is evident in the mean cover values of different life-forms per treatment. This pattern was attributed to a small number of species with very high cover under grazing exclusion, contrasting with the two grazed treatments where dominance is less pronounced. Grazed grasslands, in contrast, tend to exhibit greater similarity among themselves, when compared with grazing exclusion (Ferreira et al., 2020; Silveira et al., 2022). This results in continuous and deferred grazing being more similar in the Pampa Grasslands than in the Highland grasslands, where continuous grazing consistently demonstrates slightly higher values of species richness than deferred grazing (Andrade, 2023). However, in Highland grasslands, fire that, as discussed above, occurs alongside with grazing, may have contributed to increasing similarities between deferred grazing and grazing exclusion. Fire can rapidly consume senescent biomass as fuel and stimulate vegetation regrowth (Overbeck et al. 2005). In the studied region, fire is often applied by cattle farmers at the end of winter to remove excess biomass (Brunel et al. 2021). The use of fire benefits tussock grasses, which indeed were found to be the most dominant life form even in the deferred grazing treatment in the Highland Grasslands, at the expense of prostrated grasses. Woody species under grazing exclusion covered almost ten times more in the Pampa than in Highland grasslands, where they were limited by fire (Appendix S5). Meanwhile, in Highland grasslands, occasional fires set successional processes by woody species encroachment back periodically (Müller et al. 2012).

In agreement with our hypothesis three, the ungrazed treatments exhibited lower diversity compared to the other treatments, indicating a high dominance of some species, as well as a greater dominance of certain life forms, such as tussock grasses and shrubs. In the grazing exclusion treatments, tussocks easily reached over 50 cm in height, likely impeding the growth of other less competitive species in the grass matrix (Ferreira, et al. 2020). Additionally, we observed under grazing exclusion in the Pampa sites, high cover of ferns. Studies in unmanaged grasslands often observe the presence of ferns, as the increased humidity resulting from the accumulation of senescent biomass in tussocks

contributes to their development (Etchepare & Boccanelli 2007; Da Silveira et al. 2022). Furthermore, the greater cover of rosettes and subshrubs in deferred grazing further emphasized the preferences of grazing animals. More palatable species, such as rhizomatous and stoloniferous ones, were favored and chosen by cattle, while species with herbivore-defensive characteristics were actively avoided (Adler et al. 2001; Morris 2002). The coexistence of various life forms in the same paddock indicated low grazing pressure, as predicted in the hypothesis, allowing cattle to select which species were more palatable (Scimone et al. 2007).

The total exclusion of grazing leads to a clear transformation of grassland environments, directly impacting diversity indices at all levels (γ, α, and β). Grazing exclusion causes the loss of diversity in terms of richness per plot (α) and per paddock (γ), along with the highest values of heterogeneity (β), corroborating other studies (Lezama et al. 2014). The highest values of γ and α diversity being found in the grazed treatments of Pampa grasslands is probably linked to the historical management legacy of this region. The plant community is adapted to this disturbance, and despite the dominance in coverage of rhizomatous and stoloniferous species within this matrix, many other species thrive. In the pairwise contrasts (Appendix S7), the similarities between grazed treatments (continuous and deferred grazing) are evident, which clearly differed from grazing exclusion. In some cases, deferred grazing and grazing exclusion were not significantly distinct, likely due to the previously mentioned factors of fire or potential forest colonization.

Our study highlights how different management strategies can influence long-term environmental heterogeneity and vegetation structure, showing that diversity and patterns of dominance depend on the specific implemented management. However, context matters, and the presence or absence of fire may be crucial for community dynamics over time. Exclusion of grazing will lead to stronger changes in the plant community, with loss of grassland diversity, at sites with the absence of fire. Where fire is present – and is likely to happen if fuel accumulates and climatic conditions are suitable – sites remain as grasslands. However, the structure of vegetation, along with life form and species composition, will differ from sites without fire regime, even if the overall diversity does not fundamentally change compared to areas subjected only to grazing.

We recognize the significance of long-term experiments and encourage to establish and conduct them, as they yield valuable data on structure, dynamics and

response of grassland plant communities to disturbances, aspects not always observable in short periods. Long-term experiments also allow for the non-experimental evaluation of climate change effects as general trends of vegetation development over time can be identified, independent of short-term variation of temperature or rainfall (Gaiser et al. 2020). Overall, our results emphasize that the maintenance of grassland diversity — characterized here by different approaches — requires disturbance and thus active management, with implications for conservation policy (e.g., Tomás et al., *in press*). Which management regime is best will be ideally defined not only based on sound scientific knowledge, but also under consideration of and in partnership with land owners and managers (Baggio et al. 2021).

References

Adler, P., Raff, D., & Lauenroth, W. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479. https://doi.org/10.1007/s004420100737

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L. de M., & Sparovek, G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.xIdentificador

Andrade, B.O., Bonilha, C.L., de Abreu Ferreira, P.M., Boldrini, I.I., & Overbeck, G.E. 2016. Highland grasslands at the southern tip of the Atlantic Forest biome: management options and conservation challenges. *Oecologia Australis* 20, 37–61. https://doi.org/10.4257/oeco.2016.2002.04

Andrade, B.O., Bonilha, C.L., Overbeck, G.E., Vélez-Martin, E., Rolim, R.G., Bordignon, S.A.L., Schneider, A.A., Vogel Ely, C., Lucas, D.B., & Garcia, E.N. 2019. Classification of South Brazilian grasslands: Implications for conservation. *Applied Vegetation Science* 22: 168–184. https://doi.org/10.1111/avsc.12413

Andrade, B.O., Menezes, L. da S., Boldrini, I.I., Pillar, V.D., & Overbeck, G.E. (2023) Grassland plant community composition and dynamics: disturbance as determinants of grassland diversity. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 177–204. https://doi.org/10.1007/978-3-031-42580-6_8

Baggio, R., de Medeiros, R.B., Focht, T., da Rosa Boavista, L., Pillar, V.D., & Müller, S.C. 2018. Effects of initial disturbances and grazing regime on native grassland invasion by *Eragrostis plana* in southern Brazil. *Perspectives in Ecology and Conservation* 16: 158–165. https://doi.org/10.1016/j.pecon.2018.06.004

Baggio, R., Overbeck, G.E., Durigan, G., & Pillar, V.D. (2021) To graze or not to graze: A core question for conservation and sustainable use of grassy ecosystems in Brazil. *Perspectives in Ecology and Conservation*. https://doi.org/10.1016/j.pecon.2021.06.002

Bernardi, R.E., Holmgren, M., Arim, M., & Scheffer, M. 2016. Why are forests so scarce in subtropical South America? The shaping roles of climate, fire and livestock. *Forest Ecology and Management* 363: 212–217. https://doi.org/10.1016/j.foreco.2015.12.032

Blanchet, F.G.; Legendre, P.; Borcard, D. 2008. Forward selection of explanatory variables. *Ecology* 89 : 2623–2632. https://doi.org/10.1890/07-0986.1

Boavista, L. da R., Trindade, J.P.P., Overbeck, G.E., & Müller, S.C. 2019. Effects of grazing regimes on the temporal dynamics of grassland communities. *Applied vegetation science* 22: 326–335. https://doi.org/10.1111/avsc.12432

Boldrini, I.I. 2009. Biodiversidade dos campos do planalto das araucárias. Brasília: Ministério do Meio Ambiente, Secretaria de Biodiversidade e Florestas; 2009. 39–94.

Bond, W.J., & Keeley, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in ecology & evolution* 20: 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bond, W.J. 2021. Out of the shadows: ecology of open ecosystems. *Plant Ecology & Diversity* 14: 205-222. https://doi.org/10.1080/17550874.2022.2034065

Brunel, M., Rammig, A., Furquim, F., Overbeck, G., Barbosa, H.M.J., Thonicke, K., & Rolinski, S. 2021. When do farmers burn pasture in Brazil: a model-based approach to determine burning date. *Rangeland Ecology & Management* 79: 110–125. https://doi.org/10.1016/j.rama.2021.08.003

Caram, N., Casalás, F., Wallau, M.O., Soca, P., Pillar, V.D., Cadenazzi, M., & Boggiano, P. 2023. Biomass fine-scale variation is predictive of functional composition and diversity in grazed grassland. *Applied Vegetation Science* 26: e12714. https://doi.org/10.1111/avsc.12714

Cha, A., Chiu, C., Jost, L. 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual review of ecology, evolution, and systematics* 45: 297-324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

570 Chase, M.W. (2016) An update of the Angiosperm Phylogeny Group classification for the
571 orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean*
572 *Society*, 181, 1–20. https://doi.org/10.1111/boj.12385

573 Chase, J.M., & Myers, J.A. 2011. Disentangling the importance of ecological niches from
574 stochastic processes across scales. *Philosophical transactions of the Royal Society*
575 *B: Biological sciences* 366: 2351–2363. https://doi.org/10.1098/rstb.2011.0063

576 Cingolani, A.M., Noy-Meir, I., & Díaz, S. 2005. Grazing effects on rangeland diversity:
577 a synthesis of contemporary models. *Ecological applications* 15: 757–773.
578 https://doi.org/10.1890/03-5272

579 Collins, S.L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment.
580 *Ecology* 68: 1243–1250. https://doi.org/10.2307/1939208

581 Collins, S.L., Glenn, S.M., & Gibson, D.J. 1995. Experimental analysis of intermediate
582 disturbance and initial floristic composition: decoupling cause and effect. *Ecology*
583 76: 486–492. https://doi.org/10.2307/1941207

584 Cruz, P., De Quadros, F.L.F., Theau, J.P., Frizzo, A., Jouany, C., Duru, M., & Carvalho,
585 P.C.F. 2010. Leaf traits as functional descriptors of the intensity of continuous
586 grazing in native grasslands in the south of Brazil. *Rangeland Ecology &*
587 *Management* 63: 350–358. https://doi.org/10.2111/08-016.1

588 Etchepare, M.A., & Boccanelli, S.I. 2007. Análisis del banco de semillas y su relación
589 con la vegetación emergente en una clausura de la llanura pampeana. *Ecología*
590 *austral* 17: 159–166.

591 Fedrigo, J.K., Ataide, P.F., Azambuja Filho, J.C.R., Bertoncelli, P., & Nabinger, C. 2022.
592 Deferment associated to contrasting grazing intensities affects root/shoot biomass
593 allocation in natural grasslands. *Applied Vegetation Science* 25. 2
594 https://doi.org/10.1111/avsc.12671

595 Fedrigo, J.K., Ataide, P.F., Filho, J.A., Oliveira, L. V, Jaurena, M., Laca, E.A., Overbeck,
596 G.E., & Nabinger, C. 2018. Temporary grazing exclusion promotes rapid recovery
597 of species richness and productivity in a long-term overgrazed Campos grassland.
598 *Restoration Ecology* 26: 677–685. https://doi.org/10.1111/rec.12635

599 Ferreira, P.M.A., Andrade, B.O., Podgaiski, L.R., Dias, A.C., Pillar, V.D., Overbeck, G.E.,
600 Mendonca Jr, M. de S., & Boldrini, I.I. 2020. Long-term ecological research in
601 southern Brazil grasslands: Effects of grazing exclusion and deferred grazing on
602 plant and arthropod communities. *PLoS One* 15: e0227706.

603 Fidelis, A. 2020. Is fire always the "bad guy"?. *Flora*, 268: 151611.

604 Freitag, M., Kamp, J., Dara, A., Kuemmerle, T., Sidorova, T.V., Stirnemann, I.A., Velbert,
605 F., Hölzel, N. 2021. Post-soviet shifts in grazing and fire regimes changed the
606 functional plant community composition on the Eurasian steppe. *Global Change*
607 *Biology* 27: 388-401.

608 Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., & Leslie Jr,
609 D.M. 2006. Should heterogeneity be the basis for conservation? Grassland bird
610 response to fire and grazing. *Ecological applications* 16: 1706–1716.

611 Gaiser, E., Bell, D.M., Castorani, M.C.N., Childers, D.L., Groffman, P.M., Jackson, C.R.,
612 Kominoski, J.S., Peters, D.P.C., Pickett, S.T.A., Ripplinger, J., Zinnert, J.C. 2020.
613 Long-term ecological research and evolving frameworks of disturbance ecology.
614 *BioScience*, v. 70 (2): 141-156.

615 Golin, T. (2023) The Southern Grasslands and the expropriation of Indigenous territories.
616 South Brazilian grasslands: ecology and conservation of the Campos Sulinos.
617 Springer, 145–174. https://doi.org/10.1007/978-3-031-42580-6_7

618 Guido, A., Salengue, E., & Dresseno, A. 2017. Effect of shrub encroachment on
619 vegetation communities in Brazilian forest-grassland mosaics. *Perspectives in*
620 *ecology and conservation* 15: 52–55.

621 Heino, J., Melo, A.S., & Bini, L.M. 2015. Reconceptualising the beta diversity-
622 environmental heterogeneity relationship in running water systems. *Freshwater*
623 *Biology* 60: 223–235.

624 Hickman, K.R., Hartnett, D.C., Cochran, R.C., Owensby, C.E. 2004. Grazing
625 management effects on plant species diversity in tallgrass prairie. *Journal of Range*
626 *Management*, v. 57, n. 1, p. 58-65.

627 Hothorn, T., Bretz, F., & Westfall, P. 2008. Simultaneous inference in general parametric
628 models. *Biometrical Journal: Journal of Mathematical Methods in Biosciences* 50:
629 346–363.

630 Jacobo, E.J., Rodríguez, A.M., Bartoloni, N., & Deregibus, V.A. 2006. Rotational grazing
631 effects on rangeland vegetation at a farm scale. *Rangeland Ecology & Management*
632 59: 249–257.

633 Jardim Botânico do Rio de Janeiro. 2022. Flora e Funga do Brasil.
634 http://floradobrasil.jbrj.gov.br

635 Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E.J., & Paruelo, J.M. 2014.
636 Variation of grazing-induced vegetation changes across a large-scale productivity
637 gradient. *Journal of Vegetation Science* 25: 8–21.

638 Li, D. 2018. hillR: taxonomic, functional, and phylogenetic diversity and similarity
639 through Hill Numbers. *J. Open Source Softw.* 3: 1041.

640 Londo, G. 1976. The decimal scale for releves of permanent quadrats*. 33: 61–64.

641 Menezes, L.S., Ely, C. V, Lucas, D.B., Minervini-Silva, G.H., Velez-Martin, E.,
642 Hasenack, H., Trevisan, R., Boldrini, I.I., Pillar, V.D., & Overbeck, G.E. 2022.
643 Reference values and drivers of diversity for South Brazilian grassland plant
644 communities. *Anais da Academia Brasileira de Ciências* 94: e20201079.

645 Morris, C.D. 2002. Patch grazing of Tall Grassveld by cattle after a spring burn. *African*
646 *Journal of Range and Forage Science* 19: 107–116.

647 Müller, S.C., Overbeck, G.E., Pfadenhauer, J., Pillar, V.P. 2012. Woody species patterns
648 at forest–grassland boundaries in southern Brazil. *Flora-Morphology, Distribution,*
649 *Functional Ecology of Plants,* 207: 586-598.

650 Müller, S.C., Bergamin, R.S., Duarte, L.S., Peroni, N., Sühs, R.B., & Carlucci, M.B.
651 (2023) Mechanisms and processes shaping patterns of forest-grassland mosaics in
652 southern Brazil. South Brazilian grasslands: ecology and conservation of the
653 Campos Sulinos. *Springer*, 417–443. https://doi.org/10.1007/978-3-031-42580-
654 6_16

655 Nabinger, C., Ferreira, E.T., Freitas, A.K., Carvalho, P.C. de F., & Sant'Anna, D.M. 2009.
656 Produção animal com base no campo nativo: aplicações de resultados de pesquisa.

Campos sulinos: conservação e uso sustentável da biodiversidade. Brasília: Ministério do Meio Ambiente

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. 2023. Package 'vegan.' *Community ecology package, version* 2: 1–295.

Oliveira, J.M., & Pillar, V.D. 2004. Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. *Community ecology* 5: 197–202.

Overbeck, G.E., Müller, S.C., Fidelis, A., Pfadenhauer, J., Pillar, V.D., Blanco, C.C., Boldrini, I.I., Both, R., & Forneck, E.D. 2007. Brazil's neglected biome: the South Brazilian Campos. *Perspectives in Plant Ecology, Evolution and Systematics* 9: 101–116.

Overbeck, G.E., Müller, S.C., Pillar, V.D., & Pfadenhauer, J. 2005. Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation science* 16: 655–664.

Overbeck, G.E., & Pfadenhauer, J. 2007. Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora-Morphology, Distribution, Functional Ecology of Plants* 202: 27–49.

Overbeck, G.E., Vélez-Martin, E., da Silva Menezes, L., Anand, M., Baeza, S., Carlucci, M.B., Dechoum, M.S., Durigan, G., Fidelis, A., & Guido, A. 2022. Placing Brazil's grasslands and savannas on the map of science and conservation. *Perspectives in Plant Ecology, Evolution and Systematics* 56: 125687.

Paruelo, J.M., Oesterheld, M., Altesor, A., Piñeiro, G., Rodríguez Fábregas, C., Baldassini, P., Irisarri, G., López-Mársico, L., & Pillar, V.D. 2022. Grazers and fires: their role in shaping the structure and functioning of the Río de la Plata Grasslands. *Ecología Austral, 2022, 32: 784-805.*

Pillar, V.D.P.; Orlóci, L. 1996. On randomization testing in vegetation science: multifactor comparisons of relevé groups. *Journal of Vegetation Science*, v. 7, n. 4, p. 585-592,

Pivello, V.R., Vieira, I., Christianini, A. V, Ribeiro, D.B., da Silva Menezes, L., Berlinck, C.N., Melo, F.P.L., Marengo, J.A., Tornquist, C.G., & Tomas, W.M. 2021.

687 Understanding Brazil's catastrophic fires: Causes, consequences and policy needed
688 to prevent future tragedies. *Perspectives in Ecology and Conservation* 19: 233–255.

689 Quadros, F.L.F, Tridade, J.P.P., Bandinelli, D.G., Pötter, L. 2005. Vegetation dynamics of
690 campos under grazing/fire regimes in southern Brazil. In: *Pastoral systems in*
691 *marginal environments*. Wageningen Academic: 160-160.

692 Ripley, B.D. 2002. *Modern applied statistics with S*. springer.

693 Scimone, M., Rook, A.J., Garel, J.-P., & Sahin, N. 2007. Effects of livestock breed and
694 grazing intensity on grazing systems: 3. Effects on diversity of vegetation. *Grass*
695 *and Forage Science* 62: 172–184.

696 Silveira, F.F. 2024. Data Set: Southern Brazilian grassland diversity: anti-disturbance
697 regimes are not ideal and grazing maintains plant diversity.
698 Doi:https://doi.org/10.5281/zenodo.13893973

699 Silveira, F.F., Silva Menezes, L., Porto, A.B., & Overbeck, G.E. 2022. Environmental
700 drivers and diversity of open plant communities in grassland and wetland mosaics
701 in coastal southern Brazil. *Folia Geobotanica* 57: 1–20.

702 Sollenberger, L.E., Kohmann, M.M., Dubeux Jr, J.C.B., & Silveira, M.L. 2019. Grassland
703 management affects delivery of regulating and supporting ecosystem services. *Crop*
704 *Science* 59: 441–459.

705 Streit, H., Menezes, L.S., Pillar, V.D., & Overbeck, G.E. 2022. Intraspecific trait variation
706 of grassland species in response to grazing depends on resource acquisition strategy.
707 *Journal of Vegetation Science* 33: e13129.

708 Sühs, R. B.; Giehl, E.L.H.; Peroni, N. 2020. Preventing traditional management can cause
709 grassland loss within 30 years in southern Brazil. *Scientific Reports* 10: p. 783.

710 Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., & Milberg, P. 2016. Grazing
711 vs. mowing: A meta-analysis of biodiversity benefits for grassland management.
712 *Agriculture, Ecosystems & Environment* 222: 200–212.

713 Team, Rs. 2024. RStudio: integrated development for R. RStudio. *Inc., Boston, MA* 700:
714 879.

715 Tomás et al. 2024. Challenges in the conservation and management of Legal Reserve
716 Areas in grassland and savanna ecosystems in the face of global climate change.
717 *Pesquisa Agropecuária Brasileira*, in press.

718 Veldman, J.W., Buisson, E., Durigan, G., Fernandes, G.W., Le Stradic, S., Mahy, G.,
719 Negreiros, D., Overbeck, G.E., Veldman, R.G., & Zaloumis, N.P. 2015. Toward an
720 old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology*
721 *and the Environment* 13: 154–16

Capítulo II

Should I burn or should I graze: initial effects in the restoration of abandoned subtropical grasslands

Filipe Ferreira da Silveira, Francieli Peter da Silveira, Mateus Henrique Schenkel, Lucas Rodrigues, Guilherme Dubal dos Santos Seger, Gerhard Ernst Overbeck.

Title: Should I burn or should I graze: initial effects in the restoration of abandoned subtropical grasslands

Short title: Management effects on subtropical grasslands

Filipe F. da Silveira[1], Francieli P. da Silveira[1], Mateus Henrique Schenkel[1], Lucas S. Rodrigues, Guilherme D. S. Seger[1], Gerhard E. Overbeck[1,2].

[1] Graduate Program in Botany, Universidade Federal do Rio Grande do Sul, Brazil.
[2] Graduate Program in Ecology, Universidade Federal do Rio Grande do Sul, Brazil.
[3] Graduate Program in Biological Oceanography, Universidade Federal do Rio Grande - FURG, Brazil.

Authors and ORCID
Filipe Ferreira da Silveira - 0000-0002-1273-0655
Francieli Peter da Silveira - 0009-0008-3050-3289
Mateus Henrique Schenkel – 0009-0000-4559-2722
Lucas dos Santos Rodrigues – 0000-0003-2310-2619
Guilherme Dubal dos Santos Seger – 0000-0002-0710-3550
Gerhard Ernst Overbeck – 0000-0002-8716-5136

Correspondence
Filipe Ferreira da Silveira, Program of Botany (PPGBot/UFRGS), Universidade Federal do Rio Grande do Sul, RS, Brazil. E-mail: filipesilveferreira@hotmail.com

Funding
FFS was supported by "Bolsas Funbio–Conservando o Futuro" program, awarded by FUNBIO and Instituto Humanize.
Gerhard Ernst Overbeck was supported by CNPq (grant 310345/2018-9).

Acknowledgements
We thank the researchers and staff of the Laboratory of Grassland Vegetation Studies (LEVCamp) - UFRGS for their availability in assisting with expeditions and data collection. We thank Ana Porto, Bruno Soares, Diego Abade, Lua Cezimbra, Lucina Bittencourt, Rafael Barbosa, Sheron Silveira, Victória Meotti, William Piovesani, for their participation during data collection. For assistance in plant identification, we thank Ana Porto, Bruno Soares, Franciele Peter, Mateus Schenkel, William Piovesani. We thank Lucas Rodrigues for his insightful contributions to the statistical analysis of this work. We acknowledge the constructive comments from the thesis defense committee to which this article was submitted: Anaclara Guido Bolioli (UDELAR, Uruguay), João André Jarenkow (UFRGS, Brazil), Rosi Maria Prestes (UFRGS, Brazil). This study was partially funded by a research grant from the National Council for Scientific and Technological Development (CNPq) awarded to GEO (477618/2013-8) and by the Coordination for the Improvement of Higher Education Personnel - Brazil (CAPES) - Finance Code 001. GEO acknowledges CNPq productivity grants (310345/2018-9). FFS thanks CAPES for the scholarship (88887.684521/2022-00), was supported by the "Bolsas Funbio–Conserving the Future" program, awarded by FUNBIO and Instituto Humanize. This study is part of the LTER/PELD Campos Sulinos, supported by CNPq (CNPq grants PELD 441753/2020-5 and PQ 313315/2022-1 and by FAPERGS grant PELD 21/2551-0000776-1 to Valério De Patta Pillar). We would also like to thank the entire structure provided by the Graduate Program in Botany at the Federal University of Rio Grande do Sul.

Should I burn or should I graze: initial effects in the restoration of abandoned subtropical grasslands

ABSTRACT

Questions: How do the reintroduction of fire, grazing, and their interaction (pyric herbivory) influence the recovery of vegetation structure, species richness, and taxonomic and functional diversity in abandoned subtropical grasslands?

Location: Agronomic Experimental Station of UFRGS (EEA/UFRGS), Eldorado do Sul, RS, Brazil.

Methods: The study used a randomized block design (5 blocks) with four treatments: Burn Grazed, Burn Ungrazed, Unburned Grazed, and Control (Unburned Ungrazed). Sampling occurred in 200 fixed 1 m² plots over three surveys between 2022 and 2025 (before, immediately after, and one year after management). Data were analyzed using Generalized Linear Mixed Models (GLMM), PERMANOVA, and PCoA.

Results: Managed treatments showed significantly higher richness than the control. The combination of fire and grazing (pyric herbivory) resulted in the highest species density (average of 29.12/m²). Fire removed over 50% of the accumulated dead biomass, increasing bare soil and facilitating higher vegetation cover by the second year. Grazing alone promoted a more gradual but consistent recovery.

Conclusion: Exclusion of disturbance leads to successional stagnation and diversity loss. Burn Grazed is the most effective mechanism for restoring the typical biodiversity of grassland ecosystems, preventing the dominance of few competitive species and shrub encroachment.

Key-words: Ecological restoration, pyric herbivory, Campos Sulinos, functional diversity, senescent biomass.

Introduction

In grasslands around the world, the cessation of management, usually grazing or fire, or a combination of both, is known to have negative impacts on biodiversity, ecosystem services and thus conservation values of grasslands (Klimek et al., 2007; de Patta Pillar & Vélez, 2010; Joyce, 2014; Price et al., 2021). In many grasslands, the removal of management first leads to the accumulation of biomass of tall-growing grasses, followed by the decline of less competitive species, plant diversity, and then often to the colonization by woody species in the course of succession (Overbeck et al., 2005; Rosenthal, 2010; Fonseca et al., 2022). This pattern reflects an environmental filter that selects for conservative resource-use strategies, while species with acquisitive strategies, based on rapid resource acquisition and fast growth, tend to be excluded (HilleRisLambers et al., 2012; Pérez-Ramos et al., 2013). In some systems, periods as short as a decade may be sufficient for open grassland areas to exhibit significant changes in their physiognomy, reaching stages dominated by graminoid tussocks and shrubs (Pillar & De Quadros, 1997; Valkó et al., 2018; Sühs et al., 2020). Therefore, exclusion of fire and grazing in protected grassland areas can prove counterproductive for biodiversity maintenance, conflicting with conservation goals (Hobbs & Huenneke, 1992; Baggio et al., 2021; da Silveira et al., 2025; Guido et al., 2025). The lack of disturbances over longer periods may lead to such fundamental changes in the system that herbaceous species do not easily return, even after their reintroduction (e.g. Fidelis et al., 2014; Pearce et al., 2014; Thomas, Overbeck, et al., 2019).

These fundamental changes highlight that returning environments to their original state remains a complex challenge, as the prolonged absence of keystone grazer species can shift systems toward new stable states (Bali et al., 2008; Reijers et al., 2019; Schrama et al., 2023). In grasslands where fire and grazing are endogenous disturbances, this irreversibility is often exacerbated by the disruption of pyric herbivory, defined as the interdependent spatiotemporal interaction between fire and grazing (Fuhlendorf et al., 2009). Consequently, rewilding strategies that reintroduce large vertebrates without coupling fire regimes fail to recreate the "shifting mosaics" essential for biodiversity (Fuhlendorf et al., 2009). As demonstrated in Australian savannas, where post-fire forage quality drives faunal movement and sustains ecosystem functions, effective restoration requires re-establishing these fire-herbivore feedbacks to prevent the consolidation of simplified ecological states (Reid et al., 2023).

In the subtropical grasslands of South America, such as the South Brazilian grasslands (Campos Sulinos), grassland vegetation has historically been neglected by both scientific research and public conservation policies (Overbeck et al., 2007). This situation is exacerbated by the problem of Biome Awareness Disparity, which prioritizes forest ecosystems over open habitats, often treating grasslands as marginal systems (Silveira et al., 2022). As a result, the importance of management for grassland conservation has been repeatedly overlooked, including within protected areas, where disturbance-exclusion policies have led to the loss of the original ecological characteristics of these ecosystems (Overbeck et al., 2023; da Silveira et al., 2025). In the absence of grazing or fire, grasslands undergo profound structural changes, such as excessive accumulation of dead biomass and the expansion of shrubs and trees, resulting in reduction of grassland area and the loss of grassland-specific biodiversity (Lezama et al., 2014; Pillar & Overbeck, 2025).

In this context, the development of management strategies specifically tailored to these areas that are under successional change towards woody ecosystems becomes imperative. Importantly, in areas designated for conservation, grazing does not need to be associated with economic objectives, as is the case in most rural properties (Andrade et al., 2023) where livestock production is a key source of income. Conversely, in the conservation context, fire and grazing can be evaluated based on their effects in maintaining typical grassland biodiversity, and where management cessation over longer periods has led to successional processes towards woody vegetation, both can be important tools in ecological restoration, contributing to the recovery of vegetation structure and the maintenance of habitat heterogeneity (Buisson et al., 2019; Silveira et al., 2020).

In this study, we investigated the reintroduction of fire and grazing as tools for the recovery of grassland ecosystems after 17 years of abandonment, hypothesizing that these disturbances promote grassland vegetation recovery at three complementary levels. First, regarding structure, we expect both management regimes to reduce woody species cover and dead biomass accumulation, with fire causing a more immediate and homogeneous removal (Bond & Parr, 2010; Pausas & Keeley, 2019), while grazing ensures the continuous maintenance of an open structure through herbivory and trampling. At a second level, we anticipate that this niche vacancy and the reduction in dominance of a few competitive species will result in a direct increase in local richness and diversity (both taxonomic and functional) at the plot scale, reversing the loss of diversity and bare ground

observed in unmanaged areas (Fuhlendorf & Engle, 2001; Overbeck & Pfadenhauer, 2005; Rosenthal, 2010). Finally, we expect that the distinct disturbances and their interaction will generate communities with distinct compositions; that is, fire and grazing will act as different selective filters, creating a mosaic where species identity varies according to the applied management, thereby increasing the biotic heterogeneity and floristic differentiation of the landscape as a whole (Li et al., 2019; Pivello et al., 2021).

Methods

Study area

The study was conducted at the Agronomic Experimental Station of the Federal University of Rio Grande do Sul (EEA/UFRGS) in Eldorado do Sul, southern Brazil (Fig 1). The site is located within the South Brazilian grasslands and experiences a humid subtropical climate (Cfa according to the Köppen system), characterized by well-distributed rainfall throughout the year and distinct seasons (Overbeck et al., 2022). The regional mean annual precipitation is approximately 1,450 mm (RIO GRANDE DO SUL, 2010), while mean annual temperatures range from a maximum of 24.7°C to a minimum of 15.6°C. Mean monthly minimum temperatures during winter range from 11.5°C to 13.2°C. During this period, polar air masses may occasionally lead to the formation of isolated frost on the vegetation. The study area encompasses 27 ha and was historically managed under continuous grazing until 2006 (Podgaiski et al., 2014). Following fifteen years of abandonment, the site has undergone pronounced successional shifts, including the progressive encroachment of woody species and the invasion of *Pinus* sp., particularly in the western sector.

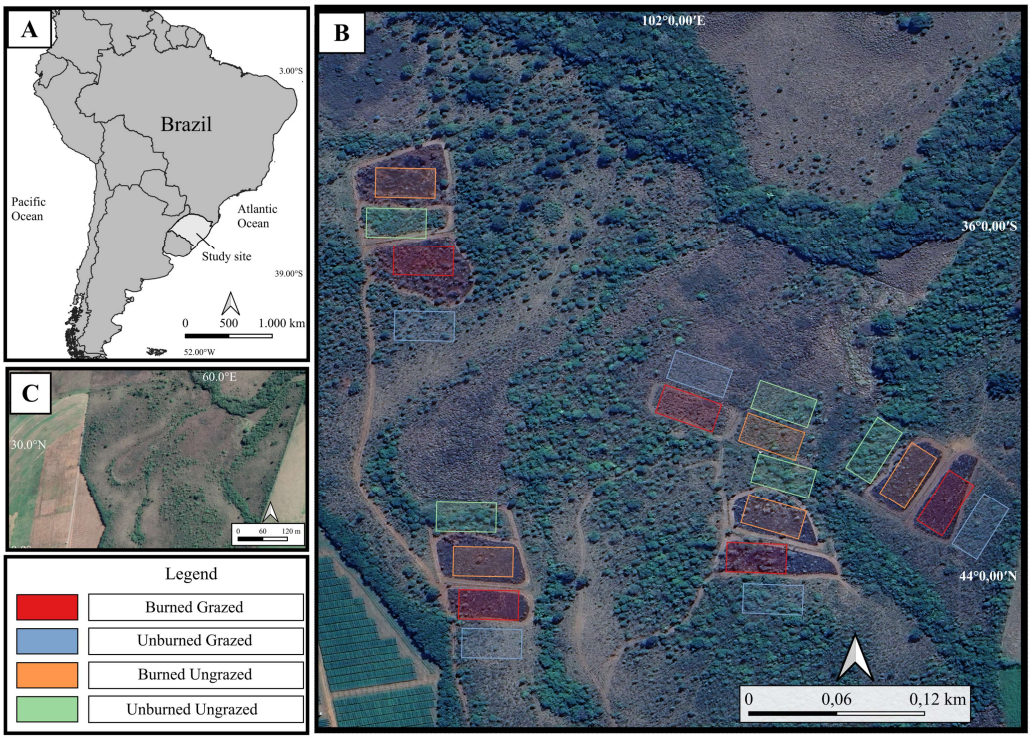


Fig. 1- (A) Geographical location of the sampling sites in Eldorado do Sul, in Rio Grande do Sul state, Brazil; (B) spatial distribution of the randomized experimental treatments at the Agronomic Experimental Station (EEA-UFRGS); and (C) temporal reference of the study area in 2016, illustrating the conditions under sheep grazing.

Experimental design

The experiment was conducted using a block design consisting of five blocks, each encompassing three management treatments plus a control: fire without grazing (Burn Ungrazed), fire with grazing (Burn Grazed), no fire with grazing (Unburned Grazed), and a control with no fire and no grazing (Unburned Ungrazed). Within each experimental plot (17 x 70 m), ten fixed 1 m² sampling units were established, spaced at least 8 m apart, and monitored throughout the study period, totaling 200 plots (Fig 1 B).

Cattle were reintroduced to the area in May 2023 (Fig. 2 F). Initially, nitrogen salt was supplied to encourage grazing in areas with accumulated dry biomass (Fig. 2 E). In August 2023, prescribed burns were applied using a drip torch with a gasoline–diesel fuel mixture (3:1) (Fig. 2 D). Fire control was ensured by a team of approximately 15 people equipped with fire beaters, and burns were conducted against the wind, directing fire fronts to converge toward the center of each plot to ensure rapid extinction (Fig. 2 G). Firebreaks were established around the burned areas by manually removing flammable vegetation and moistening the soil with water from a tanker truck and sprayers.

Cattle were allowed to move freely across the experimental area, except in fenced plots assigned to the ungrazed treatment (Fig. 2 B, F). To ensure a target forage allowance of 12% (moderate grazing pressure), corresponding to an average sward height of approximately 10–15 cm, 15 cattle were allocated. This number was calculated via regression analysis using mean vegetation height data obtained through the falling-plate method (Fig. 2 A) (Rayburn & Lozier, 2003). The experiment was implemented in September 2022, with a baseline survey conducted prior to treatment application, followed by cattle introduction in May 2023 and prescribed burning in August 2023.



Fig. 2 - Methodological overview and experimental management. A) Measurement of vegetation structure using a falling plate meter for stocking rate adjustment; B) Fencing of grazing exclusion plots; C) Baseline herbaceous survey prior to management implementation; D) Drip torch application for prescribed burning; E) Nitrogen-enriched mineral salt provided *ad libitum* to the cattle; F) Cattle accessing the grazing units; G) Execution of prescribed burning, showing fire containment via mineral soil firebreaks and wetting; H) Herbaceous plot highlighting the floristic diversity of the ground layer.

Vegetation Sampling and Structural Variables

Sampling was conducted from September 2022 to January 2025, during the spring and summer seasons. Three expeditions were carried out: the survey before the implementation of the management practices (September to December 2022), the survey after the implementation of the management practices (October to December 2023), and the survey one year later (October to January 2025). In each of the 200 sampling units, all vascular plant species were identified and their cover was estimated using the Londo decimal scale (Fig. 2 C, H) (Londo, 1976). The classification of families followed APG IV (Chase, 2016) and nomenclature followed Flora e Funga do Brasil (Jardim Botânico do Rio de Janeiro, 2026; see in Supplementary Material – Table S9). Additionally, data on vegetation structure were collected, including: average vegetation height, vegetation cover, bare soil, and total dead biomass (calculated as the sum of standing dead biomass and litter).

Data analysis

Plant communities were characterized by species richness and cover, with an emphasis on compositional diversity and life-forms. Annual cover variations were calculated as the relative percentage difference between sampling years using the formula $\Delta\,\% = \left(\frac{V_n - V_{n-1}}{V_{n-1}}\right) * 100$. In this equation, V_n represents the mean cover value in the current year, while V_{n-1} represents the value recorded in the immediately preceding year. For all analyses, mean values were calculated across ten plots per treatment for each sampling year. Since the data did not meet normality assumptions, differences among treatments were evaluated using the Kruskal–Wallis test. Whenever significant differences were detected, Dunn's post-hoc test was performed for pairwise comparisons, with p-values adjusted via the Bonferroni method ($p < 0.05$).

Simpson's diversity index (D) was calculated from mean species cover and log-transformed prior to analysis. Treatment effects on D were assessed using Generalized Linear Mixed Models (GLMM) with an inverse Gaussian distribution, fitted via the glmmPQL function. This distribution was selected because diversity values are continuous, strictly positive, and typically right-skewed, violating standard normality assumptions. Additional GLMMs were applied to cover and richness data using Beta and Negative Binomial distributions, respectively. Predictors included grazing, burning, time, and their interactions. To account for the experimental design and temporal dependency,

models incorporated a nested random effect structure (experiment within time) and a temporal autoregressive factor. This GLMM approach was chosen to accommodate non-normal distributions while simultaneously accounting for management-level fixed effects and plot-level random variation.

Community composition was assessed from both taxonomic and functional perspectives. Taxonomic distances were calculated using Bray-Curtis dissimilarity, while functional distances were derived from life-form traits using the Gower distance assigning equal weight to each of the functional traits, through the gawdis package v.0.1.5 (de Bello et al. 2021). Based on functional distances, a functional dendrogram was generated via UPGMA to calculate an abundance-based functional Sørensen similarity matrix (*Phylosor;* Nipperess et al. 2010) following Hellinger transformation. For both datasets, variations in composition and multivariate dispersion were analyzed using permutational multivariate analysis of variance (PERMANOVA) and multivariate analysis of group dispersion homogeneity (BETADISPER), respectively. To account for the experimental design, permutations were restricted within blocks and sampling units (plots). Analyses were partitioned to evaluate management effects at each time point (between-subjects) and temporal shifts within each management level (within-subjects).

Species were classified into life-form functional groups following the framework proposed by Ferreira et al. (2020), with adaptations based on morphological descriptions from the Flora e Funga do Brasil (Jardim Botânico do Rio de Janeiro, 2026) database. The classification integrated biotic attributes and spatial occupation strategies, categorizing taxa into 17 distinct types: Bulbous Geophyte, Climber, Climber Lignified, Connected Tussock, Decumbent, Herbaceous Forb, Lignified Forb, Rhizomatous, Rosette, Shrub, Solitary Tussock, Stoloniferous, Subshrub, Therophyte, Therophyte Tussock, Tree, and Xylopodium Geophyte (Supplementary Material – Table S9). This categorization accounted for shoot persistence, lignification patterns, branching architecture, and vegetative propagation, ensuring a comprehensive characterization of the community's structural and functional diversity.

All statistical analyses and data visualizations were performed in the R statistical environment v.4.4.1 (Core Team, 2024). Data manipulation was handled using the dplyr package v.1.1.4 (Wickham et al., 2023). Functional trait distances and weighting were computed using the gawdis package v.0.1.5 (de Bello et al., 2021). Dendrogram

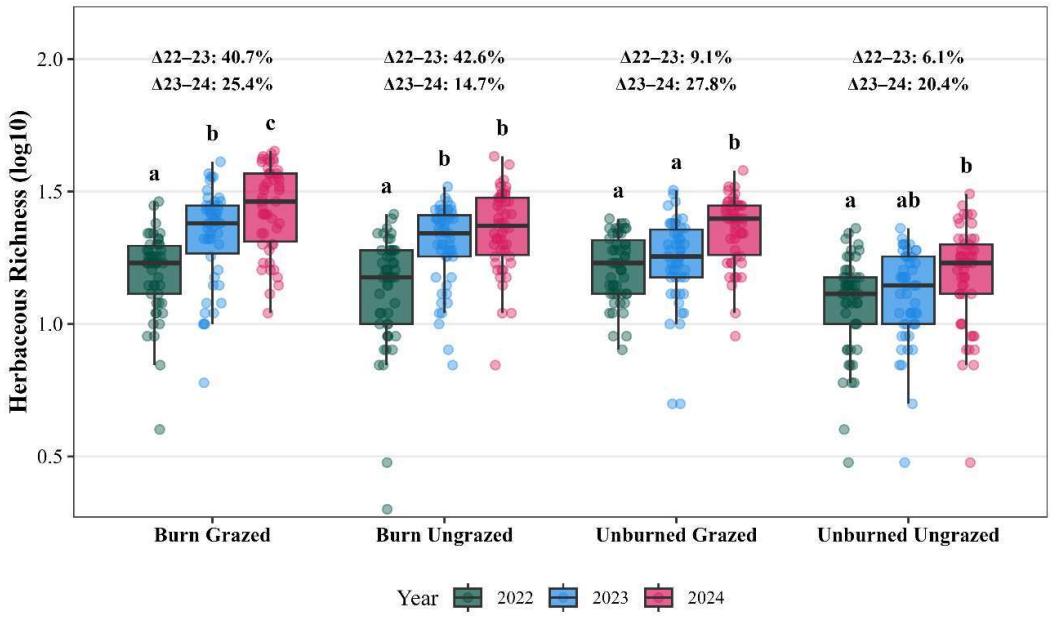
construction and phylogenetic/functional similarity metrics (Phylosor) were implemented using ape (Paradis et al., 2019), phytools (Revell, 2012) and picante (Kembel & Kembel, 2014), with matrix transformations performed via labdsv v.2.1-1 (Roberts & Roberts, 2012). The rstatix package v.0.7.2 (Kassambra, 2023) was used for Kruskal–Wallis and Dunn's tests. Multivariate analyses, including PERMANOVA (adonis2) and multivariate dispersion (betadisper), were conducted using the vegan package v.2.6-4 (Oksanen et al., 2026). Generalized Linear Mixed Models (GLMM) were implemented via the MASS package v.7.3-58.2 (Ripley, 2011), with post-hoc comparisons performed using the multcomp package v.1.4-23 (Hothorn et al., 2008). All figures and graphical representations were produced using the ggplot2 package v.3.5.1 (Wickham, 2011) and ggdist v.3.3.2 (Kay & Wiernik, 1999). The analysis code and data are available on Zenodo (Silveira, 2026).

Results

Species richness responses to fire and grazing

Mean species richness varied consistently across management regimes and sampling years, with all managed treatments (fire and/or grazing) exhibiting higher richness than the unburned and ungrazed control throughout the study (Supplementary Material – Table S1; Fig. 3). Species richness increased over time in all treatments; however, this increase was substantially more pronounced in burned plots, particularly when fire was combined with grazing. Burned and grazed plots showed the highest mean richness values in all post-treatment surveys, reaching an average of 29.12 species per 1 m^2 plot in 2024, whereas the control plots consistently exhibited the lowest values, with a mean richness of 16.46 species (Supplementary Material – Table S1). These contrasting structural patterns are visually evident in figure 4, which illustrates the differences between unmanaged areas (A–D) and managed experimental plots (E–H).

Pairwise comparisons derived from GLMMs revealed significant interactive effects between burning, grazing, and time. In the initial post-treatment survey (2022), burning significantly increased species richness in ungrazed plots ($p = 0.046$), whereas no immediate effect was detected in plots subjected to grazing alone ($p = 0.6338$). By the subsequente (2023 and 2024), however species richness had increased significantly across both grazed and ungrazed treatments ($p < 0.001$). While these GLMM results focus on richness (detailed in Supplementary Material Table S5), detailed statistical outputs regarding changes in overall community structure, including PERMANOVA results and Simpson diversity index, are provided in the Supplementary Material (Table S2).



255 Fig. 3 - Species richness of the herbaceous community across different management
256 regimes and sampling years (2022–2024). Individual sampling units are represented
257 by jittered points. Different letters above boxes indicate significant statistical differences
258 ($p < 0.05$) between years within each management regime, based on a linear model.
259 Values above columns indicate the sequential percentage change (Δ%) in mean richness
260 between consecutive years (2022–2023 and 2023–2024).
261



Fig. 4 - Characterization of sampling units under different management regimes. Unmanaged sampling units: A) Dominance of *Baccharis junciformis* (lignified forb); B) Seed dispersal of *Chromolaena laevigata* (subshrub); C) Dominance of *Paspalum exaltatum* (solitary tussock); D) Dominance of *Myrsine coriacea* (tree). Managed sampling units: E) Diverse grassland area featuring *Hyptis comaroides* (Lamiaceae), *Cypella herbertii* (Iridaceae), *Pomaria pilosa* (Fabaceae), and *Adiantopsis chlorophylla* (Pteridaceae), among others; F) *Krapovickasia flavescens* (Malvaceae) providing horizontal soil cover; G) *Richardia grandiflora* (Rubiaceae) hosting a floral visitor; H) *Eryngium horridum* (Apiaceae) with underground storage organs.

Vegetation cover

Vegetation cover dynamics were strongly influenced by management intensity and time since disturbance (Fig. 5). While treatments involving fire (Burn Grazed and Burn Ungrazed) showed a notable post-fire recovery marked by a substantial increase in cover between 2023 and 2024 (Δ +39.44% and +18.69%, respectively) their recovery trajectories differed. Burn Grazed plots only reached levels comparable to the control (Group 'a') in the final sampling year, whereas Unburned Grazed plots achieved this status a year earlier, in 2023. In contrast, the total exclusion treatment (Unburned Ungrazed) maintained consistently high and stable cover values throughout the study (Group 'a'), acting as a reference for maximum biomass accumulation, with only minor fluctuations (Δ 23–24: +3.90%; Supplementary Material – Table S3).

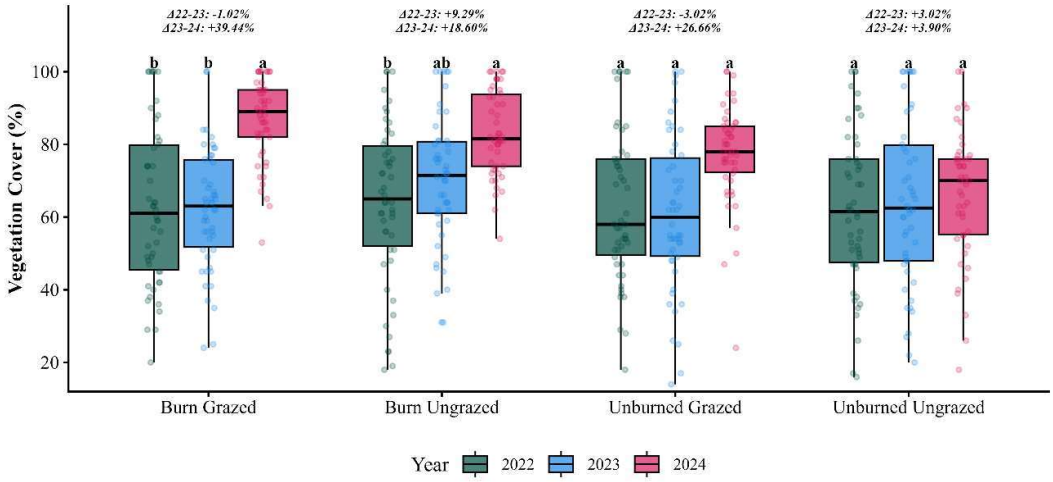


Fig. 5. Mean cumulative vegetation cover (%), calculated as the sum of individual species cover, across different management regimes: Burn Grazed, Burn Ungrazed, Unburned Grazed, and Unburned Ungrazed (2022–2024). Points represent plot-level values (jittered). Different letters above boxes indicate significant statistical differences ($p < 0.05$) between years within each management regime, based on a linear model using logit-transformed data. Values at the top indicate the relative annual percentage change (Δ%) in mean cover between consecutive years. Proportional data were adjusted for sample size and logit-transformed (adjust = 0.025) prior to statistical analysis to stabilize variance.

Structural responses

Total vegetation cover (%), estimated as the direct proportion of ground cover by living plants (independent of species composition), increased across all management treatments over the evaluated periods (Fig. 6 A). The most pronounced cumulative increase was observed in the Burned-Grazed treatment, which showed successive increments of +14% and +61% between sampling events. Average vegetation height (Fig. 6 D) presented distinct temporal patterns depending on the treatment. In both Burned-Grazed and Unburned-Grazed plots, vegetation height initially decreased (-53% and -37%, respectively) before increasing in the final period (+25% and +15%). In contrast, Unburned-Ungrazed plots maintained a stable average height throughout the temporal sequence (+1% and -0.1% change).

Dead biomass (%) was lower in burned plots compared to unburned plots following the initial sampling event (Fig. 6 B). Both burned treatments exhibited sharp initial reductions in dead biomass (-56% in grazed and -55% in ungrazed plots). Regarding exposed soil (Fig. 6 C), a pronounced transient peak was recorded during the intermediate sampling period specifically in the burned treatments. Exposed soil increased by +632% in the Burned-Grazed and +308% in the Burned-Ungrazed plots during this phase. In the subsequent period, these values decreased sharply (-74% and -80%, respectively), returning to proportions closer to the initial observations, whereas unburned treatments maintained lower and relatively stable percentages of exposed soil throughout the study.

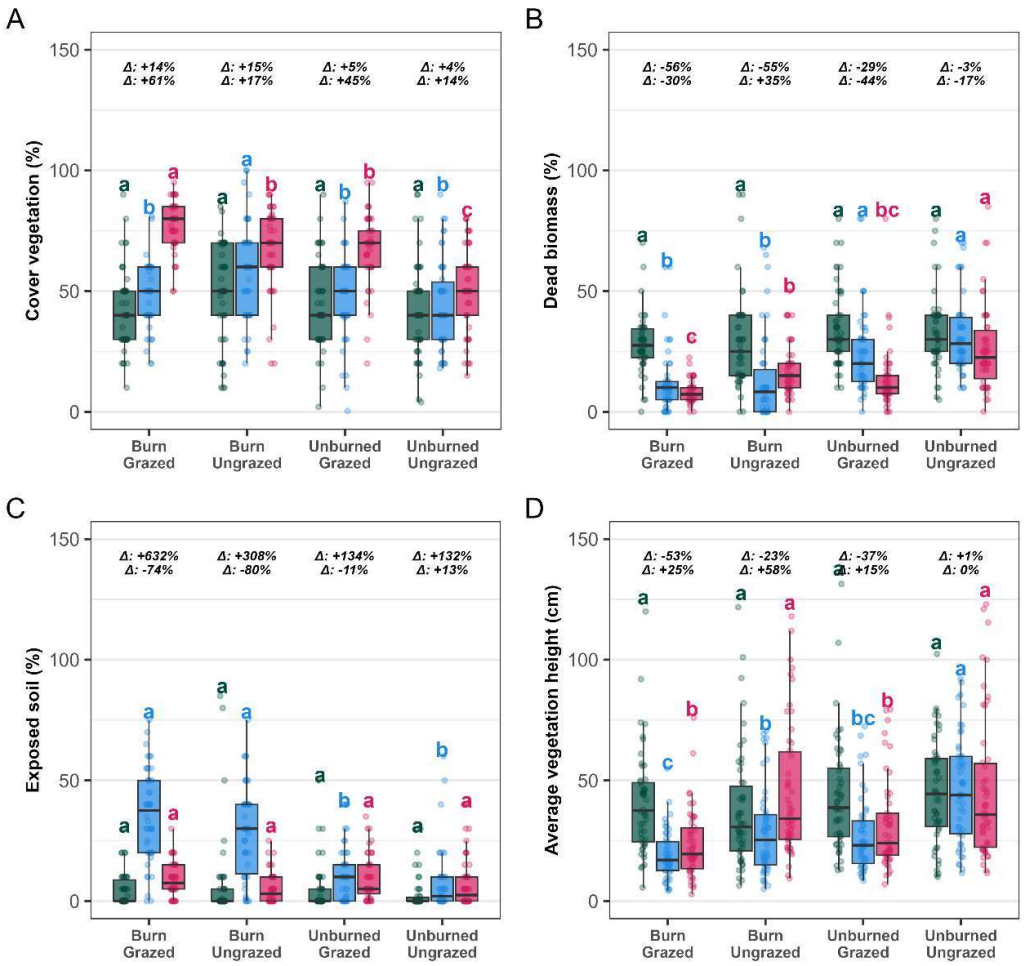


Fig. 6 - Temporal dynamics of structural environmental variables across management regimes from 2022 to 2024: (A) Cover vegetation (%), (B) Dead biomass (%), (C) Exposed soil (%), and (D) Average vegetation height (cm). Sampling units are displayed as jittered points. Different letters above boxes indicate significant statistical differences ($p < 0.05$) between management regimes within each sampling year, according to Tukey's HSD test. Values above columns indicate the annual percentage change (Δ%) between consecutive sampling years. Values displayed as 0% represent a change of -0.1% that was rounded for formatting purposes. An extreme outlier (>150 cm) was excluded from the average vegetation height analysis (D) to preserve visual scale

Vegetation cover and structural responses

Exploratory analysis of plot-level data, supported by boxplots, revealed a progressive increase in cover over time across all treatments, reflecting vegetation recovery following disturbance. Vegetation cover expanded more rapidly in burned areas where grazing was excluded, allowing for full regrowth without herbivory pressure. Conversely, in burned plots subjected to grazing, vegetation cover remained significantly lower during the second year post-fire ($p = 0.0003$), highlighting the impact of biomass consumption and trampling on regrowth.

Vegetation diversity patterns

Taxonomic composition was significantly shaped by the interaction between management strategies and environmental conditions over time. Permutational multivariate analysis of variance (PERMANOVA) revealed that management regime, time, and the set of structural variables significantly influenced species composition ($F_{11,588} = 1.22$, $R^2 = 0.022$, $p = 0.0001$). Complementarily, univariate analyses (ANOVA followed by Tukey's HSD) confirmed that each structural component (e.g., biomass, litter, and vegetation height) exhibited distinct response patterns to the treatments (Fig. 6), as indicated by the significance letters. Pairwise PERMANOVA comparisons confirmed that all management combinations resulted in distinct community structures (all $p < 0.001$ for all pairs). Specifically, the divergence between burned and unburned areas, as well as between grazed and ungrazed plots, highlights that both disturbance type and cumulative vegetation structure are primary drivers of community assembly in this system.

Generalized Linear Mixed Models (GLMM) demonstrated that management was a primary driver of diversity levels ($p < 0.001$ for all managed versus control comparisons). Post-hoc Tukey-adjusted comparisons revealed that unburned and ungrazed control plots exhibited significantly lower diversity than all managed treatments ($p < 0.001$ for all comparisons). The largest contrast was observed between the control and the burned and grazed treatment (estimate = 0.597, $p < 0.001$), followed by the burned and ungrazed (estimate = 0.436, $p < 0.001$) and the unburned and grazed treatments (estimate = 0.407, both $p < 0.001$) (Supplementary Material – Table S4).

Multivariate dispersion analysis (*betadisper*) revealed that the functional heterogeneity of the herbaceous community varied significantly as a function of the interaction between management and time ($F_{11,588} = 3.24$; $p < 0.001$). Tukey's HSD test

demonstrated that the most pronounced shifts in life-form composition stability occurred in the burned, ungrazed areas (Burn Ungrazed) when comparing the baseline year (2022) to the end of the experiment (2024) ($p < 0.01$) (Supplementary Material – Table S6**).**

In contrast, no significant differences in Simpson's diversity were detected among the managed treatments themselves (Supplementary Material – Table S4). These results indicate that the introduction of disturbance promoted an initial recovery of local (alpha) diversity relative to abandoned conditions, while differences among management types were not yet detectable during the study period.

Life-form dynamics

Life-form analyses revealed clear differences in functional composition among management regimes, with significant changes in relative cover over time (Fig. 7, Supplementary Table S7 and S8). Principal Coordinates Analysis (PCoA) confirmed these patterns, with the first two axes capturing the majority of variation in vegetation functional structure; Dimension 1 alone explained between 28.8% and 34.72% of the total inertia across regimes (Fig. 8). Functional composition differed significantly among managements in both the second (PERMANOVA: $R^2 = 0.112$, $F = 8.21$, $p = 0.001$) and third year ($R^2 = 0.117$, $F = 8.62$, $p = 0.001$). In the second year, multivariate dispersion also differed among groups ($F = 3.77$, $p = 0.011$), with pairwise comparisons indicating that Unburned Ungrazed showed distinct dispersion compared to Burn Grazed ($p = 0.005$) and Unburned Grazed ($p = 0.015$). In the third year, dispersion likewise varied among managements ($F = 3.03$, $p = 0.042$), with Unburned Ungrazed differing from Burn Grazed ($p = 0.005$) and Burn Ungrazed ($p = 0.012$). Considering temporal changes within each management, a significant effect of time was detected in all cases: Burn Grazed ($R^2 = 0.107$, $F = 8.78$, $p = 0.001$), Unburned Grazed ($R^2 = 0.051$, $F = 3.98$, $p = 0.001$), and Unburned Ungrazed ($R^2 = 0.023$, $F = 1.74$, $p = 0.001$), homogeneity of multivariate dispersion was observed ($p > 0.05$). In these regimes, the significant PERMANOVA results indicate a directional shift in functional composition (location effect), suggesting a consistent turnover of life-forms over the years. In contrast, for Burn Ungrazed, a significant temporal effect was accompanied by changes in dispersion ($R^2 = 0.073$, $F = 5.75$, $p = 0.001$), indicating that the management affected both the average composition and the heterogeneity of the functional structure over time. Pairwise comparisons between time points further detailed these shifts: in Burn Grazed and Burn Ungrazed, all year pairs differed significantly (all $p < 0.05$), with R^2 values reaching up to 0.131. In the unburned areas, although

394 significant, the temporal turnover was less pronounced, with R^2 values ranging from
395 0.009 to 0.045.
396 In the Burn Grazed treatment, woody life forms exhibited a marked reduction in
397 cover during the first interval (2022–2023), followed by an incremental increase in the
398 second period (2023–2024). Specifically, Shrubs and Trees recorded initial declines of -
399 7.06 and -4.34, respectively, with subsequent gains of +0.57 and +0.35; a similar trend
400 was observed for Subshrubs (-1.53 followed by +0.51), highlighting dynamic temporal
401 responses within woody-related categories. Among the most significant positive shifts,
402 Stoloniferous species showed a continuous and robust expansion (+3.75 and +4.73),
403 while geophytes registered varying trends, with increases of +2.85 for Bulbous Geophyte
404 and +1.91 for Xylopodium Geophyte in the first period. Conversely, Rosettes initially
405 increased (+2.89) before decreasing (-0.88), while Solitary Tussock exhibited an uninter-
406 rupted and severe reduction (-1.66 and -5.80), representing one of the most substantial
407 declines under this management. These changes are reflected in the PCoA through a clear
408 directional shift in centroids between 2022 and 2024, indicating a robust structural tran-
409 sition under the combined pressure of fire and grazing (Fig. 8).
410 In Burn Ungrazed, Shrubs (-5.98) and Trees (-4.96) also declined markedly in the
411 first period, followed by increases in the second (+2.97 and +4.38). Lignified Forbs
412 (+2.17 and +0.33) and Stoloniferous forms (+2.85 and +2.03) exhibited continuous gains.
413 Notably, Solitary Tussock showed a pronounced initial reduction (-11.94) followed by an
414 increase (+3.80), representing the strongest negative trend in the first interval. As with
415 the previous management, the PCoA centroids for the Burn Ungrazed treatment showed
416 a clear directional shift over time, reinforcing the trajectory of post-fire structural transi-
417 tion (Fig. 8).
418 In the Unburned Grazed treatment, a distinct inverse temporal pattern emerged
419 between shrubs and trees: during the first interval, shrub cover increased (+3.09) as tree
420 cover declined (-5.48), whereas in the second period, shrub cover decreased (-3.54) while
421 tree cover expanded (+4.24). Other significant gains were recorded for Connected Tus-
422 sock (+4.35) in the first period and Stoloniferous species (+3.38) in the second. Con-
423 versely, Solitary Tussock experienced a severe reduction of -6.89 during the 2023–2024
424 interval. Unlike the fire treatments, the centroids for this regime remained more closely
425 grouped in the ordination, suggesting lower temporal variation in the functional mean.
426 For this specific scenario, the ordination cumulatively retained 53.85% of the variation

(Dimension 1: 34.72%; Dimension 2: 19.13%), confirming that the multivariate gradients reliably reflect the subtle changes in vital attribute composition under isolated grazing.

In the Unburned Ungrazed control, functional composition remained comparatively stable for most life forms. Nevertheless, variations occurred within the woody strata: trees increased in the first interval (+2.40) but declined in the second (-5.75). Conversely, shrubs decreased in the first period (-5.50) but increased in the second (+5.41). Broadly, the largest absolute increases during the cumulative study period (2022–2024) occurred for Stoloniferous species in the Burn Grazed treatment (+8.48), followed by the same group in the Unburned Grazed treatment (+5.14). In contrast, the most severe reductions were recorded for Solitary Tussock under the Burn Ungrazed regime (-8.14) and for Shrubs in the Burn Grazed treatment (-6.49). This control treatment was distinguished by high multivariate dispersion and overlapping ellipses in the PCoA (Fig. 8), reflecting the greater functional heterogeneity inherent to unmanaged areas. This heterogeneity was confirmed by pairwise comparisons of the Phylosor index (Supplementary Material – Table S6). The final cumulative balance for the control treatment (2022–2024) revealed a net decline in key categories, specifically Trees (-3.35) and Solitary Tussock (-5.99). These results indicate that the absence of frequent disturbances, such as fire and grazing, can lead to significant long-term retractions in the cover of specific life forms.

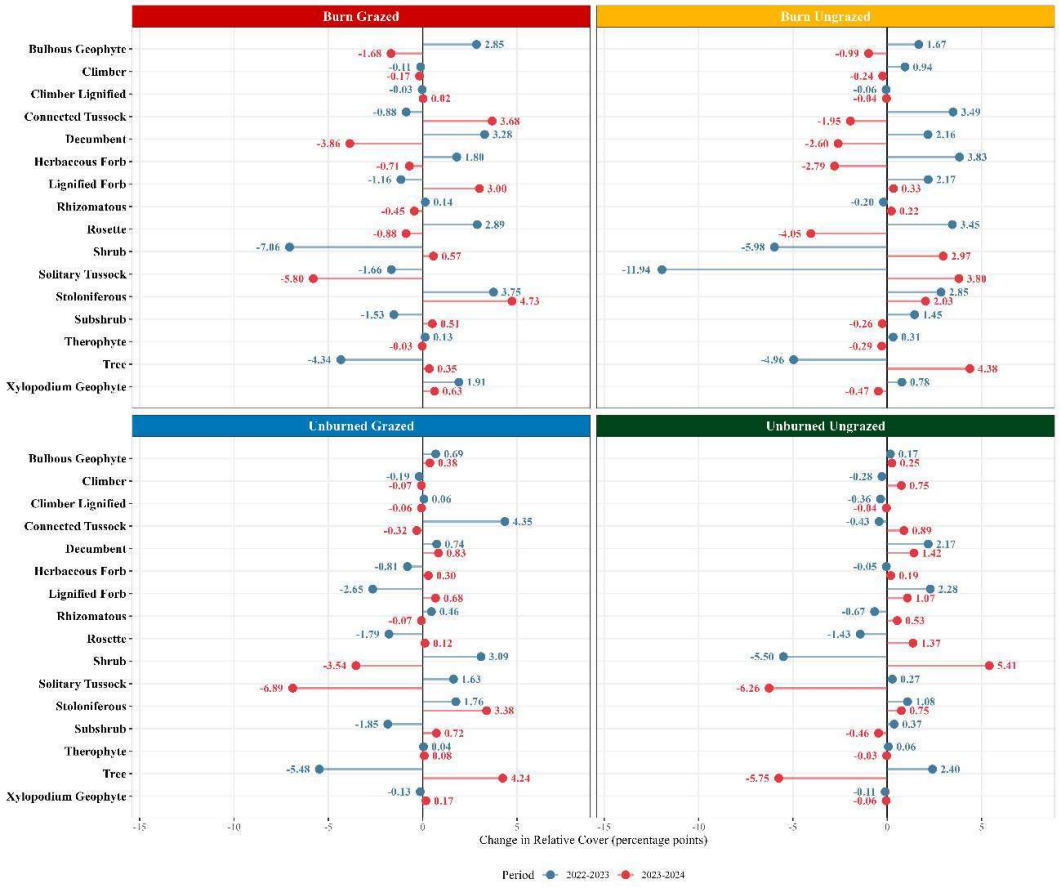
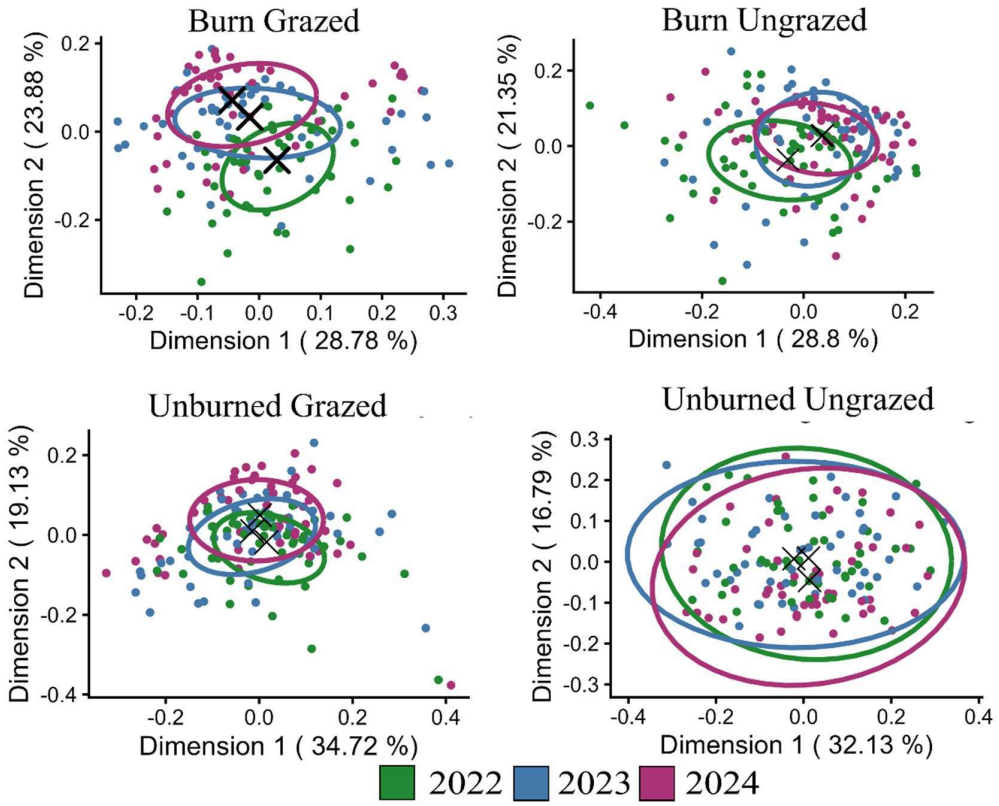


Fig 7 - Annual net change in mean relative cover (percentage points) (see in Supplementary Material – Table S8) of plant life forms across four experimental treatments: Burn Grazing (fire and cattle reintroduction), Burn Ungrazed (fire only), Unburned Grazing (cattle only), and Unburned Ungrazing (abandonment control). Blue lines represent the 2022–2023 transition, while red lines indicate the 2023–2024 period. Positive values denote an increase in dominance, while negative values indicate a reduction. The values used in this chart can be found in the supplementary material.



454 Fig. 8 - Scatterplot of functional structure under different management regimes over time.
455 Functional dissimilarity (abundance-based Phylosor) was derived from five plant traits:
456 life cycle, shoot persistence, lignification, space occupation, and branch architecture.
457 Panels distinguish management combinations: Burned Grazed, Burned Ungrazed,
458 Unburned Grazed, and Unburned Ungrazed. Colors indicate the temporal monitoringand
459 ellipses represent the multivariate dispersion (1 SD) around the group centroids ("X"),
460 reflecting the functional homogeneity (betadisper) for each year. The percentage of
461 variation explained by each principal coordinate axis is indicated in parentheses.

Discussion

Species richness responses to reintroduction of fire and grazing

Fire and grazing exclusion negatively impact taxonomic and functional diversity by reducing environmental heterogeneity and exacerbating competitive asymmetry in favor of dominant grasses (Chaneton et al., 2002; Andrade et al., 2023). Our results demonstrate that the reintroduction of management — particularly fire — acts as a critical catalyst to break this successional stagnation. This contrast was corroborated by our findings: burned treatments (Burned-Grazed and Burned-Ungrazed) exhibited a richness increase exceeding 40%, with mean species density per plot nearly doubling from the 2022 baseline after only one management cycle (Fig. 3).

In contrast, Unburned Ungrazed showed the lowest mean richness across all years, with marginal increases (0.78 in Δ 2022-2023 and 2.82 in Δ 2023-2024),), likely linked to interannual climatic stochasticity. This disparity highlights that while excluded areas remain trapped in a state of successional stagnation due to the accumulation of senescent biomass and phyto-space (both living and dead biomass) (Rice, 1993; Overbeck et al., 2018), reintroduced disturbances effectively neutralize these physical barriers. By restoring light availability at the soil level (Kitzberger, 2013) and eliminating the ecological filter imposed by woody encroachment (Sankey, 2012; Myster, 2013), the reintroduction of management triggers a rapid and non-linear recovery of grassland biodiversity, reversing the competitive exclusion process in the short term.

The slower recovery in grazed-only plots compared to burned plots highlights successional time-lags (Suding et al., 2004). These delays are likely linked to the gradual and selective nature of grazing, which maintains competition over time and limits the simultaneous opening of space for recruitment, thereby amplifying limitations associated with dispersal and soil seed bank dynamics (Facelli, 1988; Andrade, Menezes, et al., 2023). In contrast, fire promotes an abrupt removal of biomass and an immediate release of resources at the ground level—including light—creating more synchronized recruitment opportunities and reducing these lags (López-Mársico et al., 2026). The highest richness levels were reached when fire and grazing were combined (pyric herbivory), highlighting a synergistic effect that prevents competitive exclusion and allows subordinate species to persist or reestablish (Fuhlendorf et al., 2009; Limb et al., 2011; Overbeck, Andrade, et al., 2023). In the absence of these disturbances, the community tends toward a state of successional stagnation, where a few dominant perennial species monopolize resources and drive local diversity loss (Overbeck et al., 2018; Müller et al., 2023).

Vegetation cover and structural responses

The management regimes in our study promoted distinct successional trajectories. Fire provided an intense initial "reset" by removing 56% and 55% of dead biomass in Burned Grazed and Burned Ungrazed plots, respectively (Fig. 6B). This biomass removal (Fidelis et al., 2012; Fidelis, 2020) resulted in a drastic increase in exposed soil (603% and 308% — Fig. 6C), which acted as a catalyst for a 42.3% increase in vegetation cover by the second year (Fig. 5). While these gaps promote the recovery of species richness (Ferreira et al., 2020) and functional heterogeneity (Thomas et al., 2023), they also represent a transient window that requires monitoring, as such openings may facilitate the establishment of invasive species (Guido et al., 2023).

In contrast, grazing in the absence of fire (Unburned Grazed) contributed to a gradual and consistent recovery. In the first year, structural modifications were discrete—showing a 3.1% reduction in cover and an 8.6% increment in richness. However, by the second interval (2023–2024), gains in cover (26.1% - Fig. 5) and richness (28.2% - Fig. 4) more than doubled the initial values. Structurally, grazing alone contributed to an initial 134% increase in exposed soil (Fig. 6C), which was subsequently occupied by vegetation, resulting in an 11% decrease in the following year. This indicates that grazing-induced gaps, while less drastic than those created by fire, are fundamental mechanisms that favor the entry of new species and the gain of diversity over the medium term.

Ultimately, the synergy between both disturbances—pyric herbivory—acts as a regulator that prevents competitive exclusion (Fuhlendorf et al., 2009; Limb et al., 2011). This process occurs when dominant species, favored by the absence of disturbance, monopolize resources such as light and space, thereby eliminating subordinate species. In the control plots, the absence of management allowed vegetation to reach heights of 1.5 m, where the accumulation of senescent material limited light penetration and resulted in a marginal increment of only 3.6% in cover (Andrade et al., 2023). Our data confirm that the interaction between fire-driven biomass removal and grazing-mediated structural maintenance is the most effective strategy to prevent successional stagnation and preserve the typical diversity of grassland ecosystems (Fuhlendorf et al., 2009; Müller et al., 2023).

Vegetation diversity patterns

Disturbance reintroduction reverted the floristic homogenization observed under Ungrazed Unburned conditions. All managed treatments (Grazed Unburned, Ungrazed Burned, and Grazed Burned) consistently differed from the control, showing higher richness and diversity (Table GLMM; Supplementary Material – Table S4). These results indicate that the presence of disturbance, regardless of type, is essential to sustain higher diversity levels. Temporal responses differed among regimes. In Ungrazed Burned, richness increased more rapidly, whereas in Grazed Burned and Grazed Unburned the effects became more pronounced over time (Supplementary Material – Table S5). Despite differences in response timing, managed treatments converged in terms of overall diversity (Supplementary Material – Table S4).

However, species composition differed among all management combinations (in Supplementary Matterial Table S2; pairwise ADONIS comparisons), indicating that Ungrazed Burned, Grazed Burned, and Grazed Unburned did not generate equivalent communities. Thus, while disturbance regimes produced comparable diversity levels, they directed distinct compositional trajectories. In contrast, Ungrazed Unburned was associated with greater dominance and lower compositional differentiation.

Life-form Dynamics

The dynamics of life forms in our study reflect a shift in resource-use strategies, where disturbances facilitate the transition from conservative (e.g., Solitary Tussock and Xylopodium Geophyte) to acquisitive traits (e.g., Rhizomatous, Stoloniferous, and Therophyte species) (Pérez-Ramos et al., 2013). Fire exerts an initial "top-down" control by removing competitively superior woody species and opening niches for opportunistic colonizers. However, the intensity of this response is species-specific; for instance, while shrubs like *Baccharis dracunculifolia* are highly susceptible to fire (Müller et al., 2007), subshrubs such as *Austroeupatorium inulifolium* demonstrate resilience through vigorous resprouting (Mendes et al., 2024).

The Principal Coordinates Analysis (PCoA) (Figure 8) revealed contrasting trajectories among management regimes, positioning fire and grazing as key determinants of functional structure. While the Burn Grazed and Burn Ungrazed treatments showed a directional shift in centroids, suggesting a functional transition in response to disturbance, the Unburned Ungrazed (control) scenario exhibited a pattern of temporal stagnation. The high multivariate dispersion observed in the control, coupled with the near-total overlap

of ellipses between 2022 and 2024, suggests a state of ecological stasis, where the community remains compositionally and structurally unchanged despite temporal transitions. This configuration reflects a stable yet degraded equilibrium, where the dominance of woody and cespitose life-forms creates a functionally heterogeneous structure across plots that remains persistent over time. Such structural stability in the unmanaged treatment acts as a barrier to restoration, as the absence of disruptive forces (fire or grazing) prevents the vegetation from exiting a successional state to resume typical grassland dynamics.

Management exerted a consistent effect on the functional composition of communities in both the second ($p = 0.001$) and third year ($p = 0.001$). However, the significance of dispersion tests among managements in the second ($p = 0.011$) and third year ($p = 0.042$) indicates that part of the PERMANOVA signal may be driven not only by shifts in group centroids, but also by differences in within-group variability, particularly involving Unburned Ungrazed, which differed from other groups (e.g., $p = 0.005$ and $p = 0.012$). Over time, all managements showed significant changes in functional composition (Burn Grazed: $p = 0.001$; Burn Ungrazed: $p = 0.001$; Unburned Grazed: $p = 0.001$; Unburned Ungrazed: $p = 0.001$), although the magnitude of this effect was greater in burned areas, especially under grazing, and smaller in undisturbed conditions. Homogeneity of dispersion through time was maintained for Burn Grazed ($p = 0.809$), Unburned Grazed ($p = 0.677$), and Unburned Ungrazed ($p = 0.304$), indicating directional shifts in composition, whereas Burn Ungrazed showed significant heterogeneity in dispersion ($p = 0.012$), suggesting additional variation in community structure. Overall, these patterns indicate stronger temporal dynamics under fire and/or grazing regimes, while undisturbed areas exhibit more subtle changes in functional structure, see in Supplementary Matterial Table S2.

Our data highlight that grazing acts as a mitigating factor in woody encroach-ment following fire. Both burned treatments showed an initial reduction in shrub (-7.06 in Burned Grazed; -5.98 in Burned Ungrazed) and tree cover (-4.34 in Burned Grazed; -4.96 in Burned Ungrazed) between 2022 and 2023. However, during the second interval (2023–2024), the recovery of woody cover was attenuated in the pre-sence of cattle. In Burned Grazed, shrub and tree changes were limited to +0.57 and +0.35, respectively, whereas in Burned Ungrazed, these values reached +2.97 and +4.38. This suggests that

593 cattle may constrain woody densification through mecha-nisms such as seedling her-
594 bivory and trampling, preventing dominant perennials from monopolizing resources
595 (Fuhlendorf et al., 2009; Limb et al., 2011).

596 Specific life forms showed distinct resilience patterns. Stoloniferous plants exhib-
597 ited continuous gains in both burned treatments, with higher values in Burned Grazed,
598 confirming that these disturbances favor their clonal expansion. Rosettes also showed
599 substantial gains in Burned Grazed, primarily driven by the high fire resilience of species
600 like *Eryngium horridum*. For this species, fire acts as a positive stimulus rather than a
601 control measure; the destruction of aboveground biomass triggers vigo-rous resprouting
602 from thick rhizomes, which are essential for the plant's clonal growth (Fidelis et al.,
603 2008). These underground structures (see in Fig. 4-H) allow new roset-tes to emerge from
604 the same base after the main rosette flowers and dies, leading to a denser population struc-
605 ture and lateral expansion (Fidelis et al., 2008). While fire is often used by land managers
606 to eliminate *E. horridum*, our results and the literature suggest this practice is counterpro-
607 ductive as it stimulates vegetative propagation. Furthermore, their spines deter cattle her-
608 bivory, allowing them to thrive in grazed are-as. This fire-stimulated resilience is also
609 evident in other geophytes like *Zephyranthes* spp., where an intense post-fire flowering
610 was qualitatively observed in the field (Figure 9). This suggests that fire not only creates
611 colonization gaps but also acts as a physiological trigger for reproductive phases in spe-
612 cies with specialized underground reserve struc-tures.
613



Fig 9 - Post-fire ecological effects on vegetation. (A–B) After and before comparison of the same location. (C) Recovery of the herbaceous layer with fire-killed *B. dracunculifolia*. (D–F) Fruit development stages of *Zephyranthes* spp. immediately following fire implementation. (G–I) Diversity of *Zephyranthes* spp. observed in the study area post-fire management.

In the absence of disturbances (Unburned Ungrazed), the community enters a state of successional stagnation and biotic homogenization. Nearly half of the 17 monitored life forms showed marginal or no variation. Observed reduction in tree cover during the second period (2023–2024), coupled with a concomitant increase in shrubs, suggests a process is driven by self-thinning — a density-dependent mortality resulting from intense competition for resources (Belay & Moe, 2012). — and the dominance of persistent woody forms in the intermediate stratum, limiting the development of young trees and geophytic species (Andrade et al., 2023). Without the synergy of pyric herbivory, the ecosystem undergoes functional degradation as shrub encroachment limits the development of young trees and geophytic species, ultimately leading to a simplified state and the loss of typical grassland diversity (Overbeck et al., 2018).

Community composition and multivariate drivers

Our findings reinforce the premise that plant community assembly in this system does not occur stochastically but is instead driven by environmental and biotic filters established by management (Ferreira et al., 2020). The significance observed in the PERMANOVA ($p = 0.0001$) corroborates the hypothesis that anthropogenic and natural disturbances, such as fire and grazing, act as critical determinants of the phytosociological structure. The structural divergence between burned and unburned areas, as well as between grazed and exclosed plots, suggests that each management regime creates a distinct regenerative niche. While fire may act by eliminating sensitive species and favoring functional groups with resprouting strategies, grazing introduces selection pressure via defoliation and compaction, altering interspecific competition. It is worth noting that although the coefficient of determination is relatively low ($R^2 = 0.022$), which is common in complex ecological systems with high intrinsic variability, the consistency of the pairwise comparisons ($p = 0.001$) validates that the environmental heterogeneity generated by these management practices is the primary driver of local beta-diversity. Consequently, the accumulated vegetation structure is not merely a reflection of the current state, but a historical legacy of the interactions between management and time.

Conclusion

The exclusion of fire and grazing compromises the integrity of grassland ecosystems by triggering successional stagnation and a marked decline in both taxonomic and functional diversity. In the absence of these disturbances, dead biomass accumulates, forming a physical barrier that reduces light availability and restricts the establishment of subordinate species. Temporal monitoring indicates that fire rapidly increases species richness by suppressing the dominance of tussock-forming grasses and exposing bare soil, whereas grazing alone leads to a more gradual recovery, largely constrained by dispersal limitations and the time required for the occupation of newly available niches.

The interaction between fire and herbivory, under a pyric herbivory regime, emerges as the most effective regulatory mechanism for maintaining biodiversity. Fire promotes immediate structural renewal of the vegetation, while subsequent grazing limits the expansion of woody life forms and prevents shrub re-densification, thereby avoiding resource monopolization by dominant competitors. These divergent responses, characterized by the persistence of low-stature, bud-protecting life-forms (e.g., rhizomatous and stoloniferous herbs) in managed areas versus the dominance of tall woody plants (e.g., shrubs and trees) in their absence, underscore the need for management strategies that align with the ecological adaptations inherent to the system.

Therefore, the conservation of grassland diversity depends on the maintenance of disturbance regimes that sustain environmental heterogeneity. Management abandonment promotes biotic homogenization and woody encroachment, leading to functional degradation. In this context, the combined reintroduction of fire and grazing becomes essential to ensure the continuity of ecological renewal processes and the coexistence of diverse life forms, which are fundamental to long-term ecosystem resilience and conservation.

References

Andrade, B.O., Dröse, W., Aguiar, C.A. de, Aires, E.T., Alvares, D.J., Barbieri, R.L., et al. (2023) 12,500+ and counting: biodiversity of the Brazilian Pampa. *Frontiers of Biogeography*, 15(2). https://doi.or/10.21425/F5FBG59288

Andrade, B.O., Menezes, L. da S., Boldrini, I.I., Pillar, V.D., & Overbeck, G.E. (2023) Grassland plant community composition and dynamics: disturbance as determinants of grassland diversity. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 177–204. https://doi.org/10.1007/978-3-031-42580-6_8

Baez-Lizarazo, M.R., Köhler, M., & Reginato, M. (2023) A historical perspective on the biogeography of the Pampa Region: imprints of time and origins of its flora. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 101–118. https://doi.org/10.1007/978-3-031-42580-6_5

Baggio, R., Overbeck, G.E., Durigan, G., & Pillar, V.D. (2021) To graze or not to graze: A core question for conservation and sustainable use of grassy ecosystems in Brazil. *Perspectives in Ecology and Conservation*. https://doi.org/10.1016/j.pecon.2021.06.002

Bali, A., Wright, M., Bronen, R., & Okada, M. (2008) An Integrated Assessment & Evaluation of ‘ Wood Bison Reintroduction in Alaska ’ University of Alaska Fairbanks Resilience and Adaptation program.

Behling, H., Pillar, V.D., & Overbeck, G.E. (2023) Dynamics of south Brazilian grasslands during the late quaternary. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 83–99. https://doi.org/10.1007/978-3-031-42580-6_4

Belay, T.A., & Moe, S.R. (2012) Woody dominance in a semi-arid savanna rangeland - Evidence for competitive self-thinning. *Acta Oecologica*, 45, 98–105. https://doi.or/10.1016/j.actao.2012.10.006

de Bello, F., Bott-Dukat, Z., Leps, J. & Fibich, P. (2021) Towards a more balanced combination of multiple traits when computing functional differences between species. Methods in Ecology and Evolution, 12(3), 443–448. https://doi.org/10.1111/2041-210X.13537

Bencke, G.A., Dias, R.A., & Fontana, C.S. (2023) Birds of the Campos Sulinos. South

Brazilian Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 231–287. https://doi.or/10.1007/978-3-031-42580-6_10

Bond, W.J., & Parr, C.L. (2010) Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. *Biological Conservation*, 143(10), 2395–2404. https://doi.or/10.1016/j.biocon.2009.12.012

Buisson, E., Le Stradic, S., Silveira, F.A.O., Durigan, G., Overbeck, G.E., Fidelis, A., et al. (2019) Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews*, 94(2), 590–609. https://doi.or/10.1111/brv.12470

Chaneton, E.J., Perelman, S.B., Omacini, M., & León, R.J.C. (2002) Grazing, environmental heterogeneity, and alien plant invasions in temperate pampa grasslands. *Biological Invasions*, 4(1–2), 7–24. https://doi.or/10.1023/A:1020536728448

Chase, M.W. (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181, 1–20. https://doi.org/10.1111/boj.12385

De Bello, F., Bott-Dukat Z, Leps J, Fibich P 2021. Towards a more balanced combination of multiple traits when computing functional differences between species. Methods in Ecology and Evolution 12: 443-448. doi: https://doi.org/10.1111/2041-210X.13537

Facelli, J.M. (1988) Response to grazing after nine years of cattle exlusion in a Flooding Pampa grassland, Argentina. *Vegetatio*, 78(1–2), 21–25. https://doi.or/10.1007/BF00045635

Ferreira, P.M.A.A., Andrade, B.O., Podgaiski, L.R., Dias, A.C., Pillar, V.D., Overbeck, G.E., et al. (2020) Long-term ecological research in southern Brazil grasslands: Effects of grazing exclusion and deferred grazing on plant and arthropod communities. *PLoS ONE*, 15(1), e0227706. https://doi.or/10.1371/journal.pone.0227706

Fidelis, A. (2020) Is fire always the “bad guy”? *Flora: Morphology, Distribution, Functional Ecology of Plants*, 268, 151611. https://doi.or/10.1016/j.flora.2020.151611

736 Fidelis, A., Appezzato-da-Glória, B., Pillar, V.D., & Pfadenhauer, J. (2014) Does
737 disturbance affect bud bank size and belowground structures diversity in Brazilian
738 subtropical grasslands? *Flora: Morphology, Distribution, Functional Ecology of*
739 *Plants*, 209(2), 110–116. https://doi.or/10.1016/j.flora.2013.12.003

740 Fidelis, A., Blanco, C.C., Müller, S.C., Pillar, V.D., & Pfadenhauer, J. (2012) Short-term
741 changes caused by fire and mowing in Brazilian Campos grasslands with different
742 long-term fire histories. *Journal of Vegetation Science*, 23(3), 552–562.
743 https://doi.or/10.1111/j.1654-1103.2011.01364.x

744 Fidelis, A., Overbeck, G., Pillar, V.D.P., & Pfadenhauer, J. (2008) Effects of disturbance
745 on population biology of the rosette species Eryngium horridum Malme in
746 grasslands in southern Brazil. *Plant Ecology*, 195(1), 55–67.
747 https://doi.or/10.1007/s11258-007-9298-5

748 Fonseca, S.N., Moura, C.C., Farnesi, M.M., Pivello, V.R., & Machado, E.L.M. (2022)
749 Caracterização Ambiental de Campos úmidos submetidos a Queima Prescrita no
750 Parque Nacional das Sempre-Vivas (PNSV), MG. *Revista Brasileira de Geografia*
751 *Fisica*, 15(6), 3229–3243. https://doi.or/10.26848/rbgf.v15.6.p3229-3243

752 Fuhlendorf, S., & Engle, D. (2001) Restoring heterogeneity on rangelands: ecosystem
753 management based on evolutionary grazing patterns: we propose a paradigm that
754 enhances heterogeneity. *BioScience*, 51(8), 625–632. https://doi.org/10.1641/0006-
755 3568(2001)051[0625:RHOREM]2.0.CO;2

756 Fuhlendorf, S.D., Engle, D.M., Kerby, J., & Hamilton, R. (2009) Pyric herbivory:
757 Rewilding landscapes through the recoupling of fire and grazing. *Conservation*
758 *Biology,* 23(3), 588–598. https://doi.or/10.1111/j.1523-1739.2008.01139.x

759 Golin, T. (2023) The Southern Grasslands and the expropriation of Indigenous territories.
760 South Brazilian grasslands: ecology and conservation of the Campos Sulinos.
761 *Springer*, 145–174. https://doi.org/10.1007/978-3-031-42580-6_7

762 Guido, A., López-Mársico, L., Rodríguez, C., Gallego, F., Lezama, F., Baeza, S., et al.
763 (2025) Uruguayan Grasslands: A Threatened Natural Asset. *Austral Ecology*, 50(2).
764 https://doi.or/10.1111/aec.70031

765 Guido, A., Sühs, R.B., Marciniak, B., Bergamin, R.S., & Fidelis, A. (2023) Invasive alien
766 species in the Campos Sulinos: Current status and future trends. South Brazilian

Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 495–527. https://doi.or/10.1007/978-3-031-42580-6_19

Hasenack, H., Weber, E., Boldrini, I.I., & Trevisan, R. (2010) Mapa de sistemas ecológicos da ecorregião das Savanas Uruguaias em escala 1:500.000 ou superior. Porto Alegre: UFRGS.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., & Mayfield, M.M. (2012) Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics*, 43(1), 227–248. https://doi.or/10.1146/annurev-ecolsys-110411-160411

Hobbs, R.J., & Huenneke, L.F. (1992) Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology*, 6(3), 324–337. https://doi.or/10.1046/j.1523-1739.1992.06030324.x

Hothorn, T., Bretz, F., & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, 50(3), 346–363. https://doi.or/10.1002/bimj.200810425

Jardim Botânico do Rio de Janeiro. (2026) Flora e Funga do Brasil. http://floradobrasil.jbrj.gov.br

Joyce, C.B. (2014) Ecological consequences and restoration potential of abandoned wet grasslands. *Ecological Engineering*, 66, 91–102. https://doi.or/10.1016/j.ecoleng.2013.05.008

Kassambra A. (2023) Package “rstatix”: Pipe-Friendly Framework for Basic Statistical Tests. Cran, 2–94.

Kay, M., & Wiernik, B.M. (1999) ggdist: Visualizations of Distributions and Uncertainty American Statistician 53: 276–281.

Kembel, S.W., & Kembel, M.S.W. (2014) Package ‘picante.’ *R Foundation for Statistical Computing, Vienna, Austria*: https://cran. r-project. org/web/packages/picante/picante.

Kitzberger, T. (2013) Ecotones as complex arenas of disturbance, climate, and human impacts: The trans-andean forest-steppe ecotone of Northern Patagonia. Ecotones Between Forest and Grassland. *Springer*, 59–88. https://doi.or/10.1007/978-1-4614-3797-0_3

Klimek, S., Richter gen. Kemmermann, A., Hofmann, M., & Isselstein, J. (2007) Plant species richness and composition in managed grasslands: The relative importance of field management and environmental factors. *Biological Conservation*, 134(4), 559–570. https://doi.or/10.1016/j.biocon.2006.09.007

Lewinsohn, T.M., Attayde, J.L., Fonseca, C.R., Ganade, G., Jorge, L.R., Kollmann, J., et al. (2015) Ecological literacy and beyond: Problem-based learning for future professionals. *Ambio*, 44(2), 154–162. https://doi.or/10.1007/s13280-014-0539-2

Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E.J., & Paruelo, J.M. (2014) Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science*, 25(1), 8–21. https://doi.or/10.1111/jvs.12053

Li, Y., Fan, J., & Yu, H. (2019) Grazing exclusion, a choice between biomass growth and species diversity maintenance in Beijing-Tianjin Sand Source Control Project. *Sustainability (Switzerland)*, 11(7), 1941. https://doi.or/10.3390/su11071941

Limb, R.F., Fuhlendorf, S.D., Engle, D.M., Weir, J.R., Elmore, R.D., & Bidwell, T.G. (2011) Pyric herbivory and cattle performance in grassland ecosystems. *Rangeland Ecology and Management*, 64(6), 659–663. https://doi.or/10.2111/REM-D-10-00192.1

Londo, G. (1976) The decimal scale for releves of permanent quadrats. *Vegetatio*, 33, 61–64. https://doi.org/10.1007/BF00055300

López-Mársico, L., Altesor, A., Gallego, F., & Lezama, F. (2026) Fire and grazing interact to maintain open physiognomy and diversity in a South American grassland. *Journal of Environmental Management*, 404, 129488.

Medeiros, R.B. de, Saibro, J.C. de, & Focht, T. (2009) Invasão de capim-annoni (*Eragrostis plana* Nees) no bioma Pampa do Rio Grande do Sul. In: Campos Sulinos: Conservação e Uso Sustentável da Biodiversidade. 317–330.

Mendes, D. de M., Silva, R.G. da, & Farinaccio, M.A. (2024) A influência da estiagem e do fogo na família asteraceae em uma unidade de conservação ambiental no pantanal de MS, Brasil. *Revista GeoPantanal*, 36(19), 213–226.

Menegat, R. (2023) Geological Memories of South Brazilian Landscapes: From Precambrian Orogenesis to the Quaternary Coastal Plain. South Brazilian

grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 17–44.

Menezes, L.S., Ely, C. V., Lucas, D.B., Minervini-Silva, G.H., Vélez-Martin, E., Hasenack, H., et al. (2022) Reference values and drivers of diversity for South Brazilian grassland plant communities. *Anais da Academia Brasileira de Ciências*, 94(1). https://doi.or/10.1590/0001-3765202220201079

Moreira, L.F.B., de Castilhos, H.Z., & Castroviejo-Fisher, S. (2020) Something is not quite right: Effects of two land uses on anuran diversity in subtropical grasslands. *Biotropica*, 52(6), 1286–1297. https://doi.or/10.1111/btp.12836

Müller, S.C., Bergamin, R.S., Duarte, L.S., Peroni, N., Sühs, R.B., & Carlucci, M.B. (2023) Mechanisms and processes shaping patterns of forest-grassland mosaics in southern Brazil. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 417–443. https://doi.org/10.1007/978-3-031-42580-6_16

Müller, S.C., Overbeck, G.E., Pfadenhauer, J., & Pillar, V.D. (2007) Plant functional types of woody species related to fire disturbance in forest–grassland ecotones. *Plant Ecology*, 189(1), 1–14.

Myster, R.W. (2013) Ecotones between forest and grassland. S*pringer Science & Business Media,* https://doi.or/10.1007/978-1-4614-3797-0

Nipperess, D.A., Faith, D.P., Barton, K. (2010) Resemblance in phylogenetic diversity among ecological assemblages. *Journal of Vegetation Science*, 21(5), 809–820. https://doi.org/10.1111/j.1654-1103.2010.01204.x

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., et al. (2026) Package 'vegan.' Community ecology package, version, 2(9), 1–295.

Overbeck, G.E., Andrade, B.O., Vélez-Martin, E., & Pillar, V.D. (2023) Beyond protected areas: conservation of south Brazilian grasslands. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 447–473. https://doi.org/10.1007/978-3-031-42580-6_17

Overbeck, G.E., Bencke, G.A., Müller, S.C., & Pillar, V.D. (2023) The Campos Sulinos: Introduction to the book. South Brazilian Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 3–13. https://doi.org/10.1007/978-3-031-42580-6_1

Overbeck, G.E., Müller, S.C., Fidelis, A., Pfadenhauer, J., Pillar, V.D., Blanco, C.C., et

al. (2007) Brazil's neglected biome: The South Brazilian Campos. *Perspectives in Plant Ecology, Evolution and Systematics*, 9(2), 101–116. https://doi.or/10.1016/j.ppees.2007.07.005

Overbeck, G.E., Müller, S.C., Pillar, V.D., & Pfadenhauer, J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science*, 16(6), 655–664. https://doi.or/10.1111/j.1654-1103.2005.tb02408.x

Overbeck, G., & Pfadenhauer, J. (2005) Effect of fire on vegetation dynamics and plant types in subtropical grassland in southern Brazil. *Department für Ökologie*, 139.

Overbeck, G.E., Scasta, J.D., Furquim, F.F., Boldrini, I.I., & Weir, J.R. (2018) The South Brazilian grasslands – A South American tallgrass prairie? Parallels and implications of fire dependency. *Perspectives in Ecology and Conservation*, 16(1), 24–30. https://doi.or/10.1016/j.pecon.2017.11.002

Overbeck, G.E., Vélez-Martin, E., Menezes, L. da S., Anand, M., Baeza, S., Carlucci, M.B., et al. (2022) Placing Brazil's grasslands and savannas on the map of science and conservation. *Perspectives in Plant Ecology, Evolution and Systematics*, 56, 125-687. https://doi.or/10.1016/j.ppees.2022.125687

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H.S., et al. (2019) Package 'ape.' Analyses of phylogenetics and evolution, version, 2(4), 47.

de Patta Pillar, V., & Vélez, E. (2010) Extinção dos Campos Sulinos em unidades de conservação: Um fenômeno natural ou um problema ético? *Natureza & Conservação*, 8(1), 84–86. https://doi.or/10.4322/natcon.00801014

Pausas, J.G., & Keeley, J.E. (2019) Wildfires as an ecosystem service. *Frontiers in Ecology and the Environment*, 17(5), 289–295. https://doi.or/10.1002/fee.2044

Pearce, R., Lair, K., & Frasier, G. (2014) Case study: long-term livestock grazing influence on vegetation class in Coyote Flat, California, USA. *Rangelands*, 36(4), 2–12. https://doi.org/10.2111/RANGELANDS-D-14-00003.1

Pérez-Ramos, I.M., Volaire, F., Fattet, M., Blanchard, A., & Roumet, C. (2013) Tradeoffs between functional strategies for resource-use and drought-survival in Mediterranean rangeland species. *Environmental and Experimental Botany*, 87, 126–136. https://doi.or/10.1016/j.envexpbot.2012.09.004

Pillar, V.D., & Overbeck, G.E. (2025) Grazing can reduce wildfire risk amid climate

change *Science* (New York, N.Y.) 387: eadu7471. https://doi.or/10.1126/science.adu7471

Pillar, V.D., & De Quadros, F.L.F. (1997) Grassland-forest boundaries in southern Brazil. Coenoses. *Coenoses*, 119–126. https://doi.or/10.1007/978-3-0348-8722-9_17

Pivello, V.R., Vieira, I., Christianini, A. V., Ribeiro, D.B., da Silva Menezes, L., Berlinck, C.N., et al. (2021) Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation*, 19(3), 233–255. https://doi.or/10.1016/j.pecon.2021.06.005

Podgaiski, L.R., da Silva Goldas, C., Ferrando, C.P.R., Silveira, F.S., Joner, F., Overbeck, G.E., et al. (2014) Burning effects on detritivory and litter decay in Campos grasslands. *Austral Ecology*, 39(6), 686–695. https://doi.org/10.1111/aec.12132

Porto, A., Overbeck, G.E., & Salatino, A. (2021) REVISÃO E SÍNTESE Consciência Campestre : um chamado para o (re) conhecimento aos campos. *Bio Diverso*, 1(January 2022).

Price, J.N., Schultz, N.L., Hodges, J.A., Cleland, M.A., & Morgan, J.W. (2021) Land-use legacies limit the effectiveness of switches in disturbance type to restore endangered grasslands. *Restoration Ecology*, 29(S1), e13271. https://doi.or/10.1111/rec.13271

R Development Core Team. (2026) A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria. https://doi.or/10.4236/oalib.1107821

Rayburn, E., & Lozier, J. (2003) A Falling Plate Meter for Estimating Pasture Forage Mass. System, 3.

Reid, A.M., Murphy, B.P., Vigilante, T., Corporation, W.G.A., & Bowman, D.M.J.S. (2023) Pyric herbivory and the nexus between forage, fire and native and introduced large grazing herbivores in Australian tropical savannas. *Ecosystems*, 26(3), 610–626.

Reijers, V.C., Cruijsen, P.M.J.M., Hoetjes, S.C.S., van den Akker, M., Heusinkveld, J.H.T., van de Koppel, J., et al. (2019) Loss of spatial structure after temporary herbivore absence in a high-productivity reed marsh. *Journal of Applied Ecology*, 56(7), 1817–1826. https://doi.or/10.1111/1365-2664.13394

Revell, L.J. (2012) phytools: An R package for phylogenetic comparative biology (and

other things). *Methods in Ecology and Evolution*, 3(2), 217–223. https://doi.or/10.1111/j.2041-210X.2011.00169.x

Rice, S.K. (1993) Vegetation establishment in post-fire Adenostoma chaparral in relation to fine-scale pattern in fire intensity and soil nutrients . *Journal of Vegetation Science*, 4(1), 115–124. https://doi.or/10.2307/3235739

RIO GRANDE DO SUL. (2010) Atlas Climático do Rio Grande do Sul. FEPAGRO: Porto Alegre.

Ripley, B. (2011) MASS: Support Functions and Datasets for Venables and Ripley's MASS, version 7.3-9. http://R-Forge.R-project.org/projects/MASS/. R Cran, 113–120. https://doi.or/10.32614/CRAN.package.MASS

Roberts, D.W., & Roberts, M.D.W. (2012) Package 'labdsv.' Ordin Multivar.

da Rosa, Á.A.S., Kerber, L., Pinheiro, F.L., & Manfroi, J. (2023) A look into the past: fossils from the Campos Sulinos Region. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. *Springer*, 45–81. https://doi.org/10.1007/978-3-031-42580-6_3

Rosenthal, G. (2010) Secondary succession in a fallow central European wet grassland. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 205(3), 153–160. https://doi.or/10.1016/j.flora.2009.02.003

Sankey, T.T. (2012) Woody-herbaceous-livestock species interaction. Ecotones Between Forest and Grassland. *Springer*, 89–114. https://doi.or/10.1007/978-1-4614-3797-0_4

Saraiva, D., Torchelsen, F.P., Overbeck, G.E., Müller, S.C., Hasenack, H., Urruth, L.M., & da Silva, C.R. (2025) Ameaça silenciosa: análise histórica e tendências futuras da supressão dos campos naturais do bioma Pampa pela expansão agrícola. *Bio Diverso*, 5(1).

Schrama, M., Quist, C.W., Arjen De Groot, G., Cieraad, E., Ashworth, D., Laros, I., et al. (2023) Cessation of grazing causes biodiversity loss and homogenization of soil food webs. Proceedings of the Royal Society B: *Biological Sciences*, 290(2011). https://doi.or/10.1098/rspb.2023.1345

da Silva Menezes, L., Vogel Ely, C., Lucas, D.B.D.B., Minervini Silva, G.H., Boldrini, I.I., & Overbeck, G.E. (2018) Plant species richness record in Brazilian Pampa

grasslands and implications. *Revista Brasileira de Botanica*, 41(4), 817–823. https://doi.or/10.1007/s40415-018-0492-6

Silveira, F.A.O., Arruda, A.J., Bond, W., Durigan, G., Fidelis, A., Kirkman, K., et al. (2020) Myth-busting tropical grassy biome restoration. *Restoration Ecology*, 28(5), 1067–1073. https://doi.or/10.1111/rec.13202

Silveira, F. F. (2026). Should I burn or should I graze initial effects in the restoration of abandoned subtropical grasslands. *Zenodo*. https://doi.org/10.5281/zenodo.19653051.

da Silveira, F.F., Menezes, L.S., Porto, A.B., Thomas, P.A., Boavista, L. da R., Seger, G.D.S., & Overbeck, G.E. (2025) Southern Brazilian Grassland Diversity: Anti-Disturbance Regimes Are Not Ideal and Grazing Maintains Plant Diversity. *Applied Vegetation Science*, 28(4). https://doi.or/10.1111/avsc.70049

Silveira, F.A.O., Ordóñez-Parra, C.A., Moura, L.C., Schmidt, I.B., Andersen, A.N., Bond, W., et al. (2022) Biome Awareness Disparity is BAD for tropical ecosystem conservation and restoration. Journal of Applied Ecology, 59(8), 1967–1975.

Staude, I.R., Vélez-Martin, E., Andrade, B.O., Podgaiski, L.R., Boldrini, I.I., Mendonça, M., et al. (2018) Local biodiversity erosion in south Brazilian grasslands under moderate levels of landscape habitat loss. *Journal of Applied Ecology*, 55(3), 1241–1251. https://doi.or/10.1111/1365-2664.13067

Suding, K.N., Gross, K.L., & Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, 19(1), 46–53. https://doi.or/10.1016/j.tree.2003.10.005

Sühs, R.B., Giehl, E.L.H., & Peroni, N. (2020) Preventing traditional management can cause grassland loss within 30 years in southern Brazil. *Scientific Reports*, 10(1), 783. https://doi.or/10.1038/s41598-020-57564-z

Thomas, P.A., Overbeck, G.E., Dutra-Silva, R., Porto, A.B., Rolim, R.G., Minervini-Silva, G.H., et al. (2023) Ecological restoration of Campos Sulinos Grasslands. South Brazilian Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 529–552. https://doi.or/10.1007/978-3-031-42580-6_20

Thomas, P.A., Overbeck, G.E., & Müller, S.C. (2019) Restoration of abandoned subtropical highland grasslands in brazil: Mowing produces fast effects, but hay

transfer does not. *Acta Botanica Brasilica*, 33(3), 405–411. https://doi.or/10.1590/0102-33062018abb0377

Thomas, P.A., Schüler, J., Boavista, L. da R., Torchelsen, F.P., Overbeck, G.E., & Müller, S.C. (2019) Controlling the invader Urochloa decumbens: Subsidies for ecological restoration in subtropical Campos grassland. *Applied Vegetation Science*, 22(1), 96–104. https://doi.or/10.1111/avsc.12407

Turchetto, C., Segatto, A.L.A., & Freitas, L.B. (2023) Plant microevolutionary processes in the campos sulinos: Why do they matter? South Brazilian Grasslands: Ecology and Conservation of the Campos Sulinos. *Springer*, 205–229. https://doi.or/10.1007/978-3-031-42580-6_9

Valkó, O., Venn, S., Zmihorski, M., Biurrun, I., Labadessa, R., & Loos, J. (2018) The challenge of abandonment for the sustainable management of Palaearctic natural and semi-natural grasslands. *Hacquetia*, 17(1), 5–16. https://doi.or/10.1515/hacq-2017-0018

Wickham, H. (2011) Ggplot2. Wiley Interdisciplinary Reviews: *Computational Statistics*, 3(2), 180–185. https://doi.or/10.1002/wics.147

Wickham, H., Bryan, J., Kalicinski, M., Valery, K., Leitienne, C., Colbert, B., et al. (2019) Package 'readxl.' Version, 13(1).

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023) a Grammar of Data Manipulation. https://CRAN. R-project. org/package= dplyr. R package version, 3–4.

Supplementary Materials

Supplementary Material – Table S1 - Mean species richness across treatments from 2022 to 2024, calculated from 50 plots per treatment in three years of study.

Management regime	2022	Δ 2022–2023	2023	Δ 2023–2024	2024
Burned and grazed	16.48	+6.70	23.18	+5.94	29.12
Burned and ungrazed	14.64	+6.26	20.90	+3.20	24.10
Unburned and grazed	16.92	+1.52	18.44	+5.12	23.56
Unburned and ungrazed	12.86	+0.78	13.64	+2.82	16.46

Supplementary Material – Table S2 – Multivariate community composition and diversity index analysis. Multivariate (ADONIS): results from Permutational MANOVA (9,999 permutations) testing management and temporal effects. Linear Hypotheses: pairwise comparisons for the Simpson Index derived from a glmmPQL (Gaussian family). df: degrees of freedom; R^2: coefficient of determination; F: F-statistic (ADONIS); z: z-statistic (Linear Hypotheses). Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; (-) non-significant.

Analysis Type	**Comparison / Contrast**		**df**	**R^2**	**F**	**z**	***p*-value**	**Sig**
Multivariate (ADONIS)	Overall Management & Time Model		11	0.022	1.227	-	0.0001	***
Pairwise ADONIS	Burn Ungrazed	Unburned Ungrazed	9	0.043	1.445	-	0.001	***
	Burn Ungrazed	Burn Grazed	9	0.049	1.675	-	0.001	***
	Unburned Ungrazed	Unburned Grazed	9	0.045	1.505	-	0.001	***
	Burn Grazed	Unburned Grazed	9	0.051	1.726	-	0.001	***
Linear Hypotheses	Unburned Ungrazed	Burn Grazed	-	-	-	-7.400	< 0.001	***
glmmPQL (Simpson Index)	Unburned Ungrazed	Burn Ungrazed	-	-	-	-5.192	< 0.001	***
	Unburned Ungrazed	Unburned Grazed	-	-	-	-4.780	< 0.001	***
	Unburned Grazed	Burn Grazed	-	-	-	-2.619	0.0434	*
	Unburned Grazed	Burn Ungrazed	-	-	-	-0.412	0.9765	-
	Burn Grazed	Burn Ungrazed	-	-	-	2.208	0.1211	-

Supplementary Material – Table S3. Mean vegetation cover, calculated as the sum of individual species cover, and annual net changes (Δ) under different burning and grazing management regimes from 2022 to 2024. Values in the year columns represent the absolute mean percentage of vegetation cover. Delta (Δ) columns, obtained calculated as $\Delta\,\% = \left(\frac{V_n - V_{n-1}}{V_{n-1}}\right) * 100$, indicate the relative percentage change from the previous year; positive and negative values denote increases and decreases in cover, respectively.

Management regime	**2022**	**Δ 2022–2023**	**2023**	**Δ 2023–2024**	**2024**
Burned and grazed	62.9 %	-1.02 %	62.2 %	39.44 %	86.8 %
Burned and ungrazed	64.2 %	9.19 %	70.1 %	18.69 %	83.2 %
Unburned and grazed	63.0 %	-3.02 %	61.1 %	26.51 %	77.3 %
Unburned and ungrazed	62.2 %	3.05 %	64.1 %	3.90 %	66.6 %

Supplementary Material – Table S4. Pairwise comparisons of Simpson's diversity index for the herbaceous community across different management regimes. Estimates, standard errors, and z-values were obtained through Generalized Linear Mixed Models (GLMM) using an inverse Gaussian distribution and log-transformed data. Post-hoc comparisons were performed using the Tukey method. The "Unburned Ungrazed" treatment represents the abandonment control. Significant differences ($p < 0.05$) indicate where management interventions effectively altered herbaceous diversity relative to the control or other treatments.

Contrast (Treatments)	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Sig**
Unburned Ungrazed – Burn Grazed	0.60	0.09	6.756	< 0.001	***
Unburned Ungrazed – Burn Ungrazed	0.44	0.09	4.841	< 0.001	***
Unburned Ungrazed – Unburned Grazed	0.41	0.09	4.507	< 0.001	***
Unburned Grazed – Burn Ungrazed	0.03	0.09	0.340	0.987 (ns)	-
Unburned Grazed – Burn Grazed	0.19	0.08	2.267	0.106 (ns)	-
Burn Grazed – Burn Ungrazed	-0.16	0.08	-1.932	0.215 (ns)	-

Supplementary Material – Table S5. Summary of the Generalized Linear Mixed Model (GLMM) pairwise comparisons for plant cover and species richness. Contrast indicates the specific treatment comparison; Context identifies the fixed condition under which the contrast was tested; Time represents the sampling years (2022–2024). Estimate reflects the magnitude of the difference between levels on the link scale (logit for cover, log for richness); SE is the Standard Error of the estimate. The z-ratio represents the test statistic (estimate divided by SE) used to determine the p-value. Significance levels (Sig) are denoted as: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; (-) non-significant. The model includes an interaction between factors, random effects for nested experimental units, and an AR1 autoregressive temporal correlation structure.

Response Variable	Contrast	Context	Time	Estimate (± SE)	z ratio	*p*-value	Sig
Cover	Burn - Unburned	Grazed	2022	-0.056 (0.146)	-0.39	0.7	-
			2023	0.116 (0.146)	0.791	0.429	-
			2024	0.453 (0.155)	2.932	0.0034	**
		Ungrazed	2022	0.272 (0.145)	1.872	0.0612	-
			2023	0.656 (0.146)	4.501	< 0.001	***
			2024	0.584 (0.165)	3.544	< 0.001	***
	Grazed – Ungrazed	Burn	2022	-0.258 (0.145)	-1.779	0.0753	-
			2023	-0.528 (0.146)	-3.610	< 0.001	***
			2024	0.442 (0.166)	2.664	0.0077	**
		Unburned	2022	0.070 (0.146)	0.479	0.6318	-
			2023	0.012 (0.146)	0.085	0.9321	-
			2024	0.572 (0.160)	3.584	< 0.001	***
Richness	Burn - Unburned	Grazed	2022	-0.027 (0.057)	-0.48	0.6338	-
			2023	0.228 (0.053)	4.293	< 0.001	***
			2024	0.202 (0.049)	4.095	< 0.001	***
		Ungrazed	2022	0.123 (0.061)	1.995	0.046	*
			2023	0.422 (0.057)	7.353	< 0.001	***
			2024	0.418 (0.059)	7.065	< 0.001	***
	Grazed – Ungrazed	Burn	2022	0.117 (0.059)	2.003	0.0451	*
			2023	0.099 (0.052)	1.903	0.0571	-
			2024	0.183 (0.052)	3.490	< 0.001	***
		Unburned	2022	0.267 (0.060)	4.458	< 0.001	***
			2023	0.293 (0.059)	4.997	< 0.001	***
			2024	0.398 (0.058)	6.844	< 0.001	***

Supplementary Material – Table S6**.** Pairwise comparisons (Tukey's HSD post-hoc) of multivariate homogeneity of groups dispersions (*betadisper*) for herbaceous life-form composition across different management regimes and years (2022–2024). The dissimilarity matrix was calculated using the Phylosor index (abundance-based), derived from a functional dendrogram constructed using life-history traits (e.g., life cycle, lignification, and branching architecture). Significant p-values ($p < 0.05$) are highlighted in bold.

Comparison	**Comparison**	**Lower CL**	**Upper CL**	**p-value**
Burn Ungrazed-2024	Burn Ungrazed-2022	-0.05	-0.11	**0.00**
Unburned Grazed-2022	Burn Ungrazed-2022	-0.04	-0.09	**0.02**
Burn Ungrazed-2023	Burn Ungrazed-2022	-0.03	-0.08	**0.02**
Burn Grazed-2024	Burn Grazed-2022	-0.02	-0.08	**0.03**
Burn Ungrazed-2024	Burn Ungrazed-2023	-0.02	-0.08	**0.03**
Burn Grazed-2024	Burn Grazed-2023	-0.02	-0.07	**0.03**
Unburned Grazed-2024	Unburned Grazed-2023	-0.02	-0.07	**0.03**
Unburned Grazed-2022	Burn Grazed-2022	-0.01	-0.06	**0.05**
Unburned Ungrazed-2024	Unburned Ungrazed-2022	0.00	-0.06	**0.05**
Burn Grazed-2023	Burn Grazed-2022	0.00	-0.06	**0.05**
Unburned Ungrazed-2024	Unburned Ungrazed-2023	0.00	-0.06	**0.05**
Unburned Ungrazed-2023	Unburned Ungrazed-2022	0.00	-0.05	**0.05**
Unburned Grazed-2024	Unburned Grazed-2022	0.00	-0.05	**0.05**
Unburned Ungrazed-2022	Burn Ungrazed-2022	0.00	-0.05	**0.05**
Burn Ungrazed-2024	Burn Grazed-2024	0.00	-0.05	0.06
Burn Ungrazed-2023	Burn Grazed-2023	0.01	-0.05	0.06
Unburned Grazed-2023	Burn Ungrazed-2023	0.01	-0.04	0.06
Unburned Grazed-2024	Burn Ungrazed-2024	0.02	-0.04	0.07
Unburned Grazed-2023	Burn Grazed-2023	0.02	-0.04	0.07
Unburned Grazed-2024	Burn Grazed-2024	0.02	-0.03	0.07
Unburned Grazed-2023	Unburned Grazed-2022	0.02	-0.03	0.07
Unburned Ungrazed-2023	Unburned Grazed-2023	0.02	-0.03	0.07
Burn Ungrazed-2022	Burn Grazed-2022	0.03	-0.02	0.08
Unburned Ungrazed-2023	Burn Ungrazed-2023	0.03	-0.02	0.08
Unburned Ungrazed-2022	Burn Grazed-2022	0.03	-0.02	0.09
Unburned Ungrazed-2024	Unburned Grazed-2024	0.03	-0.02	0.09
Unburned Ungrazed-2023	Burn Grazed-2023	0.04	-0.02	0.09
Unburned Ungrazed-2022	Unburned Grazed-2022	0.04	-0.01	0.09
Unburned Ungrazed-2024	Burn Ungrazed-2024	0.05	0.00	0.10
Unburned Ungrazed-2024	Burn Grazed-2024	0.05	0.00	0.10

Supplementary Material – Table S7. Relative cover (%) of plant life forms under different managements from 2022 to 2024.

Life Form	Burn Grazed			Burn Ungrazed			Unburned Grazed			Unburned Ungrazed		
	2022	2023	2024	2022	2023	2024	2022	2023	2024	2022	2023	2024
Bulbous Geophyte	0.15	3.00	1.32	0.25	1.92	0.93	0.06	0.75	1.13	0.26	0.43	0.68
Climber	0.46	0.35	0.18	0.28	1.22	0.98	1.16	0.97	0.90	0.80	0.52	1.27
Climber Lignified	0.03	0.00	0.02	0.12	0.06	0.02	0.00	0.06	0.00	0.70	0.34	0.30
Connected Tussock	6.65	5.77	9.45	5.36	8.85	6.90	3.83	8.18	7.86	2.21	1.78	2.67
Decumbent	6.19	9.47	5.61	4.63	6.79	4.19	3.77	4.51	5.34	2.75	4.92	6.34
Herbaceous Forb	3.53	5.33	4.62	3.13	6.96	4.17	4.93	4.12	4.42	2.97	2.92	3.11
Lignified Forb	5.72	4.56	7.56	3.83	6.00	6.33	7.00	4.35	5.03	5.50	7.78	8.85
Rhizomatous	1.39	1.53	1.08	1.84	1.64	1.86	0.97	1.43	1.36	4.70	4.03	4.56
Rosette	9.77	12.66	11.78	8.86	12.31	8.26	15.85	14.06	14.18	6.90	5.47	6.84
Shrub	12.77	5.71	6.28	13.70	7.72	10.69	7.69	10.78	7.24	15.40	9.90	15.31
Solitary Tussock	39.81	38.15	32.35	43.00	31.06	34.86	39.83	41.46	34.57	36.43	36.70	30.44
Stoloniferous	0.65	4.40	9.13	0.74	3.59	5.62	0.38	2.14	5.52	0.86	1.94	2.69
Subshrub	6.09	4.56	5.07	5.91	7.36	7.10	4.93	3.08	3.80	3.23	3.60	3.14
Therophyte	0.03	0.16	0.13	0.00	0.31	0.02	0.06	0.10	0.18	0.00	0.06	0.03
Therophyte Tussock	0.00	0.03	0.11	0.03	0.06	0.00	0.00	0.06	0.10	0.00	0.03	0.00
Tree	6.03	1.69	2.04	7.51	2.55	6.93	8.66	3.18	7.42	17.03	19.43	13.68
Xylopodium Geophyte	0.71	2.62	3.25	0.83	1.61	1.14	0.88	0.75	0.92	0.26	0.15	0.09

Supplementary Material – Table S8. Variation of relative cover (%) of plant life forms under different managements from 2022 to 2024.

Life Form	Burn Grazed		Burn Ungrazed		Unburned Grazed		Unburned Ungrazed	
	Δ 2022-2023	Δ 2023-2024	Δ 2022-2023	Δ 2023-2024	Δ 2022-2023	Δ 2023-2024	Δ 2022-2023	Δ 2023-2024
Bulbous Geophyte	2.85	-1.68	1.67	-0.99	0.69	0.38	0.17	0.25
Climber	-0.11	-0.17	0.94	-0.24	-0.19	-0.07	-0.28	0.75
Climber Lignified	-0.03	0.02	-0.06	-0.04	0.06	-0.06	-0.36	-0.04
Connected Tussock	-0.88	3.68	3.49	-1.95	4.35	-0.32	-0.43	0.89
Decumbent	3.28	-3.86	2.16	-2.6	0.74	0.83	2.17	1.42
Herbaceous Forb	1.80	-0.71	3.83	-2.79	-0.81	0.30	-0.05	0.19
Lignified Forb	-1.16	3.00	2.17	0.33	-2.65	0.68	2.28	1.07
Rhizomatous	0.14	-0.45	-0.20	0.22	0.46	-0.07	-0.67	0.53
Rosette	2.89	-0.88	3.45	-4.05	-1.79	0.12	-1.43	1.37
Shrub	-7.06	0.57	-5.98	2.97	3.09	-3.54	-5.5	5.41
Solitary Tussock	-1.66	-5.80	-11.94	3.80	1.63	-6.89	0.27	-6.26
Stoloniferous	3.75	4.73	2.85	2.03	1.76	3.38	1.08	0.75
Subshrub	-1.53	0.51	1.45	-0.26	-1.85	0.72	0.37	-0.46
Therophyte	0.13	-0.03	0.31	-0.29	0.04	0.08	0.06	-0.03
Therophyte Tussock	0.03	0.08	0.03	-0.06	0.06	0.04	0.03	-0.03
Tree	-4.34	0.35	-4.96	4.38	-5.48	4.24	2.40	-5.75
Xylopodium Geophyte	1.91	0.63	0.78	-0.47	-0.13	0.17	-0.11	-0.06

Supplementary Material – Table S9 - Functional traits and vital attributes of the plant species. The table presents the classification of the studied species based on taxonomic identity and six functional categorical traits. Family and Species indicate taxonomic classification. Life Form describes the general growth habit. Life Cycle indicates the strategy of temporal persistence (e.g., perennial). Shoot Persist (Shoot Persistence) refers to the leaf maintenance strategy throughout the year (e.g., evergreens). Shoot Lignification distinguishes between herbaceous and woody tissues. Space Occupation describes the spatial growth form (e.g., erect, prostrate, or rosettes). Branch Architecture details the structural arrangement of the shoots (e.g., non-graminoid, nodes or compact).

Family	Species	Life Form	Life Cycle	Shoot Persist	Shoot Lignification	Space Occupation	Branch Architecture
Acanthaceae	*Hygrophila costata* Nees & T. Nees	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Acanthaceae	*Justicia axillaris* (Nees) Lindau	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Acanthaceae	*Ruellia angustiflora* (Nees) Lindau ex Rambo	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Acanthaceae	*Ruellia hypericoides* (Nees) Lindau	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Acanthaceae	*Ruellia morongii* Britton	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Acanthaceae	*Stenandrium dulce* (Cav.) Nees	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Amaranthaceae	*Gomphrena graminea* Moq.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Amaranthaceae	*Pfaffia tuberosa* (Spreng.) Hicken	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Amaryllidaceae	*Nothoscordum bivalve* (L.) Britton	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Amaryllidaceae	*Zephyranthes coerulea* (Griseb.) Baker	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Anacardiaceae	*Lithraea brasiliensis* Marchand	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Anacardiaceae	*Schinus terebinthifolia* Raddi	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Anemiaceae	*Anemia phyllitidis* (L.) Sw.	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Anemiaceae	*Anemia tomentosa* (Sav.) Sw.	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Apiaceae	*Centella asiatica* (L.) Urb.	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Apiaceae	*Cyclospermum leptophyllum* (Pers.) Sprague ex Britton & P.Wilson	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Apiaceae	*Eryngium ciliatum* Cham. & Schltdl.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact

Apiaceae	*Eryngium ebracteatum* Lam.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Apiaceae	*Eryngium elegans* Cham. & Schltdl.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Apiaceae	*Eryngium horridum* Malme	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Apiaceae	*Eryngium nudicaule* Lam.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Apiaceae	*Eryngium sanguisorba* Cham. & Schltdl.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Apocynaceae	*Forsteronia glabrescens* Müll.Arg.	Climber Lignified	Perennial	Evergreens	Lignified	Active Climbing	slender
Apocynaceae	*Orthosia scoparia* (Nutt.) Liede & Meve	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Apocynaceae	*Oxypetalum solanoides* Hook. & Arn.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Apocynaceae	*Oxypetalum tomentosum* Wight ex Hook. & Arn.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Apocynaceae	*Prestonia coalita* (Vell.) Woodson	Climber Lignified	Perennial	Evergreens	Lignified	Active Climbing	slender
Araliaceae	*Hydrocotyle bonariensis* Lam.	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Araliaceae	*Hydrocotyle exigua* (Urb.) Malme	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Arecaceae	*Syagrus romanzoffiana* (Cham.) Glassman	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Aristolochiaceae	*Aristolochia sessilifolia* (Klotzsch) Duch.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Asparagaceae	*Clara ophiopogonoides* Kunth	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Achyrocline flaccida* (Weinm.) DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Achyrocline satureioides* (Lam.) DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Ageratum conyzoides* L.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Aspilia montevidensis* (Spreng.) Kuntze	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Asteraceae	*Austroeupatorium inulaefolium* (Kunth) R.M.King & H.Rob.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Baccharis anomala* DC.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent

Asteraceae	*Baccharis articulata* (Lam.) Pers.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Baccharis caprariifolia* DC.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Baccharis coridifolia* DC.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Baccharis crispa* Spreng.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Baccharis dracunculifolia* DC.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Baccharis junciformis* DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Baccharis megapotamica* Spreng.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Baccharis psiadioides* (Less.) Joch.Müll.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Baccharis riograndensis* Malag. & J.Vidal	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Baccharis salicifolia* (Ruiz & Pav.) Pers.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Baccharis spicata* (Lam.) Baill.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Calea pinnatifida* (R.Br.) Less.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Asteraceae	*Campovassouria cruciata* (Vell.) R.M.King & H.Rob.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Campuloclinium macrocephalum* (Less.) DC.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Chaptalia integerrima* (Vell.) Burkart	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Chaptalia piloselloides* (Vahl) Baker	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Chevreulia acuminata* Less.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Chromolaena congesta* (Hook. & Arn.) R.M.King & H.Rob.	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Asteraceae	*Chromolaena hirsuta* (Hook. & Arn.) R.M.King & H.Rob.	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Asteraceae	*Chromolaena ivifolia* (L.) R.M.King & H.Rob.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent

Asteraceae	*Chromolaena laevigata* (Lam.) R.M.King & H.Rob.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Chromolaena pedunculosa* (Hook. & Arn.) R.M.King & H.Rob.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Chromolaena squarrulosa* (Hook. & Arn.) R.M.King & H.Rob.	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Asteraceae	*Chrysolaena flexuosa* (Sims) H.Rob.	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Asteraceae	*Conyza bonariensis* (L.) Cronquist	Therophyte	Bi/Annual	Bi/Annual	Herbaceous	Erect	non graminoid
Asteraceae	*Disynaphia ligulifolia* (Hook. & Arn.) R.M.King & H.Rob.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Eclipta megapotamica* (Spreng.) Sch.Bip. ex S.F.Blake	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Elephantopus mollis* Kunth	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Erechtites hieracifolius* (L.) Raf. ex DC.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Erechtites valerianifolius* (Link ex Spreng.) DC.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Facelis retusa* (Lam.) Sch.Bip.	Therophyte	Bi/Annual	Bi/Annual	Herbaceous	Erect	non graminoid
Asteraceae	*Gamochaeta americana* (Mill.) Wedd.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Gamochaeta pensylvanica* (Willd.) Cabrera	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Grazielia intermedia* (DC.) R.M.King & H.Rob.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Grazielia serrata* (Spreng.) R.M.King & H.Rob.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Gyptis tanacetifolia* (Gillies ex Hook. & Arn.) D.J.N. Hind & Flann	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Asteraceae	*Jungia floribunda* Less.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Jungia sellowii* Less.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent

Asteraceae	*Lessingianthus brevifolius* (Less.) H.Rob.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Lessingianthus rubricaulis* (Humb. & Bonpl.) H.Rob.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Lucilia acutifolia* (Poir.) Cass.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Lucilia nitens* Less.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Mikania cordifolia* (L.f.) Willd.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Asteraceae	*Mikania cynanchifolia* Hook. & Arn. ex B.L.Rob.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Asteraceae	*Mikania viminea* DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Moquiniastrum cordatum* (Less.) G. Sancho	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Moquiniastrum polymorphum* (Less.) G. Sancho	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Mutisia coccinea* A.St.-Hil.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Asteraceae	*Mutisia speciosa* Aiton ex Hook.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Asteraceae	*Neocabreria serrulata* (DC.) R.M.King & H.Rob.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Orthopappus angustifolius* (Sw.) Gleason	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Pamphalea heterophylla* Less.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Pluchea laxiflora* Hook. & Arn. ex Baker	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Porophyllum ruderale* (Jacq.) Cass.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Pterocaulon alopecuroides* (Lam.) DC.	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Asteraceae	*Pterocaulon angustifolium* DC.	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Asteraceae	*Pterocaulon balansae* Chodat	Therophyte	Bi/Annual	Bi/Annual	Herbaceous	Erect	non graminoid
Asteraceae	*Pterocaulon rugosum* (Vahl) Malme	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent

Asteraceae	*Schlechtendalia luzulifolia* Less.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Asteraceae	*Senecio brasiliensis* (Spreng.) Less.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Senecio heterotrichius* DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Senecio leptolobus* DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Senecio madagascariensis* Poir.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Asteraceae	*Senecio selloi* (Spreng.) DC.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Solidago chilensis* Meyen	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Sonchus oleraceus* L.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Stenachaenium campestre* Baker	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Stenachaenium megapotamicum* (Spreng.) Baker	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Stenachaenium riedelii* Baker	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Stenocephalum megapotamicum* (Spreng.) Sch.Bip.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Asteraceae	*Verbesina sordescens* DC.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Asteraceae	*Vernonanthura nudiflora* (Less.) H.Rob.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Asteraceae	*Vernonanthura tweediana* (Baker) H.Rob.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Begoniaceae	*Begonia cucullata* var. arenosicola (C.DC.) L.B.Sm. & B.G.Schub.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Bromeliaceae	*Bromelia antiacantha* Bertol.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Bromeliaceae	*Dyckia remotiflora* Otto & A.Dietr.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Campanulaceae	*Wahlenbergia linarioides* (Lam.) DC.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid

Cardiopteridaceae	*Citronella gongonha* (Mart.) R.A.Howard	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Celastraceae	*Monteverdia ilicifolia* (Mart. ex Reissek) Biral	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Cistaceae	*Crocanthemum brasiliensis* Spach	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Commelinaceae	*Commelina erecta* L.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Commelinaceae	*Commelina platyphylla* Klotzsch ex Seub.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Convolvulaceae	*Dichondra macrocalyx* Meisn.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Convolvulaceae	*Dichondra sericea* Sw.	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Convolvulaceae	*Evolvulus sericeus* Sw.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Cyperaceae	*Bulbostylis communis* M.G. López & D.A. Simpson	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Bulbostylis juncoides* (Vahl) Kük. ex Osten	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Carex meridionalis* (Kük.) Herter	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Carex phalaroides* Kunth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Carex sororia* Kunth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Cyperus aggregatus* (Willd.) Endl.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Cyperus brevifolius* (Rottb.) Endl. ex Hassk.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Cyperus distans* L.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Cyperus haspan* L.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Cyperus lanceolatus* Poir.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Cyperus reflexus* Vahl	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Eleocharis maculosa* (Vahl) Roem. & Schult.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Eleocharis viridans* Kük. ex Osten	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid

Cyperaceae	*Rhynchospora barrosiana* Guagl.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Rhynchospora brittonii* Gale	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Rhynchospora megapotamica* (A.Spreng.) H.Pfeiff.	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Cyperaceae	*Rhynchospora setigera* (Kunth) Griseb.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Rhynchospora tenuis* Link	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Scleria balansae* Maury ex Micheli	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Scleria distans* Poir.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Cyperaceae	*Scleria hirtella* Sw.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Dryopteridaceae	*Rumohra adiantiformis* (G.Forst.) Ching	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Euphorbiaceae	*Bernardia multicaulis* Müll.Arg.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Euphorbiaceae	*Croton gnaphalii* Baill.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Euphorbiaceae	*Croton pycnocephalus* Müll.Arg.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Euphorbiaceae	*Euphorbia selloi* (Klotzsch & Garcke) Boiss.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Euphorbiaceae	*Gymnanthes klotzschiana* Müll.Arg.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Euphorbiaceae	*Tragia bahiensis* Müll.Arg.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Fabaceae	*Betencourtia gracillima* (Benth.) L.P.Queiroz	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Fabaceae	*Betencourtia neesii* (DC.) L.P.Queiroz	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Centrosema virginianum* (L.) Benth.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Fabaceae	*Chamaecrista repens* (Vogel) H.S.Irwin & Barneby	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent

Fabaceae	*Clitoria nana* Benth.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Fabaceae	*Crotalaria tweediana* Benth.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Fabaceae	*Ctenodon falcatus* (Poir.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Fabaceae	*Desmanthus tatuhyensis* Hoehne	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Desmanthus virgatus* (L.) Willd.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Desmodium adscendens* (Sw.) DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Desmodium barbatum* (L.) Benth.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Desmodium incanum* (Sw.) DC.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Macroptilium prostratum* (Benth.) Urb.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Fabaceae	*Nanogalactia heterophylla* (Gillies ex Hook. & Arn.) L.P.Queiroz	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Fabaceae	*Pomaria pilosa* (Vogel) B.B.Simpson & G.P.Lewis	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Rhynchosia diversifolia* Micheli	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Fabaceae	*Stylosanthes leiocarpa* Vogel	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Stylosanthes montevidensis* Vogel	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Fabaceae	*Zornia burkartii* Vanni	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Gesneriaceae	*Sinningia allagophylla* (Mart.) Wiehler	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Gesneriaceae	*Sinningia elatior* (Kunth) Chautems	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Hypericaceae	*Hypericum caprifoliatum* Cham. & Schltdl.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Hypoxidaceae	*Hypoxis decumbens* L.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Iridaceae	*Cypella herbertii* (Lindl.) Herb.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid

Iridaceae	*Cypella pusilla* (Link & Otto) Benth. & Hook.f. ex B.D.Jacks.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Iridaceae	*Herbertia lahue* (Molina) Goldblatt	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Iridaceae	*Sisyrinchium micranthum* Cav.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Iridaceae	*Sisyrinchium sellowianum* Klatt	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Iridaceae	*Sisyrinchium vaginatum* Spreng.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Iridaceae	*Sisyrinchium wettsteinii* Hand.-Mazz.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Juncaceae	*Juncus microcephalus* Kunth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Juncaceae	*Juncus scirpoides* Lam.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Lamiaceae	*Cantinoa mutabilis* (Rich.) Harley & J.F.B.Pastore	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Lamiaceae	*Condea floribunda* (Briq. ex Micheli) Harley & J.F.B.Pastore	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Lamiaceae	*Cunila fasciculata* Benth.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Lamiaceae	*Hyptis comaroides* (Briq.) Harley & J.F.B.Pastore	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Lamiaceae	*Hyptis lorentziana* O.Hoffm.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Lamiaceae	*Stachys arvensis* L.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Lauraceae	*Ocotea pulchella* (Nees & Mart.) Mez	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Linaceae	*Cliococca selaginoides* (Lam.) C.M. Rogers & Mildner	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Lythraceae	*Cuphea glutinosa* Cham. & Schltdl.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Lythraceae	*Heimia apetala* (Spreng.) S.A.Graham & Gandhi	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid

Malpighiaceae	*Janusia guaranitica* (A.St.-Hil.) A.Juss.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Malvaceae	*Krapovickasia flavescens* (Cav.) Fryxell	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Malvaceae	*Krapovickasia macrodon* (A.DC.) Fryxell	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Malvaceae	*Pavonia hastata* Cav.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Malvaceae	*Sida rhombifolia* L.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Malvaceae	*Triumfetta bartramia* L.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Malvaceae	*Waltheria communis* A.St.-Hil.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Malvaceae	*Wissadula glechomifolia* (A.St.-Hil.) R.E.Fr.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Melastomataceae	*Chaetogastra gracilis* (Bonpl.) DC.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Melastomataceae	*Leandra australis* (Cham.) Cogn.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Melastomataceae	*Pleroma asperius* (Cham.) Triana	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Moraceae	*Dorstenia brasiliensis* Lam.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O.Berg	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Campomanesia aurea* O.Berg	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Eugenia hiemalis* Cambess.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Eugenia uniflora* L.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Eugenia uruguayensis* Cambess.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Myrcia cuspidata* (Mart. ex DC.) A.R.Lourenço & E.Lucas	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Myrcia glabra* (O.Berg) D.Legrand	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Myrcia multiflora* (Lam.) DC.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Myrcia palustris* DC.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent

Myrtaceae	*Myrciaria cuspidata* O.Berg	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Psidium cattleyanum* Sabine	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Myrtaceae	*Psidium salutare* (Kunth) O.Berg	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Onagraceae	*Ludwigia multinervia* (Hook. & Arn.) Ramamoorthy	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Orchidaceae	*Aspidogyne bidentifera* (Schltr.) Garay	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Orchidaceae	*Habenaria araneiflora* Barb.Rodr.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Orchidaceae	*Habenaria parviflora* Lindl.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Orchidaceae	*Prescottia densiflora* (Brongn.) Lindl.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Orobanchaceae	*Buchnera integrifolia* Larrañaga	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Orobanchaceae	*Castilleja arvensis* Schltdl. & Cham.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Oxalidaceae	*Oxalis bipartita* A.St.-Hil.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Oxalidaceae	*Oxalis brasiliensis* G.Lodd.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Oxalidaceae	*Oxalis conorrhiza* Jacq.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Oxalidaceae	*Oxalis eriocarpa* DC.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Oxalidaceae	*Oxalis floribunda* Lehm.	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Oxalidaceae	*Oxalis perdicaria* (Molina) Bertero	Bulbous Geophyte	Perennial	Geophyte	Herbaceous	Erect	graminoid
Passifloraceae	*Passiflora misera* Kunth	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Pinaceae	*Pinus* sp.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Plantaginaceae	*Mecardonia procumbens* (Mill.) Small	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Plantaginaceae	*Plantago myosuros* Lam.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact
Plantaginaceae	*Plantago tomentosa* Lam.	Rosette	Perennial	Evergreens	Herbaceous	Rosettes	compact

Poaceae	*Andropogon lateralis* Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Andropogon ternatus* (Spreng.) Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Anthaenantia lanata* (Kunth) Benth.	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Poaceae	*Aristida filifolia* (Arechav.) Herter	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Aristida flaccida* Trin. & Rupr.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Aristida jubata* (Arechav.) Herter	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Aristida laevis* (Nees) Kunth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Aristida setifolia* Kunth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Aristida venustula* Arechav.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Axonopus affinis* Chase	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Poaceae	*Axonopus argentinus* Parodi	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Chascolytrum calotheca* (Trin.) L. Essi, Longhi-Wagner & Souza-Chies	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Chascolytrum lamarckianum* (Nees) Matthei	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Chascolytrum poomorphum* (J. Presl) L. Essi, Longhi-Wagner & Souza-Chies	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Chascolytrum rufum* J.Presl	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Chascolytrum subaristatum* (Lam.) Desv.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Chascolytrum uniolae* (Nees) L. Essi, Longhi-Wagner & Souza-Chies	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Cinnagrostis viridiflavescens* (Poir.) P.M. Peterson, Soreng, Romasch. & Barberá	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Coleataenia prionitis* (Nees) Soreng	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid

Poaceae	*Cynodon dactylon* (L.) Pers.	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Poaceae	*Danthonia cirrata* Hack. & Arechav.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Danthonia secundiflora* J.Presl	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Dichanthelium sabulorum* (Lam.) Gould & C.A. Clark	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Poaceae	*Digitaria phaeothrix* (Trin.) Parodi	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Elionurus muticus* (Spreng.) Kuntze	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Eragrostis airoides* Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Eragrostis bahiensis* Schrad. ex Schult.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Eragrostis lugens* Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Eragrostis neesii* Trin.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Eragrostis plana* Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Eragrostis polytricha* Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Eriochrysis cayennensis* P.Beauv.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Gymnopogon burchellii* (Munro ex Döll) Ekman	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Hymenachne grumosa* (Nees) Zuloaga	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Imperata brasiliensis* Trin.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Jarava filifolia* (Nees) Ciald.	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Leersia hexandra* Sw.	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Poaceae	*Luziola peruviana* Juss. ex J.F.Gmel.	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Poaceae	*Melica brasiliana* Ard.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Melinis repens* (Willd.) Zizka	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid

Poaceae	*Mnesithea selloana* (Hack.) de Koning & Sosef	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Nassella filiculmis* (Delile)Barkworth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Nassella melanosperma* (J. Presl) Barkworth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Nassella neesiana* (Trin. & Rupr.) Barkworth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Nassella nutans* (Hack.) Barkworth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Panicum aquaticum* Poir.	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Poaceae	*Paspalum exaltatum* J.Presl	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum ionanthum* Chase	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum maculosum* Trin.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum nicorae* Parodi	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum notatum* Flüggé	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Poaceae	*Paspalum paniculatum* L.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum plicatulum* Michx.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum polyphyllum* Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum umbrosum* Trin.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Paspalum urvillei* Steud.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Piptochaetium bicolor* (Vahl) Desv.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Piptochaetium lasianthum* Griseb.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Piptochaetium montevidense* (Spreng.) Parodi	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Piptochaetium ruprechtianum* Desv.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Piptochaetium stipoides* (Trin. & Rupr.) Hack. ex Arechav.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid

Poaceae	*Polypogon elongatus* Kunth	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Saccharum angustifolium* (Nees) Trin.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Sacciolepis vilvoides* (Trin.) Chase	Therophyte Tussock	Bi/Annual	Bi/Annual	Herbaceous	Erect	graminoid
Poaceae	*Schizachyrium condensatum* (Kunth) Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Schizachyrium imberbe* A.Camus	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Schizachyrium microstachyum* (Desv. ex Ham.) Roseng., B.R.Arrill. & Izag.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Schizachyrium spicatum* (Spreng.) Herter	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Schizachyrium tenerum* Nees	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Setaria parviflora* (Poir.) Kerguélen	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Setaria vaginata* Spreng.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Sorghastrum pellitum* (Hack.) Parodi	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Sorghastrum setosum* (Griseb.) Hitchc.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Steinchisma decipiens* (Nees ex Trin.) W.V.Br.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Steinchisma hians* (Elliott) Nash	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Urochloa decumbens* (Stapf) R.D.Webster	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Urochloa mutica* (Forssk.) T.Q.Nguyen	Connected Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Poaceae	*Vulpia myuros* (L.) C.C.Gmel.	Therophyte Tussock	Bi/Annual	Bi/Annual	Herbaceous	Erect	graminoid
Polygalaceae	*Asemeia extraaxillaris* (Chodat) J.F.B.Pastore & J.R.Abbott	Therophyte	Bi/Annual	Bi/Annual	Herbaceous	Erect	non graminoid
Polygalaceae	*Monnina oblongifolia* Arechav.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent

Polygalaceae	*Senega adenophylla* (A.St.-Hil. & Moq.) J.F.B.Pastore	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Polygalaceae	*Senega australis* (A.W.Benn.) J.F.B.Pastore	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Polygalaceae	*Senega pumila* (Norlind) J. F. B. Pastore	Xylopodium Geophyte	Perennial	Geophyte	Lignified	Erect	non suffrutescent
Primulaceae	*Myrsine coriacea* (Sw.) R.Br. ex Roem. & Schult.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Primulaceae	*Myrsine parvula* (Mez) Otegui	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Pteridaceae	*Adiantopsis chlorophylla* (Sw.) Fée	Rhizomatous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Rubiaceae	*Borreria capitata* (Ruiz & Pav.) DC.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Rubiaceae	*Borreria dasycephala* (Cham. & Schltdl.) Bacigalupo & E.L.Cabral	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Rubiaceae	*Borreria verticillata* (L.) G.Mey.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Rubiaceae	*Coccocypselum capitatum* (Graham) C.B.Costa & Mamede	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Rubiaceae	*Galianthe fastigiata* Griseb.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Rubiaceae	*Galium equisetoides* (Cham. & Schltdl.) Standl.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Rubiaceae	*Galium hirtum* Lam.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Rubiaceae	*Galium humile* Cham. & Schltdl.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Rubiaceae	*Galium hypocarpium* (L.) Endl. ex Griseb.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Rubiaceae	*Galium noxium* (A.St.-Hil.) Dempster	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Rubiaceae	*Galium richardianum* (Gillies ex Hook. & Arn.) Endl. ex Walp.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Rubiaceae	*Richardia brasiliensis* Gomes	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting

Rubiaceae	*Richardia grandiflora* (Cham. & Schltdl.) Steud.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Rubiaceae	*Richardia humistrata* (Cham. & Schltdl.) Steud.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Rubiaceae	*Richardia stellaris* (Cham. & Schltdl.) Steud.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Rubiaceae	*Spermacoce eryngioides* (Cham. & Schltdl.) Kuntze	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Rutaceae	*Zanthoxylum fagara* (L.) Sarg.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Rutaceae	*Zanthoxylum rhoifolium* Lam.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Salicaceae	*Casearia decandra* Jacq.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Salicaceae	*Casearia sylvestris* Sw.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Sapindaceae	*Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Sapindaceae	*Cupania vernalis* Cambess.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Sapindaceae	*Dodonaea viscosa* Jacq.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Sapindaceae	*Matayba elaeagnoides* Radlk.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent
Selaginellaceae	*Selaginella muscosa* Spring	Stoloniferous	Perennial	Evergreens	Herbaceous	Prostrate	nodes rooting
Smilacaceae	*Smilax campestris* Griseb.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Solanaceae	*Solanum americanum* Mill.	Subshrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Solanaceae	*Solanum laxum* Spreng.	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Solanaceae	*Solanum mauritianum* Scop.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Solanaceae	*Solanum pseudocapsicum* L.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Solanaceae	*Solanum viarum* Dunal	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Symplocaceae	*Symplocos uniflora* (Pohl) Benth.	Tree	Perennial	Evergreens	Lignified	Erect	suffrutescent

Turneraceae	*Piriqueta selloi* Urb.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Turneraceae	*Piriqueta taubatensis* (Urb.) Arbo	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Turneraceae	*Turnera sidoides* L.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Urticaceae	*Boehmeria caudata* Sw.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Verbenaceae	*Glandularia marrubioides* (Cham.) Tronc.	Decumbent	Perennial	Evergreens	Herbaceous	Prostrate	nodes no rooting
Verbenaceae	*Lantana fucata* Lindl.	Shrub	Perennial	Evergreens	Lignified	Erect	suffrutescent
Verbenaceae	*Lippia hieraciifolia* Cham.	Lignified Forb	Perennial	Evergreens	Lignified	Erect	non suffrutescent
Verbenaceae	*Verbena litoralis* Kunth	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Verbenaceae	*Verbena sagittalis* Cham.	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Violaceae	*Anchietea pyrifolia* (Mart.) G.Don	Climber Lignified	Perennial	Evergreens	Lignified	Active Climbing	slender
Violaceae	*Pombalia bicolor* (A.St-Hil.) Paula-Souza	Herbaceous Forb	Perennial	Evergreens	Herbaceous	Erect	non graminoid
Vitaceae	*Clematicissus striata* (Ruiz & Pav.) Lombardi	Climber	Perennial	Evergreens	Herbaceous	Active Climbing	slender
Xyridaceae	*Xyris guaranitica* Malme	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid
Xyridaceae	*Xyris jupicai* Rich.	Solitary Tussock	Perennial	Evergreens	Herbaceous	Erect	graminoid

Capítulo III

Burned to Grow, Too Grazed to Stay: Deciphering the Control of Woody Encroachment in Native Grasslands

Filipe Ferreira da Silveira

Title: Burned to Grow, Too Grazed to Stay: Deciphering the Control of Woody Encroachment in Native Grasslands

Short title: Burn and graze effects on woody encroachment

Filipe F. da Silveira[1], Francieli P. da Silveira[1], William S. Piovesani, Mateus Henrique Schenkel[1], Guilherme D. S. Seger[1], Gerhard E. Overbeck[1,2].

[1] Graduate Program in Botany, Universidade Federal do Rio Grande do Sul, Brazil.
[2] Graduate Program in Ecology, Universidade Federal do Rio Grande do Sul, Brazil.

Authors and ORCID
Filipe Ferreira da Silveira - 0000-0002-1273-0655
Francieli Peter da Silveira - 0009-0008-3050-3289
William Souza Piovesani - 0000-0003-0888-0025
Mateus Henrique Schenkel – 0009-0000-4559-2722
Guilherme Dubal dos Santos Seger – 0000-0002-0710-3550
Gerhard Ernst Overbeck – 0000-0002-8716-5136

Correspondence
Filipe Ferreira da Silveira, Program of Botany (PPGBot/UFRGS), Universidade Federal do Rio Grande do Sul, RS, Brazil. E-mail: filipesilveferreira@hotmail.com

Funding
FFS was supported by "Bolsas Funbio–Conservando o Futuro" program, awarded by FUNBIO and Instituto Humanize.
Gerhard Ernst Overbeck was supported by CNPq (grant 310345/2018-9).

Acknowledgements
We thank the researchers and staff of the Laboratory of Grassland Vegetation Studies (LEVCamp) - UFRGS for their availability in assisting with expeditions and data collection. We thank Ana Porto, Bruno Soares, Diego Abade, Lucina Bittencourt, Sheron Silveira, William Piovesani, for their participation during data collection. For assistance in plant identification, we thank Bruno Soares, Franciele Peter, William Piovesani. We acknowledge the constructive comments from the thesis defense committee to which this article was submitted: Anaclara Guido Bolioli (UDELAR, Uruguay), João André Jarenkow (UFRGS, Brazil), Rosi Maria Prestes (UFRGS, Brazil). This study was partially funded by a research grant from the National Council for Scientific and Technological Development (CNPq) awarded to GEO (477618/2013-8) and by the Coordination for the Improvement of Higher Education Personnel - Brazil (CAPES) - Finance Code 001. GEO acknowledges CNPq productivity grants (310345/2018-9). FFS thanks CAPES for the scholarship (88887.684521/2022-00), was supported by the "Bolsas Funbio–Conserving the Future" program, awarded by FUNBIO and Instituto Humanize. This study is part of the LTER/PELD Campos Sulinos, supported by CNPq (CNPq grants PELD 441753/2020-5 and PQ 313315/2022-1 and by FAPERGS grant PELD 21/2551-0000776-1 to Valério De Patta Pillar). We would also like to thank the entire structure provided by the Graduate Program in Botany at the Federal University of Rio Grande do Sul.

Burned to Grow, Too Grazed to Stay: Deciphering the Control of Woody Encroachment in Native Grasslands

ABSTRACT

Questions: What are the isolated and combined effects of prescribed fire and cattle reintroduction on the density, richness, diversity, and vertical structure of the woody community in grasslands abandoned for 17 years?

Location: Agronomic Experimental Station of UFRGS (EEA/UFRGS), Eldorado do Sul, RS, Brazil.

Methods: A factorial experiment was conducted with four management regimes: Fire without Grazing, Fire with Grazing, Grazing without Fire, and Control. Woody individuals exceeding one meter in height were evaluated in 50-meter transects (total area of 1.2 hectares), classified by height classes (Small, Medium, and Large) and functional groups (grassland shrubs, pioneers, non-pioneers, and exotics).

Results: The Fire with Grazing treatment reduced woody density by 81 % compared to the control. Fire was the primary agent for reducing average height and eliminating the woody canopy. In the control plots, high richness and abundance of forest species were observed. Grazing alone did not significantly reduce woody density after advanced stages of abandonment.

Conclusion: Fire is essential for the initial impact (top-kill), but grazing acts as the maintenance agent, controlling recruitment and subsequent resprouting through herbivory and trampling. Integrated fire-grazing is the most consistent strategy to conserve the biological identity of the Pampa and reverse forest encroachment.

Key-words: Woody plant encroachment (WPE), top-kill, top-down control, pyric herbivory, ecological succession.

Introduction

Open ecosystems cover approximately 40% of the Earth's surface (Gibson, 2008). Over the last century, however, many areas have experienced a marked increase in the density and spatial extent of woody species, a process widely known as Woody Plant Encroachment (WPE) (Archer et al., 2017). This process is driven by a complex interplay of global and local factors. Among them, rising atmospheric CO_2 levels have been shown to physiologically favor C3 woody species over C4 grasses by enhancing photosynthetic and water-use efficiency, thereby accelerating growth and increasing drought tolerance (Sankey, 2012). However, the success of WPE also depends on how these physiological advantages interact with local environmental conditions and disturbance regimes. In many fire-prone systems, for instance, faster stem growth of woody species can reduce their vulnerability to fire-induced mortality by limiting the accumulation of herbaceous fine fuels that sustain intense burns (Müller et al., 2012). Nevertheless, the relative importance of these drivers varies significantly across different regions and biomes.

The dynamics of this expansion are regulated by two main sets of ecological mechanisms: bottom-up controls, associated with resource availability, and top-down controls, related to disturbance regimes (Bond, 2008). The relative importance of these controls varies according to ecosystem productivity (Andrade et al., 2023). In arid and semi-arid ecosystems, bottom-up controls tend to predominate, as water scarcity imposes strong limitations on the establishment and growth of woody species (Anderson et al., 2007; Belay & Moe, 2012). Under these conditions, encroachment occurs slowly and is strongly dependent on episodic resource pulses. In mesic and highly productive systems, by contrast, top-down controls play a central role in regulating vegetation structure. In these environments, including subtropical grasslands in southern Brazil (Overbeck et al., 2022), that are characterized by high annual water availability and the absence of severe dry periods, woody plant establishment and growth is not constrained by climate (Müller et al., 2023). Grasslands in the region are under grazing, sometimes with use of fire as a management tool (Overbeck et al., 2022). While different grazing management regimes have distinct impacts on vegetation structure and composition (e.g., Scimone et al., 2007; Fedrigo et al., 2022), traditional grazing management in the Pampa grasslands has in general proven effective in limiting woody recruitment through trampling or consumption, thereby contributing to the maintenance of grassland structure and diversity (Ferreira et al., 2020; Baggio et al., 2021; da Silveira et al., 2025).

In the absence of fire and grazing over longer periods, woody species are able to establish. As successional processes advance with time, campo shrubs – woody species typical of the grassland matrix that define the physiognomy known *as campo sujo* ('dirty grasslands') – such as *Baccharis dracunculifolia*, *Acanthostyles buniifolius*, and *Austroeupatorium inulaefolium*, tend to dominate the early stages of succession (Andrade et al., 2019; Müller et al., 2023). While these shrubs are grassland species, they already modify the vegetation physiognomy and initiate structural changes in the previously open grasslands. By providing physical structure and resources for fauna, they function as facilitative elements, attracting dispersers and increasing seed rain and local nutrient inputs (Müller et al., 2023). The microclimatic modification generated by these shrubs, such as shading and protection from environmental stress, creates favorable conditions for the establishment of pioneer tree species, which are characterized by rapid growth and adaptation to high light availability, and subsequently for non-pioneer or secondary woody species that depend on previously modified microenvironments (Müller et al., 2012, 2023; Sühs et al., 2020).

Consequently, the exclusion of fire management and grazing results in significant challenges for biodiversity conservation of grasslands, as these disturbances play a central role in maintaining environmental heterogeneity, and sustaining essential ecological cycles (e.g., nutrient mineralization and light availability) (Fidelis & Pivello, 2011). Structural changes associated with WPE have direct implications for ecosystem functions such as habitat provisioning and carbon-water dynamics. As woody biomass accumulates, a documented trade-off emerges between carbon sequestration and the maintenance of open-biome biodiversity (Pellegrini et al., 2016). In the Brazilian Cerrado, for example, total woody species richness may appear to increase with carbon storage, but the diversity of endemic savanna plants declines significantly at both local and landscape scales (Pellegrini et al., 2016; Abreu et al., 2017).

This process is driven by the transition from open formations to closed-canopy states; as tree density increases, an ecological shift occurs, typically marked by the disappearance of C4 grasses (Abreu et al., 2017). In these scenarios, the loss of open vegetation specialists, including both flora and associated fauna, is severe, as forest expansion is fundamentally incompatible with the light requirements of the herbaceous layer (Veldman et al., 2015). Despite these conservation concerns, some perspectives highlight potential benefits of WPE, particularly regarding its role in climate change mitigation

through increased carbon sequestration in woody biomass and soil (Aweto, 2024). Furthermore, in specific socio-economic contexts, encroaching species may provide secondary benefits such as fuelwood or medicinal resources (Aweto, 2024). However, a critical trade-off persists: the gains in carbon storage and provisioning services often occur at the expense of the unique biodiversity and ecological integrity of open biomes (Veldman et al., 2015; Pellegrini et al., 2016). Thus, WPE remains a primary threat to the biological identity of these ecosystems, justifying management as an essential strategy for maintaining open-biome diversity.

Despite the clear need for intervention, the restoration of long-abandoned grasslands presents significant technical challenges, and the scientific framework for restorative management is still being established. Studies suggest that simply reintroducing historical levels of disturbance may be insufficient to reverse advanced encroachment due to the resilience and resprouting capacity of established woody plants (Pillar & Vélez, 2010; Koch et al., 2022). While fire can effectively reduce accumulated biomass (top-kill), it often triggers vigorous resprouting in subtropical species (Fidelis et al., 2014). Similarly, grazing may fail to suppress woody plants once they have exceeded a certain height threshold (Bond, 2008). Therefore, current research points toward the potential synergy between fire—to reset the vegetation structure—and grazing—to suppress subsequent resprouts and recruitment—as a more effective pathway for restoration (Paruelo et al., 2022; López-Mársico et al., 2026). Nonetheless, empirical evidence from restorative efforts in long-term abandoned sites in the Pampa remains scarce, as most studies focus on the maintenance of already open systems.

In southern Brazil, exclusion of disturbances still occurs in protected areas (Overbeck et al. 2023). While allowing for the occurrence of successional processes can be a valid conservation goal, it threatens the typical biodiversity in grasslands that are suffering rapid losses due to land use change and are further threatened by inadequate management (Overbeck et al. 2023). Consequently, reintroducing management emerges as a critical tool to recover grassland ecosystems. In this study, we evaluate the effect of prescribed fire and grazing as restoration tools at a former grassland site that had been abandoned for 17 years and is undergoing Woody Plant Encroachment. Using a factorial experiment with four management regimes (fire, grazing, fire–grazing, and control), we evaluated the isolated and combined effects of prescribed burning and cattle reintroduction on the composition and structure of the woody plant community, considering density, vertical height distribution, and diversity. We hypothesize that the combined application

of fire and grazing will result in a greater reduction in woody abundance and diversity than either management applied in isolation, due to the synergistic effects of fire-induced aboveground mortality (top-kill) and subsequent mechanical suppression by livestock that will be efficient in impeding new recruitment. The data we present stems from the first two years of a long-term experiment, where we show initial effects of management on the woody plant community.

Methods

Study area

The study was carried out at the UFRGS Agronomic Experimental Station (EEA/UFRGS) in Eldorado do Sul municipality, Rio Grande do Sul State, within the South Brazilian Pampa. This region is characterized by a Cfa humid subtropical climate according to the Köppen classification, featuring well-distributed precipitation throughout the year (Overbeck et al., 2022). Regionally, the average annual rainfall is approximately 1,450 mm (RIO GRANDE DO SUL, 2010), with mean yearly temperatures ranging from 15.6°C to 24.7°C. In winter, mean monthly minimums reach between 11.5°C and 13.2°C and polar air masses can trigger sporadic frost events. The 27-hectare experimental area, which was under continuous grazing management until 2006, has since undergone fifteen years of successional changes (Podgaiski et al., 2014). These shifts are marked by the encroachment of woody plants and the presence of invasive *Pinus* sp., notably in the western portion of the site.

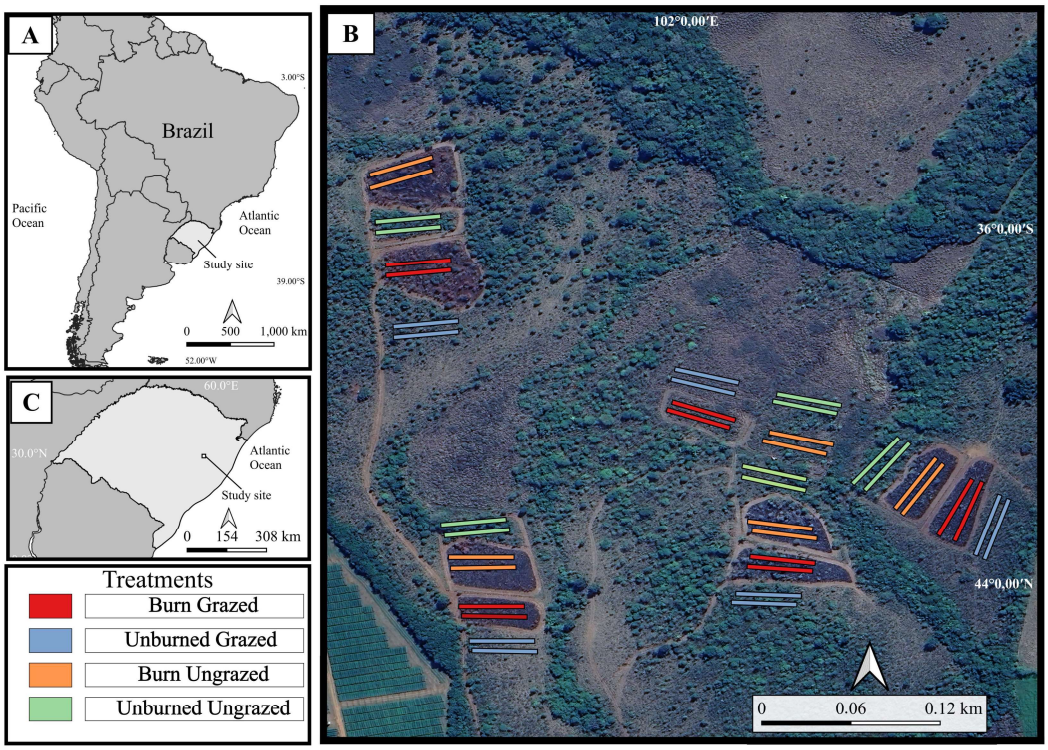


Fig. 1 - Location of the study site (A+B) at the UFRGS Agronomic Experimental Station in Eldorado do Sul, in Rio Grande do Sul state, Brazil and position of the sampling transects in the experimental blocks.

Experimental design

Within the experimental area, we established five blocks with four 35 by 70m plots each. In each block, two plots were fenced, and two plots left unfenced. One of the two fenced and one of the two unfenced plots were subjected to a prescribed burn in August 2023, after preparation of fire-breaks. Cattle had been reintroduced at the study site in May 2023, with a moderate grazing pressure level (15 animals, a number determined through regression analysis based on mean vegetation height measured using the falling-plate method proposed by (Rayburn & Lozier, 2003). To facilitate initial biomass consumption after 17 years of abandonment and thus biomass accumulation, nitrogen salt was initially provided. Cattle were allowed to move freely across the 22-hectare area, except within fenced blocks. Burns were applied using a driptorch with a fuel mixture of three parts gasoline to one part diesel. Prescribed burns were conducted against the wind, directing the fire edges toward the center of the blocks to ensure rapid flame extinction. Thus, the experimental design consisted of four treatments in a randomized design: Burn Ungrazed (fire without grazing), Burn Grazed (fire with grazing), Unburned Grazed (grazing without fire), and Unburned Ungrazed (control). Within each plot, we evaluated woody species composition along two 50-m transects established at a minimum distance of 8 meters from each other. In January 2025, we recorded all woody species taller than 1 meter and their respective heights, located within 3 meters on both sides of the transect centerline. The total sampling effort encompassed 12,000 m² (1,2 ha), distributed across 40 rectangular sampling units of 300 m² (50 × 6 m) each. To account for differences in sample unit sizes and facilitate comparison with other studies, woody plant abundance and species richness were standardized to a 100m² area.

Vegetation Sampling

Sampling was conducted in January 2025, in southern hemisphere summer. Plant height was recorded using a measuring tape and individuals were classified into three height classes: Intermediate (100–199 cm), Tall (200–299 cm), and Very Tall (≥ 300 cm). Identified species were further categorized into functional groups – Grassland Shrubs, Alien trees, Pioneer trees or Non-Pioneer trees – Supplementary Material Table S1. Botanical families were classified according to the APG IV system (Chase, 2016), and nomenclature was standardized following the Flora do Brasil (Jardim Botânico do Rio de Janeiro, 2026).

Data analysis

Statistical analyses and data visualizations were performed in R (R Development Core Team, 2026) primarily utilizing the glmmTMB package, v. 1.1.10 (Brooks et al., 2017) for model construction, performance for model metrics, vegan for multivariate analyses, v. 2.7.1(Oksanen et al., 2026), and ggplot2 v. 4.0.1, for visualizations. The effects of fire and grazing on mean woody height were tested using a two-way Analysis of Variance (ANOVA) followed by Tukey's HSD post-hoc tests for pairwise comparisons.

The effect of experimental treatments on woody plant density was evaluated using Generalized Linear Mixed Models (GLMM) with a Negative Binomial distribution (nbinom2) and a log link function, accounting for the randomized block design as a random effect. To allow for a direct comparison of proportional changes in density relative to the control (Ungrazed/Unburned), model coefficients were exponentiated to obtain Incidence Rate Ratios (IRR).

Species richness (the total number of species per plot) and woody diversity, quantified by the Simpson Index (1-D), were analyzed via Linear Mixed Models (LMM) with a Gaussian distribution and identity link function, also incorporating block as a random effect. Model fit for both density and diversity were assessed using the marginal R-squared (R_m^2), which represents the variance explained exclusively by the management treatments, calculated according to the Nakagawa method (Nakagawa & Schielzeth, 2013). Model assumptions and residual distributions were validated using the DHARMa diagnostic framework (Hartig, 2024), which employs a simulation-based approach to assess overdispersion and ensure the adequacy of the chosen error distributions.

Non-metric Multidimensional Scaling (NMDS) was performed based on Bray-Curtis dissimilarity index calculated from species abundance data. Statistical differences in species composition among treatments were tested using Permutational Multivariate

Analysis of Variance (PERMANOVA) via the *adonis2* function, with permutations restricted within blocks (strata) (Oksanen et al., 2024). The robustness of the PERMANOVA was further validated by testing the homogeneity of multivariate dispersions using the *betadisper* function. Finally, significant species vectors were fitted onto the ordination using the *envfit* function (999 permutations) to identify which taxa most strongly contributed to the differentiation between management regimes (Anderson, 2001). The analysis code and data are available on Zenodo (Silveira, 2026).

Results

Variation in woody abundance across management regimes

The woody community structure was significantly influenced by management practices, particularly those involving fire. Mean woody plant abundance was 7.47 (SD = 6.16) individuals/100m2 in Burn Grazed treatment, compared to 39.6 (SD = 8.76) individuals/100m2 in Unburned Ungrazed (Fig. 2). Treatments with only one of the two processes showed high variability, reflecting heterogeneous effects of the disturbances and of post-disturbance recruitmente processes. Generalized Linear Mixed Models (Negative Binomial) revealed that management regimes accounted for 66.8% of the observed variance in woody density (R^2_m = 0.668). Compared to the control (Intercept = 5.47, $p < 0.001$), the combined effect of fire and grazing (Burn Grazed) resulted in the most substantial reduction in woody plant density (IRR = 0.19, $p < 0.001$), followed by fire alone (Burn Ungrazed; IRR = 0.53, $p = 0.010$). In contrast, cattle grazing in the absence of fire (Unburned Grazed) did not significantly alter woody density compared to the control (IRR = 0.82, $p = 0.362$, see in Supplementary Material – Table S2).

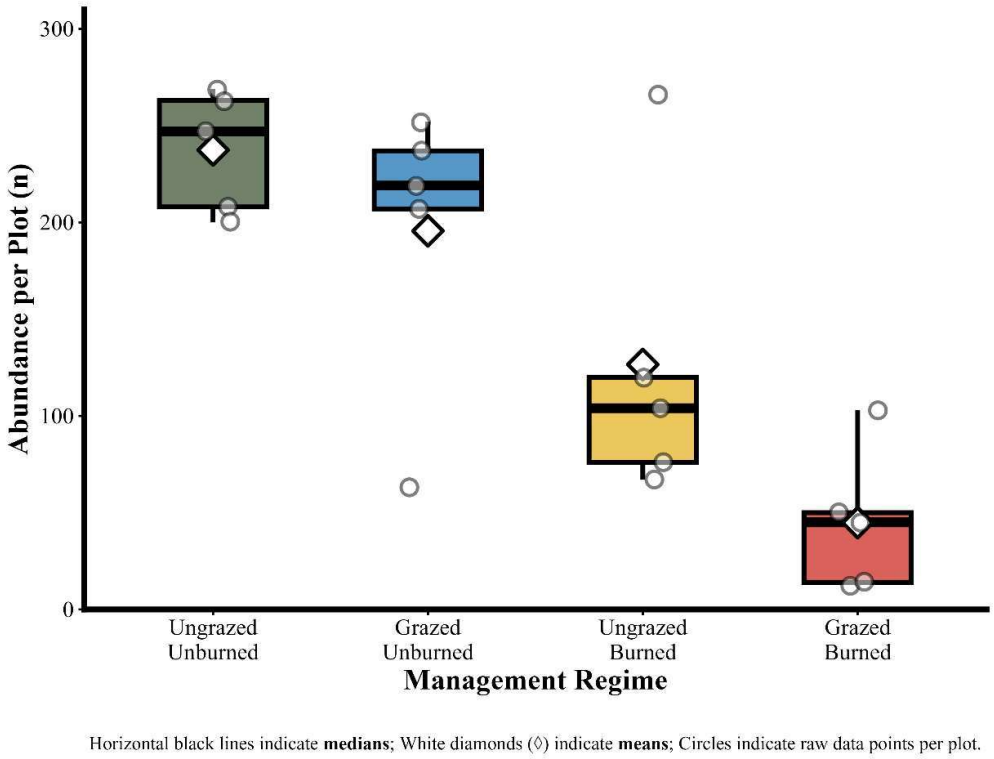


Fig. 2 - Abundance of woody individuals per plot under different management regimes. Boxplots represent the interquartile range (25-75%), internal horizontal black lines represent medians, white diamonds indicate means, and circles represent raw data points per plot.

Diversity Patterns and Richness

Woody species richness also differed markedly among treatments (Table X). Fire suppression allowed for the maintenance of higher woody plant richness, with the Unburned Ungrazed treatment reaching a mean of 3.77 species/$100m^2$. The introduction of fire in the Burn Ungrazed areas resulted in a substantial decrease to 2.9 species per plot. The most rigorous environmental filter was observed under the combined disturbance of the Burn Grazed plots, where mean species richness dropped to only 1.20 species/$100m^2$.

Table 1 - Mean species richness and abundance (± SD) standardized for 100 m² under different management treatments. Distinct letters indicate statistical significance by Tukey's test ($p < 0.05$). Each treatment consists of 10 sampling units.

Management	Mean Abundance	Tukey	SD Abundance	Mean Richness	Tukey	SD Richness
Unburned Ungrazed	39.6	a	5.28	3.77	a	0.69
Unburned Grazed	32.6	ab	12.7	2.90	ab	1.15
Burn Ungrazed	21.1	bc	13.5	2.10	bc	0.66
Burn Grazed	7.47	c	6.16	1.20	c	0.34

Functional Groups and Height Structure

The woody community exhibited distinct shifts in successional composition and vertical structure across regimes. Fire suppression (unburned areas) preserved the integrity of the non-pioneer group, which reached its peak richness (R = 15) and abundance (n = 186) under the Unburned Ungrazed regime. In contrast, the combined Burn Grazed treatment caused a drastic decline in pioneer tree abundance (from 475 in the control to 49) and a simplification of the community, which became dominated by grassland shrubs (accounting for 69% of the total abundance in this treatment) (Supplementary Material – Table S4.; Fig. 3).

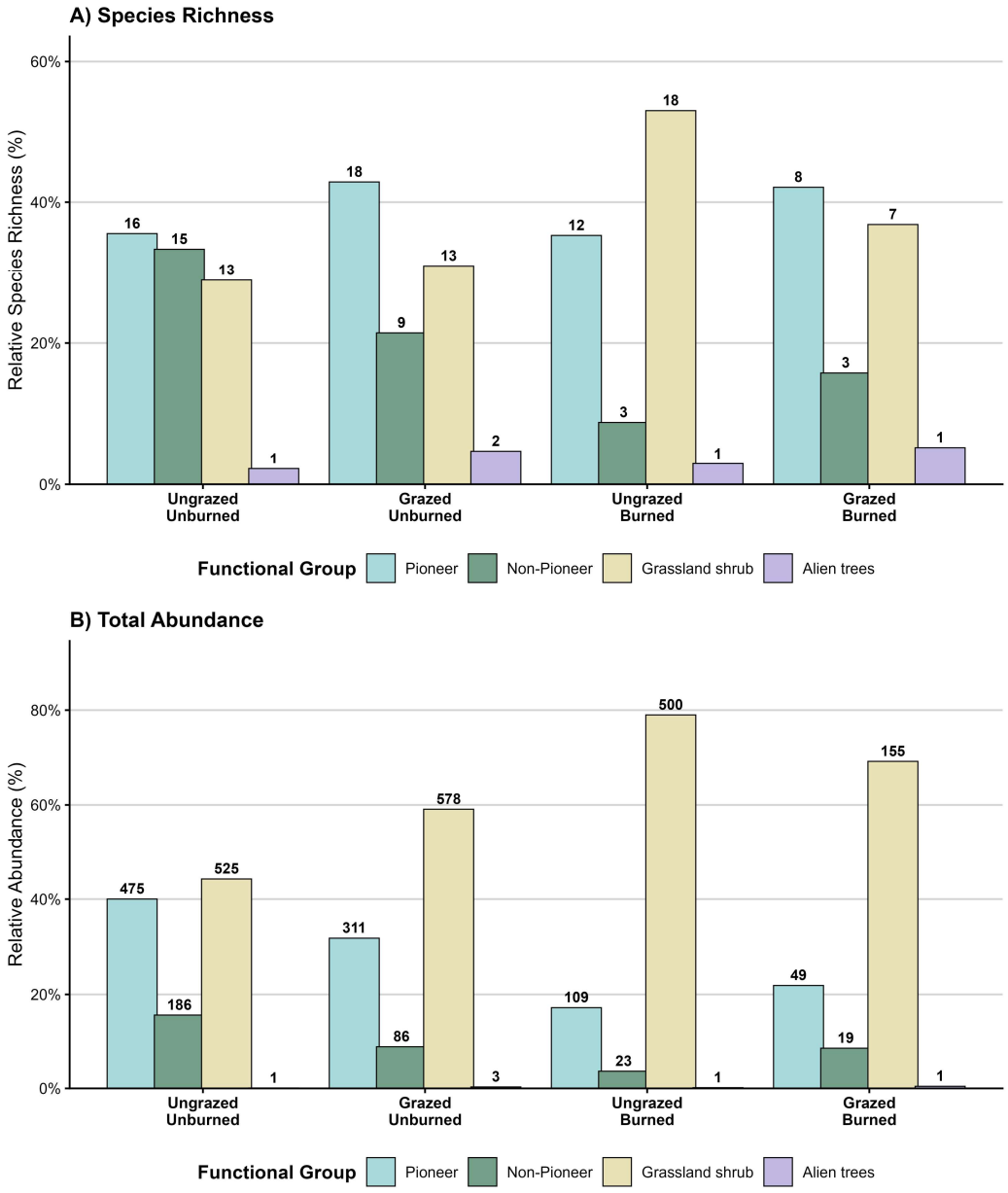


Fig. 3 - Relative richness and abundance of woody species by functional group under different management regimes. The plots display (A) Relative Species Richness (%) and (B) Relative Abundance (%), categorized into four functional groups: Pioneer, Non-pioneer, Grassland shrub, and Alien trees. Management treatments are represented on the horizontal axis: Unburned Ungrazed, Unburned Grazed, Burned Ungrazed, and Burned Grazed. Numbers above the bars indicate the absolute species richness (in A) and the total number of individuals (in B) recorded for each category.

This structural simplification was also reflected in the vertical stratification (Fig. 4). Fire exerted a strong and highly significant effect on woody height structure structure ($F_1 = 224.12$, $p < 0.0001$), reducing the contribution of medium and tall individuals. While unburned treatments exhibited a more balanced distribution between intermediate and taller individuals, burned treatments were strongly dominated by small and intermediate-height classes. Grazing had a weaker but significant effect on height ($F_1 = 11.34$, $p < 0.001$), while the interaction between fire and grazing was not statistically significant ($F_1 = 0.71$, $p = 0.397$), indicating predominantly additive effects.

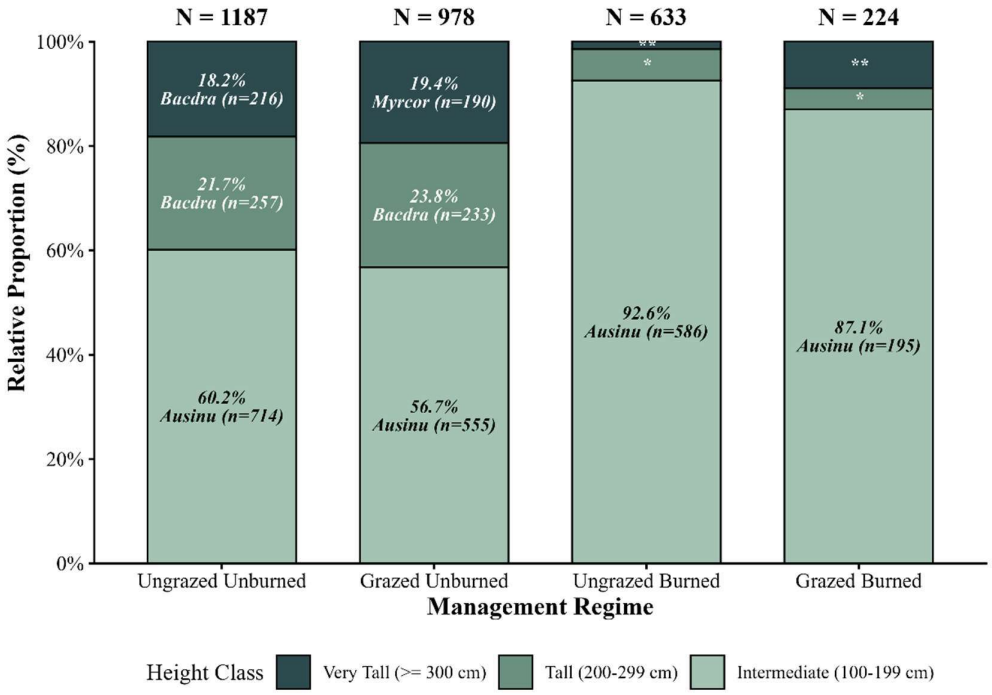


Fig. 4 –- Relative proportion of tree height classes, represented by stacked bars, across four management regimes: Unburned Ungrazed, Unburned Grazed, Burn Ungrazed, and Burn Grazed. Height classes are categorized from Small (100–199 cm), Intermediate (200–299cm) to Tall (≥ 300 cm), as indicated by the color scale. The total individual count per treatment is denoted above each bar. Values within bar segments represent the relative percentage and absolute number of individuals (n) of the most abundant species for each category. * Tall class in the Ungrazed Burned (4 %, n = 9) and in the Grazed Burned (6 %, n = 38); ** Very Tall class in the Ungrazed Burned (1.4%, n = 9) and in the Grazed Burned (8.9 %, n = 20).

Dominant woody species abundance across different management regimes

The NMDS ordination revealed a clear differentiation in woody community composition among treatments (Stress = 0.173; Fig. 5). Permutational Multivariate Analysis Variance confirmed that management regimes significantly altered species composition ($R^2 = 0.179$, $p = 0.001$; Supplementary Material – Table S3). Plots exposed to fire, especially those also grazed, occupied a distinct region of the ordination space. The test for homogeneity of multivariate dispersions was non-significant ($p = 0.756$), indicating that observed patterns are driven by species turnover (substitution) rather than differences in within-group variance.

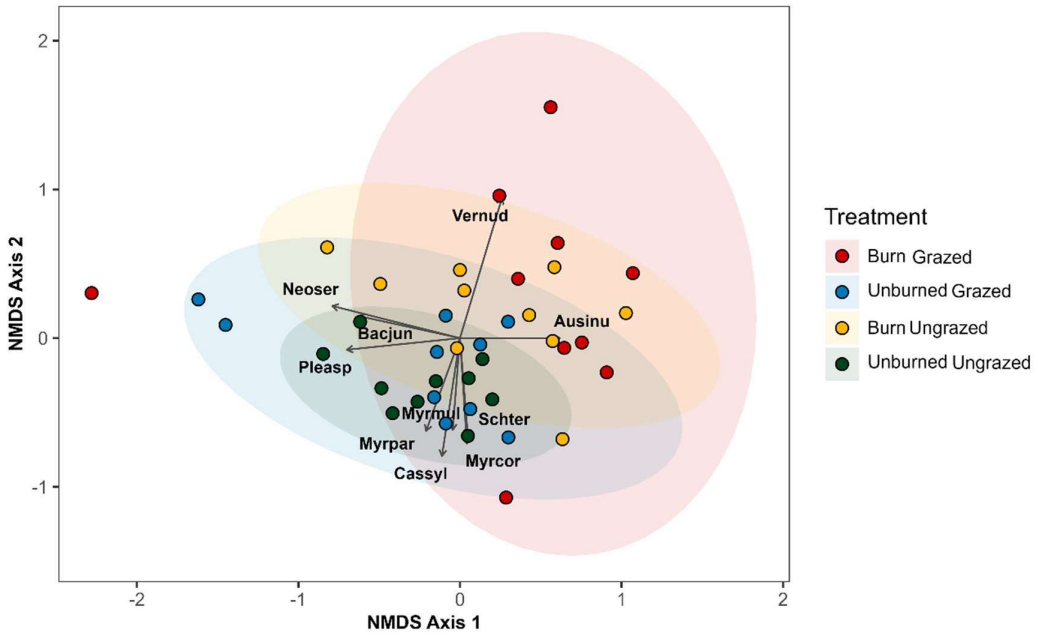


Fig. 5 - Non-metric multidimensional scaling (NMDS) ordination of woody community composition (Stress: 0.17). Ellipses denote 95% confidence intervals for each treatment. Vectors (arrows) indicate the direction of the steepest increase in species abundance (*envfit*), with arrow length and R^2 values reflecting the strength of correlation with the ordination axes. Significant species ($p < 0.05$): **Vernud**: *Vernonanthura nudiflora* ($R^2 = 0.37$, $p = 0.002$); **Neoser**: *Neocabreria serrulata* ($R^2 = 0.26$, $p = 0.023$); **Cassyl**: *Casearia sylvestris* ($R^2 = 0.25$, $p = 0.011$); **Myrcor**: *Myrsine coriacea* ($R^2 = 0.2$, $p = 0.020$); **Pleasp**: *Pleroma asperius* ($R^2 = 0.19$, $p = 0.028$); **Myrpar**: *Myrsine parvula* ($R^2 = 0.17$, $p = 0.035$); **Schter**: *Schinus terebinthifolia* ($R^2 = 0.17$, $p = 0.045$); **Bacjun**: *Baccharis junciformis* ($R^2 = 0.16$, $p = 0.043$); **Myrmul**: *Myrcia multiflora* ($R^2 = 0.15$, $p = 0.049$); and **Ausinu**: *Austroeupatorium inulaefolium* ($R^2 = 0.14$, $p = 0.048$).

Dominance patterns also shifted; Unburned treatments were characterized by the prevalence of *Baccharis dracunculifolia* and *Austroeupatorium inulifolium*, alongside *Myrsine coriacea* and *Schinus terebinthifolia*. In the Burn Ungrazed treatment, *A. inulifolium* became heavily dominant, representing more than half of the individuals. Species vectors (e.g., *Vernonanthura nudiflora*, *Neocabreria serrulata*) contributed significantly to plot dispersion, reflecting a clear shift in community assembly (Fig. 6).

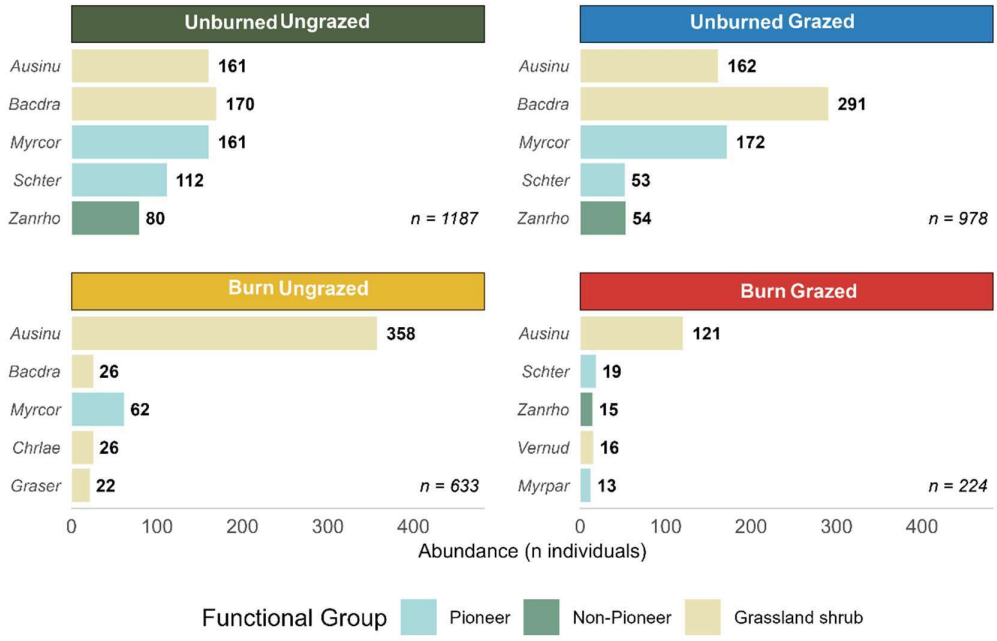


Fig. 6 - Dominant woody species abundance across different management regimes. Horizontal bars represent the top 5 most abundant species for each treatment: Unburned Ungrazed, Unburned Grazed, Burn Ungrazed, and Burn Grazed. Species names are presented as acronyms. Ausinu – *Austroeupatorium inulaifolium*, Bacdra – *Baccharis dracunculifolia*, Myrcor – *Myrsine coriacea*, Schter – *Schinus terebinthifolia*, Zanrho – *Zanthoxylum rhoifolium*, Chrlae – *Chromolaena laevigata*, Graser – *Grazielia serrata*, Vernud – *Vernonanthura nudiflora*, Myrpar – *Myrsine parvula*. Colors indicate functional groups: Pioneer, Non-Pioneer, and Grassland shrub. The total number of individuals recorded in each treatment is indicated.

Discussion

Our results demonstrate that management regimes significantly shape woody community structure and composition. The combination of fire and grazing (Burn Grazed) was the most effective treatment for re-establishing open grassland conditions, promoting the sharpest reductions in woody species richness and abundance (Table 1; Supplementary Material – Table S2). In contrast, the absence of fire, regardless of grazing, allowed the maintenance of higher woody density and richness, supporting structurally and compositionally more complex communities with greater representation of non-pioneer species, consistent with successional advancement under disturbance exclusion (Supplementary Material – Table S4). Notably, grazing alone (Unburned Grazed) did not significantly alter these woody parameters compared to the control (Unburned Ungrazed), indicating that fire is the primary driver suppressing woody encroachment. Burned treatments, particularly when combined with grazing, simplified the community by reducing both Pioneer and Non-Pioneer species, shifting composition toward assemblages typical of open grasslands (Table S3). These changes were accompanied by marked differences in vertical structure, with burned regimes characterized by smaller individuals and distinct assemblages relative to unburned areas, indicating a reorganization toward early structural stages. Collectively, these results indicate that the reintroduction of fire, particularly when combined with grazing, reorganizes the community toward simpler assemblages typical of open grassland systems.

In contrast, the similarity between the Unburned Grazed treatment and the control indicates that grazing alone was ineffective in altering the community structure. This lack of significant difference suggests that 17 years of management exclusion allowed woody species to attain heights and structural complexity that surpass the control capacity of cattle. The statistical model captured this structural stability ($R_m^2 = 0.668$), suggesting that the system has reached a state in which herbivory alone cannot overcome the physical barrier imposed by established vegetation, reinforcing the persistence of encroachment (Liu et al. 2019).

Beyond absolute density, management regimes significantly reshaped woody community composition. The multivariate analysis confirms that these shifts are driven by a species turnover process rather than internal group variance, indicating a clear replacement of taxa under different disturbances. This turnover reflects compositional divergence directly linked to disturbance filters (HilleRisLambers et al. 2012).

Specifically, the association of certain pioneer species with unburned treatments highlights how fire exclusion facilitates the consolidation of encroachment-driving taxa, such as *Myrsine coriacea*, *Schinus terebinthifolia*, and *Zanthoxylum rhoifolium*. These species, which possess a Pioneer successional status and characterize a more advanced stage of woody expansion compared to typical Grasslands shrub species, have been previously identified as forest-associated taxa that act as colonizers of open environments (Müller et al. 2007, 2012; Gautreau & Lezama 2009). Thus, their dominance under fire exclusion reflects both their colonizing ability and their sensitivity to subsequent disturbance.

The link between these compositional patterns and demographic structure is evident in the height distribution of individuals. For these three pioneer species combined, only 139 individuals were recorded in fire-managed treatments, 125 of which were under 2 meters tall. This scenario likely results from post-disturbance recruitment from the seed bank; however, their concentration in lower height classes indicates that individuals remain confined within the fire-trap, being repeatedly subjected to top-kill and prevented from reaching fire-resistant stages (Capozzelli et al. 2020; Mndela et al. 2025). Conversely, in unburned treatments, 633 individuals were sampled, with 347 measuring up to 2 meters in height. The presence of taller individuals indicates escape from the fire-trap, allowing investment in secondary stem development, which increases structural resistance and reduces susceptibility to top-kill (Capozzelli et al. 2020).

Fire acts as a selective environmental filter (HilleRisLambers et al. 2012) that promotes a structural reset of the vegetation through top-kill, directly influencing height distribution and community organization. Our findings suggest that while fire is the primary agent responsible for breaking canopy dominance, subsequent management determines the trajectory of recovery. In the absence of grazing, the woody community exhibits rapid numerical recovery and re-establishment of density (Fuhlendorf et al. 2009). Conversely, in the presence of grazing, the interaction between fire and herbivory maintains woody populations at reduced levels and confined to smaller size classes, preventing vertical escape of recruits. This pattern is consistent with the piro-herbivory framework, in which fire generates a magnet effect that concentrates herbivore activity in recently burned patches (Capozzelli et al. 2020; Mndela et al. 2025). In this leader–follower system, fire initiates top-kill, while herbivores reinforce suppression through browsing and trampling, maintaining individuals within the fire-trap.

Species-specific responses further illustrate these mechanisms. *Baccharis dracunculifolia*, a dominant species in abandoned areas, showed a drastic reduction in burned treatments, consistent with its high fire sensitivity and lack of resprouting capacity (Müller et al. 2007). In contrast, *Austroeupatorium inulifolium* (p = 0.048) exhibited strong post-fire recovery via resprouting, becoming dominant in Burn Ungrazed (358 of 633 individuals; Mendes et al. 2024). However, its sharp reduction in Burn Grazed indicates that cattle effectively suppress resprouting species, acting as a maintenance filter on post-fire recovery dynamics (Mndela et al. 2025).

At the functional level, management effectively reversed woody encroachment by reducing Non-Pioneer (forest-type) species. In the control, this group comprised 186 individuals and 15 species, whereas in Burn Grazed it declined to 19 individuals and 3 species, indicating substantial progress toward open grassland conditions. This shift reflects not only species loss but also functional turnover aligned with grassland dynamics (Pittarello et al. 2016).

The exclusion of disturbances in grassland conservation areas has repeatedly been identified as a major threat to ecosystem integrity (Belsky, 1992; Harrison et al. 2003; Overbeck et al. 2018; da Silveira et al. 2025). Our results reinforce that grazing alone is insufficient to reverse advanced encroachment. Fire is essential as the initial disturbance, performing top-kill and breaking structural dominance, while cattle act as maintenance agents, exerting top-down control via herbivory and trampling on recruits. The lower variability observed in Burn Grazed (SD = 6.16) indicates that this integrated regime provides the most consistent control of woody expansion. We therefore recommend the implementation of combined fire and grazing management to restore encroached grasslands. Continuous monitoring is essential to ensure that new recruits remain confined within the fire-trap, preventing escape via secondary stem development and the re-establishment of woody encroachment (Mndela et al. 2025).

Conclusion

The reintroduction of fire combined with grazing (Burn Grazed) proved to be the most effective strategy for reversing woody encroachment and restoring open grassland conditions. This management drastically reduced woody density and maintained individuals confined to lower height classes, indicating that the interaction between disturbances is essential to keep juvenile individuals and resprouts within the fire-trap. While fire promotes top-kill and structural reset, grazing prevents the return of woody species after disturbance by limiting vertical growth, stem diameter increase and lignification, thereby constraining the re-establishment of woody dominance. Restoration occurred through a clear process of species turnover, with fire and grazing acting as selective filters that reduced forest-associated taxa and substantially decreased Non-Pioneer species. In contrast, disturbance exclusion and grazing alone were ineffective, as woody vegetation reached a structurally stable state beyond the control capacity of cattle. Given its lower variability and consistent outcomes, the integrated fire–grazing regime emerges as the most reliable strategy for Pampa grassland conservation.

Future perspectives should focus on long-term monitoring to ensure that individuals remain confined within the fire-trap, preventing escape through height growth and stem diameter increase/lignification, and the re-establishment of woody encroachment. In addition, defining optimal fire regimes, particularly in terms of burn frequency, is essential to maximize management effectiveness without compromising ecosystem integrity. Complementary assessments of soil responses to this management are also necessary to ensure the long-term sustainability of the recommended practices.

References

Abreu, R.C.R., Hoffmann, W.A., Vasconcelos, H.L., Pilon, N.A., Rossatto, D.R., & Durigan, G. (2017) The biodiversity cost of carbon sequestration in tropical savanna. *Science Advances*, 3(8). https://doi.or/10.1126/sciadv.1701284

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), 32–46. https://doi.or/10.1111/j.1442-9993.2001.01070. x

Anderson, T.M., Metzger, K.L., & McNaughton, S.J. (2007) Multi-scale analysis of plant species richness in Serengeti grasslands. *Journal of Biogeography*, 34(2), 313–323. https://doi.or/10.1111/j.1365-2699.2006.01598.x

Andrade, B.O., Bonilha, C.L., Overbeck, G.E., Vélez-Martin, E., Rolim, R.G., Bordignon, S.A.L., et al. (2019) Classification of South Brazilian grasslands: Implications for conservation. *Applied Vegetation Science*, 22(1), 168–184. https://doi.or/10.1111/avsc.12413

Andrade, B.O., Dröse, W., Aguiar, C.A. de, Aires, E.T., Alvares, D.J., Barbieri, R.L., et al. (2023) 12,500+ and counting: biodiversity of the Brazilian Pampa. *Frontiers of Biogeography*, 15(2). https://doi.or/10.21425/F5FBG59288

Archer, S.R., Andersen, E.M., Predick, K.I., Schwinning, S., Steidl, R.J., & Woods, S.R. (2017) Woody Plant Encroachment: Causes and Consequences. *Rangeland systems: Processes, management and challenges*. 25–84. https://doi.or/10.1007/978-3-319-46709-2_2

Aweto, A.O. (2024) Is woody plant encroachment bad? Benefits of woody plant encroachment—A review. *Landscape Ecology*, 39, 21. https://doi.org/10.1007/s10980-024-01823-1

Baggio, R., Overbeck, G.E., Durigan, G., & Pillar, V.D. (2021) To graze or not to graze: A core question for conservation and sustainable use of grassy ecosystems in Brazil. *Perspectives in Ecology and Conservation.* https://doi.org/10.1016/j.pecon.2021.06.002

Barbosa, L. M. (2017). Lista de espécies indicadas para restauração ecológica para diversas regiões do estado de São Paulo. Instituto de Botânica, São Paulo, Brazil.

Belay, T.A., & Moe, S.R. (2012) Woody dominance in a semi-arid savanna rangeland -

Evidence for competitive self-thinning. *Acta Oecologica*, 45, 98–105. https://doi.or/10.1016/j.actao.2012.10.006

Belsky, A. J. (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, 3(2), 187-200. https://doi.org/10.2307/3235679

Bond, W.J. (2008) What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics,* 39(1), 641–659. https://doi.or/10.1146/annurev.ecolsys.39.110707.173411

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, 9(2), 378–400. https://doi.or/10.32614/rj-2017-066

Capozzelli, J.F., Miller, J.R., Debinski, D.M., & Schacht, W.H. (2020) Restoring the fire–grazing interaction promotes tree–grass coexistence by controlling woody encroachment. Ecosphere, 11(2). https://doi.org/10.1002/ecs2.2993

Chase, M.W. (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181, 1–20. https://doi.org/10.1111/boj.12385

Fedrigo, J.K., Ataide, P.F., Azambuja Filho, J.C.R., Bertoncelli, P., & Nabinger, C. (2022) Deferment associated to contrasting grazing intensities affects root/shoot biomass allocation in natural grasslands. *Applied Vegetation Science*, 25(3). https://doi.or/10.1111/avsc.12671

Ferreira, P.M.A.A., Andrade, B.O., Podgaiski, L.R., Dias, A.C., Pillar, V.D., Overbeck, G.E., et al. (2020) Long-term ecological research in southern Brazil grasslands: Effects of grazing exclusion and deferred grazing on plant and arthropod communities. *PLoS ONE*, 15(1). https://doi.or/10.1371/journal.pone.0227706

Fidelis, A., & Pivello, V.R. (2011) Deve-se usar o fogo como instrumento de manejo no Cerrado e Campos Sulinos? *Biodiversidade Brasileira*, 1(2), 12–25. https://doi.or/10.37002/biodiversidadebrasileira.v1i2.102

Fuhlendorf, S.D., Engle, D.M., Kerby, J., & Hamilton, R. (2009) Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conservation*

Biology, 23(3), 588–598. https://doi.or/10.1111/j.1523-1739.2008.01139.x

Gautreau, P.; Lezama, F. (2009). Clasificación florística de los bosques y arbustales de las sierras del Uruguay. *Ecologia austral*, 19(2), 81-92.

Gibson, D.J. (2008) Grasses and Grassland Ecology. Oxford University Press: New York. https://doi.or/10.1093/oso/9780198529187.001.0001

Hartig, F. (2024) DHARMa - Residual Diagnostics for HierARchical Models. R package version 0.4.7.

Harrison, S., Inouye, B.D., Safford, H.D. (2003) Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology*, 17(3), 837-845. https://doi.org/10.1046/j.1523-1739.2003.01633.x

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., & Mayfield, M.M. (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43(1), 227–248. https://doi.or/10.1146/annurev-ecolsys-110411-160411

Jardim Botânico do Rio de Janeiro. (2026) Flora e Funga do Brasil. http://floradobrasil.jbrj.gov.br

Liu, Y., Shi, Z., Gong, L., Cong, R., Yang, X., & Eldridge, DJ (2019) Is the removal of aboveground shrub biomass an effective technique to restore a shrub-encroached grassland? *Restoration Ecology*, 27(6), 1348-1356. https://doi.org/10.1111/rec.13012

Mendes, D. de M., Silva, R.G. da, & Farinaccio, M.A. (2024) A influência da estiagem e do fogo na família asteraceae em uma unidade de conservação ambiental no pantanal de MS, Brasil. *Revista GeoPantanal*, 36(19), 213–226. https://doi.org/10.55028/geop.v19i36.20329

Mndela, M., Barrett, A. S., & Brown, L. R. (2025) Fire and herbivory control shrub encroachment and restore herbaceous vegetation in mesic grasslands of South Africa. *Plant Ecology & Diversity*, 18(1-2), 25-38. https://doi.org/10.1080/17550874.2025.2537152

Müller, S.C., Bergamin, R.S., Duarte, L.S., Peroni, N., Sühs, R.B., & Carlucci, M.B. (2023) Mechanisms and processes shaping patterns of forest-grassland mosaics in southern Brazil. South Brazilian grasslands: ecology and conservation of the

Campos Sulinos. *Springer*, 417–443. https://doi.org/10.1007/978-3-031-42580-6_16

Müller, S.C., Overbeck, G.E., Pfadenhauer, J., & Pillar, V.D. (2007) Plant functional types of woody species related to fire disturbance in forest–grassland ecotones. *Plant Ecology*, 189(1), 1–14.

Müller, S.C., Overbeck, G.E., Blanco, C.C., Oliveira, J.M., Pillar, V.D. (2012) South Brazilian forest-grassland ecotones: dynamics affected by climate, disturbance, and woody species traits. In: Ecotones between forest and grassland. *New York*, NY: Springer New York, 2012. 167-187. https://10.1007/978-1-4614-3797-0_7

Müller, S.C., Overbeck, G.E., Pfadenhauer, J., & Pillar, V.D. (2012) Woody species patterns at forest-grassland boundaries in southern Brazil. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 207(8), 586–598. https://doi.or/10.1016/j.flora.2012.06.012

Nakagawa, S., & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. https://doi.or/10.1111/j.2041-210x.2012.00261.x

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., et al. (2026) Package 'vegan.' Community ecology package, version, 2(9), 1–295.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., et al. (2024) vegan: Community Ecology Package.

Overbeck, G.E., Vélez-Martin, E., Menezes, L. da S., Anand, M., Baeza, S., Carlucci, M.B., et al. (2022) Placing Brazil's grasslands and savannas on the map of science and conservation. *Perspectives in Plant Ecology, Evolution and Systematics*, 56, 125687. https://doi.or/10.1016/j.ppees.2022.125687

Overbeck, G.E., Scasta, J.D., Furquim, F.F., Boldrini, I.I., Weir, J.R. (2018) The South Brazilian grasslands–A South American tallgrass prairie? Parallels and implications of fire dependency. *Perspectives in Ecology and Conservation*, 16(1), 24-30. https://doi.org/10.1016/j.pecon.2017.11.002

Pellegrini, A.F.A., Socolar, J.B., Elsen, P.R., & Giam, X. (2016) Trade-offs between savanna woody plant diversity and carbon storage in the Brazilian Cerrado. *Global change biology*, 22(10), 3373–3382. https://doi.or/10.1111/gcb.13259

Pittarello, M., Probo, M., Lonati, M., & Lombardi, G. (2016) Restoration of sub-alpine shrub-encroached grasslands through pastoral practices: effects on vegetation structure and botanical composition. *Applied Vegetation Science*, 19(3), 381-390.

Podgaiski, L.R., da Silva Goldas, C., Ferrando, C.P.R., Silveira, F.S., Joner, F., Overbeck, G.E., et al. (2014) Burning effects on detritivory and litter decay in Campos grasslands. *Austral Ecology*, 39(6), 686–695.

R Development Core Team. (2026) A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria. https://doi.or/10.4236/oalib.1107821

Rayburn, E., & Lozier, J. (2003) A Falling Plate Meter for Estimating Pasture Forage Mass. System, 3.

Rio Grande do Sul. (2010) Atlas Climático do Rio Grande do Sul. FEPAGRO: Porto Alegre, Brazil. pp.76-99.

Sankey, T.T. (2012) Woody-herbaceous-livestock species interaction. Ecotones Between Forest and Grassland. *Springer*, 89–114. https://doi.or/10.1007/978-1-4614-3797-0_4

Scimone, M., Rook, A.J., Garel, J.P., & Sahin, N. (2007) Effects of livestock breed and grazing intensity on grazing systems: Effects on diversity of vegetation. *Grass and Forage Science*, 62(2), 172–184. https://doi.or/10.1111/j.1365-2494.2007.00579.x

da Silveira, F.F., Menezes, L.S., Porto, A.B., Thomas, P.A., Boavista, L. da R., Seger, G.D.S., & Overbeck, G.E. (2025) Southern Brazilian Grassland Diversity: Anti-Disturbance Regimes Are Not Ideal and Grazing Maintains Plant Diversity. *Applied Vegetation Science*, 28(4). https://doi.or/10.1111/avsc.70049

Silveira, F. F. (2026). Too Burned to Grow, Too Grazed to Stay: Deciphering the Control of Woody Encroachment in Native Grasslands. Zenodo. https://doi.org/10.5281/zenodo.19655848

Sühs, R.B., Giehl, E.L.H., & Peroni, N. (2020) Preventing traditional management can cause grassland loss within 30 years in southern Brazil. *Scientific Reports*, 10(1), 783. https://doi.or/10.1038/s41598-020-57564-z

Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G.W., et al. (2015) Where Tree Planting and Forest Expansion are Bad for Biodiversity and Ecosystem Services. *BioScience*, 65(10), 1011–1018. https://doi.or/10.1093/biosci/biv118

Supplementary Material Table S1. Floristic summary of identified woody species, arranged by botanical family, indicating functinal group (Pioneer, Non-Pioneer, Alien species or Grassland shrub) based on a specialized literature review (Lorenzi, 2003; Soares & al., 2008; Boldrini, 2009; Müller et al., 2012; Heiden & Pirani, 2016; Barbosa et al., 2017; Pirani & Groppo, 2026).

Family	Species	Successional Status	Main Reference
Anacardiaceae	*Lithraea brasiliensis* Marchand	Pioneer	Müller et al. (2012)
	Schinus sp.	Pioneer	Müller et al. (2012)
	Schinus terebinthifolia Raddi	Pioneer	Müller et al. (2012)
	Schinus weinmanniifolia Engl.	Pioneer	Müller et al. (2012)
Arecaceae	*Syagrus romanzoffiana* (Cham.) Glassman	Non-pioneer	Barbosa et al. (2015)
Asteraceae	*Achyrocline satureioides* (Lam.) DC.	Grasslands shrub	Barbosa et al. (2015)
	Austroeupatorium inulifolium (Kunth) R.M.King & H.Rob.	Grasslands shrub	Boldrini (2009)
	Baccharis anomala DC.	Grasslands shrub	Barbosa et al. (2017)
	Baccharis articulata (Lam.) Pers.	Grasslands shrub	Barbosa et al. (2017)
	Baccharis caprariifolia DC.	Grasslands shrub	Barbosa et al. (2017)
	Baccharis coridifolia DC.	Grasslands shrub	Barbosa et al. (2017)
	Baccharis crispa Spreng.	Grasslands shrub	Barbosa et al. (2017)
	Baccharis dracunculifolia DC.	Grasslands shrub	Müller et al. (2012)
	Baccharis junciformis DC.	Grasslands shrub	Heiden (2016)
	Baccharis megapotamica Spreng.	Grasslands shrub	Barbosa et al. (2017)
	Baccharis punctulata DC.	Grasslands shrub	Barbosa et al. (2017)
	Baccharis spicata (Lam.) Baill.	Grasslands shrub	Barbosa et al. (2017)
	Chromolaena laevigata (Lam.) R.M.King & H.Rob.	Grasslands shrub	Barbosa et al. (2017)
	Chromolaena pedunculosa (Hook. & Arn.) R.M.King & H.Rob.	Grasslands shrub	Barbosa et al. (2017)
	Disynaphia ligulifolia (Hook. & Arn.) R.M.King & H.Rob.	Pioneer	Barbosa et al. (2017)

	Grazielia serrata (Spreng.) R.M.King & H.Rob.	Grasslands shrub	Barbosa et al. (2017)
	Moquiniastrum polymorphum (Less.) G.Sancho	Pioneer	Barbosa et al. (2017)
	Neocabreria serrulata (DC.) R.M.King & H.Rob.	Grasslands shrub	Barbosa et al. (2017)
	Senecio brasiliensis (Spreng.) Less.	Grasslands shrub	Barbosa et al. (2017)
	Vernonanthura nudiflora (Less.) H.Rob.	Grasslands shrub	Barbosa et al. (2017)
	Vernonanthura tweedieana (Baker) H.Rob.	Grasslands shrub	Boldrini (2009)
Cardiopteridaceae	*Citronella gongonha* (Mart.) R.A.Howard	Non-pioneer	Barbosa et al. (2017)
Erythroxylaceae	*Erythroxylum argentinum* O.E.Schulz	Non-pioneer	Barbosa et al. (2017)
Euphorbiaceae	*Gymnanthes klotzschiana* Müll.Arg.	Non-pioneer	Müller et al. (2012)
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke	Non-pioneer	Barbosa et al. (2017)
Lauraceae	*Ocotea pulchella* (Nees & Mart.) Mez	Non-pioneer	Müller et al. (2012)
Melastomataceae	*Leandra australis* (Cham.) Cogn.	Pioneer	Barbosa et al. (2017)
	Miconia cinerascens Miq.	Pioneer	Barbosa et al. (2017)
	Miconia hyemalis A.St.-Hil. & Naudin	Pioneer	Barbosa et al. (2017)
	Pleroma asperius (Cham.) Triana	Grasslands shrub	Flora do Brasil (2026)
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	Non-pioneer	Barbosa et al. (2017)
Myrtaceae	*Campomanesia aurea* O.Berg	Pioneer	Barbosa et al. (2017)
	Eugenia hyemalis Cambess.	Pioneer	Barbosa et al. (2017)
	Eugenia uniflora L.	Pioneer	Müller et al. (2012)
	Myrcia glabra (O.Berg) D.Legrand	Non-pioneer	Barbosa et al. (2017)
	Myrcia multiflora (Lam.) DC.	Non-pioneer	Müller et al. (2012)
	Myrcia palustris DC.	Pioneer	Barbosa et al. (2017)
	Myrciaria cuspidata O.Berg	Non-pioneer	Barbosa et al. (2017)
	Myrciaria tenella (DC.) O.Berg	Non-pioneer	Barbosa et al. (2017)
	Psidium cattleyanum Sabine	Pioneer	Müller et al. (2012)
Onagraceae	*Ludwigia multinervia* (Hook. & Arn.) Ramamoorthy	Grasslands shrub	Barbosa et al. (2017)
Pinaceae	*Pinus* sp.	Alien species	Flora do Brasil (2026)
Primulaceae	*Myrsine coriacea* (Sw.) R.Br. ex Roem. & Schult.	Pioneer	Müller et al. (2012)
	Myrsine loefgrenii (Mez) Imkhan.	Pioneer	Barbosa et al. (2017)

	Myrsine parvula (Mez) Otegui	Pioneer	Barbosa et al. (2017)
Proteaceae	*Grevillea robusta* A.Cunn. ex R.Br.	Alien species	Lorenzi (2003)
Rosaceae	*Prunus myrtifolia* (L.) Urb.	Non-pioneer	Müller et al. (2012)
Rutaceae	*Citrus limon* (L.) Burm.f.	Alien species	Pirani; Groppo (2026)
	Zanthoxylum fagara (L.) Sarg.	Non-pioneer	Barbosa et al. (2017)
	Zanthoxylum rhoifolium Lam.	Non-pioneer	Barbosa et al. (2017)
Salicaceae	*Casearia sylvestris* Sw.	Pioneer	Müller et al. (2012)
Sapindaceae	*Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl.	Pioneer	Müller et al. (2012)
	Cupania vernalis Cambess.	Non-pioneer	Müller et al. (2012)
	Dodonaea viscosa (L.) Jacq.	Pioneer	Müller et al. (2012)
	Matayba elaeagnoides Radlk.	Non-pioneer	Müller et al. (2012)
Solanaceae	*Solanum mauritianum* Scop.	Grasslands shrub	Soares et al. (2008)
	Solanum pseudocapsicum L.	Grasslands shrub	Soares et al. (2008)
Symplocaceae	*Symplocos uniflora* (Pohl) Benth.	Pioneer	Barbosa et al. (2017)

Supplementary Material – Table S2. Detailed results of the Generalized Linear Mixed Models (GLMM) for woody plant density and Simpson diversity index (1-D). The models evaluate the effects of fire and cattle grazing management in a randomized block design.

Model	Parameter	Std Error	*P* value	Sig	R_m^2	Dispersion (*p*)
Density	Burn Ungrazed	0.272	0.010	**	0.668	0.224
	Burn Grazed	0.284	< 0.001	***		
	Unburned Grazed	0.269	0.362	ns		
Simpson	Burn Ungrazed	0.079	0.011	*	0.333	0.800
	Burn Grazed	0.079	0.006	**		
	Unburned Grazed	0.079	0.144	ns		

Supplementary Material – Table S3. Multivariate analysis of woody community composition. Statistical summary of the Permutational Multivariate Analysis of Variance (PERMANOVA) based on Bray-Curtis distances and the test for homogeneity of multivariate dispersions (Betadisper). The models evaluate the effects of fire and cattle grazing management while accounting for the randomized block design (strata). The R^2 value represents the proportion of total community variance explained by the management treatments. The Betadisper results validate the PERMANOVA by confirming that observed differences are driven by centroid shifts (species substitution) rather than unequal within-group variances. Significant effects are indicated by: *** $p < 0.001$; ns for non-significant results ($p \geq 0.05$).

Analysis	Factor	Df	Sum of Sqs	R^2	F value	P value	Sig
PERMANOVA	Treatment	3	2.1933	0.179	2.6188	0.001	***
	Residuals	36	10.0504	0.821			
	Total	39	12.243	1.000			
Betadisper	Dispersion	3.0	0.034	-	0.397	0.756	ns

Supplementary Material – Table S4. Species richness and total abundance (number of individuals) categorized by plant functional groups in response to different management types. Management categories include combinations of grazing presence/absence (Grazed/Ungrazed) and fire occurrence or suppression (Burned/Unburned). Functional groups distinguish between grassland species (Grasslands), pioneer woody species, non-pioneer woody species, and exotic species (Alien species).

Vegetation category	Parameter	Burn Grazed	Unburned Grazed	Burn Ungrazed	Unburned Ungrazed
Grasslands Shrubs	Richness	7	13	18	13
	Abundance	155	578	500	525
Alien trees	Richness	1	2	1	1
	Abundance	1	3	1	1
Pioneer trees and shrubs	Richness	8	18	12	16
	Abundance	49	311	109	475
Non-pioneer tress and shrubs	Richness	3	9	3	15
	Abundance	19	86	23	186
Total	Richness	19	42	34	45
	Abundance	224	978	633	1187

Capítulo IV

Entre a impercepção botânica e a consciência campestre: desafios e possibilidades para o ensino do bioma Pampa na educação básica

Filipe Ferreira da Silveira, Sheron Ferreira da Silveira, Francieli Peter da Silveira, Guilherme Dubal dos Santos Seger, Gerhard Ernst Overbeck

Entre a Impercepção Botânica e a Consciência Campestre: Desafios e Possibilidades para o Ensino do Bioma Pampa na Educação Básica

From Botanical Imperception to Grassland Consciousness: Challenges and Prospects for Pampa Biome Instruction in Basic Education

Filipe F. da Silveira[1*], Sheron F. da Silveira[1], Francieli P. da Silveira[1], Julian Silveira Diogo de Ávila Fontoura[2], e Gerhard E. Overbeck[13].

[1] Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Botânica, Porto Alegre, Rio Grande do Sul, Brasil.

*e-mail: filipesilveferreira@hotmail.com

[2] Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Educação, Porto Alegre, Rio Grande do Sul, Brasil.

[3] Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Ecologia, Porto Alegre, Rio Grande do Sul, Brasil.

Filipe Ferreira da Silveira – **ORCiD**: 0000-0002-1273-0655 – **ID Lattes:** 3159324243187479

Sheron Ferreira da Silveira – **ORCiD**: 0009-0007-5596-0809 – **ID Lattes:** 7015014251877619

Francieli Peter da Silveira – **ORCiD**: 0009-0008-3050-3289– **ID Lattes:** 1986625334208670

Julian Silveira Diogo de Ávila Fontoura – **ORCiD**: 0000-0001-8507-6538– **ID Lattes:** 7808693167946729

Gerhard Ernst Overbeck – **ORCiD**: 0000-0002-8716-5136– **ID Lattes:** 7199331941689392

TÍTULO CURTO: EDUCAÇÃO E PAMPA: DA INVISIBILIDADE À CONSCIÊNCIA.

Resumo

A invisibilização dos campos na sociedade e nos currículos prejudica a conservação do Pampa. Apesar do vasto conhecimento científico disponível, o público ainda o desconhece, uma clara disparidade na percepção de biomas. Na educação, barreiras como a impercepção botânica, o viés florestal e lacunas curriculares impedem que os campos sejam vistos como ecossistemas legítimos. Este artigo discute esses desafios na educação básica e propõe a Alfabetização Ecológica para aproximar a ciência da escola. Com base em práticas reais, sugerimos estratégias que valorizam a biodiversidade regional e o afeto pelo território, defendendo que uma Consciência Campestre é essencial para formar cidadãos comprometidos com os campos sulinos.

Palavras-chave: práticas pedagógicas, viés florestal, biodiversidade regional, alfabetização ecológica, campos naturais.

Abstract

The invisibility of grasslands in society and school curricula hinders the conservation of the Pampa. Despite the vast scientific knowledge available, the general public remains largely unaware of this biome—a clear disparity in biome perception. In education, barriers such as botanical imperception, forest bias, and curricular gaps prevent grasslands from being recognized as legitimate ecosystems. This article discusses these challenges in basic education and proposes Ecological Literacy as a way to bridge the gap between science and the school environment. Based on real-world practices, we suggest strategies that value regional biodiversity and territorial attachment, arguing that a Grassland Awareness is essential for forming citizens committed to the southern grasslands.

Keywords: *pedagogical practices; forest bias; regional biodiversity; ecological literacy; natural grasslands.*

Introdução

Os ecossistemas abertos ocupam uma parcela significativa da superfície terrestre e desempenham papel central na manutenção da biodiversidade global (Gibson, 2008). No sudeste da América do Sul, destaca-se o bioma Pampa, segundo-menor bioma brasileiro, caracterizado por uma fisionomia predominantemente campestre, moldada por uma longa história evolutiva associada a distúrbios naturais, como o fogo e o pastejo. Apesar de sua relevância ecológica, cultural e histórica, o Pampa permanece amplamente invisibilizado no imaginário social e educacional, sendo frequentemente interpretado como um ambiente empobrecido ou como um estágio degradado de formações florestais (Overbeck et al., 2007, 2023; Porto et al., 2020). A literatura científica recente tem evidenciado a elevada biodiversidade associada aos campos naturais, com estimativas que ultrapassam 12.500 espécies registradas para o bioma Pampa como um todo (Andrade et al., 2023). De forma geral, a biodiversidade do Pampa, bem como os processos ecológicos que moldam os seus ecossistemas, hoje são bem conhecidos. Contudo, esse expressivo acúmulo de conhecimento contrasta com a baixa percepção social acerca de sua importância, configurando o que Silveira et al. (2022) denominam Biome Awareness Disparity (BAD): biomas florestais recebem mais atenção que biomas não-florestais, como o Pampa. Tal disparidade entre produção científica e reconhecimento social contribui para a continuidade de processos de degradação e supressão dos campos naturais, frequentemente legitimados por discursos conservacionistas baseados em modelos florestais hegemônicos. A falta de consideração dos ecossistemas campestres nas políticas de conservação no Brasil tem sido apontada pela ciência (Overbeck et al., 2007, 2015). No contexto escolar, essa invisibilização evidencia um distanciamento entre o currículo e os territórios vividos. Essa lacuna demanda o que Kitzmann e Asmus (2012) definem como ambientalização sistêmica: um processo de ressignificação de conteúdos e metodologias que busca integrar a dimensão socioambiental de forma transversal. Superar esse cenário é um imperativo legal e

pedagógico, fundamentado no Plano Nacional de Educação (Lei 13.005/2014), que estabelece, em seu Artigo 2º (inciso X), a promoção da sustentabilidade socioambiental e o respeito à diversidade como diretrizes educacionais. Sob esta perspectiva, a escola assume o papel de promotora de uma inovação curricular (Kitzmann; Asmus, 2012), um processo de microescala que modifica ideias e práticas pedagógicas a partir do chão da escola. Através dessa ótica, a valorização do Bioma Pampa e dos seus campos como sistemas ecológicos legítimos alinha-se à unidade temática "Vida e evolução" da Base Nacional Comum Curricular (BNCC), que preconiza o estudo da distribuição da biodiversidade nos principais ecossistemas brasileiros e as interações entre seres humanos e ambiente. Assim, repensar as práticas pedagógicas torna-se essencial para que o conhecimento científico sobre a fauna e flora locais fundamente alternativas de convivência sustentável, transformando a escola em um espaço de fortalecimento de vínculos e de uso consciente dos recursos naturais para o presente e o futuro. Nesse sentido, este artigo tem como objetivo discutir os desafios conceituais e curriculares associados ao ensino do bioma Pampa na educação básica e apresentar a Alfabetização Ecológica como um referencial teórico capaz de orientar práticas pedagógicas voltadas à construção de uma Consciência Campestre. Essa consciência pressupõe a formação do 'sujeito ecológico' (Carvalho, 2012), aquele que se constitui por meio de uma relação ética, política e sensível com o entorno. Para além da transmissão de informações, busca-se uma dimensão formativa que mobilize valores e identidades, permitindo que o educando se reconheça como parte integrante e responsável pela sustentabilidade dos sistemas naturais onde está inserido.

1.1 Invisibilização dos campos naturais: impercepção botânica e viés florestal

A marginalização dos ecossistemas campestres no debate ambiental e educacional está associada a dois agravantes conceituais inter-relacionados: a impercepção botânica e o viés florestal. A impercepção botânica, termo proposto por Ursi e Salatino (2022) como alternativa a *botanical blindness*, refere-se à dificuldade de reconhecer as plantas como

organismos vivos centrais nos ecossistemas, frequentemente relegadas ao papel de pano de fundo da paisagem. Essa limitação perceptiva compromete a compreensão dos processos ecológicos e reduz o interesse pelos componentes vegetais da biodiversidade. No entanto, este componente é de fundamental importância nos ecossistemas, já que a vegetação - ou as comunidades de plantas - não só é responsável pela produtividade primária, processo fundamental nos ecossistemas, mas também constitui o habitat para a maior parte da fauna. Ademais, a dinâmica dos ecossistemas muitas vezes depende da dinâmica da vegetação; isso fica muito claro no caso dos ecossistemas campestres, onde é a biomassa do estrato herbáceo, formado principalmente por gramíneas, que é o alimento para os grandes herbívoros ou o combustível para o fogo. O viés florestal, por sua vez, diz respeito à tendência de atribuir maior valor ecológico e conservacionista às formações florestais, em detrimento de ecossistemas abertos, como campos e savanas (Overbeck et al., 2015). Esse viés sustenta a interpretação equivocada dos campos naturais como ambientes incompletos ou degradados, cuja conservação estaria condicionada à regeneração florestal. Tal perspectiva ignora a estabilidade ecológica, a funcionalidade, os serviços ecossistêmicos e a história evolutiva milenar dos ecossistemas campestres já evidenciados por diversos estudos, além de desconsiderar o papel de distúrbios naturais na manutenção de sua biodiversidade (Veldman et al., 2015). No caso do bioma Pampa, esses vieses contribuem para a invisibilização de sua flora predominantemente herbácea, composta por uma elevada diversidade de formas de vida, estratégias funcionais e adaptações ecológicas (Porto et al., 2021). A ausência de extensas formações florestais, as quais são frequentemente associadas a uma noção simplificada de "natureza conservada", reforça a percepção social dos campos como espaços vazios ou subutilizados, o que se reflete tanto em políticas públicas quanto em materiais didáticos e práticas pedagógicas.

Método

Trata-se de um artigo de natureza teórico-reflexiva, ancorado na literatura científica e na sistematização de práticas educativas desenvolvidas no âmbito da educação básica, sem a pretensão de avaliar. O percurso metodológico iniciou-se pela constituição de um *corpus* bibliográfico representativo, operado por meio de buscas em bases de dados como Google Acadêmico e Periódicos CAPES. Utilizando descritores como "Bioma Pampa", "Ensino de Botânica", "Alfabetização Ecológica" e "*Botanical blindness*" – neste último em inglês pois são utilizados diversos termos para se referirem ao seu significado como Cegueira Botânica ou Impercepção Botânica por exemplo - , os critérios de inclusão priorizaram obras que fundamentam o fenômeno da disparidade de percepção entre biomas (BAD) e a ecologia de ecossistemas abertos, confrontando-os com o referencial teórico-crítico da educação.

Complementarmente, realizou-se um mapeamento curricular centrado na análise da Base Nacional Comum Curricular (BNCC), com o objetivo de identificar habilidades que, embora de caráter nacional e generalista, apresentassem a plasticidade necessária para a inserção das especificidades regionais e dos processos ecológicos do Pampa. Essa análise documental serviu de suporte para a subsequente seleção e sistematização de práticas educativas e recursos lúdicos sugeridos, como o jogo "Super Trunfo dos Campos Sulinos" e o projeto "Jardim das Percepções". A escolha dessas experiências obedeceu a critérios de relevância técnica, especificamente seu potencial para o enfrentamento do viés florestal e da impercepção botânica, e de viabilidade de aplicação no cotidiano da escola pública. Finalmente, a análise dessas práticas deu-se de forma descritivo-reflexiva, buscando evidenciar a potência dessas estratégias frente ao referencial da Alfabetização Ecológica. Ressalta-se que o estudo não pretende a avaliação empírica de impactos em grupos amostrais, mas sim a construção de uma síntese teórica que sustente a transposição didática

do conhecimento científico para o fortalecimento da consciência campestre no ambiente escolar.

Análise

1. Currículo, território e a ausência do Pampa na educação formal

A escola desempenha papel central na construção de sentidos sobre natureza, ambiente e conservação (de Lima Gomes et al., 2025). Entretanto, essa função é atravessada por disputas simbólicas materializadas no currículo, que não é um documento neutro, mas um aparato de reprodução ideológica e de manutenção de relações de poder (Althusser, 1985; Ferraro, 2014). Sob essa ótica, o currículo atua como um território onde se definem quais conhecimentos são legítimos, influenciando diretamente a produção de identidades e subjetividades (da Silva, 1996). No contexto brasileiro, essa tensão fica evidente na Base Nacional Comum Curricular (BNCC): ao estabelecer orientações gerais para o ensino de Ciências e Biologia, o documento silencia o bioma Pampa, excluindo-o quanto a sua caracterização entre os ecossistemas nacionais (BRASIL, 2017), revelando como as escolhas curriculares podem invisibilizar territórios e biodiversidades regionais. A lacuna curricular invisibiliza os Campos Sulinos — ecossistemas de gramíneas que abrangem o Pampa e as áreas de altitude do Sul do Brasil — comprometendo o reconhecimento de sua relevância ecológica, histórica e cultural. A omissão do Pampa nos documentos oficiais que normatizam os currículos escolares, reforça a centralidade de outros biomas e limita a contextualização da biodiversidade regional. Como consequência, observa-se uma insegurança docente no trato de conteúdos relacionados aos campos naturais, uma vez que estudos de Dill e Carcinatto (2020) e Santos et al. (2016) já apontam o desconhecimento dos professores a respeito de temáticas vinculadas ao ambiente natural em que vivem.

Essa vulnerabilidade pedagógica sugere que a omissão do Pampa nos documentos oficiais impacta a própria base de conhecimentos que sustenta a profissão. Conforme as

proposições de Tardif (2014), o saber que o professor mobiliza não é uma entidade isolada ou puramente técnica, mas uma construção intrinsecamente vinculada ao reconhecimento coletivo. No caso dos ecossistemas campestres, a ausência de uma validação institucional e curricular acaba por deslegitimar o saber docente, pois a autoridade do professor sobre o que ensinar não provém apenas de sua cognição individual, mas de um sistema social que chancela esse conhecimento como relevante. Dessa forma, o "saber ensinar" o Pampa deve ser compreendido como um processo relacional e não como um conjunto estático de informações biológicas. Ensinar Ciências é, essencialmente, um ato de interação entre sujeitos; logo, a construção de uma consciência sobre o bioma depende de um jogo de expectativas e negociações constantes entre o docente e seus alunos (Tardif, 2014). Quando o território é ignorado pelas esferas que organizam o trabalho escolar, o professor perde o amparo necessário para desenvolver saberes experienciais significativos, o que compromete a execução de um projeto educativo que de fato instrua e transforme a percepção dos estudantes sobre o seu próprio entorno socioambiental. O professor, nesse cenário, não apenas "não sabe o conteúdo" técnico, mas carece de saberes experienciais e de uma base de conhecimento profissional que relacione a ciência da conservação com a didática das ciências, dificultando a transposição de temas locais para o plano de aula. Essa lacuna de conhecimento é justificada por Zanini et al. (2020) como reflexo de um baixo envolvimento prático com o ecossistema local e do reduzido tempo destinado pelas escolas para atividades que possibilitem a interação direta com a natureza. O distanciamento físico e cultural em relação à natureza, intensificado pelos estilos de vida mediados por telas nos centros urbanos, fragiliza a memória botânica e a construção de vínculos afetivos com a biodiversidade local.

2. Articulação entre as habilidades da BNCC e o Pampa

As habilidades da BNCC elencadas na Tabela 1 constituem um recorte analítico selecionado para este estudo, evidenciando que, embora o documento nacional não

menciona nominalmente o Bioma Pampa, suas diretrizes são suficientemente amplas para permitir a inserção de temáticas regionais e de conservação. Essa autonomia pedagógica possibilita que o docente, mesmo sem ser um especialista no assunto, utilize o cotidiano como recurso: a presença de plantas ruderais em meios-fios ou terrenos baldios oferece um contato prático imediato, mobilizando verbos centrais da Base como observar, identificar e descrever. Para a construção desse conhecimento situado, o docente deve articular a abertura — o planejamento estratégico de inserção do bioma no cronograma dos 200 dias letivos — e a oferta, que consiste na transposição didática das competências. Exemplos disso incluem a investigação de mecanismos reprodutivos da fauna nativa (EF08CI07), a montagem de cadeias alimentares contextualizadas com espécies locais (EF04CI04) ou a análise da importância ecológica da flora, fauna e funga na criação de unidades de conservação (EF09CI12; EF07CI08).

Tabela 1

Articulação entre as Habilidades de Ciências da BNCC e Propostas de Contextualização para a Valorização do Bioma Pampa e Ecossistemas do Rio Grande do Sul.

Ano	Unidades Temáticas	Objetos de conhecimento	Habilidades	Sugestões de assunto para a valorização campestre
2º Ano	Vida e evolução	Seres vivos no ambiente Plantas	(EF02CI04) Descrever características de plantas e animais (tamanho, forma, cor, fase da vida, local onde se desenvolvem etc.) que fazem parte de seu cotidiano e relacioná-las ao ambiente em que eles vivem.	Plantas e animais nativos do Bioma Pampa, como graxaim, ema, colhereiro, quero-quero, jacaré-de-papo-amarelo e plantas como o aguapé, a pitangueira, o butiázeiro, e o capim-dos-pampas
2º Ano	Vida e evolução	Seres vivos no ambiente Plantas	(EF02CI06) Identificar as principais partes de uma planta (raiz, caule, folhas, flores e frutos) e a função desempenhada por cada uma delas, e analisar as relações entre as plantas, o ambiente e os demais seres vivos.	Através de fotos mostrar a diversidade de órgãos vegetais e múltiplas estratégias ecológicas para lidar com o ambiente: trepadeiras, geófitas, xerófitas, touceiras, prostradas, lenhosas.
3° Ano	Vida e evolução	Características e desenvolvimento dos animais	(EF03CI04) Identificar características sobre o modo de vida (o que comem, como se reproduzem, como se deslocam etc.) dos animais mais comuns no ambiente próximo.	Aspectos ecológicos sobre fauna nativa, usando exemplos atrativos como o boto-de-lahille e a pesca cooperativa na Barra de Imbé – Litoral RS
3° Ano	Vida e evolução	Características e desenvolvimento dos animais	(EF03CI05) Descrever e comunicar as alterações que ocorrem desde o nascimento em animais de diferentes meios terrestres ou aquáticos, inclusive o homem	Abordar aspectos ecológicos sobre o não compartilhamento de nicho entre adultos e filhotes, e metamorfose usando espécies de borboletas e anfíbios nativas
3° Ano	Vida e evolução	Características e desenvolvimento dos animais	(EF03CI06) Comparar alguns animais e organizar grupos com base em características externas comuns (presença de penas, pelos, escamas, bico, garras, antenas, patas etc.).	Usando exemplos múltiplos de animais nativos de grupos distintos.

4º Ano	Vida e evolução	Cadeias alimentares simples	(EF04CI04) Analisar e construir cadeias alimentares simples, reconhecendo a posição ocupada pelos seres vivos nessas cadeias e o papel do Sol como fonte primária de energia na produção de alimentos	Elaborar com estudantes diferentes ambientes e possíveis animais que ali vivem. Através disso o estudante perceberá que dependendo do ambiente a cadeia alimentar mudará, pois os organismos-chave também mudarão. Exemplos: ecossistema litorâneo aquático, dunoso, urbano, banhado, campestre. Exemplo: Cadeia natural – capim – lagarta de borboleta-oitenta-e-oito – sabiá – gavião-caboclo Cadeia Antrópica: capim – gado – humano É possível unir o exemplo de cadeia alimentar natural com a cadeia alimentar antrópica em uma única teia alimentar relacionando os consumidores primários com capim
4º Ano	Vida e evolução	Cadeias alimentares simples	(EF04CI07) Verificar a participação de microrganismos na produção de alimentos, combustíveis, medicamentos, entre outros.	Desenvolver com estudante a consciência de que decompositores reciclam a matéria orgânica para absorção vegetal, diferentemente com o que acontece com detritívoros que apenas fragmentam e auxiliam no processo de diminuição do tamanho da matéria orgânica. Usar exemplo do urubu e falar sobre o *alloprening* com o Carcará.
5º Ano	Matéria e energia	Ciclo hidrológico	(EF05CI02) Aplicar os conhecimentos sobre as mudanças de estado físico da água para explicar o ciclo hidrológico e analisar suas implicações na agricultura, no clima, na geração de energia elétrica, no provimento de água potável e no equilíbrio dos ecossistemas regionais (ou locais).	Contextualizar o ciclo hidrológico, topografia do estado com o atual cenário de eventos climáticos extremos, vivenciados com as enchentes de maio de 2024, e possíveis ações de mitigação de impactos.
5º Ano	Matéria e energia	Ciclo hidrológico	(EF05CI03) Selecionar argumentos que justifiquem a importância da cobertura vegetal para a manutenção	Abordar com estudantes o efeito esponja que o banhado exerce, contextualizando com o viés conservacionista do

			do ciclo da água, a conservação dos solos, dos cursos de água e da qualidade do ar atmosférico.	ecossistema e demais serviços ecológicos que ele executa.
7º Ano	Vida e evolução	Diversidade de ecossistemas	(EF07CI07) Caracterizar os principais ecossistemas brasileiros quanto à paisagem, à quantidade de água, ao tipo de solo, à disponibilidade de luz solar, à temperatura etc., correlacionando essas características à flora e fauna específicas.	Abordar as diferenças entre ambientes de vegetação aberta e fechada no Rio Grande do Sul, criando hipóteses sobre seu funcionamento que poderão ser sanadas através de pesquisas ou do docente.
7º Ano	Vida e evolução	Fenômenos naturais e impactos ambientais	(EF07CI08) avaliar como os impactos provocados por catástrofes naturais ou mudanças nos componentes físicos, biológicos ou sociais de um ecossistema afetam suas populações, podendo ameaçar ou provocar a extinção de espécies, alteração de hábitos, migração etc.	Pensar em conjunto com a turma em hipóteses de mitigação de impactos, ações executadas desde o último evento pelos tomadores de decisão, levando em consideração a preservação de áreas úmidas, vegetação ripária com o viés da absorção e escoamento como serviço ecossistêmico às cidades.
8º Ano	Vida e evolução	Mecanismos reprodutivos	(EF08CI07) Comparar diferentes processos reprodutivos em plantas e animais em relação aos mecanismos adaptativos e evolutivos	Usar exemplo de plantas nativas, como o xaxim, araucária e o butiá, assim como ovíparos (tesourinha), ovovivíparos (arraias ou tubarões) e vivíparos, marsupiais (gambá, catita) e placentários nativos (anta, gato-palheiro)
9º Ano	Vida e evolução	Preservação da biodiversidade	(EF09CI12) Justificar a importância das unidades de conservação para a preservação da biodiversidade e do patrimônio nacional, considerando os diferentes tipos de unidades (parques, reservas e florestas nacionais), as populações humanas e as atividades a eles relacionados.	Apresentar aos estudantes algumas UC presentes no nosso estado, as principais espécies vegetais e animais encontradas e a importância da convivência em harmonia com a natureza por meio de exemplos de extrativismo sustentável por povos originários e quilombolas.

Eixo de discussão

1. Alfabetização ecológica como referencial para o ensino do bioma Pampa

Diante dos desafios conceituais e curriculares que permeiam o ensino do Pampa, a Alfabetização Ecológica, conforme proposta por Capra et al. (2006), oferece um arcabouço teórico capaz de subsidiar a transposição do conhecimento científico para o ambiente escolar. Essa abordagem parte da compreensão dos sistemas naturais como redes interconectadas, enfatizando processos, relações e dinâmicas ecológicas, em oposição a uma visão fragmentada e estática da natureza. No contexto do bioma Pampa, a Alfabetização Ecológica possibilita a abordagem de conceitos complexos e, muitas vezes, contraintuitivos, como o papel ecológico do fogo e do pastejo. Estudos recentes demonstram que a exclusão desses distúrbios pode resultar em perda de diversidade e alterações estruturais nos ecossistemas campestres (Müller et al., 2007, 2012; Overbeck et al., 2023; da Silveira et al., 2025). Assim, compreender o manejo pastoril e a pecuária sustentável como ferramentas de conservação constitui um elemento central para a superação de visões simplistas que classificam toda intervenção humana como necessariamente degradante. Também permitem discutir a relação entre seres humanos e natureza, e a dependência das economias humanas dos recursos naturais. A Alfabetização Ecológica é concebida como uma ferramenta pedagógica essencial para enfrentar a crise da educação, partindo da premissa de que o desequilíbrio dos ecossistemas contemporâneos reflete um desequilíbrio prévio da mente humana (Stone et al., 2006). Essa perspectiva favorece a articulação entre o conhecimento científico, os saberes locais e as práticas culturais, promovendo uma compreensão ampla e contextualizada do Pampa como um sistema ecológico dinâmico. Ao reconhecer o território como espaço educativo e valorizar a realidade concreta dos educandos, tal abordagem dialoga diretamente com a pedagogia pós-crítica, transformando a percepção ambiental em um compromisso ético e social. Sob a ótica de Tomaz Tadeu da Silva, essa problemática transcende a questão ambiental, pois o

currículo deve ser compreendido como um "documento de identidade", cujo papel central é responder que tipo de ser humano se deseja formar e quais identidades sociais devem ser construídas (Silva, 1999). Nesse contexto, a escola assume uma responsabilidade estratégica, uma vez que o currículo opera precisamente no nexo entre a transmissão do conhecimento e a produção de identidades, nunca sendo um artefato neutro, mas sim intrinsecamente ligado a relações de poder (da Silva, 1996, 2016). Essa produção de identidade converge para a constituição do sujeito ecológico (Carvalho, 2012), deslocando a Educação Ambiental de uma abordagem meramente informativa para uma experiência de pertencimento. Ao articular a ideia de sujeito ecológico à Consciência Campestre, favorecem-se processos educativos que promovem o engajamento com a realidade dos campos sulinos, transformando o saber botânico em um modo de vida comprometido com o território. Assim, a reconstrução do senso de pertencimento ao território e a valorização dos ecossistemas regionais configuram-se como uma estratégia política de um currículo voltado para a emancipação e a liberdade, promovendo o que se denomina "pedagogia da possibilidade" em oposição às formas de alienação contemporâneas (da Silva, 2016).

2. Estratégias pedagógicas para a construção de uma Consciência Campestre

A educação voltada ao Pampa demanda a ruptura com o ensino meramente descritivo. Propõe-se, em seu lugar, a convergência entre o conhecimento científico e o engajamento sensível com os ecossistemas que compõem essa parcela dos campos sulinos. Essa conexão é fundamental para a conservação, pois as atitudes individuais são guiadas mais por emoções e valores do que meramente por conhecimentos teóricos (do Nascimento & Araújo-de-Almeida, 2009). Assim, o estabelecimento de "laços estreitos" com o meio ambiente torna-se o eixo central da Educação Ambiental, permitindo que o estudante recupere a ideia de pertencimento e entenda que "conhecer para preservar" envolve uma nova aliança entre humanos e natureza (Reigota, 2017). Ao aproximar os educandos dos elementos bióticos e abióticos do Pampa desde os anos iniciais, a escola transforma a

informação em valor, combatendo a invisibilidade do bioma e fomentando o respeito necessário para a sua sobrevivência e dignidade.A sistematização de práticas pedagógicas desenvolvidas no âmbito da educação básica indica que estratégias lúdicas e dialógicas ampliam as possibilidades de aprendizagem e favorecem a superação da impercepção botânica (Gozzer, 2023; Santos & Soffiatti, 2024). Entre essas estratégias, destacam-se atividades estruturadas em quatro eixos complementares: apresentação dialógica do tema, jogos educativos, práticas artísticas com elementos botânicos e experiências sensoriais. O estabelecimento de vínculos com a botânica pressupõe, inicialmente, a promoção de atividades sensoriais que permitam a interação direta entre o estudante e o universo vegetal. Um exemplo bem-sucedido dessa abordagem é o projeto de extensão da UFRGS, "Jardim das Percepções", originado do Jardim Sensorial (da Silveira, 2018), que utiliza a dinâmica dos sentidos para abordar aspectos morfológicos e ecológicos das plantas. Ao estimular os alunos a tocar, cheirar e explorar diferentes texturas e odores, essa prática não apenas favorece o engajamento, mas também evoca memórias afetivas que fortalecem a conexão com o ambiente natural. No cotidiano escolar, essa estratégia pode ser ampliada por meio de hortas ou espaços não formais que priorizem a flora nativa regional. A introdução de espécies nativas com usos populares — sejam elas medicinais e temperos (carqueja, marcela e capim-limão) ou frutíferas e ornamentais (butiá, pitanga, araçá e cerejeira-do-mato) — permite que o conteúdo biológico dialogue com o saber cultural e a realidade local. De modo complementar, o uso de ferramentas lúdicas, como o jogo "Super Trunfo dos Campos Sulinos" (Santos, 2022), consolida conceitos de forma integrada e contextualizada. Ao associar espécies campestres a seus respectivos habitats e níveis tróficos, tais recursos combatem a "impercepção botânica" e o "viés florestal", valorizando a biodiversidade herbácea e arbustiva muitas vezes negligenciada nos materiais didáticos tradicionais. Outros recursos pedagógicos, como álbuns ilustrados, jogos de cartas e atividades de memória, têm se mostrado ferramentas promissoras para apoiar o trabalho docente (Silveira et al., 2022,

2023, 2025). Tais estratégias não têm como finalidade a avaliação de resultados de aprendizagem, mas a ampliação do repertório pedagógico disponível aos professores e o fortalecimento de práticas alinhadas à Alfabetização Ecológica.

Conclusão

Este artigo contribui para o campo da educação básica ao oferecer um roteiro de transposição didática que converte lacunas da BNCC em oportunidades de inovação curricular, provendo ao docente ferramentas analíticas e recursos lúdicos contextualizados para o ensino do Pampa. No entanto, reconhecem-se os limites desta reflexão, centrada na análise teórica e em proposições metodológicas, o que demanda futuras investigações de cunho empírico que avaliem a recepção e a eficácia dessas estratégias no cotidiano escolar. Como agenda de pesquisa, abre-se a necessidade de investigar a formação continuada de professores sob a lente da ambientalização sistêmica e de desenvolver materiais didáticos que aprofundem a interdisciplinaridade, consolidando o bioma não apenas como objeto de estudo, mas como um eixo central de uma pedagogia do território.

A invisibilização do bioma Pampa no imaginário social, nos currículos escolares e nas práticas pedagógicas constitui um dos principais desafios para sua conservação. A superação desse quadro exige a construção de uma Consciência Campestre, entendida como o reconhecimento dos campos sulinos enquanto sistemas ecológicos legítimos, dinâmicos e historicamente moldados por interações entre processos naturais e práticas humanas. No campo educacional, esse desafio implica repensar currículos, formar professores e desenvolver estratégias pedagógicas que articulem botânica, ecologia e cultura, valorizando a biodiversidade regional e o território como espaço educativo. A Alfabetização Ecológica emerge, nesse contexto, como um referencial teórico potente para subsidiar a transposição do conhecimento científico para a educação básica, promovendo uma compreensão mais integrada e crítica dos ecossistemas campestres.

Em consonância com perspectivas pedagógicas críticas, defende-se que o ensino deve emergir da realidade concreta dos educandos, reconhecendo seus territórios, saberes e experiências.

Nessa mesma direção, a construção de uma educação comprometida com a sustentabilidade implica a formação do sujeito ecológico, conforme proposto por Isabel Carvalho (2012). Trata-se de um sujeito que se constitui na relação ética, política e sensível com o meio ambiente, deslocando a educação ambiental de uma abordagem meramente informativa para uma dimensão formativa mais ampla, na qual valores e identidades são mobilizados. No contexto deste estudo, a ideia de sujeito ecológico articula-se à construção de uma Consciência Campestre ao favorecer processos educativos que promovem pertencimento, responsabilidade socioambiental e engajamento com a realidade dos Campos Sulinos. Somente por meio de uma educação que reconecte ciência, escola e território será possível transformar a subjetividade contida nos versos da canção Sol, Sul, Terra e Cor, do compositor Leonardo, deixe de ser apenas uma herança cultural distante para se tornar uma vivência cotidiana: “Eu quero andar nas coxilhas, sentindo as flechilhas das ervas do chão, ter os pés roseteados de campo...”. Ao promover essa integração, assegura-se que o contato direto com a natureza se traduza não apenas em experiência estética, mas na constituição de um sujeito cuja relação com o mundo fundamente uma responsabilidade ética com a conservação do Pampa, transformando o "sentir o chão" em um compromisso existencial com a vida.

Agradecimentos

Agradecemos à CAPES pela concessão da bolsa de estudos (88887.684521/2022-00) e ao programa 'Bolsas FUNBIO – Conservando o Futuro', viabilizado pelo FUNBIO e Instituto Humanize. Agradecemos também à Universidade Federal do Rio Grande do Sul (UFRGS), em especial a toda a estrutura e apoio oferecidos pelo Programa de Pós-Graduação em Botânica (PPGBot)

Financiamento

Filipe Ferreira da Silveira – Bolsa de estudos CAPES (88887.684521/2022-00);

Bolsa FUNBIO – Conservando o Futuro viabilizada pelo Instituto Humanize.

Contribuições de Autoria

Conceitualização: FFS, SFS, FPS, JSDAF, GEO. Curadoria de dados: FFS. Análise formal: FFS, SFS, FPS, JSDAF, GEO. Aquisição de financiamento: GEO. Investigação: FFS, SFS, JSDAF, FPS. Metodologia: FFS, SFS, FPS, JSDAF. Administração do projeto: FFS. Recursos: GEO. Programas: GEO. Supervisão: JSDAF , GEO. Validação: SFS, FPS, JSDAF, GEO. Visualização: FFS, SFS, FPS, JSDAF, GEO. Redação - rascunho original: FFS. Redação - revisão e edição: FFS, SFS, FPS, JSDAF, GEO.

Conflito de Interesse

As pessoas autoras declaram não haver conflitos de interesse a informar.

Disponibilidade dos Dados

Os dados integrais analisados durante o estudo atual estão apresentados no corpo do manuscrito.

Conformidade Ética

Não se aplica.

Referências

Althusser, L. (1985). Aparelhos ideológicos de Estado: Nota sobre os aparelhos ideológicos de Estado (E. Presença, Ed.). Graal.

Andrade, B. O., Dröse, W., Aguiar, C. A. de, Aires, E. T., Alvares, D. J., Barbieri, R. L., Beretta, M. S., Bordignon, S. A. L., Blanco, C. C., Brandão, A. S., Brassaloti, R. A., Brauwers, V. V., Brito, R., Camargo, A., Cancelli, R. R., Castanho, C. T., Chuvas, S. N., Chomen-de-Cebreiros, M., Cordazzo, C. V., . . . Overbeck, G. E. (2023). 12,500+ and counting: Biodiversity of the Brazilian Pampa. Frontiers of Biogeography, 15(2). https://doi.org/10.21425/F5FBG59288

Brasil. (2017). Base Nacional Comum Curricular: Educação Infantil e Ensino Fundamental. Ministério da Educação.

Carvalho, I. C. M. (2012). Educação ambiental: a formação do sujeito ecológico. 6. ed. São Paulo: Cortez.

da Silva, T. T. (1996). Identidades terminais: As transformações na política da pedagogia e na pedagogia da política. Vozes.

da Silva, T. T. (2016). Documentos de identidade: Uma introdução às teorias do currículo. Autêntica.

da Silveira, F. F. (2018). Adaptação do uso de Jardim Sensorial como objeto de aprendizagem no ensino de botânica no Ensino Fundamental. Trabalho de Conclusão de Curso. Universidade Federal do Rio Grande do Sul.

da Silveira, F. F., Menezes, L. S., Porto, A. B., Thomas, P. A., Boavista, L. da R., Seger, G. D. S., & Overbeck, G. E. (2025). Southern Brazilian Grassland Diversity: Anti-Disturbance Regimes Are Not Ideal and Grazing Maintains Plant Diversity. Applied Vegetation Science, 28(4), e70049. https://doi.org/10.1111/avsc.70049

de Lima Gomes, R. L., Brandão, A. A., do Nascimento Araujo, I. R., da Silva Melo, E. H., da Silva, P. M., & das Neves, R. F. (2025). Linha evolutiva: Proposta de recurso lúdico para o ensino da evolução das plantas terrestres. In Realize Editora (Ed.), Anais do XI Congresso Nacional de Educação (CONEDU). Realize Editora.

Dill, M. A., & Carniatto, I. (2020). Concepções de meio ambiente e Educação Ambiental de professores do ensino fundamental I. Revista Brasileira de Educação Ambiental (RevBEA), 15(5), 152–172. https://doi.org/10.34024/revbea.2020.v15.9928

Ferraro, J. L. S. (2014). Althusser, educação, estado e (re) produção. Revista Contemporânea de Educação, 9(17), 4–23, 1-20. https://doi.org/10.20500/rce.v9i17.1712

Gozzer, E. K. (2023). Gamificação em roteiros ambientais: Um estudo de caso sobre a impercepção botânica. Trabalho de Conclusão de Curso. Instituto Federal do Espírito Santo.

Kitzmann, D. I. S.; Asmus, M. L (2012). Ambientalização sistêmica do currículo ao socioambiente.

Müller, S. C., Overbeck, G. E., Pfadenhauer, J., & Pillar, V. D. (2007). Plant functional types of woody species related to fire disturbance in forest–grassland ecotones. Plant Ecology, 189(1), 1–14.

Müller, S. C., Overbeck, G. E., Pfadenhauer, J., & Pillar, V. D. (2012). Woody species patterns at forest-grassland boundaries in southern Brazil. Flora: Morphology, Distribution, Functional Ecology of Plants, 207(8), 586–598. https://doi.org/10.1016/j.flora.2012.06.012

do Nascimento, M. V. É., & Araújo-de-Almeida, E. (2009). Importância da realização de trilhas participativas para o conhecimento e conservação da diversidade biológica: Uma análise da percepção ambiental. REMEA - Revista Eletrônica do Mestrado em Educação Ambiental, 23, 1-11.

Overbeck, G. E., Müller, S. C., Fidelis, A., Pfadenhauer, J., Pillar, V. D., Blanco, C. C., Boldrini, I. I., Both, R., & Forneck, E. D. (2007). Brazil's neglected biome: The South Brazilian Campos. Perspectives in Plant Ecology, Evolution and Systematics, 9(2), 101–116. https://doi.org/10.1016/j.ppees.2007.07.005

Overbeck, G. E., Vélez-Martin, E., Scarano, F. R., Lewinsohn, T. M., Fonseca, C. R., Meyer, S. T., Müller, S. C., Ceotto, P., Dadalt, L., Durigan, G., Ganade, G., Gossner, M. M., Guadagnin, D. L., Koch, K., Kottspirit, A., Moreno-Mateos, D., Pahl, B. E., Pillar, V. D., Silveira, F. A., . . . Weisser, W. W. (2015). Conservation in Brazil needs to include non-forest ecosystems. Diversity and Distributions, 21(12), 1455–1460. https://doi.org/10.1111/ddi.12380

Overbeck, G.E., Andrade, B.O., Vélez-Martin, E., & Pillar, V.D. (2023) Beyond protected areas: conservation of south Brazilian grasslands. South Brazilian grasslands: ecology and conservation of the Campos Sulinos. Springer, 447–473. https://doi.org/10.1007/978-3-031-42580-6_17

Pillar, V. D., & Overbeck, G. E. (2025). Nature conservation policies are biased toward forests and neglect grassy ecosystems worldwide. Science, 388(6747). https://doi.org/10.1126/science.adx7441

Porto, A. B., Rolim, R. G., Thomas, P. A., Silveira, F. F. da, Taffarel, E. S., & Overbeck, G. E. (2019). O uso do fogo para controlar invasão por pinus: Estudo de caso no Parque Nacional da Lagoa do Peixe. In Anais do Seminário Regional de Espécies Exóticas Invasoras. SEMA.

Porto, A. B., Overbeck, G. E., & Salatino, A. (2021). Consciência Campestre: Um chamado para o (re)conhecimento aos campos. Bio Diverso, 1(1),1-25.

Reigota, M. (2017). O que é educação ambiental. Brasiliense.

Santos, J. O. dos. (2016). Análise da percepção ambiental acerca do bioma Caatinga por parte dos docentes de uma escola pública do município de Patos, Paraíba. Revista de Geociências do Nordeste, 2, 753–769. https://doi.org/10.21680/2447-3359.2016v2n0id10524

Santos, R. B. dos. (2022). Super Trunfo dos Campos Sulinos: Desenvolvimento de ferramenta pedagógica e de experiências sobre a flora nativa de uso popular do Sul do Brasil. Trabalho de Conclusão de Curso. Universidade Federal do Rio Grande do Sul.

Santos, C. A. L. C. dos, & Soffiatti, P. (2024). Estratégia interdisciplinar no ensino de botânica: Utilização da arte para superação da impercepção botânica. Diálogos em educação: Olhares multidisciplinares sobre a aprendizagem, 3, 245–259. https://doi.org/10.47402/ed.ep.c240232020911

Silveira, F. A. O., Ordóñez-Parra, C. A., Moura, L. C., Schmidt, I. B., Andersen, A. N., Bond, W., Overbeck, G. E., Durigan, G., & Fidelis, A. (2022). Biome Awareness Disparity is BAD for tropical ecosystem conservation and restoration. Journal of Applied Ecology, 59(8), 1967–1975.

Silveira, F. F. da, Marchioretto, R., Silveira, S. F. da, & Pereira, M. J. R. (2022). Biodiversidade gaúcha na escola: Álbum de Figurinhas Mamíferos do Rio Grande do Sul. Bio Diverso, 2(1), 152-163.

Silveira, F. F. da, Souza, M. A. de A. L. de, Porto, A. B., Marchioretto, R. M., & Silveira, S. F. da. (2023). Pife Ecológico. In M. C. de C. Moço, M. Deprá & R. T. D. da Rosa (Eds.), Jogos para formar cientistas (1ª ed., pp. 247–260). Editora Ilustração. https://doi.org/10.46550/978-65-85614-36-8.247-260

Silveira, S. F. da, Peter-da-Silveira, F., Silveira, F. F. da, Fontoura, J. S. D. de Á., & Overbeck, G. E. (2025). Memória Campestre: Jogo para apresentar a flora do bioma Pampa. EduCAPES. https://educapes.capes.gov.br/handle/capes/1131809

Stone, M. K., Barlow, Z., & Capra, F. (2006). Alfabetização ecológica: A educação das crianças para um mundo sustentável. Cultrix. p. 312-312.

Ursi, S., & Salatino, A. (2022). Nota Científica - É tempo de superar termos capacitistas no ensino de Biologia: Impercepção botânica como alternativa para 'cegueira botânica'. Boletim de Botânica, 39, 1–4. https://doi.org/10.11606/issn.2316-9052.v39p1-4

Veldman, J. W., Overbeck, G. E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G. W., Durigan, G., Buisson, E., Putz, F. E., & Bond, W. J. (2015). Where tree planting and forest expansion are bad for biodiversity and ecosystem services. BioScience, 65(10), 1011–1018. https://doi.org/10.1093/biosci/biv118

Zanini, A. M., Vendruscolo, G. S., Milesi, S. V., Zanin, E. M., & Zakrzevski, S. B. B. (2020). Percepções de estudantes do sul do Brasil sobre a biodiversidade da Mata Atlântica. Interciência, 45(1), 15–22.