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Natália de Freitas Medeiros

RESTORING OPEN BIOMES: evidence, gaps, and the threats of tree planting

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Natália de Freitas Medeiros

RESTORING OPEN BIOMES: evidence, gaps, and the threats of tree planting

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NATÁLIA DE FREITAS MEDEIROS

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No dia 26 de agosto de 2025, às 08:00 horas, na sala de reuniões e vídeo conferência G493, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) Natália de Freitas Medeiros, orientando(a) do Professor Fernando Augusto de Oliveira e Silveira, intitulada: **“Restoring open biomes: evidence, gaps, and the threats of tree planting”**. Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) Fernando Augusto de Oliveira e Silveira, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Giselda Durigan (IPA/SP), Gerhard Ernst Overbeck (UFRGS), Jerônimo Boelsums Barreto Sansevero (UFRRJ), Soizig Le Stradic (INRAE) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

☒ (X) Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;

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A banca indica esta tese aos Prêmios CAPES e UFMG de teses? ☒ (X) SIM ☐ () NÃO

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

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GENERAL ABSTRACT

Restoring open ecosystems is challenging because of misguided restoration actions, an overall lack of knowledge on how to enhance ecosystem resilience and uncertainties on how to measure restoration success in ecologically meaningful ways. Active interventions are often required to enhance recovery of open ecosystems, and long-term monitoring and management are recommended as recovery rates are often extremely slow. Tree-oriented, carbon-based, practices have extensively expanded in many ecosystems, including forested and open ones. However, the consequences of tree planting are not fully understood. For instance, tree planting programs often overestimate the potential of increasing carbon sequestration, while largely overlooking the negative impacts on biodiversity and ecosystem services. Reflecting on how to enhance restoration, especially for open ecosystems, this thesis aims to fill up some gaps and gather accumulated evidence on this topic to steer future restoration programs. In the first chapter of this thesis, I assessed the global impact of tree planting on the biodiversity of open-canopy ecosystems using a meta-analysis. I found that tree planting fails to achieve the biodiversity of open-canopy reference ecosystems. This pattern remained consistent regardless of whether the trees planted were native or exotic. In the second chapter, I sought to understand where and how restoration of tropical open ecosystems has been done using a systematic review and found that studies were largely context-dependent. I found an inconsistent usage of restoration techniques to different sources of degradation and less than half of the indicators evaluated were monitored consistently through time. Moreover, because I found severe issues in primary data reporting, I propose a checklist for minimum research reporting information and a more complete multilingual standardized guideline. In the third chapter I explored the identity of species planted and seeded in restoration tropical open ecosystems, and I found that

most of them were native to the restored open ecosystem, but herbs and forbs were relatively underrepresented compared to trees and shrubs. Finally, in the fourth chapter I developed a field case study to examine the effects of tree encroachment on sites adjacent to pine plantation. I found that that native herbaceous plant cover decreased with the increase in tree cover and the same pattern was observed for forb species richness and frequency, as well as plant-pollinator interaction richness and abundance. Overall, this thesis reveals that current restoration in open ecosystem approaches often rely heavily on tree planting, which may only partially recover biodiversity and potentially undermine herbaceous communities and plant-pollinator interactions in open ecosystems. To improve restoration outcomes, future efforts must adopt ecologically informed planting designs, increase the representation of herbs, forbs and shrubs, ensure long-term monitoring, and implement standardized reporting protocols to strengthen restoration science and practice globally.

Key words: open ecosystems; restoration ecology; ecosystem resilience; tree planting; biodiversity; plant-pollinator interactions; meta-analysis; systematic review

RESUMO GERAL

A restauração de ecossistemas abertos é desafiadora devido a ações de restauração mal direcionadas, à falta de conhecimento geral sobre como aumentar a resiliência desses ecossistemas e às incertezas sobre como medir o sucesso da restauração de maneira ecologicamente significativa. Intervenções ativas são frequentemente necessárias para promover a recuperação desses ecossistemas, e o monitoramento e manejo de longo prazo são recomendados, já que as taxas de recuperação costumam ser extremamente lentas. Práticas focadas em árvores e baseadas em carbono têm se expandido amplamente em muitos ecossistemas, tanto florestais quanto abertos. No entanto, as consequências do plantio de árvores não são totalmente compreendidas. Por exemplo, programas de plantio de árvores frequentemente superestimam o potencial de aumento do sequestro de carbono, ao mesmo tempo em que negligenciam os impactos negativos sobre a biodiversidade e os serviços ecossistêmicos. Refletindo sobre como aprimorar a restauração, especialmente de ecossistemas abertos, esta tese busca preencher algumas lacunas e reunir evidências acumuladas sobre o tema para apoiar futuras ações de restauração. No primeiro capítulo desta tese, avaliei o impacto global do plantio de árvores na biodiversidade de ecossistemas de dossel aberto usando uma meta-análise. Encontrei que o plantio de árvores não é capaz de atingir a biodiversidade dos ecossistemas de referência abertos. Esse padrão manteve-se consistente independente se as árvores plantadas eram nativas ou exóticas. No segundo capítulo, busquei entender onde e como a restauração de ecossistemas abertos tropicais têm sido realizada usando uma revisão sistematizada, e descobri que os estudos eram amplamente dependentes do contexto. Encontrei um uso inconsistente de técnicas de restauração para diferentes fontes de degradação, e menos da metade dos indicadores avaliados têm sido monitorados consistentemente ao longo do tempo. Além disso, como encontrei problemas graves no reporte de dados primários, propus

uma lista de verificação com informações mínimas para serem reportadas em pesquisas, e um guia multilíngue padronizado mais completo. No terceiro capítulo, explorei a identidade das espécies plantadas e semeadas na restauração de ecossistemas tropicais abertos, e descobri que a maioria delas era nativa do ecossistema de referência, mas herbáceas estavam relativamente sub-representadas em comparação com árvores e arbustos. Finalmente, no quarto capítulo, desenvolvi um estudo de caso de campo para avaliar os efeitos do adensamento de árvores em áreas adjacentes a plantações de pinheiros. Constatei que a cobertura de plantas herbáceas nativas diminuiu com o aumento da cobertura arbórea, e, o mesmo padrão foi observado para riqueza e frequência de espécies de plantas herbáceas não-graminosas, bem como para riqueza e abundância de interações planta-polinizador. De maneira geral, essa tese revela que as atuais abordagens de restauração frequentemente dependem fortemente do plantio de árvores, o qual pode apenas parcialmente recuperar a biodiversidade e potencialmente prejudica as comunidades de herbáceas e interações planta-polinizador em ecossistemas abertos. Para melhorar os resultados da restauração, esforços futuros devem adotar projetos de plantio ecologicamente direcionados, garantindo monitoramento a longo prazo e implementando protocolos padronizados para reportar os dados e, globalmente fortalecer a ciência e a prática da restauração.

Palavras-chave: ecossistemas abertos; restauração ecológica; resiliência de ecossistema; plantio de árvores; biodiversidade; interações planta-polinizador; meta-análise; revisão sistemática

RÉSUMÉ GENERAL

La restauration des écosystèmes ouverts est difficile en raison d'actions de restauration mal orientées, d'un manque général de connaissances sur la manière d'améliorer la résilience des écosystèmes et d'incertitudes quant aux façons de mesurer le succès de la restauration de manière écologiquement pertinente. Des interventions actives sont souvent nécessaires pour favoriser la récupération de ces écosystèmes, et un suivi ainsi qu'une gestion à long terme sont recommandés, car les taux de régénération sont souvent extrêmement lents. Les pratiques axées sur les arbres et fondées sur le stockage du carbone se sont largement répandues dans de nombreux écosystèmes, qu'ils soient forestiers ou ouverts. Cependant, les conséquences de la plantation d'arbres ne sont pas encore entièrement comprises. Par exemple, les programmes de plantation d'arbres surestiment souvent le potentiel d'augmentation de la séquestration du carbone, tout en négligeant largement les impacts négatifs sur la biodiversité et les services écosystémiques. Dans le but d'améliorer la restauration, en particulier celle des écosystèmes ouverts, cette thèse vise à combler certaines lacunes et à rassembler les connaissances accumulées sur le sujet afin de guider les futures actions de restauration. Dans le premier chapitre de cette thèse, j'ai évalué l'impact global de la plantation d'arbres sur la biodiversité des écosystèmes à canopée ouverte à travers une méta-analyse. J'ai constaté que la plantation d'arbres ne permet pas d'atteindre la biodiversité des écosystèmes à canopée ouverte de référence. Cette tendance est restée constante, que les arbres plantés soient indigènes ou exotiques. Dans le deuxième chapitre, j'ai cherché à comprendre où et comment la restauration des écosystèmes ouverts tropicaux a été mise en œuvre. J'ai constaté, à travers une revue systématique, que les études étaient largement dépendantes du contexte. L'utilisation des techniques de restauration variait de manière incohérente selon les sources de dégradation, et moins de la moitié des indicateurs évalués faisaient l'objet d'un suivi constant dans le temps.

De plus, en raison de problèmes importants liés à la qualité des données, je propose une liste de vérification pour les informations minimales à rapporter dans les recherches, ainsi qu'une ligne directrice standardisée, plus complète et multilingue. Dans le troisième chapitre, j'ai exploré les espèces plantées et semées dans les écosystèmes ouverts tropicaux restaurés, et j'ai constaté que la plupart étaient indigènes de l'écosystème restauré. Toutefois, les herbes et plantes herbacées étaient relativement sous-représentées par rapport aux arbres et aux arbustes. Enfin, dans le quatrième chapitre, j'ai mené une étude de terrain pour comprendre les effets de l'envahissement par les arbres dans des zones adjacentes à des plantations de pins. J'ai constaté que le recouvrement de plantes herbacées indigènes diminuait avec l'augmentation du recouvrement arboré, et que le même schéma se retrouvait pour la richesse et la fréquence des espèces herbacées, ainsi que pour la richesse et l'abondance des interactions plante-pollinisateur. Dans l'ensemble, cette thèse révèle que les approches actuelles de restauration reposent souvent fortement sur la plantation d'arbres, ce qui peut ne restaurer la biodiversité que partiellement et potentiellement nuire aux communautés herbacées et aux interactions plante-pollinisateur dans les écosystèmes ouverts. Pour améliorer les résultats de la restauration, les efforts futurs devront adopter des schémas de plantation informés écologiquement, assurer un suivi à long terme et mettre en œuvre des protocoles de rapport standardisés afin de renforcer la science et la pratique de la restauration à l'échelle mondiale.

Mots-clés: écosystèmes ouverts ; restauration écologique; résilience des écosystèmes ; plantation d'arbres ; biodiversité ; interactions plantes-pollinisateurs ; méta-analyse ; revue systématique

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GENERAL INTRODUCTION

The current loss of natural ecosystems and decline of biodiversity, coupled with the climatic emergency that characterizes the Anthropocene, have demanded urgent local and global, coordinated actions. Human activities have impacted the environment drastically by consuming natural resources more than Earth's ability to generate and maintain systems functioning (Ripple *et al.* 2024). In this context, ecological restoration has emerged as a strategy to reverse humanity's increasing ecological footprint. Advances in restoration science and practice are expected under the support of the United Nations Decade on Ecosystem Restoration 2021-2030 (UN Environment Programme 2019). The UN incentives offer an unprecedented opportunity to improve our understanding of ecological foundations and enhance methods to refine its practices, promoting the development of new strategies for habitat-tailored interventions as well as better evaluate restoration success.

The Society for Ecological Restoration (SER) proposes that ecosystem restoration should encompass a *continuum* of restorative activities that goes from reducing the impacts to fully recovering the native ecosystem (Figure 1). Different actions could be applied in ecosystem restoration, including one or more approaches from natural to assisted regeneration and reconstruction (Gann *et al.* 2019). Natural regeneration may occur when degradation factors are removed, and the ecosystem is left to regenerate by itself. On the other hand, the reconstruction approach occurs if biota arrival is entirely or almost entirely dependent on human actions. In turn, the assisted regeneration approach comprises many active interventions that assist or prompt ecosystem regeneration, such as soil rehabilitation, soil translocation, removal or control of exotic species, reintroduction of native species, planting, seeding, reapplying ecological disturbance regimes (ie. fire), etc. Regardless of the chosen approach, it is important

to highlight that ecosystem restoration differs from ecological restoration as the first has a broader goal while the last one always has biodiversity and ecological integrity targets (Gann *et al.* 2019). For instance, remediation and rehabilitation actions aiming solely on the delivery of ecosystem services are included in ecosystem restoration but cannot be considered as ecological restoration (Figure 1). Ecological restoration, therefore, can apply different approaches (natural regeneration, assisted regeneration and reconstruction – the last two being considered as active restoration) but has a focus in recovering the native ecosystem integrity and biodiversity.

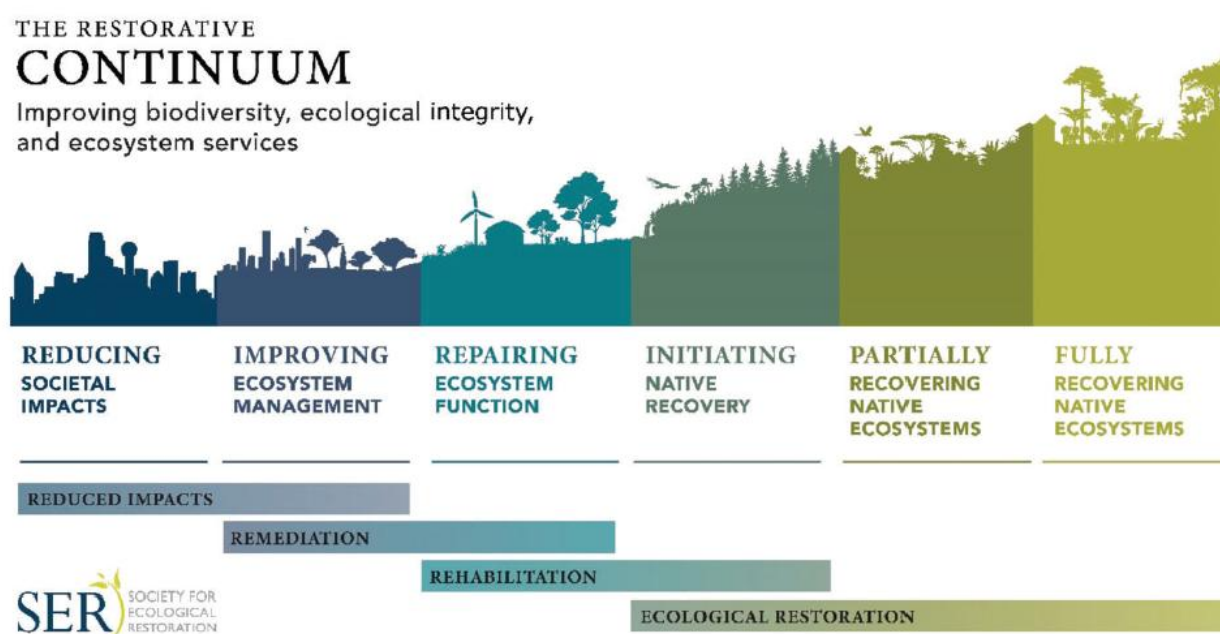


Figure 1 – The restorative continuum proposed by the Society of Ecological Restoration (SER) with different restoration activities from reducing the impacts on a degraded site to fully recovering a native ecosystem. Figure extracted from Gann *et al.* (2019).

We face a critical moment to focus on ecological restoration and move it forward. This is also an opportunity to overcome Biome Awareness Disparity (Silveira *et al.* 2022), a recognized failure to value the importance of all ecosystems in conservation and restoration policy. Historical, persistent, and pervasive forest-oriented focus (e.g. Veldman *et al.* 2015b) has resulted in multiple biases: open ecosystem restoration research and management have received far less attention than those of forested ecosystems (Török *et al.* 2021; Silveira *et al.* 2022; Tölgyesi *et al.* 2022). Moreover, many actions have been misguided and based on forest ecology rather than open ecosystem ecology (Bond *et al.* 2019; Silveira *et al.* 2020; Buisson *et al.* 2022). For instance, we should avoid the use tree cover as a reliable indicator for restoration success of open ecosystems (Scogings 2023). Moreover, many open ecosystems have been wrongly considered as degraded forests (Lahiri *et al.* 2023), which contributes to the assumption that they are biodiversity-poor and cannot provide essential ecosystem services, thus reducing their value to society (Silveira *et al.* 2020). In Africa, extensive areas of grassy ecosystems have been targeted for tree planting ‘restoration’ under the assumption that these ecosystems are deforested or degraded (Bond *et al.* 2019; Parr *et al.* 2024). Hence, the research stimulus supported by UN Decade is expected to allow improvements in ecological restoration for every type of ecosystem, through different strategies, minimizing or reversing the degradation effects of human ecological footprint.

One of the main restoration strategies that has been applied worldwide is tree planting (IUCN-DC 2011; Bond *et al.* 2019; Fagan *et al.* 2022). Under the assumption that tree planting can improve biodiversity (Hartley 2002) in forested ecosystems and that large-scale tree planting can help sequester CO₂ (Bastin *et al.* 2019), many initiatives have spread all over the globe (IUCN-DC 2011; Fagan *et al.* 2022). Global-scale maps have suggested priority areas for planting, based on factors such as soil quality, rainfall and maximizing carbon absorption (Bastin *et al.* 2019; WRI 2025; Fesenmyer *et al.* 2025). Reforestation, which refers to forest

planting on land that was previously a forest (FRA 2020), is well encouraged. However, monoculture tree plantings like *Pinus* sp. or *Eucalyptus* sp. plantations may result in undesired impacts for biodiversity (Wang *et al.* 2022; Simões *et al.* 2024). Furthermore, tree planting has been shown to be especially problematic when forests/stands are introduced to lands where no former forests existed (Veldman *et al.* 2015a; Veldman *et al.* 2015b; Bond *et al.* 2019). Such cases characterize afforestation practices (FRA 2020).

Afforestation and tree invasion in adjacent native sites modify open ecosystem natural structure, composition and functioning, causing native species loss and homogenization (Briske *et al.* 2024; Moyano *et al.* 2024). Caution should be taken for tree planting and guidance could be improved by considering which tree species are planted (native vs. exotic) as well as the plantation diversity (monoculture vs. mixed species) and how they are planted (density and configuration of plantation) (Kremer *et al.* 2025). Beyond that, global-scale maps need to integrate small-scale refined information to allow more precise and effective restoration actions, especially in mosaic landscapes. Restoration efforts cannot overlook the damages of prioritizing tree planting for carbon capture demands as this practice can cost the biodiversity and integrity of open ecosystems (Jackson *et al.* 2005; Abreu *et al.* 2017; Veldman *et al.* 2019b)

Open ecosystems are formed by a dominant herbaceous cover of graminoids and forbs, that can have scattered shrubs and trees, and thus, are naturally open-canopy ecosystems (Bond 2019; Stevens *et al.* 2022). Grassland-savanna mosaics and other open ecosystems (Figure 2) are biodiversity-rich natural ecosystems that evolved under endogenous disturbances including fire and large herbivores, which both play a major role in their functioning and dynamics (Veldman *et al.* 2015a; Buisson *et al.* 2019; Török *et al.* 2021). Besides, edaphic constraints are also important for these open ecosystem dynamics, which altogether with the endogenous disturbances, restrict tree growth and establishment (Buisson *et al.* 2019). Encroachment of

naturally open ecosystems has been occurring due to suppression of endogenous disturbances causing negative consequences for native biodiversity (Wieczorkowski & Lehmann 2022).

Most of the plant diversity in open ecosystems, comparable to forests (Murphy *et al.* 2016), are in the herbaceous layer, comprising shade-intolerant graminoid and forb species (Castilho Silva *et al.* 2024). For instance, in Cerrado, the most biodiverse savanna in the world, there are seven herbaceous species for each tree species (Ribeiro & Walter 2008). Beyond the biodiversity importance, open ecosystems regulate water supply and nutrient cycling as well as promote soil erosion control and carbon sequestration (Zhao *et al.* 2020). They also provide diverse ecosystem services for millions of people (Lehmann & Parr 2016), including medicinal plants, food, fodder for animals, fuel, timber and non-timber products (Fleischmann *et al.* 2022). Despite being biodiversity-rich and highly valuable for multiple ecosystem services, open ecosystems are severely threatened by different pressures, such as invasive species, changing in fire regimes, woody encroachment, wood extraction, agricultural conversion, livestock production, mining, urbanization, afforestation, and climate change (Veldman *et al.* 2015b; Fernandes *et al.* 2018; Török *et al.* 2021). Therefore, conservation and restoration of degraded open ecosystems is not only desirable, but it is also required in order to avoid compromise biodiversity, ecosystem functioning and ecosystem services provision (Pilon *et al.* 2025).

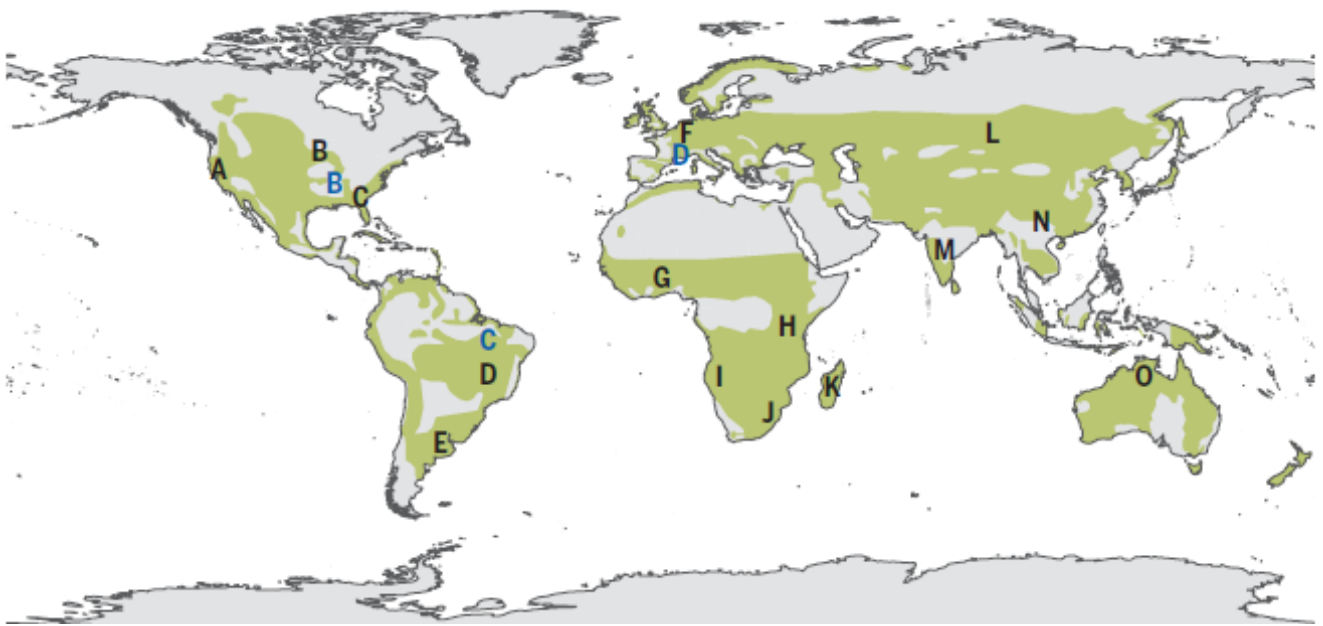


Figure 2 – The distribution of old-growth grasslands in tropical and temperate regions and some examples of their diversity. Figure extracted from Buisson *et al.* (2022): Letters in black in the map = (A) California coastal grasslands on Mount Tamalpais, USA; (B) Curtis Tallgrass

Prairie Restoration, Wisconsin, USA; (C) Longleaf pine (*Pinus palustris*) savanna, North Carolina, USA; (D) Grassland in the Espinhaço mountain range, Minas Gerais, Brazil; (E) Subtropical grasslands in Rio Grande do Sul, southern Brazil; (F) Alpine meadow in the Alps, Vanoise National Park, France; (G) A highrainfall grassy savanna in Mole National Park, Ghana; (H) The Serengeti ecosystem in Tanzania; (I) The grasslands in the Kavango Catchment, Angola; (J) Grassland in the Drakensberg, South Africa; (K) Grassland and tapia savannas on Ibity mountain, Madagascar; (L) Petrophytic steppe in Khakassky Zapovednik State Nature Reserve, Russia; (M) Eravikulam Shola grasslands, India; (N) Oak savanna in South Yunnan, YuanJiang region, China; (O) Mesic savanna in the Northern Territory, Australia.

Restoration of open ecosystems has been challenging both because of misguided restoration actions and an overall lack of knowledge on how to improve ecosystem resilience and how to measure restoration success in ecologically meaningful ways (Ruiz-Jaen & Aide, 2005; Wortley *et al.* 2013; Buisson *et al.* 2021; Lyons *et al.* 2023). In some open ecosystems, ecological restoration through natural regeneration is not always possible (Zaloumis 2013; Le Stradic *et al.* 2018; Wellstein *et al.* 2024), and the recovery rates are often extremely low (Jaunatre *et al.* 2014; Nerlekar & Veldman 2020). Because of this, active interventions to enhance recovery as well as long-term monitoring and adaptive management are required. As highlighted before, tree-oriented, carbon-based practices have extensively expanded in many ecosystems (Fagan *et al.* 2022), including forested and open ones. However, the consequences of tree planting are not fully understood.

To address ways of enhancing restoration, especially for open ecosystems, this thesis aims to fill up gaps and gather accumulated evidence on this topic to improve our knowledge in different aspects of ecological restoration, especially considering one widespread promoted

restoration strategy worldwide: tree planting. Specifically, the first chapter of this thesis is a meta-analysis that assesses the global impact of tree planting on biodiversity and ecosystem functioning of forested and open ecosystems. The second chapter is a systematic review that aims to understand where and how restoration of tropical open ecosystems has been done. The third chapter explores the species origin and growth-form in planted and seeded restored open ecosystems in the tropics. Finally, the fourth chapter of this thesis focuses on a field case study to comprehend the effects of tree encroachment on sites adjacent to pine plantation, especially focusing on native plants and plant-pollinator interactions. Figure 3 synthesizes the focuses and interconnectedness of all chapters

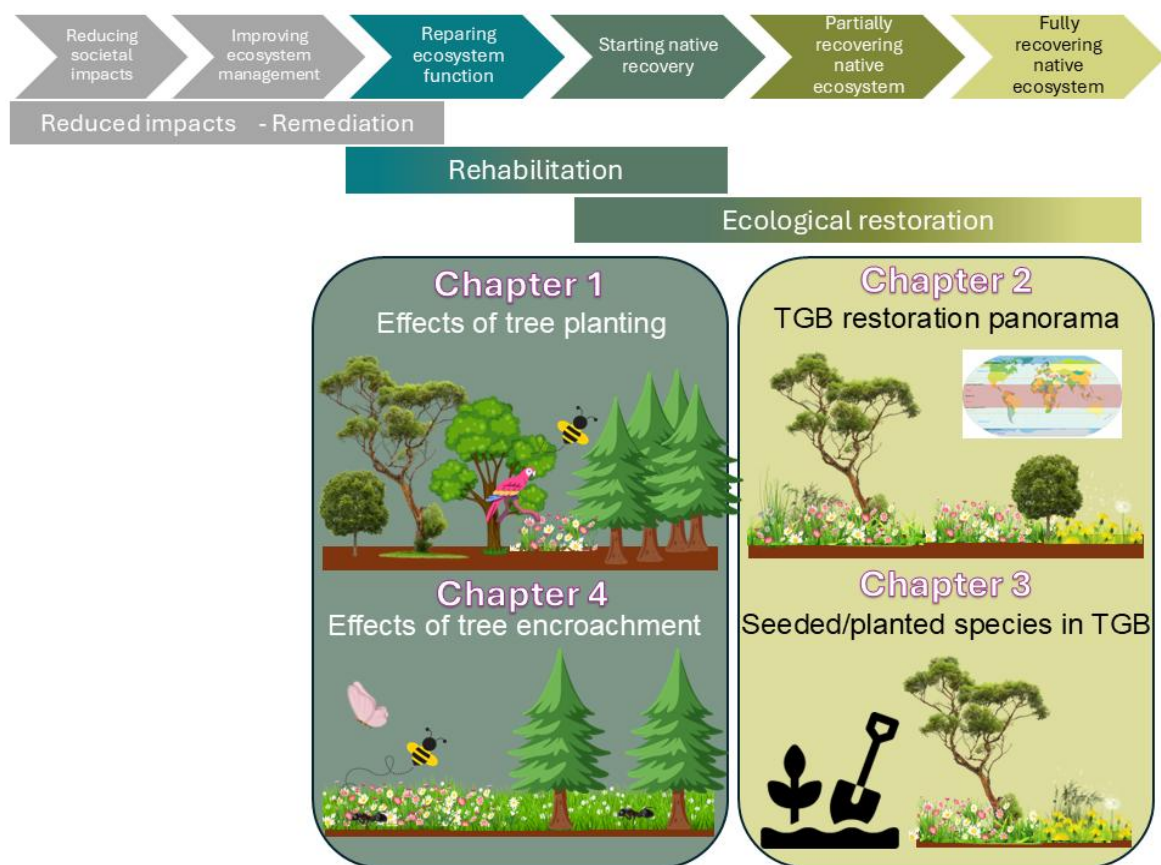
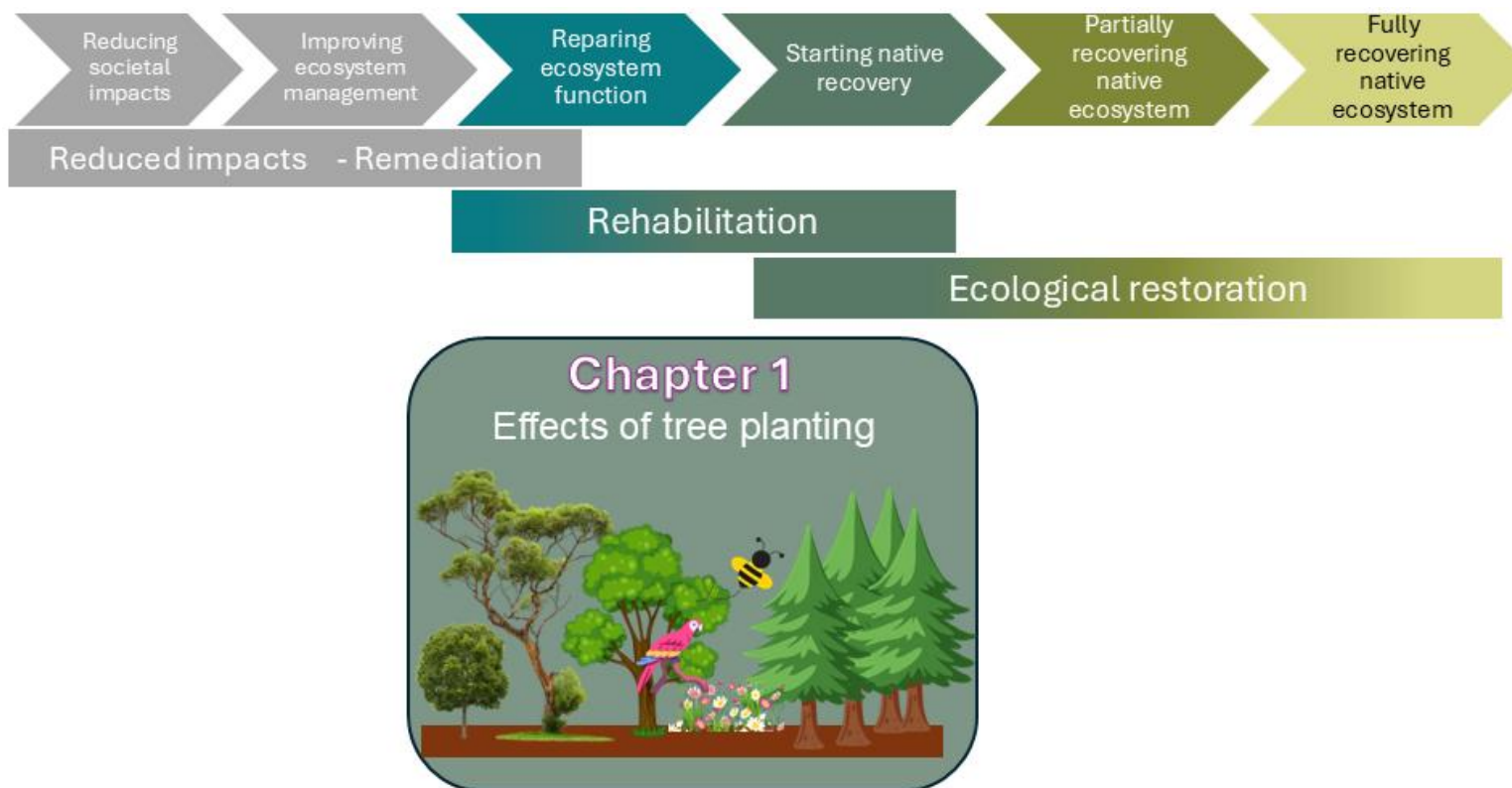


Figure 3 – Summary of the thesis chapters with their respective main focus, under the restoration *continuum*. TGB = Tropical Grassy Biomes

CHAPTERS

CHAPTER 1: TREE PLANTING CANNOT ACHIEVE BIODIVERSITY LEVELS OF OPEN CANOPY ECOSYSTEMS – A GLOBAL META-ANALYSIS



1.1 Abstract

Assessing the impacts of tree planting on biodiversity is critical, given its widespread encouragement across diverse ecological contexts and planting designs, each of which can lead to markedly different outcomes. The effects of tree planting on biodiversity can vary widely depending on ecological contexts, such as whether it occurs in natural grassland or savanna systems as well as the planting method, techniques used, and species selection. Here, we conducted a global meta-analysis to evaluate the effects of tree planting on taxonomic biodiversity of plants, vertebrates and invertebrates in open ecosystems, regardless of the plantation objective. We expect tree planting to have overall insufficient recovery when compared to an open native reference ecosystem. As hypothesized, tree planting cannot enhance native biodiversity compared to its level in native reference ecosystems. This pattern held consistently despite the origin of planted species. Notably, we had no data to run analyses to compare tree planting against a degraded site, or to consider the effects of other moderators, such as plantation age, due to data constraints. Our findings highlight that, although tree planting is a widely advocated strategy, it does not guarantee the recovery of taxonomic biodiversity, especially for open ecosystems.

Key-words: tree planting, ecological restoration, open ecosystems, degraded land recovery

1.2 Introduction

Tree planting is increasingly advocated as a major strategy to combat climate change through carbon sequestration (Bastin *et al.* 2019; Mo *et al.* 2023; Kirschbaum *et al.* 2024). Globally, governments, organizations and landowners are investing in large-and small-scale tree planting initiatives (Brancalion & Holl 2020), driven by diverse objectives, such as livelihood support through agroforestry and degraded land restoration (Fleischman *et al.* 2022). However, tree planting is also implemented as monocultures for timber production (Lugo *et al.* 1990), which can lead to negative biodiversity outcomes (Kirschbaum *et al.* 2024). Regardless of motivation, the global expansion of tree planting has wide-ranging impacts, from benefits like carbon sequestration, soil restoration and economic development (Malkamäki *et al.* 2018; Allek *et al.* 2023) to drawbacks, such as native habitat loss, reduced water availability due to carbon-water trade-offs, unsustainable land use and social conflicts (Jackson *et al.* 2005; Brancalion & Holl 2020; Fleischmann *et al.* 2022; Wang *et al.* 2022; Kremer *et al.* 2025; Li *et al.* 2025; Prober *et al.* 2025). Given the rapid rise of tree planting for environmental, economic and social purposes (Fagan *et al.* 2022), a quantitative assessment of its outcomes for native biodiversity is urgently needed.

Tree planting outcomes vary considerably with ecosystem type, species selection, and planting techniques. Reforestation (establishment of forest on land that formerly were closed-canopy systems) and afforestation (establishment of forest on land that are not forest ecosystems) differ fundamentally in their biodiversity responses (Fagan *et al.* 2022) due to the ecosystem type where trees are planted. Ecological theory and empirical evidence suggest that tree planting can benefit biodiversity in deforested sites. However, in open-canopy ecosystems (e.g., grasslands, savannas), tree planting often reduces biodiversity, by favouring shade-tolerant species at the expense of native specialized and light-dependent flora and fauna

(Veldman *et al.* 2015a; Abreu *et al.* 2017; Bond 2019). Despite this, generalist species might be favoured, but empirical data on tree planting impacts in open ecosystems remains scarce. The shift to shaded conditions under plantations alters ecosystem structure, disadvantaging open-canopy specialists (Valladares *et al.* 2016), and disrupting disturbance regimes like fire, which are critical for native species regeneration (Jackson *et al.* 2005; Bond *et al.* 2019). Thus, while tree planting may enhance biodiversity in closed-canopy ecosystems (Nakamura *et al.* 2017), it may also have different impacts for some open-canopy ecosystems, like savannas, which support high ground-layer diversity adapted to disturbances like fire and herbivory (Veldman *et al.* 2015a; Bond 2019).

Another factor that influences plantation outcomes is the diversity of planting techniques. Mixed-species plantations (polycultures) promote structural heterogeneity and higher species richness than monocultures (Liu *et al.* 2018; Kremer *et al.* 2025), though their success depends on species selection and long-term management (Kremer *et al.* 2025). Conversely, nucleation (patch-based planting) offers a cost-effective alternative, fostering landscape heterogeneity with fewer resources (Zahawi *et al.* 2013). Furthermore, older plantations generally support greater biodiversity than younger ones (Wang *et al.* 2021), but poorly planned initiatives risk wasting financial and human resources (Rana *et al.* 2022). Thus, local ecological context, species origin (native vs. exotic) and planting design are critical to favour biodiversity in tree plantings.

Assessing tree planting impacts on biodiversity require careful evaluation. Many studies use degraded sites as a control, particularly when their primary goal is other than biodiversity conservation. Evaluating the effects of tree planting by comparing it to a reference ecosystem and to a degraded site enables a more comprehensive evaluation of the outcomes (Atkinson *et al.* 2022). Here, we aim to improve our understanding of the ecological impacts of tree planting, focusing on its impacts to taxonomic biodiversity of open ecosystems. Because we want to have

a broad understanding of how different types of planting trees could impact biodiversity of open ecosystems, we aim to encompass any type of tree planting regardless of its objective (biodiversity/restoration goal or not). We will test a general hypothesis that tree planting enhances native biodiversity relative to degraded sites (Negative Control) for savannas and shrublands but not for grasslands. Moreover, we expect that only planting trees will fail to match reference levels in native open ecosystems (Positive Control). We also expect that the outcomes will be mediated by species origin and planting technique. Specifically, we predict: (1) greater biodiversity deficits in exotic versus native tree plantings; (2) worse outcomes for monoculture plantations compared to other plantation techniques.

1.3 Methods

We conducted a global meta-analysis of peer-reviewed articles to assess the effects of tree planting on taxonomic biodiversity, focusing on species richness, abundance and diversity indices. Our search encompassed studies published in English up to December 2020 in the Web of Science and Scopus databases. To identify relevant studies, we used a combination of keywords searched in the title, abstract and keywords of the published studies, as follows: (afforestation OR afforested OR restoration OR restored OR recovery OR reforestation OR reforested OR rehabilitation OR rehabilitated) AND (“tree plant*” OR “tree cover*”) AND (biodiversity OR diversity OR richness OR abundan* OR composition OR “ecosystem function*” OR “ecosystem service*” OR ecoservice* OR ecoservice*). This three-pronged search strategy aimed to capture the breadth of tree planting research while restricting results to studies evaluating biodiversity or ecosystem functioning (see Figure 4).

1.3.1 Screening process and database creation

The screening process involved three sequential stages to ensure data quality and relevance. First, we evaluated titles and abstracts to exclude studies not involving field-based tree planting, such as laboratory and greenhouse experiments. Next, full texts of the remaining papers were assessed against three criteria: (1) explicit documentation of planting a large number of trees over broad areas (e.g. excluding small-scale plantings like hedgerows and windbreaks); (2) focus on biodiversity metrics (excluding studies measuring only survival, growth, or biomass, of planted species); and (3) provision of primary data of the impacts of tree planting on terrestrial native species richness, abundance and diversity indices in open ecosystems (grasslands, shrublands and savannas). This screening also excluded studies on riparian buffers or aquatic systems as well as studies on forests and other types of ecosystems.

Finally, we applied a conservative third screening to select studies with quantifiable data to run meta-analyses, namely sample sizes, mean of the response variables and any measurement of variability associated to the mean that could be converted into standard deviations. The elected studies must also have compared tree plantation to a positive (reference native ecosystem) or negative (degraded site) control. We considered native reference ecosystems as positive controls and degraded sites as negative controls (see Atkinson *et al.* 2022; Medeiros *et al.* 2024). We had different types of reference ecosystems, including grassland, shrubland and savanna ecosystems. The negative control included bare soil from mine sites and degraded pastures, among others, which were all grouped together as negative control. Studies comparing plantations to active land used (e.g., croplands) or using ambiguous terms (e.g., “stand”) without plantation details were excluded. For the selected studies after these three screenings, we extracted metadata to run the meta-analyses.

1.3.2 Data collection and analyses

We systematically extracted all available data from the selected studies in our database. Since some studies evaluated multiple target variables, or provided spatially independent replicates, a single paper could yield multiple reports for our analyses. For each report we collected general metadata including country, original ecosystem, protect area status, urban context and distance to reference sites (when available). We also recorded detailed plantation characteristics: number of tree species planted, geographic origin of the planted species (native, exotic or both), if tree planting occurred along with other plant growth-forms, planting technique (monoculture, mixed plantation, nucleation or agroecosystem), plantation age (classified as very young (0-10 years), young (11-20 years), mature (21-30 years), or old (>30 years)), primary management goal (economic, revegetation/rehabilitation or ecological restoration), and post-planting management practices. For biodiversity metrics, we extracted sample sizes, means and variability measures (Standard Error or Standard Deviation, SE or SD) for both plantations (treatment) and their paired controls (positive PC or negative NC). Our response variables included species richness, abundance and diversity indices (Table 1). Variables associated to ecosystem functioning were not included in our analysis at this time.

Quantitative biodiversity data were obtained directly from tables or extracted from figures using ImageJ (Schneider *et al.* 2012). All SE values were converted into SD prior to analyses. To maintain data integrity, we excluded exotic species from biodiversity metrics when explicitly identified in the original studies. For studies reporting hierarchical classifications (e.g., understory trees vs shrubs) we prioritized total values (e.g., “understory species richness”) to avoid redundancy, but retained disaggregated data when total was unavailable. When studies presented seasonal data, we consistently used wet-season measurements to standardize comparisons.

To test our hypotheses, we used all recorded data to calculate Hedges' g effect sizes, which standardize differences in biodiversity between plantations and controls (PC or NC). Positive effect size means that biodiversity in plantations is higher than in control, while negative effect size means that biodiversity is lower in plantation than in control. Furthermore, we ran analyses including moderators that have at least 10 independent comparisons, to ensure statistical robustness and minimize bias (Pincus *et al.* 2011). Moderators of mixed model meta-analysis included: (1) species origin of the plantation (native, exotic or both); and (2) planting technique as reported in the original paper. Reports lacking clear moderator data were excluded from the respective analyses. All analyses were implemented in R using the "metafor" package (Viechtbauer 2010), with figures generated using "orchaRd" package (Nakagawa *et al.* 2023).

Table 1. Information retrieved from original elected studies and further classification and definition/examples used in a global meta-analyses of tree planting and biodiversity.

Information retrieved	Classification	Definition/Examples
Original ecosystem	● Grassland ● Shrubland ● Savanna	● Sandy grassland, steppe ● Shrubby steppe ● Cerrado <i>sensu stricto</i>
Protected area	● Yes ● No	● National Park, biological station

		● Rural property
Planting technique	● Monoculture ● Mixed plantation	● One species planted in rows (e.g., pine plantation) ● Two or more species planted in rows (e.g., pine and oak plantation)
Plantation management	● Yes ● No	● Use of herbicides, thinning, or any other management ● No intervention
Main management objective	● Economic ● Revegetation/Rehabilitation ● Ecological restoration	● Timber production ● Increase vegetation cover and/or rehabilitate a degraded site ● Establish a sustainable ecosystem similar to the reference site

Biodiversity measurement	● Species richness	● Number of different species
	● Species abundance	● Number of individuals or density
	● Biodiversity index	● Shannon, Jaccard, Chao-1, rarity, evenness, equitability

1.4 Results

Our systematic search initially identified 1,094 papers which were reduced to 12 after duplicate removal and the rigorous three-stage screening process (details in Figure 5). These studies yielded 106 individual registers to our database. All selected studies compared tree plantations to reference native open ecosystems with 55 reports in grasslands, eight in shrublands, and 43 in savannas. Notably, none of the studies were conducted in urban areas, and only three of them (23 reports) were within protected areas. More than half of the cases (58.3% - 81 reports) did not report the distance to native reference sites, limiting our ability to assess proximity effects. Tree planting initiatives predominantly focused on monocultures or mixed-tree species, with only one study incorporating herbaceous species alongside trees at a Cerrado *sensu stricto* vegetation (Laste *et al.* 2019). Geographically, the studies were unevenly distributed, with the highest representation from Argentina (4 studies with 34 reports), Brazil (3 studies with 46 reports), Spain (2 studies with 6 reports), China (2 studies with 16 reports), and Ireland (1 study with 4 reports).

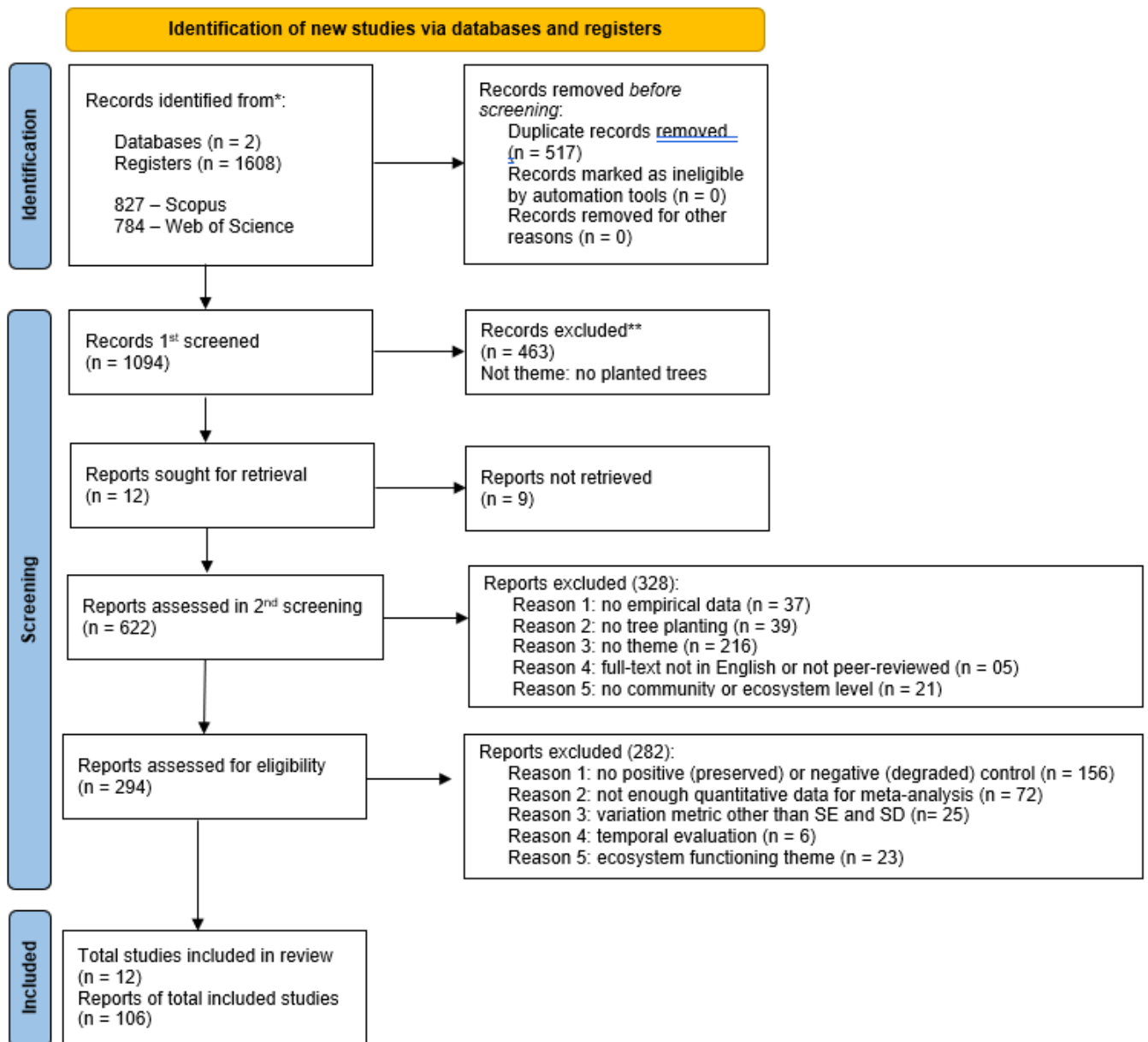


Figure 4 – PRISMA fluxogram (Preferred reported items for systematic reviews and meta-analysis) of our database creation with inclusion and exclusion criteria on each screening.

Our analysis included 106 reports comparing tree plantations to native reference open ecosystems positive controls, which measured species richness (48 reports), abundance (36), and diversity indices (22). Plants were the most studied taxa (73 reports), followed by invertebrates (29 reports) and vertebrates (4 reports). Regarding the design of tree plantations, we found that 69.8% involved the planting of only a single species (74 reports), which were

mostly planted aiming for economic (25 reports), carbon sequestration (18 reports), restoration (14 reports) and afforestation (12 reports) purposes. Three reports had a recovery reason (mitigation, rehabilitation and/or revegetation) while two have not provided this information. In terms of species origin, more than half of the reports (61.3%) described plantations consisting exclusively of exotic tree species, whereas 31.1% reported the use of native tree species. Additionally, four reports included a mix of both native and exotic species, and one report planted a hybrid exotic species. No information regarding origin was available for 3 reports (2.8%).

Our analysis revealed that only two plantation designs have been used: monoculture was the most frequently reported planting technique, accounting for 69.8% of the reports, followed by mixed plantations (27.4%). Three reports have not provided this information. Moreover, plantation age varied considerably across studies, with nearly half (46.2%) classified as either very young (0 to 10 years) or young (11 to 20 years), while 41.5% were classified as mature plantations (21 to 30 years). Older plantations (>30 years) constituted only 5.7% (six reports), and 2.8% of the reports lacked explicit data on plantation age, with an additional four reports (3.8%) that have provided age estimates that did not align with our predefined classification intervals. Finally, it is important to highlight that due to data constraints we were unable to run some analysis, such as the effects of tree planting compared to a degraded site control and the effects of some moderators such as plantation age and plantation distance to a native patch. Moreover, we initially aimed to compare the effects for each type of open ecosystem (grassland, shrubland and savanna), but we had to merge them under ‘open ecosystem’ to have only one robust general pattern. Similarly, we merged the different response variables (richness, abundance and diversity index) of plants, invertebrates and vertebrates into one ‘biodiversity effect’.

1.4.1 Meta-Analysis

Overall, tree planting had a negative effect on biodiversity compared to positive controls (Figure 5). This pattern remained consistent regardless of the planted species origin (Figure 6). However, regarding tree planting techniques (Figure 7), we found a negative effect for monoculture plantations and an absence of effect for mixed species plantations. Although we found such pattern, our Rosenthal's number for this analysis (-103) suggested that this is not a robust result as additional studies have the power to change it.

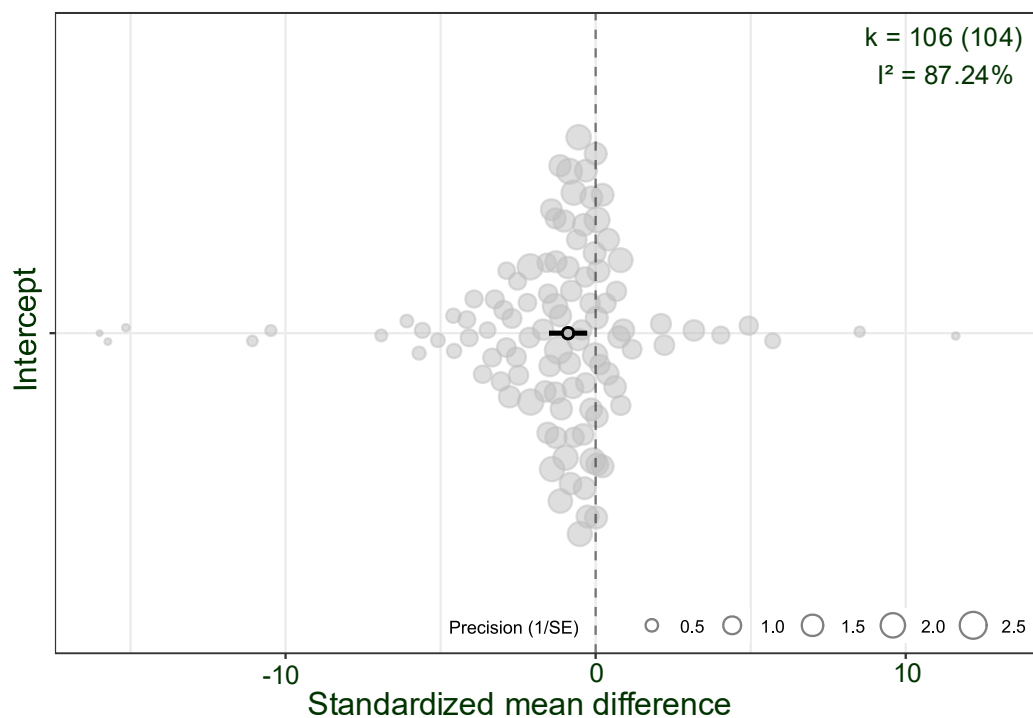


Figure 5 – Overall effects of tree planting on terrestrial taxonomic biodiversity compared to a native reference open ecosystem (positive control). The centroids of the polygons indicate the point estimate of the combined standardized mean difference between plantations and controls, while their outer edges indicate the 95% confidence interval limits. Polygons intersecting the null effect axis (vertical line 0) indicate absence of effect; K = number of reports included in the meta-analysis; I^2 = percentage of variability in effect sizes due to heterogeneity between studies; Fail-safe N = 4196.

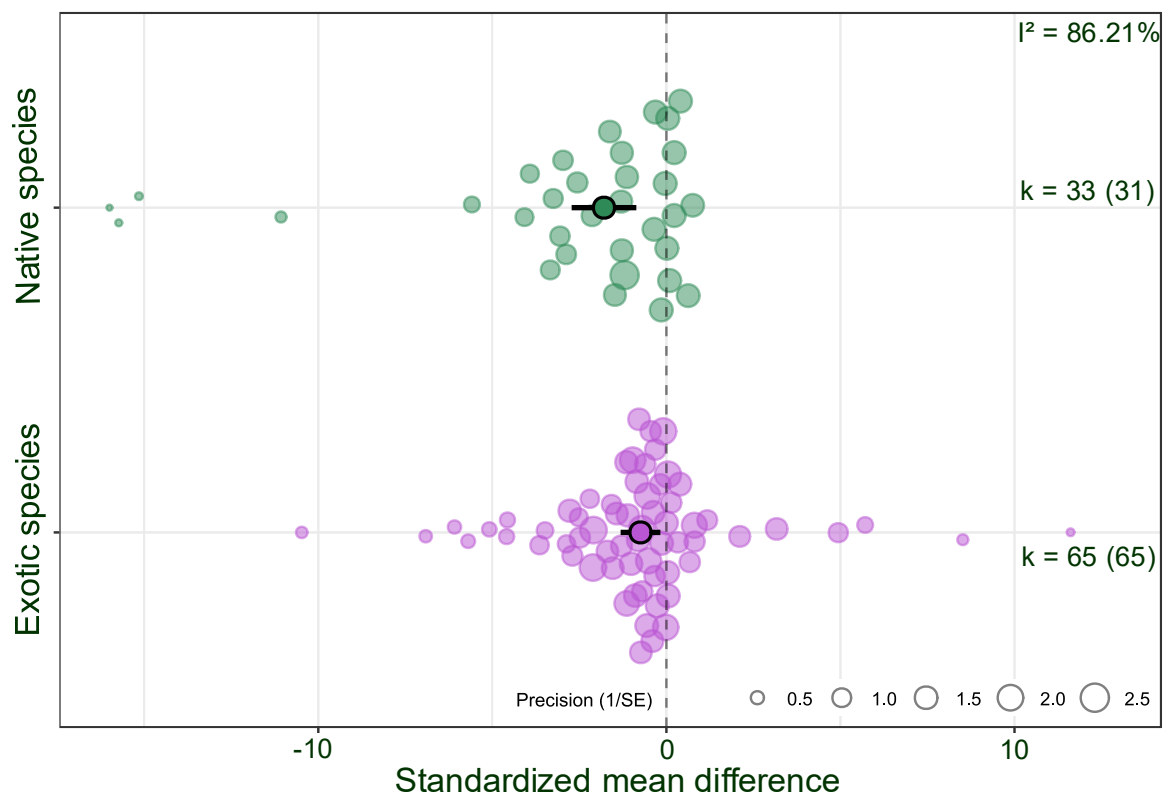


Figure 6 – Effects of planting exotic and native species trees on terrestrial taxonomic biodiversity compared to a native reference open ecosystem (positive control). Only classes with ≥ 10 observations were included. The centroids of the polygons indicate the point estimate of the combined standardized mean difference between plantations and controls, while their outer edges indicate the 95% confidence interval limits. Polygons intersecting the null effect axis (vertical line 0) indicate absence of effect. K = number of reports included in the meta-analysis; I^2 = percentage of variability in effect sizes due to heterogeneity between studies; QM = 0.038; Fail-safe N = 4196.

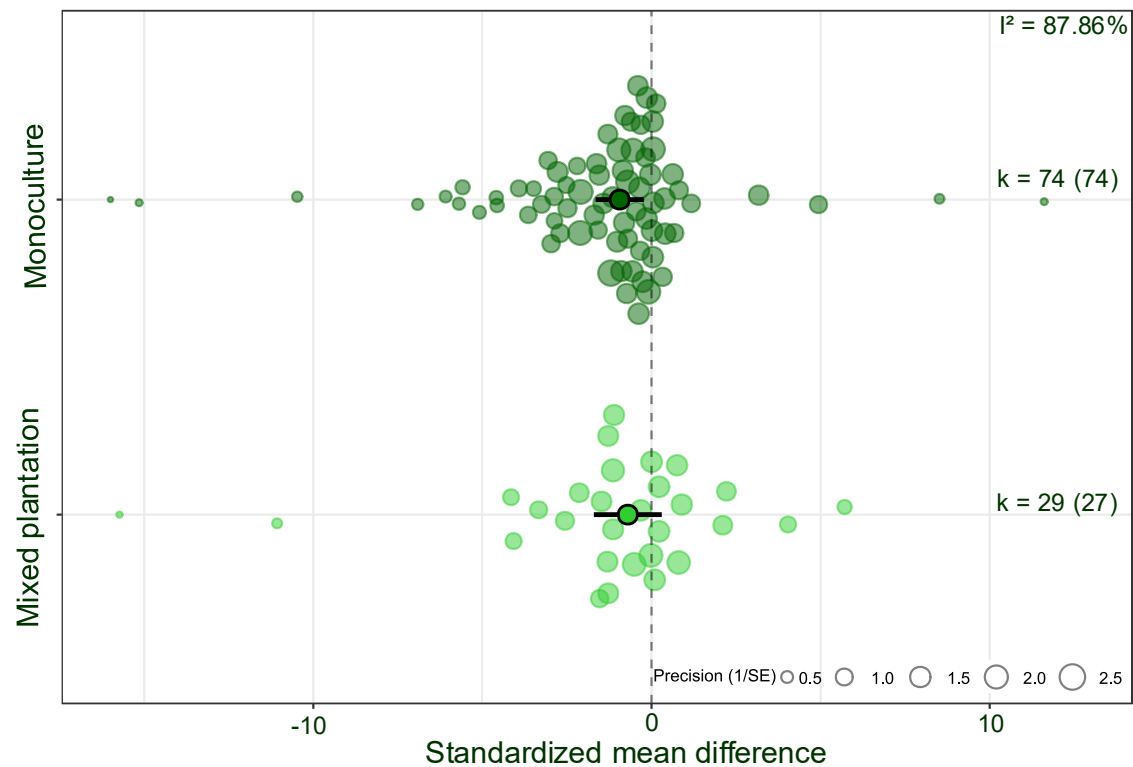


Figure 7 – Effects of different tree planting techniques on terrestrial taxonomic biodiversity compared to a native reference open ecosystem (positive control). Only classes with ≥ 10 observations were included. The centroids of the polygons indicate the point estimate of the combined standardized mean difference between plantations and controls, while their outer edges indicate the 95% confidence interval limits. Polygons intersecting the null effect axis (vertical line 0) indicate absence of effect. K = number of reports included in the meta-analysis; I^2 = percentage of variability in effect sizes due to heterogeneity between studies; $QM = 0.65$; Fail-safe $N = -103$.

1.5 Discussion

Our meta-analyses revealed that tree planting is ineffective in reaching biodiversity levels of plants, invertebrates and vertebrates of the native reference open ecosystems. Despite

combining 106 individual reports, our analyses are derived from only 12 studies that included diverse ecosystems, such as heathlands, dry grasslands, grasslands, shrubby steppes, subtropical grasslands, sandy grasslands, shrub grasslands, steppes, and *Cerrado*. In many of these ecosystems, tree planting is often ecologically inappropriate, as they are naturally treeless. On the other hand, some of them, such as the Cerrado, are characterized by sparse tree cover, which could justify tree planting at low densities (Veldman *et al.* 2015a; Bond 2019). Nonetheless, such tree planting should occur along with other growth-forms like grasses and forbs, which was not frequent conducted in the evaluated studies.

The paucity of research in these open ecosystems may reflect a growing recognition of the unsuitability of tree planting in such contexts (Veldman *et al.* 2015b), suggesting that alternative techniques are being appropriately prioritized in open ecosystems (see Arruda *et al.* 2023; Pilon *et al.* 2023). However, it could also indicate a critical gap in monitoring and reporting of tree planting interventions, highlighting that despite increasing global afforestation efforts, few studies evaluate their outcomes. This disparity likely stems from the historical undervaluation of open ecosystems and the persistent misconception that they represent degraded states requiring tree-based restoration to reach a ‘climax’ state (see Lahiri *et al.* 2023). Further complicating this issue, many studies were excluded from our analyses due to their reliance on tree cover as a proxy for success – a metric poorly correlated with biodiversity outcomes in open ecosystems (Scogings 2023).

Our main finding is that plantations supported lower biodiversity than reference ecosystems, a finding that aligns with a previous study (Atkinson *et al.* 2022) that evaluated taxonomic, functional, and phylogenetic diversity indices for woody and non-woody ecosystems. Beyond confirming previous findings, our overall biodiversity response was consistent despite the planted species origin. This underscores the inefficacy of tree planting for biodiversity recovery, even when using native species. Such tree planting efforts thus

represent a waste of time, resources and biological material (Coleman *et al.* 2021; Rana *et al.* 2022).

Tree planting might improve biodiversity relative to degraded sites for some open ecosystems like savannas, though we found that they never matched reference open ecosystem levels. This partial recovery highlights a critical limitation of current practices: the massive focus on trees alone (Medeiros *et al.* 2024). Tree-only plantings are typical in commercial forestry and are often justified by the concern that other plant growth forms may negatively affect tree performance, potentially reducing economic returns (Estrada-Villegas & Schnitzer 2018). Yet, even in closed-canopy ecosystems, biodiversity recovery requires structural and functional complexity that monocultures or tree-dominated plantings cannot provide. Effective restoration must integrate multiple approaches – a paradigm that shifts from “tree planting” (see Duarte & Gandolfi 2017).

Our analysis of the effects of different planting techniques reveals no clear guidance for restoration practices aiming to enhance biodiversity. Although we found that mixed plantations would have more positive outcomes than monocultures in enhancing biodiversity, our result is not robust and further field studies should be done to better access such information. The potential of mixed plantations lies in their design: when properly planned with complementary species (Liu *et al.* 2018) they can enhance resource use efficiency, boost productivity (Pretzsch and Schütze 2016) and improve carbon sequestration compared to monocultures. Additionally, mixed plantations can allow for diversified production under different rotation periods, but all of these benefits depend on the selected species. Poorly chosen mixtures can create unfavourable conditions by increasing the risk of disease outbreaks or reducing soil fertility due to asymmetric competition (Liu *et al.* 2018). Hence, careful planning and appropriate species selection (see Liu *et al.* 2018; Di Sacco *et al.* 2021) have the potential to foster increases in both biodiversity and productivity. Future research investigating optimal planting densities (Gabira

et al. 2023) to maximize diversity while maintaining productivity gains can be carefully encouraged for savanna ecosystems as long as tree planting co-occurs that of forbs and grasses and is spaced enough to maintain the continuous herbaceous ground cover typical of savannas.

We identified several critical gaps in current tree planting research regarding its effects on biodiversity. Assessments mainly focus on plants, while fungi, microorganisms, and vertebrates were significantly underrepresented. This limited taxonomic scope constrains our understanding of how tree planting affects the entire community. Moreover, our ability to investigate how some factors modulate restoration outcomes, such as the distance to native open reference ecosystems and plantation age, was limited due to either frequent omission of key methodological details or to data variability. Our screening process excluded many studies due to a lack of control, either positive (reference native ecosystem) or negative (degraded sites), which is a concern already raised by previous studies (Gann *et al.* 2019; Medeiros *et al.* 2024). To address these limitations and considering a restoration context, we recommend future studies to 1) expand biodiversity monitoring in planted areas to include underrepresented taxa; 2) systematically report management practices and spatial context of the plantations; 3) incorporate restoration controls in study designs; and 4) document species selection criteria for planting as well as planting configuration.

1.6 Conclusion

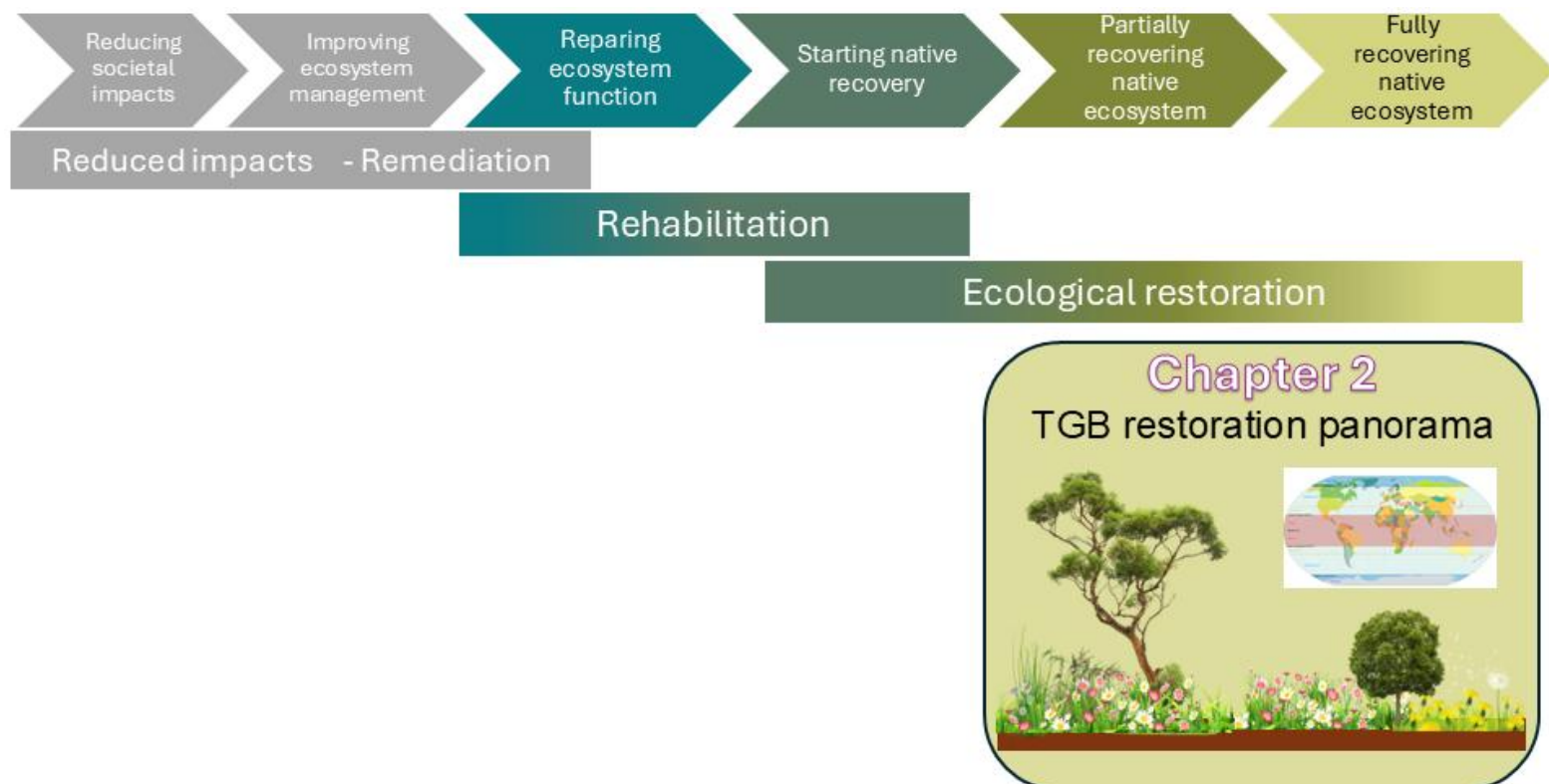
Our study aligns with previous synthesis that explored tree planting effects on biodiversity across multiple trophic levels (see Atkinson *et al.* 2022; Wang *et al.* 2022; Kremer *et al.* 2025). However, our study takes one step further by investigating the effects of tree planting on biodiversity only exploring plantations in open ecosystems, regardless of their main

goal. Our overall trend was reinforced despite the origin of planted trees: tree planting could not reach the biodiversity levels of reference native open ecosystems.

One limitation of our study is the lack of sufficient comparisons that hampered hierarchical meta-analyses that would explore the effects in the three different open ecosystem types: grasslands, shrublands and savannas. Further, other limitations of our study is meta-analysis approach not being suitable for compositional diversity data, which is also a key measurement to realistic estimates biodiversity effects of tree planting (see Prober *et al.* 2025). Furthermore, strategies that incorporate growth-forms beyond trees as well as other taxonomic groups rather than plants are encouraged to foster biodiversity recovery. We, thus, highlight that despite tree planting being widely promoted, planting only trees cannot ensure the return of biodiversity.

CHAPTER 2: SYSTEMATIC REVIEW OF FIELD RESEARCH REVEALS CRITICAL SHORTFALLS FOR RESTORATION OF TROPICAL GRASSY BIOMES

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2.1 Abstract

Scientists and policymakers are becoming aware of the pressing need to restore tropical grassy biomes (TGB), which are home to unique biodiversity and provide essential ecosystem services to hundreds of millions of people. However, TGB face increasing threats, including the forest- and tree-centric approaches that promote their degradation though we still lack a systematic assessment of where and how TGB restoration research has been done to guide policy and practice. We synthesised knowledge on field restoration experiments by conducting a systematic literature review to map TGB restoration field studies, examine the association of restoration techniques and degradations sources, and investigate the diversity of indicators used to monitor restoration outcomes. TGB restoration was concentrated at Brazilian and Australian savannas, with large blindspots in Asia, Africa, and northern and western South America. Studies were largely context-dependent, with an inconsistent usage of restoration techniques to different sources of degradation. Less than half of the indicators evaluated were monitored consistently through time, often using a low-dimensional approach related to ecosystem functioning. Few studies manipulated fire, herbivores and soils, the key drivers for the re-establishment of TGB dynamics. Unfortunately, many studies lacked negative (degraded ecosystems), positive (reference ecosystems) controls, or both, impairing attempts to robustly determine restoration outcomes. Our overview of field research on TGB restoration highlights that research needs improvement to refine our ability to assess, plan, implement and monitor restoration. Severe issues with experimental designs and data reporting are identified as barriers to find generality and upscale TGB restoration to meet the goals of the UN Decade on Ecosystem Restoration. Our synthesis calls for enhanced field experiments, transparent data reporting, and quantitative syntheses to guide large-scale TGB restoration. The overall lack of knowledge on improving resilience and measuring outcomes hampers meaningful comparisons

between studies and hinders synthetic views essential for determining appropriate restoration techniques for different degradation sources and suitable monitoring indicators. To overcome the scarcity of reliable and transparent data supporting TGB restoration, we propose a simple checklist for minimum research reporting information and a more complete multilingual standardized guideline.

Key-words: ecological restoration, ecological synthesis, grassland, savanna, shrubland, transparent science, reproducibility, guidelines

2.2 Introduction

The need to restore ecosystems has never been more urgent due to ever increasing degradation rates. As a response to this trend, the United Nations has launched the Decade on Ecosystem Restoration 2021-2030, aiming to catalyse global restoration efforts to reverse ecosystem degradation, protect biodiversity, mitigate climate change, and support human livelihoods. Our capacity to achieve such goals relies largely on knowledge built for the different stages of the restoration process, including assessment, planning, designing, implementing, management and monitoring (Gann *et al.* 2019). Such knowledge builds on multiple sources and field restoration experiments are essential to test the generality of hypotheses, calibrate and validate models, and to provide realistic cost-benefit estimates. Moreover, ecological restoration must also move forward and overcome Biome Awareness Disparity to include all types of biomes (Török *et al.* 2021; Silveira *et al.* 2022). The goals of the United Nations Decade of Ecosystem Restoration are ambitious but will remain utopic and unfeasible without truly embracing the diversity of Earth's ecosystems combined with solid theory, predictive models and accumulated empirical data.

Tropical grassy biomes (TGB) encompass the world's ancient tropical and subtropical megadiverse grasslands, shrublands and savannas. They are dominated by a continuous herbaceous layer with variable degrees of woody cover (Bond 2019). TGB have evolved with fire and large herbivores playing a major role in their functioning, structure, and dynamics (Veldman *et al.* 2015a; Buisson *et al.* 2019). In addition to these two drivers, edaphic factors can also shape and maintain these naturally open-canopy ecosystems (Buisson *et al.* 2019). Despite their megadiversity and provision of vital ecosystem services for hundreds of millions of people (Lehmann & Parr 2016; Bengtsson *et al.* 2019), TGB cover and biodiversity are declining due to multiple pressures, such as agricultural conversion, livestock production,

mining, urbanization, afforestation, exotic species invasion, novel fire regimes, woody encroachment and climate change (Veldman *et al.* 2015b; Bardgett *et al.* 2021).

Threats to TGB are not only due to different degradation pressures but also because of historical misunderstandings, undervaluation, and insufficient knowledge and protection (Parr *et al.* 2014; Pausas & Bond 2019; Silveira *et al.* 2022; Tölgyesi *et al.* 2022; Pilon *et al.* 2023). Despite covering nearly 40% of the land (Dinerstein *et al.* 2017), a restoration policy, science, and practice framework for TGB is still in their infancy (Silveira *et al.* 2022) given that clear definitions of reference ecosystems have emerged only recently (Bond & Parr 2010; Veldman *et al.* 2015a). For example, despite the long history of TGB degradation, the first field TGB restoration experiment (Lovera & Cuenca 1996) was published nearly a century after Warming's (1895) seminal plant ecology book based on Neotropical savannas (Figure 8). This relatively recent restoration history resulted in misguided actions (Silveira *et al.* 2022), such as tree-oriented, and often carbon-based, practices that continuously have been expanding on TGB (Fagan *et al.* 2022; Nerlekar *et al.* 2023). Therefore, TGB are extensively threatened by multiple degradation pressures, scientific overlooked and misguided practices.

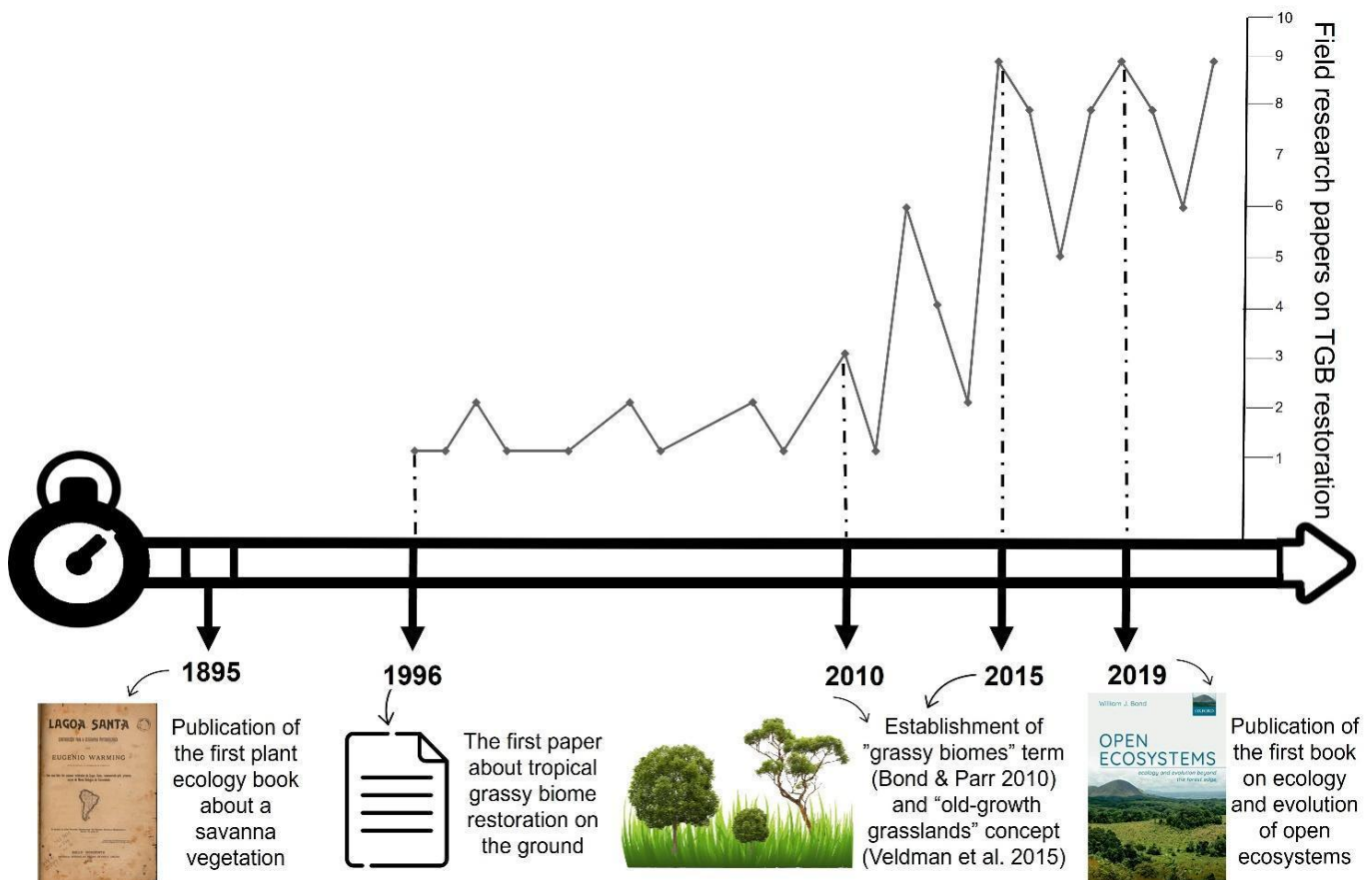


Figure 8 – Timeline showing cornerstones in the history of tropical grassy biomes (TGB) ecology and restoration. The curve above the timeline shows the recent and poorly developed restoration framework with the publication of very few papers addressing field restoration papers.

Although challenging, recent efforts have attempted to increase the knowledge underpinning TGB restoration (Buisson *et al.* 2019). Such studies have demonstrated the need for active interventions given extremely slow recovery rates and natural regeneration of TGB (Nerlekar & Veldman 2020). Proper management of livestock and wild herbivores, tree, and shrub control (i.e., removal and cutting), invasive species control and prescribed fires are among the key strategies to restore TGB (Buisson *et al.* 2019). The efficiency of such strategies should be evaluated by long-term monitoring of species composition, community structure and

ecosystem functioning, which should assess the resilience to endogenous disturbances (Buisson *et al.* 2019). Nonetheless, TGB restoration is still constrained by an overall lack of knowledge on how to improve ecosystem resilience (Buisson *et al.* 2019, 2022). Therefore, mapping field restoration experiments is pivotal to precisely identify bottlenecks in TGB restoration and overcome practical challenges.

Several global reviews on restoration research have emerged (see Wortley *et al.* 2013; Atkinson *et al.* 2022) but, in contrast to forests, syntheses specifically focusing on TGB restoration are beginning to emerge only recently on a regional scale (Carbutt & Kirkman 2022; Medeiros *et al.* 2022; Pilon *et al.* 2023). Broad and detailed mapping of field restoration experiments encompassing sources of degradation, restoration strategies and indicators usage is needed to support achieving the target agenda for TGB restoration (Buisson *et al.* 2021). Such overview will provide the baseline for developing novel and refined strategies for TGB habitat-tailored interventions. Therefore, here, we aim to fill this knowledge gap by conducting a systematic literature survey and providing the first empirical synthesis of TGB restoration research, along with the techniques and approaches used. Specifically, we mapped restoration field research, identified the major drivers of habitat degradation, evaluated the most used restoration techniques, and assessed the diversity of monitoring strategies. Finally, to tackle the remarkable disparity found in data reporting of in our database, we provide a multilanguage checklist of minimum standards for data reporting on TGB restoration to foster future research designs and quantitative syntheses.

2.3 Methods

2.3.1 Literature review

To assess where and how TGB restoration research is being conducted, we carried out a systematic literature review of peer-reviewed articles (does not require ethical approval) that conducted field restoration research. We used both the Web of Science and Scopus databases to perform the searches, considering studies published in English from January 1945 to December 2022 and using the following keywords: (“grassy biome” OR “grassland” OR “meadow” OR “prairie” OR “rangeland” OR “savanna*” OR “steppe” OR “shrubland” OR “cerrado”) AND (“afforestation” OR “afforested” OR “restoration” OR “restored” OR “recovery” OR “recovered” OR “reforestation” OR “reforested” OR “rehabilitation” OR “rehabilitated” OR “revegetation” OR “revegetate”) AND (“tropical” OR “subtropical”). Given the wide diversity of terms to describe TGB (Bond 2019) and commonly misused terms, we used all these words to encompass as much restoration research as possible.

Research on ecological restoration should aim to improve the state and/or functionality of a degraded, damaged, or destroyed ecosystem towards re-establishing the native ecosystem (Gann *et al.* 2019). The initial state of degradation is key for dictating the possibility of restoration as well as the most appropriate approach to be undertaken. In some cases, a novel ecosystem needs to be created due to high levels of degradation (Hobbs *et al.* 2009). We considered an ecosystem as degraded or damaged when it experienced deleterious impacts that reduced biodiversity and ecosystem functioning (Gann *et al.* 2019) due to exogenous disturbances or shifts in endogenous disturbance regimes. We assessed degradation as quantitatively (time-zero data) or qualitatively self-reported. In the last case, the site targeted for restoration must have had some anthropogenic impact (e.g., oil spill, mechanical clearance, human-induced fire, etc.) or previous land use (e.g., mining, livestock production, farming, etc.) that explicitly resulted in degradation. Therefore, degraded sites did not necessarily imply having a negative control. We considered that research had a negative control when restoration

outcomes were compared with data collected at a time-zero, at a degraded site without interventions or undergoing degradation. Furthermore, we considered that research had a positive control when studies compared restoration outcomes to a target reference ecosystem.

In the first screening, we checked the paper title and abstract to exclude studies focusing on improving site conditions with objectives unrelated to ecological restoration, such as crop planting and pastureland for livestock. We also exclude studies done under laboratory and greenhouse conditions. To refine our database, we ran a second screening evaluating the full text of remaining papers to assess whether studies (1) were conducted in tropical or subtropical grassy biomes; (2) disclosed information on degradation, and (3) applied at least one restoration technique aiming for ecological restoration. To match the first criterion, research must have been done within 30 to -30° latitude and should be classified as a grassland, shrubland or savanna biome (Dinerstein *et al.* 2017). We decided to exclude wetlands and ecotones, even if located within the boundaries of TGB, due to their unique characteristics, functioning and restoration needs. To match the second criterion, research must have been done on a degraded site and should not have been restricted to the management of native areas (e.g., fire management inside a savanna protected area). Thus, we included papers reporting perturbations in the fire/grazing regime but excluded those aiming to understand the role of herbivores and fire in TGB dynamics even if they provide knowledge support to guide future restoration and conservation management (e.g., Alvarado *et al.* 2018; Pilon *et al.* 2021). In the end, we only included 15 papers that clearly provided enough information on changes in fire regime as a degradation source (Appendix F) and 27 papers that reported grazing pressure due to livestock as a degradation source (Appendix G). Finally, to match the third criterion, research should have been carried out an intervention within the restoration *continuum* (Gann *et al.* 2019) ultimately aiming to (re)establishing a native TGB.

2.3.2 Data collection and analyses

To map TGB restoration, we retrieved geographic coordinates, biome type and sources of degradation for each site from eligible papers. We plotted the geographic coordinates of each field experiment using QGIS and classified biome types as savanna, grassland, or shrubland based on original descriptions. We plotted the geographical coordinate of the restoration site into a global biome map (Dinerstein *et al.* 2017), in 28% of the cases when the reference ecosystem was unspecified and upon the use of ambiguous terms (i.e. open forest). Despite inconsistencies with more precise, local-scale maps, we chose Dinerstein *et al.* (2017) as a source of mapping because it uses a hierarchical classification and is a widely used system for biome classification worldwide allowing our study to be comparable to others. Coordinates falling outside the area covered by TGB were excluded. Papers for which we were unable to identify the reference ecosystems (i.e. used ambiguous terms with no geographical coordinates) were also excluded.

We classified the sources of degradation into few categories, even if they often involve multiple drivers of loss of biodiversity and ecosystem functioning. For example, crop plantation often involves soil disturbance, fertilization, and invasive species. Hence, despite the diversity of disturbance histories, we operationally classified sources of disturbance into the following categories: afforestation, agriculture, exotic species, fire, livestock, and mining, or classified studies as having two and three sources of degradation (more details in Appendix C). Furthermore, we were unable to classify three studies that did not provide clear causes of degradation even after contacting corresponding authors.

We recorded the degradation and restoration time length based on data provide by the original studies. To identify the most common strategies for TGB restoration, we extracted information on manipulation of the main drivers (fire, herbivores, soil), and the restoration techniques provided in the original papers (natural regeneration, seed sowing, planting, topsoil

transfer, etc., or a combination – see Appendix E). We considered natural regeneration as a technique of passive restoration in cases where the regeneration process started after the cessation of an exogenous disturbance that has caused degradation. Hence, resilience after endogenous disturbances (i.e. fire and grazing) was not considered as a restoration technique, because, in this case, disturbances are part of TGB functioning rather than a source of degradation. Finally, we examined the diversity of indicators used to measure restoration success (e.g. Ruiz-Jaen & Aide 2005; Wortley *et al.* 2013; Prach *et al.* 2019), the frequency intervals and length of monitoring. To accommodate the diversity of indicators into workable categories, we classified all indicators into the six attributes or categories use by the Society for Ecological Restoration (SER): absence of threats, ecosystem function, external changes, physical conditions, species composition and structural diversity (Gann *et al.* 2019).

Because some papers assessed restoration outcomes in more than one degraded area and/or applied more than one restoration treatment, we considered each independent restoration experiment as our sample unit. However, because papers employed the same indicators to measure restoration success for monitoring analyses, we considered the paper as our sample unit to avoid inflating our database. We built alluvial diagrams connecting the sources of degradation to restoration techniques when both data were available. Moreover, we explored the overlap in the use of the six SER attributes using Venn diagrams. All analyses and figures were made using R and Inkscape software.

2.4 Results

After excluding duplicates, we retrieved 1,256 papers, but only 90 papers matched our inclusion criteria (Figure 9; Appendix A). The first paper on TGB restoration was published in

1996, and despite a recent increase in average publication/year, the total number of papers was never above 10/year (Figure 8). These 90 papers generated 155 TGB field restoration experiments. Most experiments were concentrated in Brazil (50%), Australia (17%), South Africa (6%) and USA (6%), with the other 13 countries accounting for less than 5% each (Figure 10). We noticed large unstudied TGB in Asia, sub-Saharan Africa, and North-western South America. Furthermore, most restoration research aimed at restoring savannas (61%), followed by grasslands (32%) and shrublands (8%). The Brazilian Cerrado was the most commonly biome target for restoration, whereas other biomes appeared only rarely in the database.

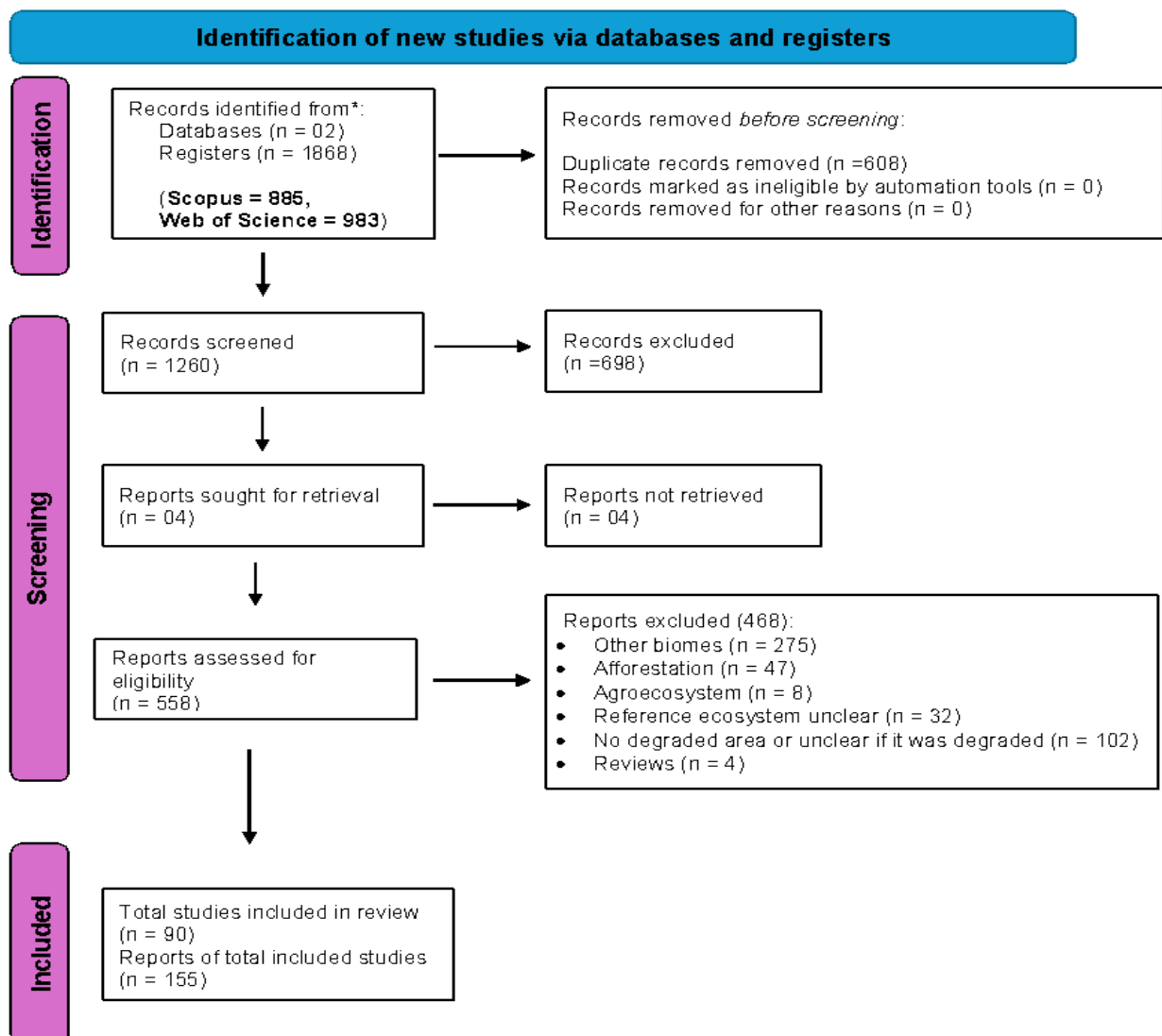


Figure 9 – PRISMA fluxogram (Preferred reported items for systematic reviews and meta-analysis) of the systematic review on Tropical Grassy Biomes field restoration experiments of our database creation with inclusion and exclusion criteria on each screening.

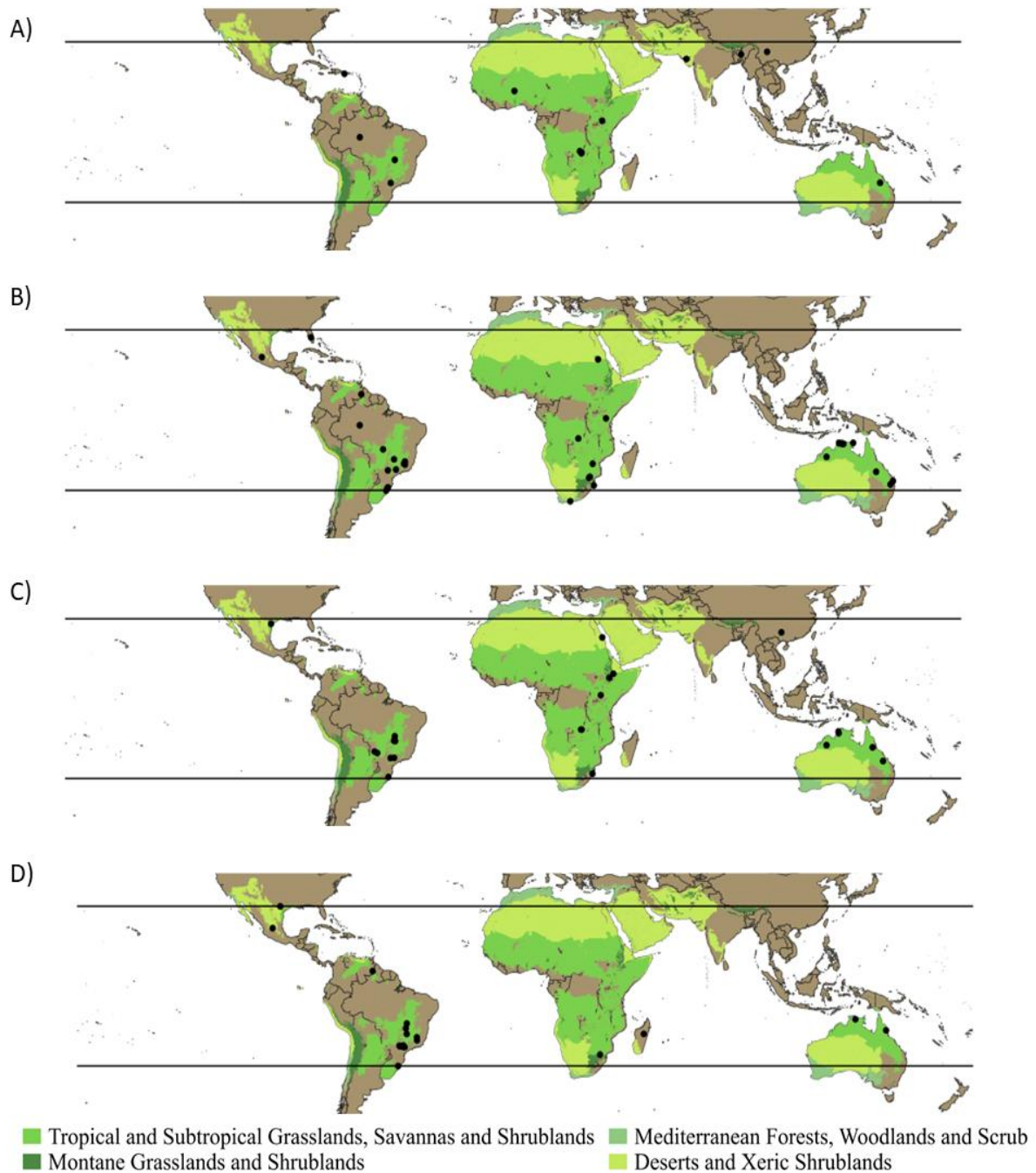


Figure 10 – Systematic mapping of tropical and sub-tropical grassy biome (TGB) restoration. Each field restoration experiment conducted at different biomes (*sensu* Dinerstein *et al.* 2017)

are represented according to their restoration control: (a) both positive and negative controls; (b) only positive control (reference TGB site); (c) only negative control (degraded site without restoration intervention); (d) no restoration control (neither positive nor negative controls).

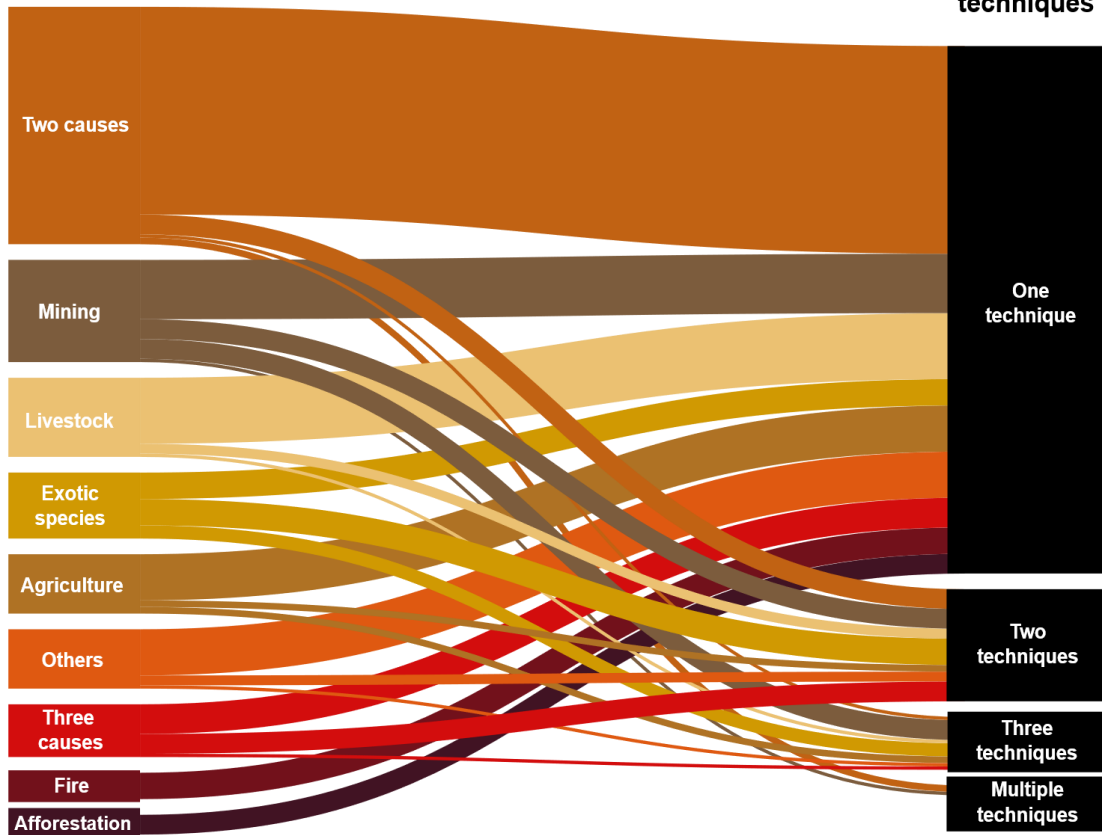
Restoration experiments were implemented in areas with a broad diversity of degradation sources. Forty-one percent of restoration sites were degraded by multiple sources, with the combination of livestock and exotic species (25%) appearing as the most frequent degradation cause. Additional degradation causes included mining (14%), livestock (10%), agriculture (8%), exotic species (6%), perturbation of fire regimes (6%), combination of agriculture, livestock and exotic species (5%), and afforestation (4%). Other minor causes (1-3% of cases) include woody encroachment, desertification, oil spill, urban development, and diverse combinations of degradation sources (Appendices B and C). Three papers provided equivocal causes creating bare soils and were classified as unknown causes.

Only 29% of studies quantified degradation state of time-zero and the remaining provided qualitatively assessments of degradation. Eleven papers with sites degraded by fire qualitatively assessed changes in at least one dimension of fire regime (severity, frequency or, seasonality) while only four fire-related papers support the degradation by fire quantitatively. Those fire degraded papers encompassed 23 sites from which 13 were restored using natural regeneration while only five sites applied some fire management. Regarding the grazing pressure, 19 out of 27 papers qualitatively reported livestock as a degradation source, and eight papers quantified the effects of overgrazing. Furthermore, we also evaluated how long sites had been under degradation and for how long restoration experiments had been implemented. Degradation time ranged from a year to more than a century, but 67% of the papers did not disclose this information precisely. Restoration experiments were relatively recent with more than half of the cases occurring from one to 10 years (59%), and 12% spanned more than 30

years of intervention. Unfortunately, 29% of the experiments did not provide precise data on the onset of the experiments.

Despite most TGB restoration experiments conducted in sites with multiple degradation sources, 73% applied a single restoration technique (Figure 11A). Natural regeneration (22.3%) and fire management (21.8%) were the most commonly used techniques, followed by physical interventions (9.5%), planting or seed sowing species (9.1%), chemical interventions (4.5%), gradual livestock removal (3.2%), and the combination of chemical intervention with physical intervention and planting or seed sowing (3.2%). Other less used techniques include translocation, hay transfer, topsoil spreading and the combination of different techniques (Appendices D and E). When we explored the relationship between the different combinations of degradation sources and restoration techniques applied, we found the same general pattern: the dominant usage of one technique for different types of degradation scenarios (Figure 11B). Surprisingly, 40% of restoration experiments did not manipulate any driver of TGB distribution. Currently, 28% of restoration experiments managed soil properties, 23% managed fire, and 4% managed large herbivores. Some studies manipulated fire and soil simultaneously (3%) whereas others manipulated both fire and herbivores (2%).

A)
Sources of
degradation



B)
Two or three
sources of
degradation

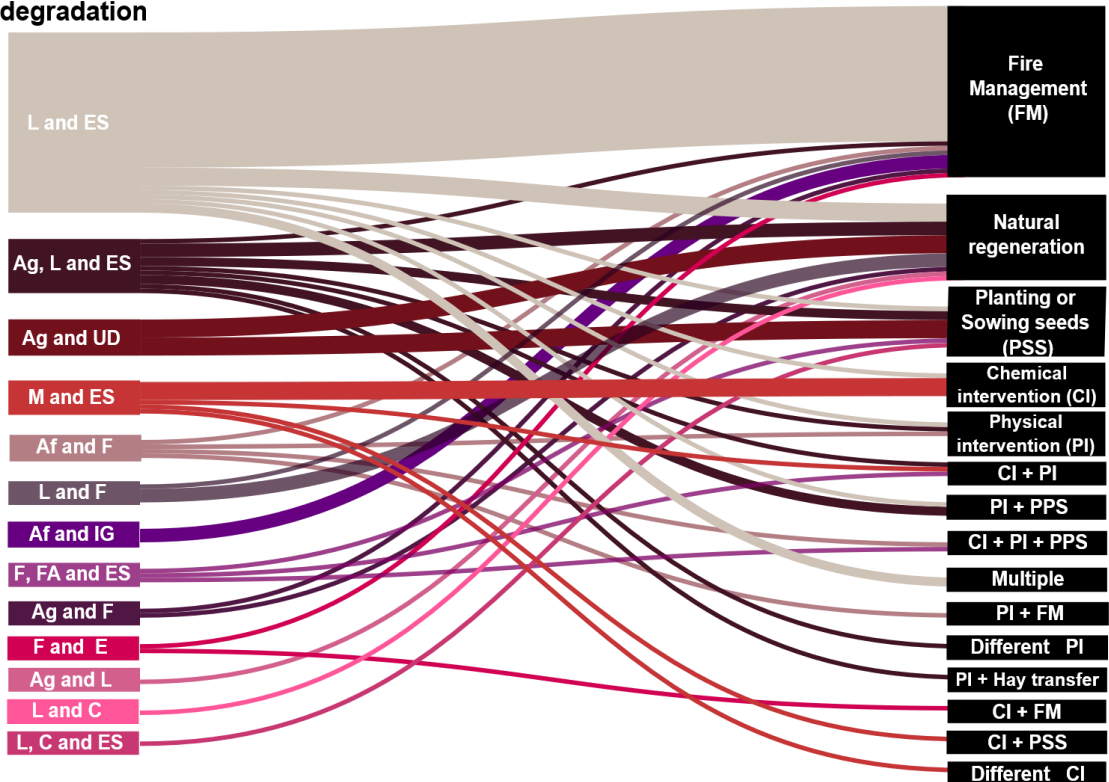


Figure 11 – A poor match between different sources of degradation (left) to restoration technique (right) applied to tropical grassy biomes. The general pattern is presented in figure 11A and the degradation sources combinations are presented in detail in figure 11B as the following: livestock (L), exotic species (ES); agriculture (Ag), urban development (UD), mining (M), afforestation (Af), fire (F), feral animals (FA), invasive grass (IG), encroachment©), chopping©). In both figures (A and B), the width of lines linking the source of degradation and restoration technique indicates how many times each type of technique was applied for the same degradation context.

We assessed aspects regarding evaluation of restoration outcomes and surprisingly found that 32% of experiments lacked either a positive control (native reference ecosystem) or a negative control (degraded site with no intervention or undergoing degradation). Only 12% of cases implemented both controls, while 37% compared the restoration site to a positive control and 19% compared to a negative control (Figure 10). Studies used 1019 indicators to measure restoration success, encompassing a wide range of measurements. Unfortunately, most indicators were not monitored through time or information in the original papers was not clearly provided (Figure 12A). As a result, only 501 indicators were monitored temporally with monitoring lengths ranging from weeks to years. Despite a wide diversity of attempts to evaluate restoration success over time (Figure 12B), monitoring was not consistent through time, suggesting opportunistic assessments. Indicators used to monitor restoration success were mostly concentrated on ecosystem functioning (150 indicators) and species composition (150). Structural diversity (91), physical conditions (81) and absence of threats (29) were less monitored whereas ‘external changes’ was the only attribute without temporal assessment. Unfortunately, no study evaluated all six SER attributes simultaneously over time, with most cases (85%) of monitoring using from one to three attributes (Figure 12C). The combination of

species composition, structural diversity and ecosystem function attributes was the most frequent approach in TGB restoration experiments.

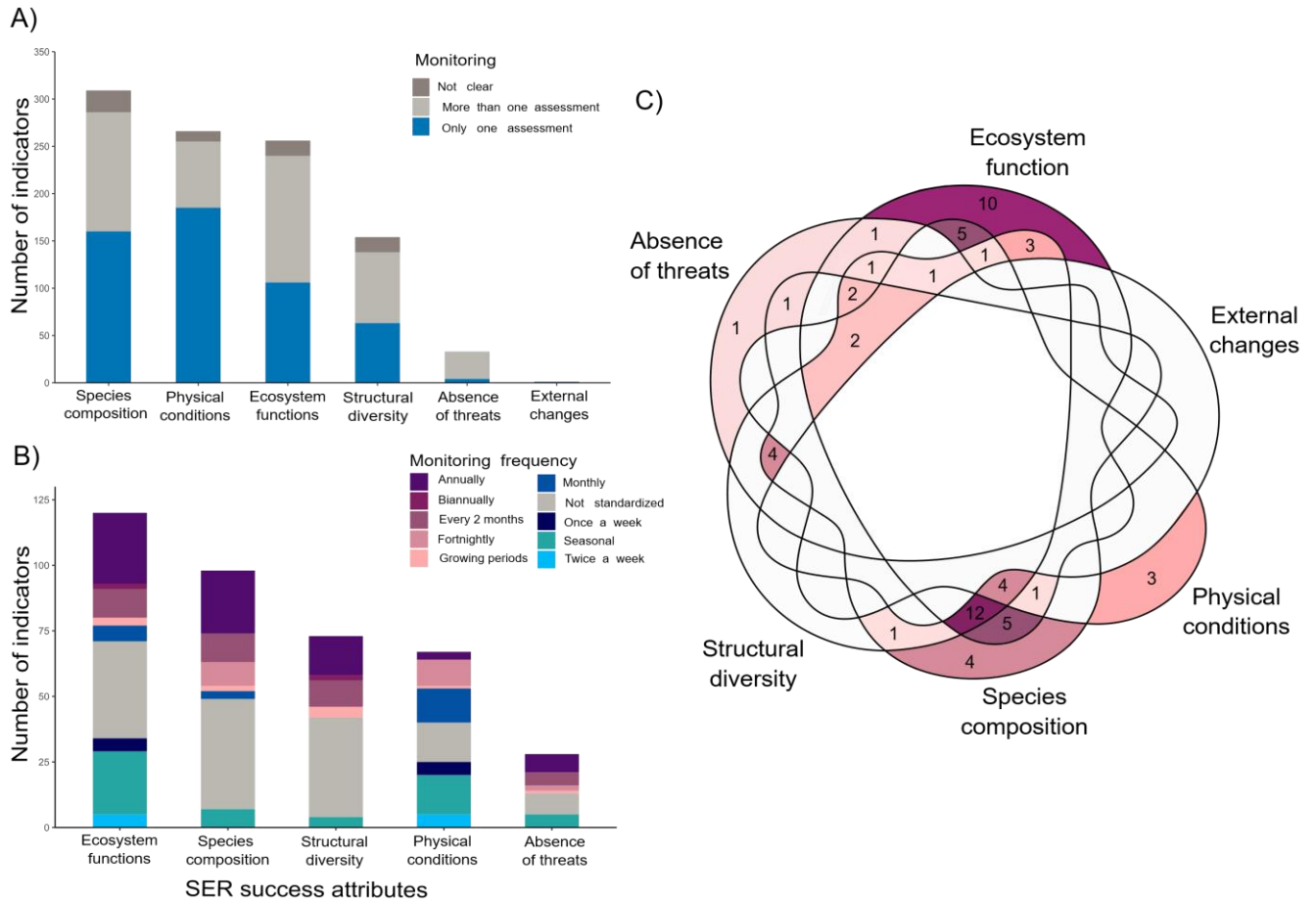


Figure 12 – Monitoring interval frequency for indicators of restoration success in tropical grassy biomes (A-B). Indicators were classified into SER success attribute categories and monitoring restoration success has been historically done mostly with low-dimensional approaches as shown by low overlap at all six SER success attributes for the 51 papers that applied monitoring (B).

2.5 Discussion

Our synthesis of TGB restoration highlights multiple methodological shortfalls, incomplete data reporting and several blindspots preventing overall assessments of restoration outcomes. Key knowledge improvements identified were the incorporation the drivers of ecosystem functioning (Buisson *et al.* 2019) into field experimental settings and the establishment minimum standards of data reporting to evaluate outcomes. Context-dependency identified in TGB experiments prevents assessment of overall recommendations of restoration techniques and monitoring. Identifying the source of degradation is key for developing appropriate restoration strategies (Holl *et al.* 2023), however, one third of restoration experiments applied natural regeneration as a single restoration technique regardless of the degradation source. Whenever sites were monitored, the length was shorter than recommended for TGB (Nerlekar & Veldman 2020). Hence, ecologically-sound restoration and monitoring frameworks should be implemented in future restoration studies.

Incorporating TGB functioning into restoration practice is imperative for enhancing ecosystem resilience (Coutinho *et al.* 2023). Despite TGB having evolved with endogenous disturbances and specific edaphic conditions (Veldman *et al.* 2015a; Buisson *et al.* 2019), only 55% of the experiments manipulated fire, herbivores, or soils, and only 5% simultaneously manipulate two drivers. Excluding disturbances in TGB has been proven unwarranted (Alvarado *et al.* 2018) and restoration of disturbance regimes are proposed as a critical restoration tool (Buisson *et al.* 2019). Soil chemical, physical and biological properties are key to prevent biological invasion and should be targeted for recovering TGB functionality. We thus highlight that restoration frameworks in TGB must focus on re-establishing resilience to endogenous disturbances and the edaphic properties (Lira-Martins *et al.* 2022; Gerrits *et al.*

2023), otherwise, restored TGB are unlikely to deliver positive long-term outcomes (Giles *et al.* 2022).

TGB restoration should address the multiple degradation sources that threaten their conservation and resilience (Bardgett *et al.* 2021). Multiple active restoration techniques are required to restore TGB under multiple degradation sources (Pilon *et al.* 2023) since they can produce profound impacts, such as the complete removal of soils and subsoils as well as legacies of fertilizers and herbicides (Török *et al.* 2021; Wolfsdorf *et al.* 2021). Nevertheless, 73% of TGB restoration experiments have applied a single technique, mostly natural regeneration and fire management, regardless of the degradation source. This is problematic because restoration techniques should be linked to degradation sources (Holl *et al.* 2023), which have a lasting influence on biodiversity recovery (Atkinson *et al.* 2022). Moreover, natural regeneration has a limited capacity to restore some TGB (Cava *et al.* 2018; Nerlekar & Veldman 2020) and likely results in pronounced recovery debts (Moreno-Mateos *et al.* 2017). Fire management, on the other hand, is a recommended technique for TGB restoration as it represents the reintroduction of a natural endogenous disturbance driver. However, caution should be taken to ensure the benefits of fire reintroduction (DAWE 2022). Therefore, we recommend the implementation of multiple active techniques that have proven positive effects on TGB restoration, such as fire management or topsoil translocation when soil disturbances occurred (Lira-Martins *et al.* 2022; Gerrits *et al.* 2023).

Inconsistent methods to evaluate TGB restoration represent another barrier to support decision-making and adjusting legislation. Monitoring was mostly restricted to two or three attributes, with no study addressing the six attributes recommended by SER (Gann *et al.* 2019). This result aligns with previous reviews (Ruiz-Jean & Aide 2005; Wortley *et al.* 2013) of restoration outcomes. Furthermore, monitoring had no consistent intervals and spanned very short periods of time (69% of studies <5 years), which is insufficient to determine restoration

trajectories in TGB (Nerlekar & Veldman 2020). The first steps towards adequate assessments of TGB restoration are clearly to determine the reference ecosystem, report time-zero data and establish control sites (Gann *et al.* 2019). Issues concerning the reference ecosystem have already emerged (Ruiz-Jean & Aide 2005; Wortley *et al.* 2013), highlighting the need for a clear reference site and the need to establish at least two sites to capture the target ecosystem variance. We had to exclude 27 papers for not reporting the reference ecosystem, while a third of experiments lacked any control site and most of them lacked data to confirm the degradation state. Therefore, we recommend experiments to report time-zero data as well as clearly determine the reference ecosystem and include both positive and negative controls to provide a broad understanding of restoration trajectories through monitoring.

The lack of time-zero reporting is especially concerning in cases of novel fire regimes and grazing pressure because those are endogenous disturbance in TGB. In such cases, it is imperative to report historical data on fire and herbivore regimes instead of qualitative reports. Changes in fire regime patterns can have different impacts depending on the changes in fire components (i.e., intensity, frequency, seasonality, and type) and characteristics (i.e., severity, extent, patchiness, ignition type). Fire events can either promote the growth of many TGB species and inhibit woody plant encroachment or do the opposite (DAWE 2022). Understanding how fire and herbivores affect vegetation structure as well as species composition and ecosystem resilience is vital to select adequate restoration techniques. TGB restoration experiments in sites degraded by perturbations in fire regime and overgrazing must include historical data of fire and herbivore regimes and, for fire degradation, it should clearly discriminate which fire component and characteristic changed.

Future TGB restoration experiments should be expanded throughout the tropics since research was geographically concentrated in Brazilian and Australian savannas. The relative high concentration of studies in Brazil is explained by increasing land use change in the

Cerrado, the most biodiverse savanna in the world (Strassbourg *et al.* 2017). On the other hand, montane grasslands and shrublands have been also increasingly threatened (Christmann & Menor 2021), but were significant blindspots in our review. These biomes have high diversity, endemism (Madriñan *et al.* 2013) and provide many ecosystem services (Mengist *et al.* 2020), but still remain poorly studied (Christmann & Menor 2021). Moreover, we also found absence of restoration studies in African and Indian TGB, regions where biodiversity studies have been raising only recently (Rabarivola *et al.* 2019; Nerlekar *et al.* 2022) but where open ecosystems are increasingly threatened by agriculture and afforestation (Nerlekar *et al.* 2023). The misinterpretation of African and Asian savannas as wastelands with low conservation value has been pointed as a legacy of colonial forestry (Nerlekar *et al.* 2022; Lahiri *et al.* 2023), though old-growth grasslands and savannas are recognized at least one million years ago (Ratnam *et al.* 2016). Such biodiversity knowledge shortfall and misguided policies undermine TGB restoration efforts. We thus reinforce the need of a better assessment of montane grasslands and shrublands as well as African (Nsikani *et al.* 2023) and Indian TGB restoration efforts (Lahiri *et al.* 2023).

Our review highlights the idiosyncratic essence of TGB restoration and the need to enhance field experiments to support quantitative syntheses and meta-analyses guiding large-scale restoration policy and practice (e.g. Gerrits *et al.* 2023; Pilon *et al.* 2023). We also show that TGB restoration is still constrained by an overall lack of knowledge on how to improve ecosystem resilience and how to measure restoration success in ecologically and functionally meaningful ways. Both the effectiveness of restoration techniques and the transparent details of monitoring practices are not fully comparable among studies, preventing us to synthesize practical knowledge that is essential to determine appropriate restoration techniques for different degradation sources.

To overcome methodological shortcomings, incomplete data reporting and context-dependency key recommendations include incorporating ecosystem functioning drivers into experimental settings, establishing minimum data reporting standards, and considering the source of degradation for effective restoration strategies to allow tracking restoration outcomes beyond the focused experiment. Concerns arose about the lack of reporting historical data for novel fire regimes and grazing pressure, emphasizing the need to understand the impacts of endogenous disturbances on TGB. Given the relatively low number of studies, restoration research urges to be encouraged in all TGB, specially in montane grasslands in African and Indian TGB where we found knowledge gaps. These studies need to incorporate TGB drivers, use active techniques to accelerate natural regeneration and carefully select a suitable set of multidimensional indicators based on SER recommendations (Gann *et al.* 2019).

2.6 Practical guidelines with minimum standards for data reporting and enhanced experimental settings

Emerging frameworks in restoration science and practice are expected under the United Nations Decade on Ecosystem Restoration (2021-2030) (e.g., Copeland *et al.* 2021). However, persistent knowledge gaps prevent us from synthesizing knowledge on TGB restoration to inform future policy and practice. Our review clearly points out the urgent need of additional field restoration experiments in TGB and the need to overcome critical issues in primary research that preclude comparability and reproducibility, which dictates the reliability and generality of methods and results (Powers & Hampton 2019). Hence, we propose a simple checklist (Table 2) and a multilingual practical guideline for minimum standards of data reporting and enhancement of field TGB restoration experiment designs.

Table 2 – Elementary restoration research information at site level. Information was filled up only as an example (no real data). For the reference and control sites, monitoring has to be informed in relation to the restoration date on the restoration site.

Project name: <i>Grassland restoration in montane ecosystem</i> RESTORATION SITE Degradation source(s): <i>sugarcane cropland</i> Restoration technique(s): <i>seed sowing (2000)</i> Adaptative management: <i>resowing 5 years after the first seed sowing and reestablishment of natural fire regime</i> Restoration site location(s): <i>10° 20' N and 76° 20' E</i> Monitoring before the restoration date: <i>yes (data collected before seed sowing in 2000)</i> Monitoring after the restoration date: <i>yes (data collected in 2005 and 2010)</i> REFERENCE SITE Reference ecosystem type: <i>montane grasslands</i> Reference site location(s): <i>Nilgiri Hills (10° 58' N and 76° 48' E)</i> Monitoring before the restoration date: <i>no</i> Monitoring after the restoration date: <i>yes (data collected in 2010)</i> CONTROL SITE Restoration control type: <i>abandoned sugarcane field without seed sowing</i> Restoration control site location(s): <i>10° 35' N and 76° 20' E</i> Monitoring before the restoration date: <i>yes (data collected in 2000)</i> Monitoring after the restoration date: <i>no</i>
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Global quantitative comparisons among TGB restoration experiments are prevented due to poor data reporting and a wide variation of degradation sources, restoration techniques and selection of monitoring indicators. Restoration science is often context-dependent and cross-studies comparisons are not always possible (Gerstner *et al.* 2017). Nevertheless, clear, detailed, and transparent data reporting has the potential to provide support for overcoming challenges in restoration outcome predictions (Gerstner *et al.* 2017; Brudvig & Catano 2021). For example,

predictive relative recovery trajectories over time allowed for model building in forest restoration (Poorter *et al.* 2021) but this step is currently unachievable for TGB due to the paucity of empirical data and poor data reporting. Failure to report methods and results in sufficient detail to allow correct interpretation, replicability, and data extraction, severely compromises cross-studies comparisons and attempts to synthesize applicable ecological knowledge (Gerstner *et al.* 2017).

We proposed a step back focusing on improving transparent data reporting because standardizing field experiment reporting has the potential to enhance our capacity to understand generalities and develop new theories based on empirical and functional relationships across spatial and temporal scales (McCleery *et al.* 2023). Our guidelines consist of a multilingual checklist (Appendix H) that can be easily implemented in ecological restoration projects. The guidelines can also be used in sites where new ecosystems will be created and/or interventions have other goals within the restorative *continuum* (Gann *et al.* 2019). Our guideline is a tool for restoration practitioners, scientists and decisions-makers aiming to increase the value of scientific evidence and moving TGB restoration experiments towards a more open, reliable, and transparent science (O’Dea *et al.* 2021; McCleery *et al.* 2023). Below we discussed the main issues regarding data reporting and provided suggestions for minimum standards for data reporting and experimental designs with a full checklist (see Appendix H for the English version; complete version in the published study).

First, providing clear and transparent information on the study site is mandatory. We were unable to determine the reference ecosystem for 209 restoration sites and to overcome such failures in disclosing detailed information on the reference ecosystem, we plotted the geographical coordinates into a global biome map (Dinerstein *et al.* 2017). However, we acknowledge that our approach is scale-dependent and cannot be used as a panacea. We also suggest that a standardised nomenclature should be sought while confusing terms must be

avoided. Recently, a critical review of common terms and concepts used in forest landscape restoration was done (Stanturf *et al.* 2023), and available frameworks for open biomes (Bond 2019; Copeland *et al.* 2021) can work as a starting point.

A second issue refers to the clarification on degradation history, which includes information relative to exogenous disturbances and perturbations of endogenous disturbances regimes. TGB restoration experiments were implemented in sites under multiple degradation sources and sometimes multiple interventions were applied. In such cases, information was not transparent enough to allow data retrieval. For instance, it was challenging to determine the effectiveness of each technique and for different degradation contexts. Moreover, identifying degradation history can be tricky since there are no universally applicable indicators for ecosystem degradation and restoration (Bardgett *et al.* 2021). Consequently, quantification of fire and grazing impacts is needed to allow cross-studies comparisons. Thus, we suggest that a full diagnostic assessment of the physical, chemical and biological conditions of the degraded site should be reported along with a clear disclosure whether there has been any perturbation in the natural disturbance regimes (Keeley & Pausas 2019). Refined, precise and detailed information of initial conditions before restoration should be more useful for identifying trends and conclusions among different studies.

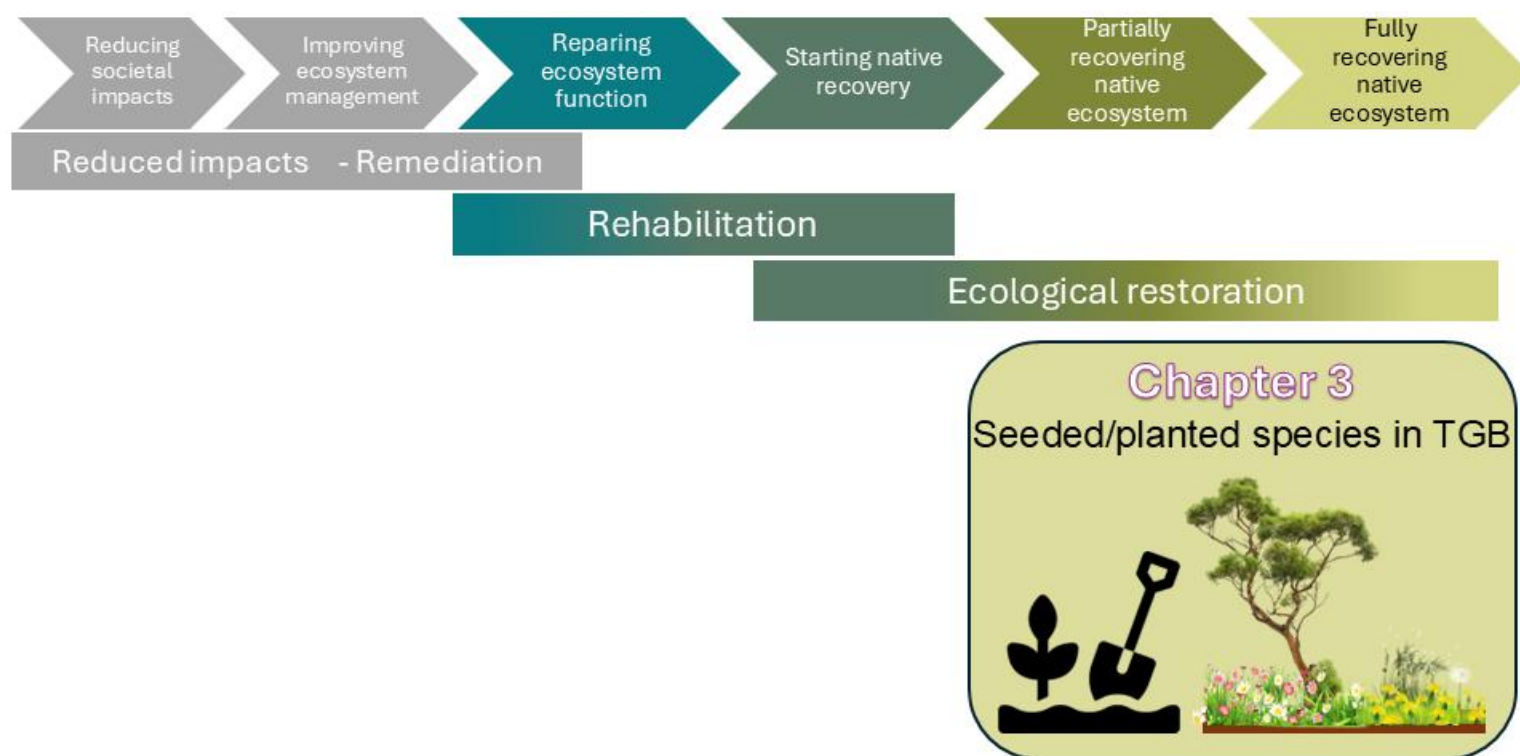
The third major issue is the description of the restoration setting. Basic information concerning the methods and results must be systematically and transparently reported to allow comparisons (Gerstner *et al.* 2017). A third of experiments provided no information on restoration controls, while 10% did not provide enough information on the number and composition of species planted or seeded. To overcome these limitations, we suggest minimum standards for setting restoration experiments that include detailed information on the restoration controls, restoration strategies and monitoring indicators (see Appendix H).

2.7 Conclusions

Our review provides a synthesis of the state of knowledge of field experiments on TGB restoration allowing us to identify critical shortcomings and future research priorities. We found knowledge gaps and poor data reporting in TGB restoration research as well as a need to incorporate TGB drivers in restoration and to better evaluate outcomes. Severe issues in primary data report prevented us to integrate field experiments and provide more refined recommendations for future TGB restoration research and management. However, to overcome this issue, we provided a guideline to enhance data reporting which would allow broader quantitative assessments to support decision-making across different ecological contexts. The implementation of our proposed checklist is expected to support future TGB restoration projects by allowing standardizing terminology, methodology and data reporting. We hope that our synthesis contributes effectively to the UN Decade on Ecosystem Restoration moving TGB restoration to the forefront and enhancing our abilities to restore these megadiverse yet overlooked ecosystems

CHAPTER 3: WHAT ARE WE PLANTING IN ECOLOGICAL RESTORATION OF TROPICAL OPEN ECOSYSTEMS? A SYSTEMATIC REVIEW OF FIELD EXPERIMENTS

This chapter has been accepted and is under publication process to Acta Botanica Brasilica as a scientific note and is still under review.



3.1 Abstract

Tropical grasslands, savannas, and shrublands comprise open ecosystems that are experiencing growing anthropogenic pressures and lack theoretical and practical knowledge on ecological restoration. Natural regeneration in these ecosystems is very slow and often unfeasible, making planting and seeding increasingly important restoration techniques. We conducted a systematic review to investigate the richness, origin, and functional groups of the plant species used to restore tropical open ecosystems. Identifying species and their functional groups used in restoration experiments allows us to better plan, implement, and monitor restoration. We identified 220 plant species introduced to restore tropical open ecosystems in 37 controlled restoration sites located in Brazil, Australia, the USA, Kenya, Venezuela, South Africa, and Congo. Nearly 55% of plant species were shrubs or trees, and 80% were native to the country where they were used. Strikingly, 51% of the plants were used only once. We found no evidence of biotic homogenization in the restoration of tropical open ecosystems. Only six reintroduced species were classified as endangered, suggesting an untapped potential for enhancing conservation-oriented restoration. Our results indicate that despite the predominant use of native species, woody species remain disproportionately planted compared to herbaceous species, which constitute the bulk of diversity in grasslands and savannas.

Key-words: active restoration, grassland, savanna, shrubland, tropics, tropical ecosystem, tropical grassland biome

3.2 Introduction

Ecological restoration is a global priority in the context of the emergent climate and biodiversity crises. Global restoration efforts are increasingly supported by the United Nations Decade on Ecosystem Restoration (2021-2030), but a forest-centric view still dominates the scientific, governmental, and media arenas (Silveira *et al.* 2022). Restoration efforts in tropical open ecosystems (ancient grasslands, shrublands, and savannas) are relatively scarce despite increasing degradation levels (Buisson *et al.* 2022). Open ecosystems are characterized by graminoids, herbs, forbs, and shrubs. For instance, grasslands have no trees, and some savannas are known to have seven herbaceous plants for each wood species (Ribeiro & Walter 2008). Moreover, open ecosystems feature a unique ecosystem functioning driven by soil properties, fire regimes, and large herbivores, which play important roles in shaping vegetation (Buisson *et al.* 2019). Open ecosystems are also biodiversity-rich, with many endemic and threatened species (Veldman *et al.* 2015a; Bond 2019; Buisson *et al.* 2019). Therefore, there is a pressing need to restore open ecosystems, aiming to protect their high biodiversity through effective management of their main ecosystem drivers, including disturbance, hydrological, and edaphic properties.

Active restoration approaches, including species reintroduction and active management, can yield better restoration outcomes in open ecosystems, as natural regeneration in these ecosystems is extremely slow or may never happen, depending on the degree of degradation (Nerlekar & Veldman 2020). Consequently, planting and seeding native species have been employed as main techniques aimed at enhancing the resilience of open ecosystems and contributing to the maintenance of biodiversity of restored sites (Wiederhecker *et al.* 2024). In addition to species reintroduction, other main active restoration strategies in open ecosystems include tree cutting, invasive species control, livestock and wild herbivore management,

prescribed fires, and soil acidification (Buisson *et al.* 2019; Haddad *et al.* 2021; Buisson *et al.* 2022; Pilon *et al.* 2023; Lira-Martins *et al.* 2024). Therefore, the efficiency of open biome restoration ultimately relies on active approaches, with planting and/or seeding native species playing important roles in restoring diverse and resilient ecosystems (Lyons *et al.* 2023).

The use of native species in restoration has been recommended for decades, but non-native species are still commonly used in forest restoration (D'Antonio & Meyerson 2002; Simões *et al.* 2024). The benefits of non-native species in restoration can be due to their faster growth and the income provision to landowners (timber, forage, fruit). Despite this, the choice for non-native species may also be constrained by the low availability of native species on the market (Vidal *et al.* 2020; Faria *et al.* 2025), which is especially true for herbaceous species, the main component of open ecosystems (Castilho Silva *et al.* 2024). Furthermore, despite recent attempts to synthesize the common practices in the restoration of tropical open ecosystems (Pilon *et al.* 2023; Medeiros *et al.* 2024), a knowledge gap remains about the identity and richness of plant species used in active restoration approaches. Assessing the species pool used in restoration efforts in tropical open ecosystems can provide important insights into the effectiveness of these initiatives. In particular, it can help evaluate their potential to recover the diverse herbaceous layer, protect endangered species, and mitigate biotic homogenization.

To address this gap, we investigated the restoration species pool used to restore tropical open ecosystems. Specifically, we examined the richness, origin (native or non-native), and growth forms. Under the hypothesis that restoration practices follow the vegetation structure of open ecosystems, we expect grasses, forbs, and shrubs to be the most commonly reintroduced species, with a lower proportion of trees to match the open biome vegetation structure. Moreover, under the assumption that restoration is grounded in ecological theory (Barbosa-Dias *et al.* 2025), we expect the preferential reintroduction of native species instead of non-

native ones. Finally, to address the potential of conservation-oriented restoration in open ecosystems (Volis 2019), we examined the conservation status of the reintroduced species.

3.3 Methods

To assess the richness and functional groups of plant species used in active open biome restoration - defined as the world's ancient grasslands, shrublands and savannas (Bond 2019), we carried out a systematic literature review of peer-reviewed articles using Web of Science and Scopus databases using the following keywords: (“grassy biome” OR “grassland” OR “meadow” OR “prairie” OR “rangeland” OR “savanna*” OR “steppe” OR “shrubland” OR “cerrado”) AND (“afforestation” OR “afforested” OR “restoration” OR “restored” OR “recovery” OR “recovered” OR “reforestation” OR “reforested” OR “rehabilitation” OR “rehabilitated” OR “revegetation” OR “revegetate”) AND (“tropical” OR “subtropical”). Details of the search engine and paper screening are provided in Medeiros *et al.* (2024). Hence, we only included controlled studies with data obtained in the field (laboratory and greenhouse research were excluded), focusing on ecological restoration (crop planting and pastureland for livestock were excluded). However, here, we used only a subset of studies, including only those that applied active restoration techniques, including species reintroduction as well as seedling planting and direct seeding (see Appendix I). Studies must also provide a list of reintroduced species directly on degraded open ecosystems. We retrieved geographic coordinates and the identification of the reintroduced species, and used the Kew database (POWO 2024) to correct species names and record the origin (native or non-native, depending on where they were planted or seeded), life cycle (annual or perennial), and growth form. We completed the growth form for 11 species using the Reflora database (FFB 2024) because such information was not

available in the Kew database. Besides, we assumed that all shrubs and trees were perennials, and we used the IUCN Red List (IUCN 2024) to retrieve species conservation status.

We conducted an ANOVA test to assess the richness of different growth forms and a GLM to evaluate the origin of planted species used in open biome restoration. All analyses were performed in the R program (R Core Team 2025) using *dplyr*, *tidyr*, and *ggplot2* packages. We made an alluvial graph to present the relationship between plant growth forms and the biome in which they were planted. To do so, we needed to assign only one growth form to each plant species; thus, we adopted a conservative approach in which, for example, if a plant species could assume an herbaceous or subshrub form, we assigned it as herb, while if it could assume a shrub or tree form, we assigned it as shrub. Hence, we classified as herbs all herb, herb-climbing-subshrub, herb-shrub, and herb-subshrub-shrub because the species could be herbaceous. Following the same criteria, we classified as shrubs all shrub, shrub-tree, subshrub, and subshrub-shrub. All other graphs were made using the *ggplot2* package in the R program.

3.4 Results

The surveyed papers provided 37 restoration experiments from 29 studies that met our criteria for inclusion (see Appendix I). Nine sites from six studies only provided information on the richness of species planted without providing a specific species list (e.g., mixed grassland species, native species, high number of species), and were excluded from our analyses. Most experiments were concentrated in Brazil (43%), Australia (22%), the USA (19%), followed by Kenya (5%), Venezuela (5%), South Africa (3%) and Congo (3%). Moreover, we had nine experiments in grasslands, 16 in savannas and only three in shrublands.

Globally, 220 species from 45 families were reintroduced, with Poaceae (60 species), Fabaceae (47 species) and Asteraceae (14 species) standing out as the most common families (Figure 13; Appendix J). Regarding species growth form, only 45.6% of the species were herbaceous and 53.8% were shrubs or trees, reintroduced mainly into savannas, particularly in Brazil, Venezuela and Congo (Figure 14 and 15). Besides, we have not found a difference between herbs and woody species (Figure 16; $p>0.05$).

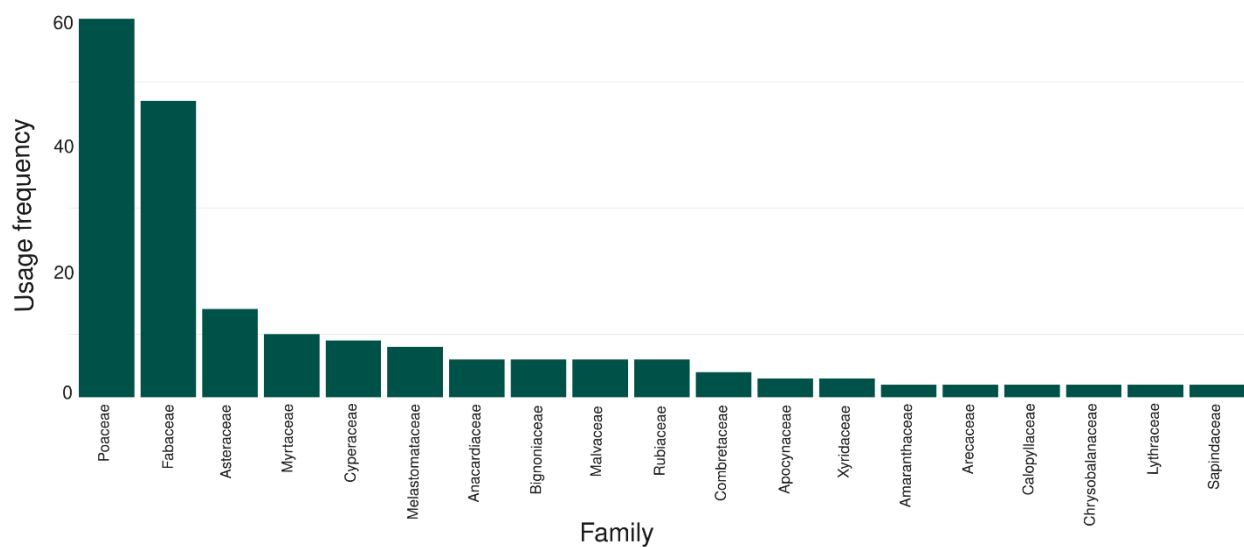


Figure 13. The richness of plants used in tropical open ecosystem active restoration research experiments through planting or seeding. Plant richness is grouped by families. Family used only once are not represented on this figure and includes: Acanthaceae, Annonaceae, Araliaceae, Boraginaceae, Caryocaraceae, Convolvulaceae, Dilleniaceae, Eriocaulaceae, Euphorbiaceae, Gentianaceae, Haloragaceae, Lycopodiaceae, Malpighiaceae, Metteniusaceae, Moraceae, Ochnaceae, Plantaginaceae, Polygalaceae, Rutaceae, Santalaceae, Smilacaceae, Solanaceae, Urticaceae, Verbenaceae, Vochysiaceae.

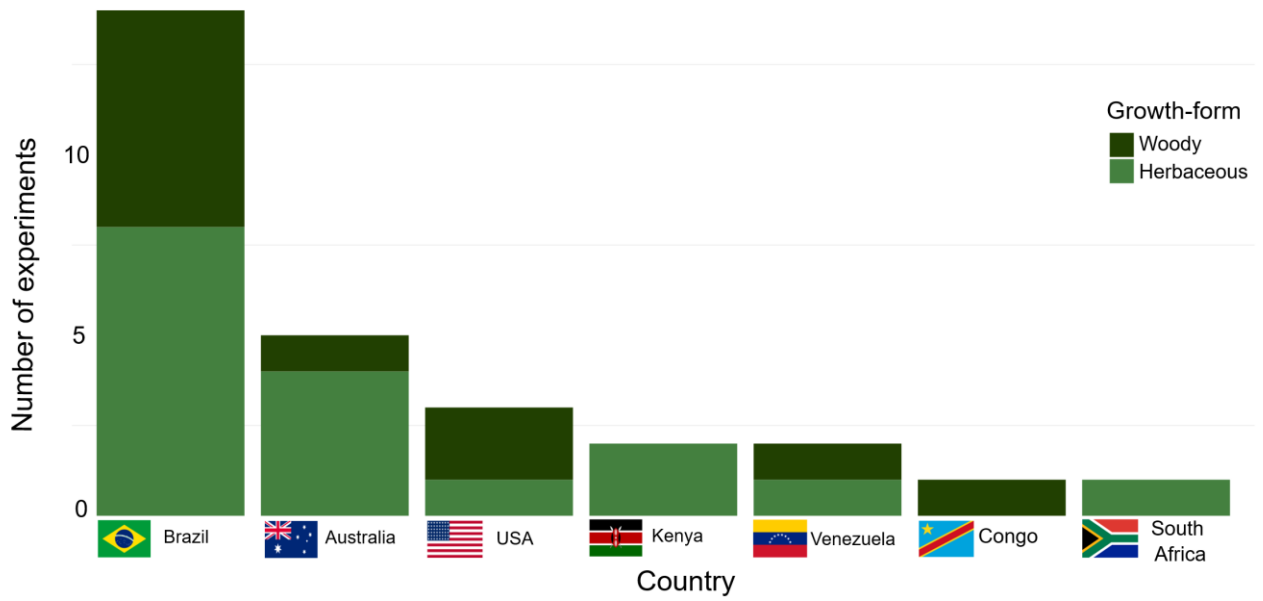


Figure 14. The growth-form of the plants used in tropical open ecosystem active restoration research experiments through planting or seeding experiments by country.



Figure 15. The proportion of herbaceous, shrub and tree species (total of 220 species) used in active restoration of tropical open ecosystems: grassland (nine experiments), shrubland (three experiments) and savanna (16 experiments). The proportion of each growth-form is represented by the thickness of the lines connecting the plants (in the left side) to the tropical open ecosystem where they were planted/seeded (in the right side). It is important to note that we adopted a conservative approach to classify the plant growth-form. For example, we considered it as herbaceous even if the plant could be an herb or a sub-shrub; we considered it as a shrub even if the plant could be a shrub or a tree. The numbers at the left panel indicate the number of species introduced in each functional group.

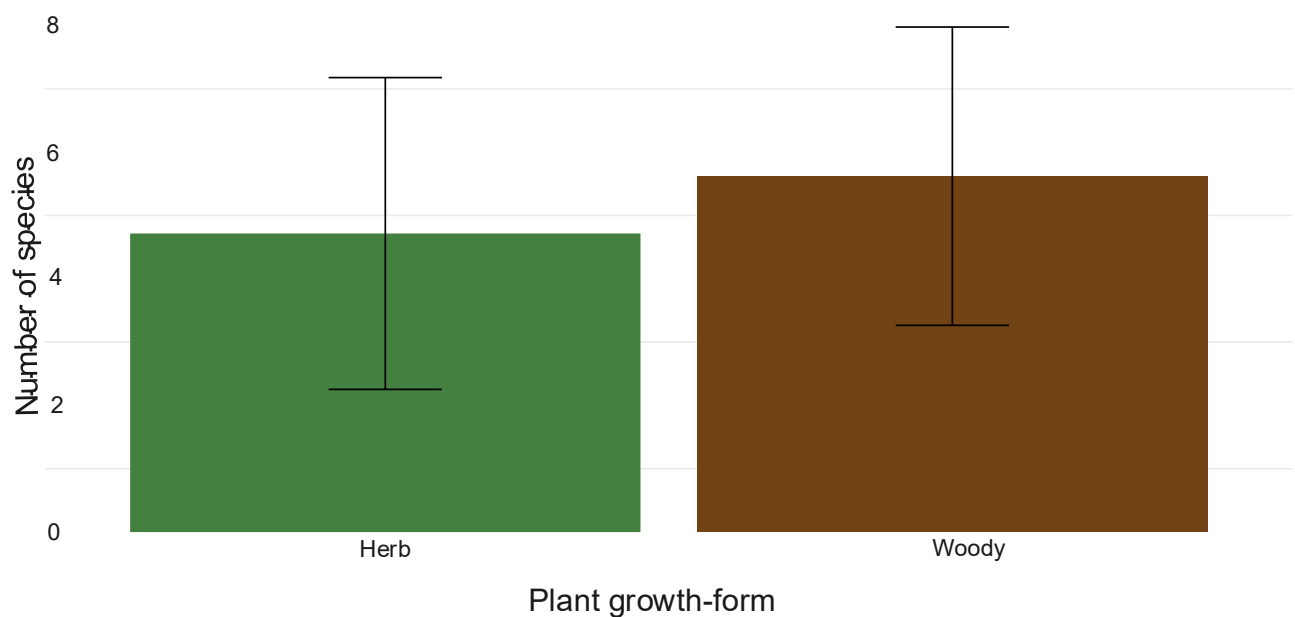


Figure 16. Mean number of plant species planted in open ecosystem restoration experiments, depending on their growth form: herbs (grass, forbs, graminoids) or woody species (ANOVA; $n = 29$ experiments; $p > 0.05$; $F = 0.0706$. mean $\pm$ SE)

Regarding species life cycles, we found 180 species perennial, 12 annuals, eight annual/perennial, and two annual/biennial species. Information was missing for 18 species. As we expected, nearly 80% of the species were native to the country (Figure 17 and 18, $p < 0.001$), indicating that few non-natives are used to restore open ecosystems. Most non-native species reintroduced belonged to Poaceae (12), Fabaceae (3) and Gentianaceae (1) families, including invasive, fast-growing invasive African grasses such as *Urochloa eminii* and *Urochloa dictyoneura* planted in Venezuela, and forage legumes such as *Stylosanthes scabra* and *Stylosanthes hamata* planted in Australia. Ten of the 37 restoration experiments used at least one non-native species, usually without a clear justification. Moreover, we found that only 24 species were planted in more than five restoration experiments, while most species (107 plant species) were used only once (Figure 19). Among species with available IUCN classifications, most were listed as ‘Least Concern’ (76 species). Additionally, four species were classified as ‘Vulnerable’ (*Eucalyptus populnea*, *Dipteryx alata*, *Mimosa caesalpiniiifolia*, *Metrosideros polymorpha*), three species as ‘Endangered’ (*Cynodon dactylon*, *Amburana cearensis*, *Andropogon leucostachyus*), two species as ‘Near Threatened’ (*Eucalyptus camaldulensis*, *Pterogyne nitens*) and one species as ‘Data Deficient’ (*Myracrodruon urundeuva*). IUCN classification was unavailable for 145 species.

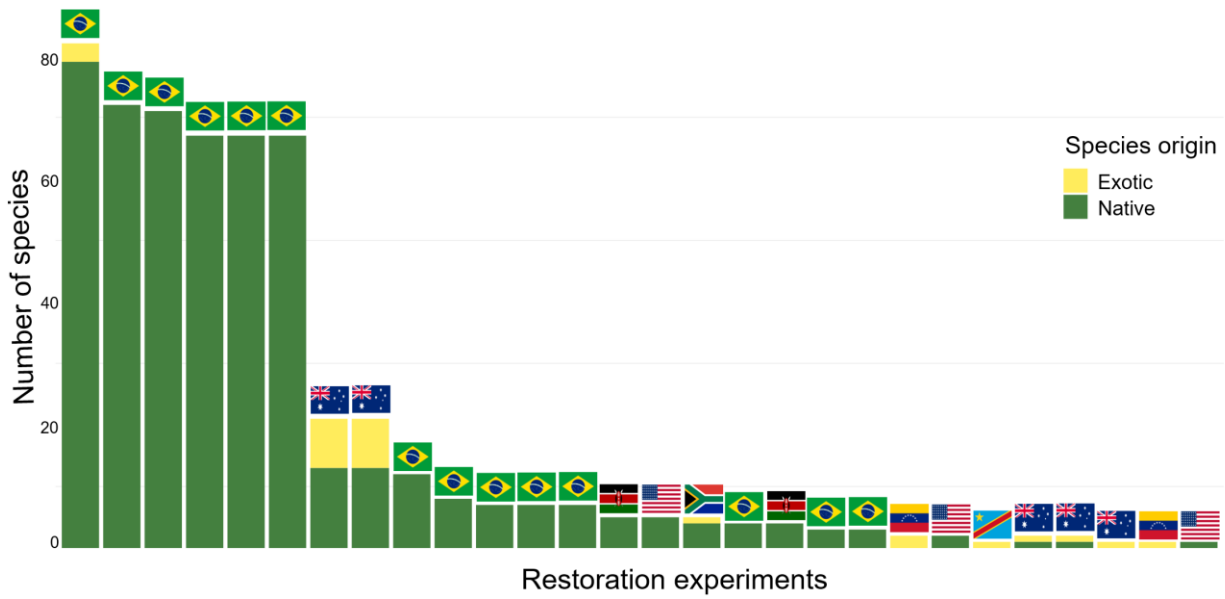


Figure 17. The origin of plants used in the 28 restoration experiments of tropical open ecosystem active restoration through planting or seeding. Note that we found another nine experiments of planting/seeding species in TGB that were not represented here because they have not provided the plant species identification.

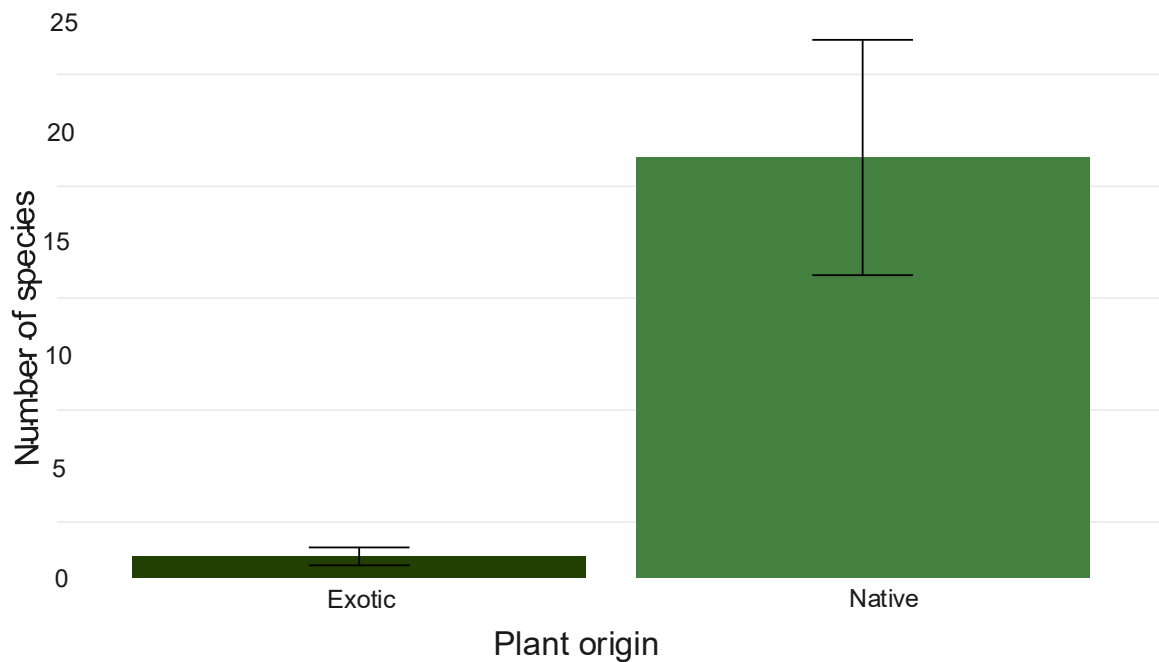


Figure 18. Mean number of species planted in open ecosystem restoration experiments,

depending on their origin: native or exotic plant species. ($n = 29$ experiments; $p < 0,001$; z value = 15.048, mean $\pm$ SE). GLM (formula = number_plants ~ origin, family = "poisson")

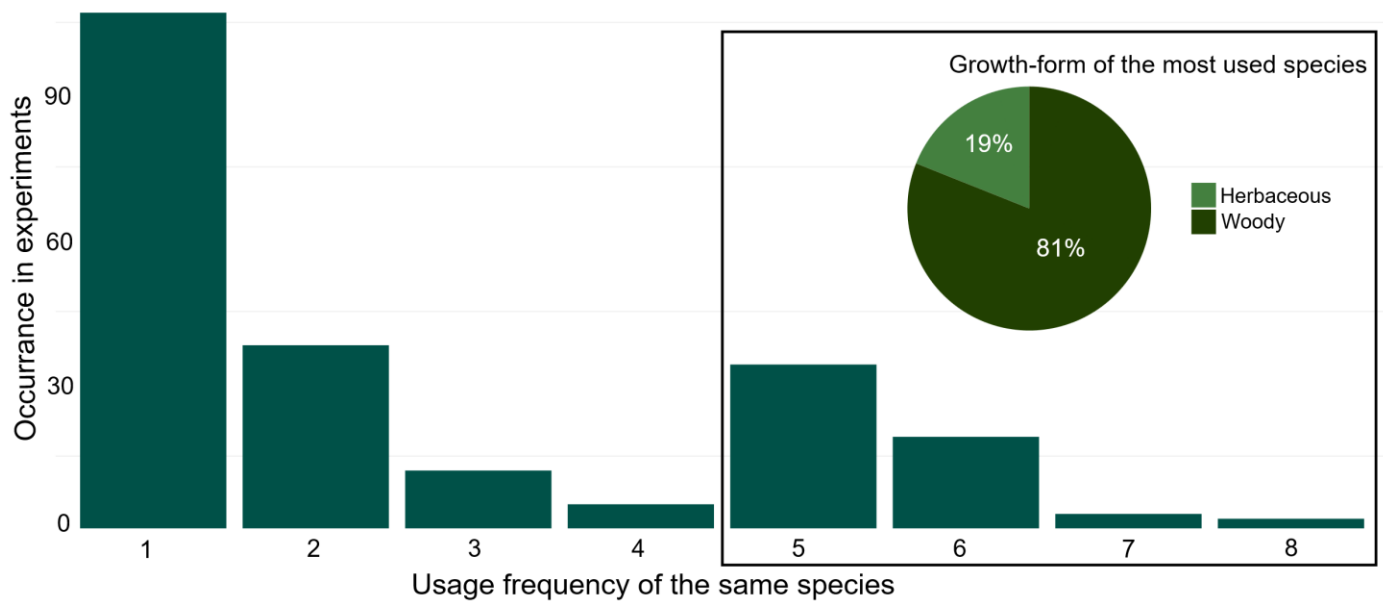


Figure 19. The bar graph represents how many times a single species was used in different tropical open ecosystem restoration experiments. The circle graph represents the growth-form proportion of the most used species (those used in five to eight experiments).

3.5 Discussion

Our review is based on a relatively low number of studies and *in situ* restoration experiments, highlighting the scarcity of controlled restoration studies of tropical open ecosystems using standardized, reproducible and clear protocols (Medeiros *et al.* 2024). This emphasizes the importance of improving and expanding restoration science to support policies that promote and assist the restoration of open ecosystems worldwide (Lyons *et al.* 2023).

Despite a relatively high richness of plant families retrieved in restoration experiments, we still need to increase species richness in the restoration species pool for open ecosystems, as most experiments reintroduced less than three species from all plant families. Tropical open ecosystems are extremely species-rich (Murphy *et al.* 2016), and increasing taxonomic, functional and phylogenetic diversity in plantings is likely to promote more biodiverse and resilient restored ecosystems (Buisson *et al.* 2022; Mazzochini *et al.* 2024). For example, grasses are important in open ecosystems, but forbs also have an important, yet underappreciated role in these ecosystems, as they promote biodiversity by supporting pollinators and herbivores (Siebert *et al.* 2024). Thus, we highlight the need to diversify the restoration species pool and encourage the reintroduction of forbs in open biome restoration (Silveira *et al.* 2020; Nerlekar *et al.* 2024).

The mismatch between the planted species pool and the reference open biome, like savannas and grasslands, was identified here. Only 45% of the species were herbaceous, despite savannas having an herb:wood species ratio of nearly 7:1 (Ribeiro & Walter 2008; Castilho Silva *et al.* 2024). Herbaceous species dominance in open ecosystems is often neglected in open biome restoration, exemplified by a 1:1 herbs and woody species ratio (Supplementary Material – Fig. S1; $p > 0.05$). Savannas were the main type of biome targeted in restoration experiments. This biome comprises open-canopy ecosystems with sparse and low-stature trees (Bond 2019) that have no benefits from increasing tree density, which results in the loss of shade-intolerant herbaceous species (Wieczorkowski & Lehmann 2022). A positive example is the use of shrubs to restore shrublands in the USA. To better align restoration efforts with open ecosystems ecology, we reinforce that trees and shrubs should be more carefully used, respecting their proportions in the native open ecosystems, especially in grasslands and savannas (Buisson *et al.* 2022).

Most of the reintroduced species were native; however, the reintroduction of common non-native species raises concerns, as they are fast-growing invasive grasses and forage legumes. Combining fast-growing grasses and N-fixing species usually stems from the idea that the restoration of open ecosystems needs to increase vegetation cover and improve soil nutrients, a misconception derived from forest restoration (Silveira *et al.* 2020). For example, many plant species in open ecosystems do not form mutualistic interactions with mycorrhizal fungi because they have evolved root specializations (Abrahão *et al.* 2019), thus not requiring fertilization or inoculation treatment (Silveira *et al.* 2020). Frequently, experiments had no clear justification for using non-native species. Perhaps, outdated paradigms from the 1990's such as ideas stemming from forest restoration (Lovera & Cuenca 1996; Cuenca *et al.* 1998), may help explain the use of non-native species in some cases. Another possible reason for using non-native species is the fact that legislation often fails to recognize the value of native herbaceous species in recovery and rehabilitation projects (Pimenta & Fonseca 2021). Finally, another possibility is the paucity of native seedlings in the market (Ladouceur & Mayfield 2017).

Regarding the species life cycle, we found that most of the species were perennial, which is consistent with the evolution of strategies to deal with natural disturbance regimes common to open ecosystems, such as recurrent fires and grazing (Bond & Midgley 2001). Many open ecosystems are characterized by species with persistent niches, which describe the strategies that allow species to survive and grow under high disturbance regimes (Bond & Midgley 2001). However, woody species were the most commonly reintroduced species (Fig. 2), which contrasts with our expectations and supports the idea that the restoration of grasslands and savannas is disconnected from ecological theory (Barbosa-Dias *et al.* 2025). To overcome this misconception, focus should be given to herbs and forbs in grasslands and shrubs in shrublands through the development of cultivation and propagation protocols (Vidal *et al.* 2020).

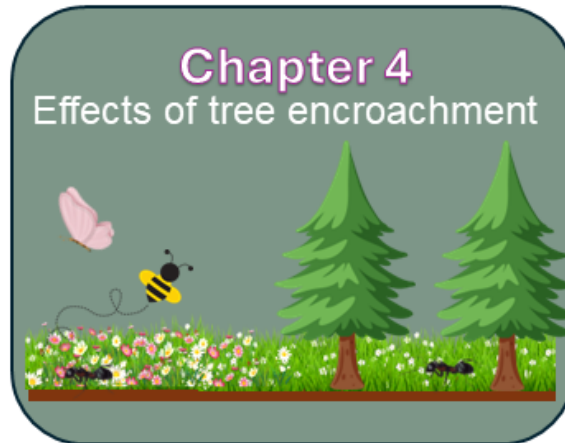
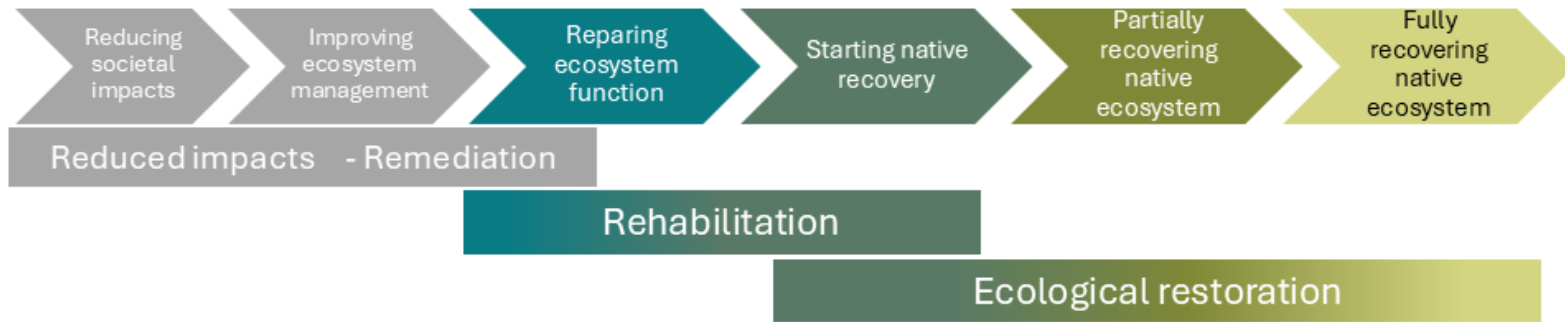
Concerns have been raised about the extent to which common restoration practices favour widespread and easily grown species with high survival and propagation knowledge promoting biotic homogenization in restored sites (Holl *et al.* 2022). In some cases, restored forests can be floristically more similar to one another than to reference ecosystems (Almeida *et al.* 2025). In tropical open ecosystems, the idea of biotic homogenization is not supported, given that a few herbaceous species have been reintroduced in more than five experiments. However, homogenization may have gone undetected because of low species richness in open biome restoration globally.

Conservation-oriented restoration stems from the idea of reintroducing threatened species as a complementary approach to traditional restoration (Volis 2019). Most of the reintroduced species had an IUCN classification unavailable or were listed as ‘Least Concern’, which points out that open biome restoration has an untapped potential to move towards conservation-oriented practices by reintroducing threatened plant species and integrating restoration efforts into broader conservation efforts (Volis 2019). Besides, the species pool used in the active restoration of open ecosystems through species reintroduction remains relatively small compared to the high plant biodiversity and endemism of tropical grasslands, shrublands and savannas (Murphy *et al.* 2016). Our results agree with those of Vidal *et al.* (2020), who found an underrepresentation of savanna specialists in nurseries, which may lead to afforestation and to other negative consequences for the native diversity. This result calls for further experiments that explore and enhance the diversity of plant species reintroduced in open biome restoration, reducing the dissimilarity between restored sites and reference ecosystems.

Overcoming species propagation barriers, aiming at diversifying the restoration species pool of herbaceous species would be vital to promote the reintroduction of a more diverse array of plant species in the restoration of open ecosystems (Vidal *et al.* 2020; Faria *et al.* 2025). Despite the predominant use of native species, focus is still given to woody species in many

places. The reintroduction of forbs along with grasses to restore biodiverse and more resilient open ecosystems should be encouraged. Poorly planned tree plantations pose a threat to local floras, resulting in plantings that are floristically more similar to one another than to the regional species pool, even in forest restoration (Almeida *et al.* 2025). Moreover, the woody species focus undermines the key roles the herbs and forbs play in ecosystem functioning (Siebert *et al.* 2024). The species choice should respect the vegetation structure of the target open biome, which means that the herb:woody species ratio should ideally match that of the native reference ecosystem.

CHAPTER 4: HOW DOES PINE COLONIZATION AFFECT HERBACEOUS NATIVE PLANTS AND THEIR POLLINATORS IN A MEDITERRANEAN GRASSLAND ECOSYSTEM?



4.1 Abstract

Land-use changes have been driving extinctions and colonization worldwide, leading to species replacement and biotic homogenization. Pine monocultures have replaced many open ecosystems, and such tree cover increment has impacted their herbaceous diversity as they harbor many light-demanding species. Because pollinators rely on plant species, they can also be affected by changes in plant community structure. In this context, the main objective of this chapter is to understand how pine colonization from *Pinus nigra* plantations impacts native grassland biodiversity and pollination functioning. We found that native herbaceous plant cover decreased with the increase in tree cover and the same pattern was observed for forb species richness and frequency, as well as plant-pollinator interaction richness and abundance. Different pollinator groups presented different sensitivities to increasing tree cover and herbaceous composition only changed with contrasting land-use change: species were similar in preserved and encroached sites but differed from plantation sites. Our results highlight that pine plantations must be avoided in open ecosystems due to negative effects on native herbaceous plants while restoration interventions are required to recover herbaceous richness and abundance as well as enhance plant-pollinator interactions. We suggest that in addition to pine removal, other adaptive management interventions, like grazing management and seeding native species, may be needed to restore the encroached areas and maintain the original open vegetation.

Key-words: encroachment, tree colonization, tree invasion, steppe, grassland, pollination

4.2 Introduction

Human actions have drastically impacted the environment by consuming natural resources and degrading many Earth's ecosystems (Ripple *et al.* 2024). One human activity that changes the environment and impacts biodiversity and ecosystem functioning is tree planting. Trees have been planted for timber production for centuries (Minghe & Gary 1999; Bennet & Kruger 2013), and recently, tree planting has intensified due to climate change mitigation potential (IUCN-DC 2011; Fagan *et al.* 2022). On the one hand, plantations can increase carbon sequestration, but on the other, they promote homogeneous environments that often have an understory poor in native and shade-intolerant species, especially in monoculture plantations and in plantations of non-native species (Abreu & Durigan 2011; Milani *et al.* 2020; Wieczorkowski & Lehmann 2022; Prangel *et al.* 2023).

Among planted trees, pines are among the most common because they grow and produce wood quickly, showing a good average yield (Brown & Ball 2000; Cubbage *et al.* 2020). The magnitude of pine plantation impacts depends on many factors from the species planted, its functional traits (Hedman *et al.* 2000), planting densities (Gómez-Aparicio *et al.* 2009), where they were planted, and how much the species can spread over adjacent sites in the landscape (Rigot *et al.* 2014; Taylor *et al.* 2016). Monoculture stands tend to have habitat structures and biotic communities more homogeneous when compared to mixed plantations. However, the impacts can be similar, depending on the proportion of each pine species in the mix (Oxbrough *et al.* 2012). Even if the planted species naturally occur in forests, the plantations lead to environmental changes. Hence, multiple impacts can result from planting pine trees, and their extent depends upon the pine species and environmental properties as well as the plantation configuration. For example, *Pinus sylvestris* plantations result in lower herbaceous cover in the understory, lower soil pH and lower organic matter and phosphorus content compared to natural forests (Marcos *et al.* 2007). *Pinus radiata* plantations can also alter litter composition and the structure of benthic macroinvertebrate communities in streams (Martínez *et al.* 2013).

Pine monocultures have been planted in various landscapes worldwide due to different reasons from economic to climate change migration (Tulod *et al.* 2017; Manrique & Franco 2020). These monocultures have also been replacing native ecosystems, including vast areas of savannas and grasslands, while also causing other undesirable and harmful effects like invading adjacent areas (Curtis *et al.* 2019; Briske *et al.* 2024; Moyano *et al.* 2024). Tree cover increment in such open ecosystems is detrimental to biodiversity since those ecosystems have many light-demanding species that can be displaced by shadow casted by high tree cover (Abreu *et al.* 2011; Veldman *et al.* 2015a; Pellegrini *et al.* 2016; Stevens *et al.* 2017). For instance, even though declines in species richness could be offset by increases in forest specialist species, a global meta-analysis has shown that species richness of forbs and graminoids (C₃ and C₄) decreases with woody cover increases, and substantial losses of species are highlighted as they are not replaced (Wieczorkowski & Lehmann 2022). Hence, shade-intolerance of herbaceous plants from open ecosystems underscores their strong dependency on vegetation openness structure.

Open ecosystem vegetation structure, composition and functioning are modified by afforestation, leading to native species loss and homogenization (Pérez-Gómez *et al.* 2025). Moreover, similar negative impacts have been reported in adjacent sites when tree planted species spread. For instance, pine invasions can reduce species richness and plant cover whether encroaching from forests in native range or from plantations in introduced range (Taylor *et al.* 2016). The impacts of such shifts can go beyond plants and affect species interactions. Changes in herbaceous composition and abundance can impact species interactions as plant-associated organisms can be affected by those changes. For instance, grassland afforestation in Estonia declined biodiversity and ecosystem services like pollination and natural pest regulation (Prangel *et al.* 2023). Negative impacts on pollination can ultimately reduce ecosystem resilience capacity and compromise its sustainability. On the other hand, moderate levels of

shrub encroachment in Spanish alpine grassland presented an increase in flower visitor diversity and plant-plant competition (Lara-Romero *et al.* 2016). Therefore, abundance and richness of pollinators can be impacted by changes in native vegetation as it alters floral availability.

Pollinators are an important group for ecosystem resilience due to their role in plant sexual reproduction. This is particularly concerning because negative impacts on pollinators due to pine encroachment can compromise the resilience of the grassland ecosystems by reducing native plant reproductive success. The effects of pine plantations on biodiversity, plants and pollinators in open environments, including adjacent encroached sites, remain poorly understood. However, there is emerging evidence suggesting that rarer and more specialized interactions can disappear with increasing tree encroachment, decreasing overall network stability (Pérez-Gomez *et al.* 2025). Understanding these impacts more thoroughly is crucial for biodiversity conservation, especially given the decline of native plants and pollinators (Schatz *et al.* 2021; Yang *et al.* 2023).

Some effects of non-native pine plantations on native biodiversity have been demonstrated. However, those related to various densities of pine encroachment on open ecosystems have yet to be thoroughly documented. Here, we aim to investigate how pine colonization from *Pinus nigra* plantations impacts native grassland biodiversity and functioning. We expect pine encroachment to negatively impact herbaceous native plants and pollinators. Specifically, we expect the diversity of pollination interactions will reduce and homogenize with increasing pine encroachment. To test these hypotheses, we predict: (1) increases in pine cover will decrease abundance and richness of flora (herbaceous plants and forb flowers), pollinators and plant-pollinator interactions in encroached sites, with even lower values in plantation sites; (2) increases in pine cover will change the composition of the herbaceous communities, with different species composition assigned to native grassland, encroached and plantation sites.

4.3 Methods

4.3.1 Site description

This study was carried out in *Causse Méjean*, within the *Cévennes* National Park (44°16' N and 3°24' E), a Jurassic limestone plateau at elevations ranging from 800 and 1250m, Southern France. This plateau has a karst topography with poor and dry soils that support a steppe-like native grassland (Lepart *et al.* 2000; Tison *et al.* 2014). Besides native grasslands, which are grazed by native fauna and livestock (mainly sheep – Osty *et al.* 1994; Marty *et al.* 2003; Mutillod *et al.* 2024), the landscape of *Causse Méjean* is also composed of other land uses, such as, wood production over large areas (mainly with the exotic species *Pinus nigra nigra*) and cereal cultivation on small plots (especially in the depressions) (Marty *et al.* 2003). The grasslands belong to the Mediterraneo-montane steppes EUNIS habitat type (code E1.51, European Environment Agency 2019) and encompass several protected native species. Common species that characterize these grasslands are *Bromopsis erecta*, *Stipa pennata* and various *Festuca* spp. (Poaceae), *Helianthemum apenninum* and *Helianthemum oelandicum* (Cistaceae), *Coronilla minima*, *Ononis striata*, and various *Anthyllis* spp. and *Genista* spp. (Fabaceae), *Aster alpinus*, *Inula montana* and *Leucanthemum graminifolium* (Asteraceae), *Teucrium rouyanum* and *Thymus serpyllum* (Lamiaceae), *Rhinanthus pumilus* (Orobanchaceae) and *Linum suffruticosum* (Linaceae) (European Environment Agency 2019). The region has a mixed continental and Mediterranean climate, characterized by cold wet winters and hot dry summers (Caplat *et al.* 2006), mean annual precipitation is around 950mm, with average monthly minimum temperature of -2°C in January and mean monthly maximum temperature of 23°C in July (Meteoblue 2025).

4.3.2 *Experimental design*

We identified 12 sites on the *Causse Méjean*, in each of which we established a block design (n=12) of four 10m×10m plots in each block, with at least 50m distance between plots, to encompass four different types of land use contexts, hereafter named “treatments” (Figure 20): native grassland (preserved control, 0% of pine cover, n=12 plots), grassland colonized with <50% of ground surface covered by pine trees (projection of canopy; n = 12 plots), grassland colonized with >50% of ground surface covered by pine trees (projection of canopy; n = 12 plots), and pine monoculture plantations (negative control, plantation with 45-90% canopy projection; n = 12 plots). We therefore had a total of 48 plots arranged in the 12 blocks. In each plot, tree cover was visually estimated by the same person, who assigned the percent cover of pine trees, the total percentage of herbaceous plant cover and the total percentage cover of forb flowers. Visual estimations were done by dividing the plot into four parts and visualizing how much of it was covered by tree cover, herbaceous plants and forb flowers (see dashed lines in the Fig. 25). Evaluations were done either in the morning or in the afternoon (9am to 5:30pm).

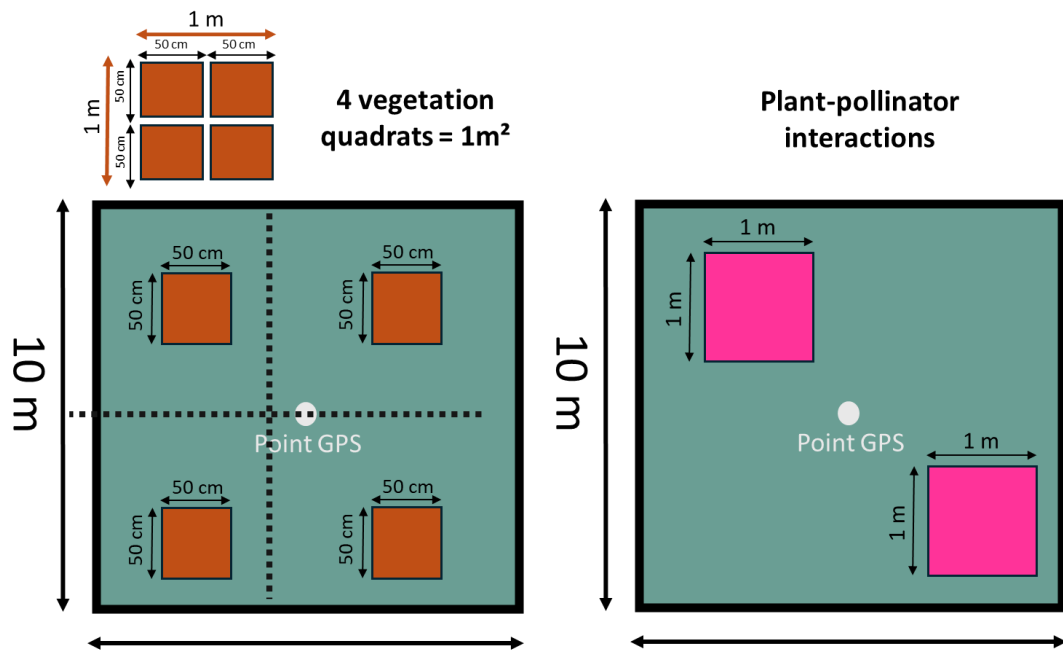


Figure 20. Experimental design in each of our plots (10x10m): plant sampling on the left, with the plot divided into four quadrats and the subplots (in brown) established in the centre of each quadrat; and plant-pollinator interactions sampling on the right, with random subplots of 1x1m (in pink).

4.3.3 Plant sampling

To evaluate forb species diversity, we established four 50×50cm subplots in each of the 48 plots. We divided the plot into four quadrats and set the subplot at the centre of each quadrat (Figure 20). In June 2024, we recorded forb composition in each subplot to assess the plant species richness. To evaluate species richness at the plot level, we considered all forb species present in the four subplots. To evaluate species frequency, we calculated the frequency of each species in each plot: if a species was present in one subplot, it was assigned a frequency of 1; in two subplots, a frequency of 2; in three subplots, a frequency of 3; in four subplots, a frequency of 4; when absent of all subplots it was assigned a frequency of 0.

4.3.4 *Plant-pollinator interactions sampling*

We sampled plant-pollinator interactions in each plot for one hour, in total, when pollinators were more active: from 09:00am to 5:30pm. Sampling occurred twice: 30 minutes before mid-June and 30 minutes after mid-June, alternating morning and afternoon whenever possible. Because pollinators are sensitive to weather conditions, the sampling was carried out on days when average temperatures ranged from 16°C to 30°C, without rain and strong winds (> 30 km/h).

We established random 1m x 1m flowering patches and recorded all forbs flowering in the patch. The number of patches depended on flower cover on each plot as some of them had just a few flowers (some plantation plots even had no flowers). Moreover, because flowers had an aggregation distribution in some plots, we established the subplots aiming to maximize interaction sampling by encompassing the maximum forb diversity and heterogeneity in the plot. However, it is important to highlight that the total sampling time remained the same across all plots (1 hour/plot). We observed plant-pollinator interactions and recorded all events in which insects touched the reproductive parts of a visiting flower. We considered all insects touching the reproductive part of a flower as being potential pollinators even if they may not be well recognized for that. For example, some studies show that orthopterans could participate in pollination (Micheneau *et al.* 2010). Because we did not capture the insects, we identified them to the Order level and allocated them to insect functional morphotypes as follows: Acari, Coleoptera, Diptera (hoverfly, fly, bee fly), Heteroptera, Hymenoptera (ant, wasp, small native bee, big native bee, domestic bee – *Apis mellifera*), Lepidoptera, Orthoptera, and Thysanoptera.

4.3.5 *Statistical analyses*

All analyses were done in R program using different packages (R Core Team 2025). First, we analysed the effect of the treatments on vegetation response variables: total herbaceous

cover, forb species richness and forb flower cover. To do so, Generalized Linear Models (GLM) were fitted with a quasibinomial distribution for covers (percentage data) and with a Poisson distribution for species richness (count data), using the “stats” package. All models were followed by pairwise contrast comparisons with a sidak adjustment when significant (“emmeans” and “multcomp” packages – Lenth R 2025; Hothorn *et al.* 2008). We evaluate the effect of the treatments on forb community composition by running a classical multidimensional scaling of Principal Coordinates Analysis (PCoA) based on Bray-Curtis dissimilarities calculated on plant frequencies (package “vegan” – Oksanen *et al.* 2025), for a total of 128 species on the 48 plots. We tested for dissimilarity in community composition between treatments with a pairwise distance (PERMANOVA), calculated with pairwise adonis tests with Bray-Curtis distances and 999 permutation (package “vegan” - Oksanen *et al.* 2025).

To study the effect of the treatments on plant-pollinator networks, we built one network for each plot, and then, extracted the abundance of interactions and interaction richness for each network or plot, using the “bipartite” package (Dormann *et al.* 2008, 2009). Then, a GLM was fitted with Poisson distribution for these two response variables to evaluate the effect of each treatment. All models were followed by pairwise contrast comparisons with a sidak adjustment when significant. Besides, we combined the 12 networks of each treatment to explore the five most important plant and pollinator species according to centrality degree (taxa with more connections; Cagua *et al.* 2019). Finally, we studied the effect of treatments on some specific pollinators. We selected the three groups of bees (big native bees, small native bees, and domestic bees) because they are known to be particularly effective pollinators (Ballantyne *et al.* 2017). We also explored the pollinator groups that had more than 50 interactions in total, considering the 48 plots: Coleoptera, Heteroptera, Diptera (fly, hoverfly, bee fly) and Hymenoptera (ant).

4.4 Results

We found lower herbaceous cover, forb species richness, forb flower cover, plant-pollinator interaction richness and abundance at plantations compared to native grasslands and the two levels of colonization (Figures 21 to 26). We also observed differences in interaction abundance when some pollinator group was particularly evaluated (Appendix M). We found that herbaceous coverage ranged from 0.5 to 100%, while forb plant richness ranged from two to 35 species per plot and forb flower cover from 0 to 40%. We also found a total of 131 different herbaceous forb species in our 48 plots, with the ten most frequent species being attractive for pollinators: *Potentilla verna* (35 plots), *Helianthemum oelandicum* (34 plots), *Galium pumilum* (31 plots), *Coronilla minima* (30 plots), *Teucrium montanum* (29 plots), *Ononis striata* (28 plots), *Globularia bisnagarica* (26 plots), *Linum suffruticosum* (26 plots), *Anthyllis vulneraria* (25 plots), *Galium corrudifolium* (25 plots).

Grassland had the highest herbaceous plant cover while the lowest values were under pine plantation ($p < 0.001$; Figure 21), with intermediate values for the colonization treatments (no difference among colonization $<50\%$ and $>50\%$). We found the same pattern for forb flower cover ($p < 0.001$; Figure 22). For the forb species richness, we found a slightly different pattern but still with the highest richness in grassland and the lowest in the plantation ($p < 0.001$; Figure 23): the treatment colonization $<50\%$ had intermediate values, while colonization $>50\%$ had values similar to both grassland and colonization $<50\%$. Species composition changed among treatments (PERMANOVA = $p < 0.05$; Figure 24), and we could clearly identify that grassland and colonization treatments have different species composition than pine plantation.

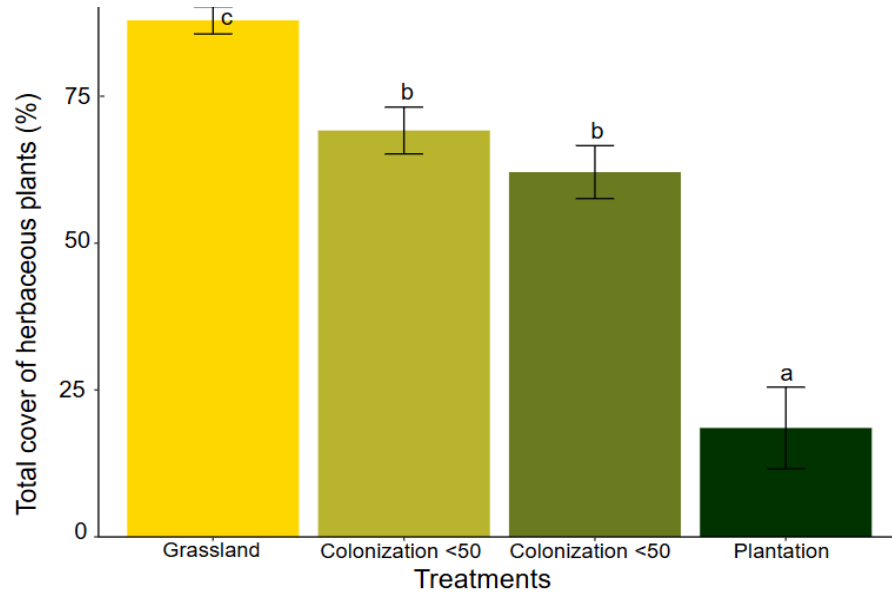


Figure 21. Mean total percentage of herbaceous cover (monocotyledons and forbs) decreases from grassland to colonization and plantation treatments (mean $\pm$ SE; $X^2 = 86.05$; $p < 0.001$; $n = 48$ plots of 10×10 m quadrats)

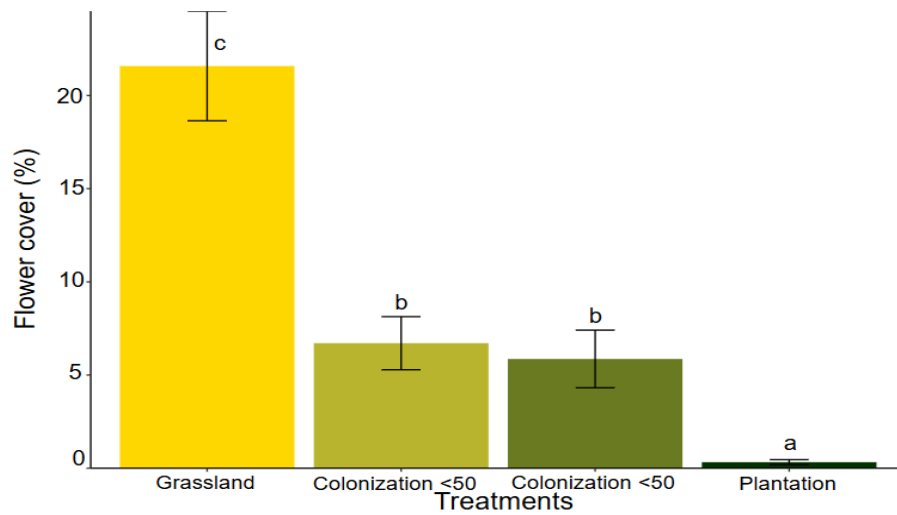


Figure 22. Mean of forb flower cover (%) decreases from grassland to colonization and plantation treatments (mean $\pm$ SE; $X^2 = 3.78$; $p < 0.001$; $n = 48$ plots of 10×10 m quadrats)

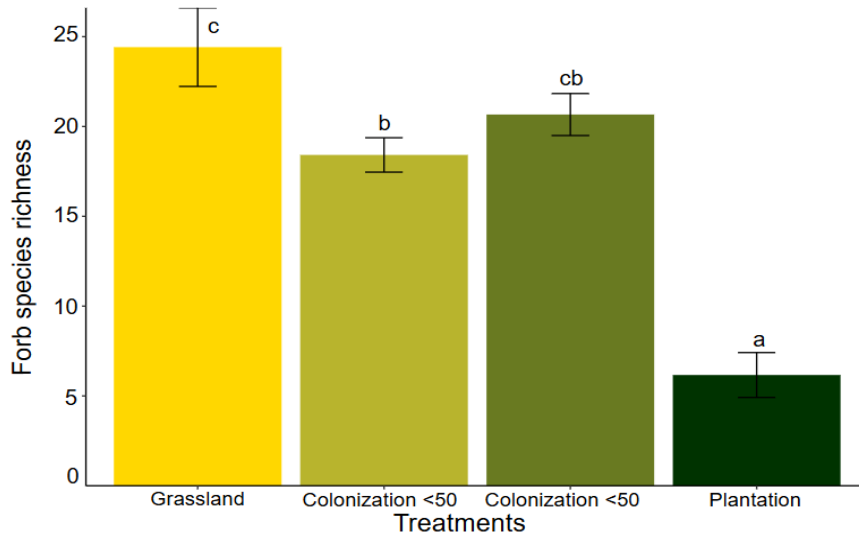


Figure 23. Mean richness of forbs in grassland, pine colonization and pine plantation (mean $\pm$ SE; $X^2 = 141.08$; $p < 0.001$; $n =$ four 50x50cm quadrats/plot) in Mediterranean grasslands

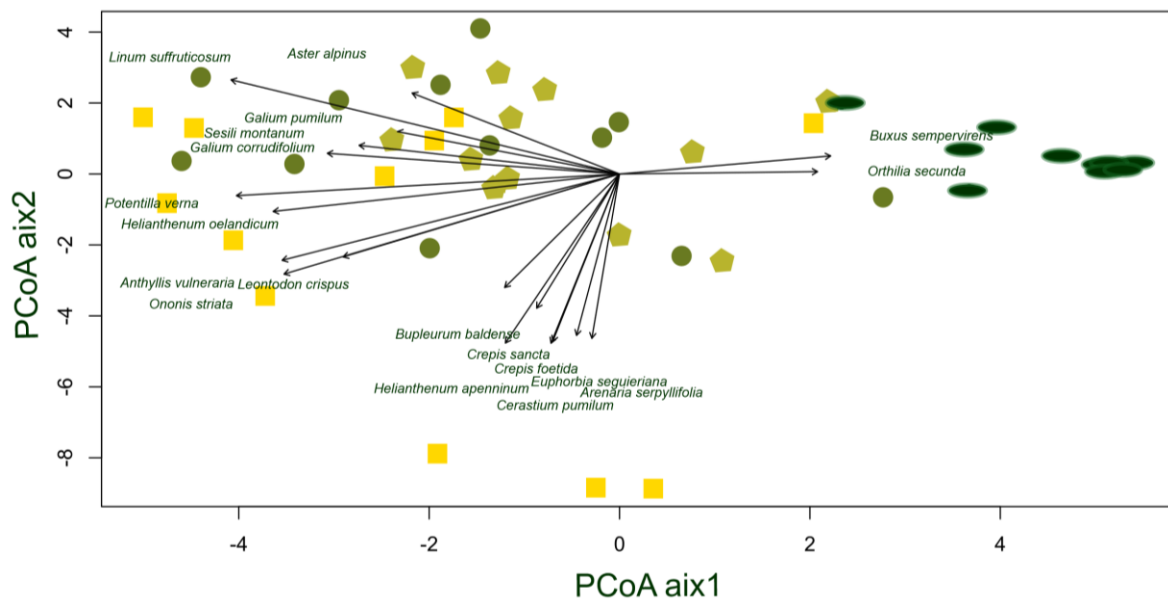


Figure 24. Plant species composition of each treatment: grassland (yellow squares); colonization <50% (light green pentagons); colonization >50% (light-dark green dots); plantation (dark green ellipses). Indicator species are highlighted. Stress = 0.12

Regarding plant-pollinator interactions, we found that interaction richness was statistically similar among grassland, colonization <50% and colonization >50%, but lower in pine plantation ($p < 0.001$; Figure 25). Nonetheless, we found that plant-pollinator interaction abundance differed among treatments, with the highest values in grassland, followed by colonization <50%, colonization >50% and plantation ($p < 0.001$; Figure 26). When we looked into the interaction abundance of the different groups of pollinators, we found that flies (Diptera), hoverflies (Diptera) and ants (Hymenoptera) showed the most abundant interactions in grassland and the lowest in plantation, with colonization treatments having intermediate values (Appendix M). Bee-flies (Diptera), domestic bees (Hymenoptera) and big wild bees (Hymenoptera) were not found in plantation plots, and only bee-flies and domestic bees were sensitive to the other treatments ($p < 0.001$), being more abundant in grassland than in colonization (Appendix M). Additionally, small bees (Hymenoptera) and Coleoptera had similar numbers of interactions among the treatments ($p = 0.67$ and $p = 0.26$, respectively; Appendix M).

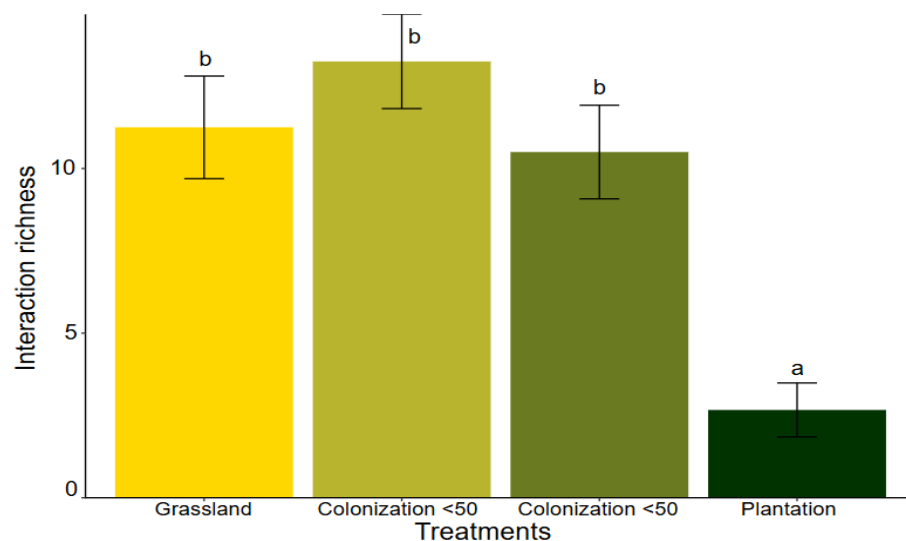


Figure 25. Mean plant-pollinator interaction richness is higher in grassland and colonization treatments than in plantation treatment (mean $\pm$ SE; $X^2 = 82.57$; $p < 0.001$; $n = 96$ of 30 min surveys) in Mediterranean grasslands.

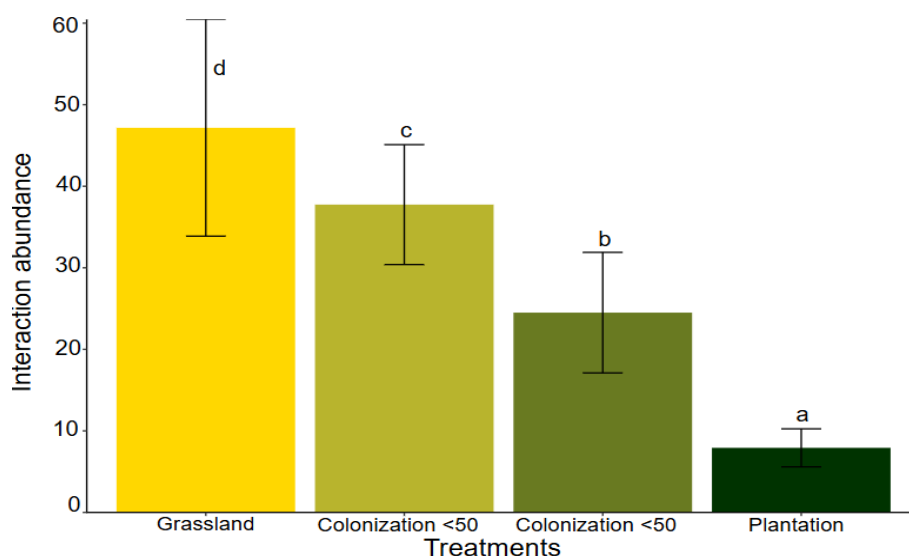


Figure 26. Mean plant-pollinator interaction abundance decreases from grassland to colonization <50%, colonization >50% and plantation (mean $\pm$ SE; $X^2 = 356.28$; $p < 0.001$; $n = 96$ of 30 min surveys) in Mediterranean grasslands.

Finally, the five plant species with the highest centrality degree for the grassland treatment were: *Euphorbia seguieriana* (722 interactions), *Linum suffruticosum* (236 interactions), *Thymus serpyllum* (174 interactions), *Leucanthemum graminifolium* (110 interactions) and *Helianthemum apenninum* (76 interactions). *Linum suffruticosum* and *Euphorbia seguieriana* were among the five most important species in colonization <50% (124 and 88 interactions, respectively) while only *Euphorbia seguieriana* was found under pine colonization >50% (176 interactions). The most important plant species in pine plantations were completely different from those in the grassland treatment, and only *Helianthemum oelandicum* was common among colonization treatments and plantation (see the full list in Appendix K and network interactions in Appendices N-Q). The most important pollinator groups in the grassland treatment were flies (626 interactions), ants (260 interactions), hoverflies (242 interactions), coleoptera (86 interactions) and bee-flies (80 interactions). Flies, ants and

Coleoptera were also among the most important pollinator groups in the other three treatments, but with a much smaller number of interactions (see the full list in Appendix L and network interactions in Appendices N-Q). Hoverflies were an important pollinator group in both colonization treatments, but bee-flies were only important for the grassland.

4.5 Discussion

According to our expectations and previous research (Taylor *et al.* 2016; Wieczorkowski & Lehmann 2022; Pérez-Gómez *et al.* 2025), pine encroachment had negative impacts on herbaceous native plants and pollinators of a native grassland. The increase in pine cover reduced native herbaceous cover and richness as well as pollinator interaction abundance and richness, albeit different for different groups of pollinators. The important flowering plant species in the native grassland habitat were markedly different from the pine plantation, with *Fragaria viridis* and *Pyrola chlorantha* only occurring in plantations. Pollinator groups also varied in relative importance to plant-pollination network interactions. Nonetheless, we found that herbaceous species composition was similar in native grassland and colonization plots while different from plantation plots. This result indicates that although species composition changes among treatments, it may happen due to the degree of degradation (spontaneous encroachment vs. plantation) instead of only the increase in tree cover. Therefore, non-native pine plantations can have different impacts on native biodiversity and functioning of grasslands, with pine encroachment in adjacent native sites negatively affecting herbaceous species cover and forb richness and frequency as well as flower resources, which impact pollination by reducing and homogenizing plant-pollinator interactions. These results agree with a previous assessment (Pérez-Gómez *et al.* 2025).

Woody encroachment is known to reduce herbaceous plant diversity in open ecosystems worldwide and can present different trajectories due to the colonization and establishment of woody species (de Souza *et al.* 2022; Wieczkowski & Lehmann 2022). According to a meta-analysis encompassing tropical and temperate grassy ecosystems, species richness moderately decreases when encroachment reaches 33% and strongly decreases at 66%, with forbs being more sensitive than graminoids (Wieczkowski & Lehmann 2022). In our study, we found a reduction in herbaceous forb richness and frequency due to pine encroachment. However, we have also explored how these reductions could impact other biodiversity groups, like pollinators, that rely on resources provided by these herbaceous plants. Changes in plant community structure, as found here, can impact pollinator visitation patterns and, consequently, plant reproductive success (Biella *et al.* 2019; Hederström *et al.* 2024). Pine encroachment affected the abundance of pollinators and the richness of interactions, which decreased from grassland treatment to colonization <50%, colonization >50% and plantation. Therefore, owing to tree cover increases, both loss of forb species and reduction in pollination occurred, indicating a cascade of events that deeply changes the native ecosystem and compromises its resilience (Lundberg & Moberg 2003; Hirayama *et al.* 2025).

The disruption of pollination interactions has a key consequences in ecosystem functioning, as reproductive success of many flowering plants depends on animal pollinators (Ollerton *et al.* 2011; Hachuy-Filho *et al.* 2020; Schatz *et al.* 2021). Plant-pollinator interactions can be affected by changes in plant community as interaction richness and abundance decreases with reduction in plant abundance or loss of plant species with high interaction frequency (Biella *et al.* 2019; Hachuy-Filho *et al.* 2020; Lanuza *et al.* 2025). We detected decreases in forb richness and frequency as well as the fact that dominant species in grassland plant-pollinator network were markedly different from pine plantations. All these changes in the plant community among the different treatments highlight reduction and composition changes in

available flower resources for pollinators, which can respond differently to the shifts. For instance, canopy closeness was negatively associated to floristic diversity and abundance as well as lower plant-pollinator network stability in Mediterranean heathland in Iberian Peninsula (Pérez-Gómez *et al.* 2025).

It is critical to emphasize that interactions may be lost before pollinators (Valiente-Banuet *et al.* 2015), and to understand how interactions are lost or changed, we have grouped pollinators to provide additional information regarding the ongoing processes in plant-pollinator interactions. Our results indicate that small wild bees curiously have no sensitivity to the different treatments, which can perhaps occur due to the replacement of species from open environments by other species from closed environments. On the other hand, bee-flies, domestic bees and big wild bees seem to be very sensitive to environmental changes among treatments. Such sensitivity is especially highlighted for bee-flies as, in addition to being absent in colonization and plantation treatments, they are an important group of pollinators in grasslands (Johnson & Dafni 1998; Kastinger & Weber 2001; Lanuza *et al.* 2025). In our grassland network bee-flies had multiple visit records once they arrived in the forb flower patch, and they were linked to plant species that were also present in colonization like *Anthyllis montana*, *Aster alpinus*, *Linum suffruticosum* and *Thymus serpyllum*. Bee-flies can visit numerous taxa of different families and their activity is strongly dependent on weather conditions, with lower activity in shade (Kastinger & Weber 2001). These observations suggest that although bee-fly encounters may appear infrequent or random, their activity is likely influenced by microhabitat conditions such as shade promoted by tree cover increase in colonization and plantation treatments.

It is possible that along with interaction losses, shifts in resource usage patterns also occurred among the different treatments (Hirayama *et al.* 2025). The reductions in floral resources (forb richness and flower abundance) that we found may favor generalist and

abundant pollinators, decreasing specialization within ecological networks, and increasing interspecific pollen deposition, which negatively impact plant reproduction (Maruyama *et al.* 2018; Hachuy-Filho *et al.* 2020). Following this, our data supports that generalist pollinators like flies and Coleoptera are important pollinators in all treatments, indicating a possible decrease in network specialization. However, we need detailed information to assess such knowledge and further analyses encompassing interacting species identification will better support our understanding regarding plant-pollinator network configuration. At present, it is reasonable to assume that the observed decrease in herbaceous forb richness and frequency had a direct negative effect on pollination, with varying responses among pollinator groups.

We found that regardless of tree cover amount, colonization plots had similar species composition to native grasslands. Their composition, however, differs from pine plantation plots. This pattern highlights that extinctions and colonization as well as species replacement are expected to occur due to land-use change (Bagaria *et al.* 2019). Hence, we strength that pine plantation, especially with fast-growing exotic species, must be avoided in grasslands since all biodiversity facets explored here change in the plantation. Moreover, our composition finding suggests that this is a biodiversity facet less sensitive to tree cover increases, supporting the assumption that pollinator differences found between colonization and grassland plots are due to changes in forb cover and flower resources rather than forb composition. The overlap of species composition among native and colonization sites can assist future restoration as species pool are still in the encroached sites and may favor the development of native species. Therefore, forb biodiversity facets are differently impacted by pine encroachment with species composition altering due to land-use change and highlighting the importance of avoiding tree plantations in grassland ecosystems.

Future management practice aiming to restore encroached grasslands ecosystem should aim to remove pine trees (Bartolomé *et al.* 2000). Such removal in addition to traditional

grazing practices could allow the recovery of native herbaceous cover and may support the species richness increase as encroached sites are nearby native conserved sites. Because we found an overlap for species composition community in native grassland and colonization plots, recolonization from the seedbank could also happen. However, it may require active species reintroduction as seed banks have been documented as a constraint for Mediterranean dry grasslands (Buisson *et al.* 2021). Moreover, restoration may demand long-term management along with removal of woody invasive species and restoration of grazing regimes with active introduction of native species to restore pollination function (Zeidler *et al.* 2021, 2022; Hirayama *et al.* 2025). In this context, restoration of Mediterranean dry grasslands has presented two major constraints: (1) poor contribution of seed rain and seed bank, and (2) low establishment of perennial species (Buisson *et al.* 2021). Thus, target species richness may fail to be achieved, especially for sites with higher density of trees, demanding other adaptive management practices to ensure restoration success. Low intensity grazing, hay-mulch addition and seeding native species are among the techniques with potential great results as found in other open ecosystems (e.g. Helbing *et al.* 2023; Szentes *et al.* 2024). Considering that the region has historical and mostly extensive livestock management, the proposed grazing technique can be beneficial to restore the ecosystem and value the use of the territory at the same time. Nonetheless, grazing alone may not be enough as negative impacts of encroachment have been reported for other Mediterranean mountain grasslands despite livestock management (Gómez-García *et al.* 2023). Therefore, in addition to pine removal and other potential adaptive management interventions aimed at restoring encroached areas, it is imperative to emphasize that the establishment of pine plantations must be avoided in open ecosystem regions or, at least, it must be held responsible regarding ecological damages to adjacent sites.

4.6 Conclusion

Land-use changes, such as the expansion of pine monocultures, have led to species replacement and biotic homogenization worldwide (Olden 2006; Bagaria *et al.* 2019). We found that in a Mediterranean steppe-like native grassland impacted by exotic pine plantation, both plants and pollinators were negatively affected. Native herbaceous plant cover, forb species richness and frequency, as well as plant-pollinator interaction richness and abundance decreased with the increase in tree cover. Moreover, pollinator groups had different sensitivities to increasing tree cover, with big wild bees and bee-flies being less frequent and even absent in colonization and plantation. Further analyses to investigate how each species may change their interactions and their importance for plant-pollinator networks can provide promising outcomes to better understanding pine impacts. Moreover, one limitation of our study that can be overcome in future research is related to our unique season sampling. Further investigations considering plant phenologies are encouraged. Another interesting finding in our study that have management impacts is that herbaceous composition was similar in preserved and encroached sites but differed from plantation sites. Pine removal, in addition to other adaptive management interventions, like grazing management and seeding native species can be promising restoration managements. Our results highlight that pine plantations must be avoided in open ecosystems and restoration interventions should be encouraged in order to recover herbaceous richness and abundance as well as enhance plant-pollinator interactions. Restoration of encroached areas to maintain the original open and light woodland vegetation that dominated the European landscape before the massive impacts of human dominance (Pearce *et al.* 2023, 2024) is a concern for biodiversity conservation and protection.

FINAL CONSIDERATIONS

This thesis advances our scientific understanding of ecological restoration in tropical open ecosystems by integrating accumulated evidence and exploring the impacts and limitations of tree planting and encroachment. Through a global meta-analysis, I quantified the biodiversity outcomes of tree planting in open-canopy ecosystems, showing that overall plantations cannot reach biodiversity levels of native reference ecosystems. Moreover, the overreliance on forest-based approaches risks promoting biotic homogenization and degradation in naturally open ecosystems.

The field study in a Mediterranean steppe-like grassland demonstrated that pine encroachment negatively affects native herbaceous cover, forb diversity, and plant–pollinator interactions. These results underscore the threat that tree expansion poses to biodiversity in open ecosystems and highlight the ecological risks of afforestation. Effective restoration of encroached areas requires not only pine removal but also the use of adaptive management techniques such as seeding and grazing management to recover herbaceous vegetation and associated ecosystem functions.

The systematic review of tropical grassy biome (TGB) restoration studies highlighted severe geographic and methodological biases. Restoration efforts are heavily concentrated in Brazil and Australia, with critical blind spots in Africa and Asia. Restoration techniques are often misaligned with degradation drivers, and long-term, multidimensional monitoring remains rare. Furthermore, poor experimental designs and inconsistent data reporting limit cross-study comparisons and the development of generalizable insights. To address these gaps, I propose a minimum reporting checklist and a multilingual standardized guideline, aimed at

improving transparency, data quality, and the global comparability of restoration research. Furthermore, when I evaluated the diversity and identity of plant species used in restoration of tropical open ecosystems, I found a strong overrepresentation of woody species, despite herbaceous taxa constituting the bulk of biodiversity in these ecosystems. Most species were used only once, and few were of conservation concern, indicating limited consideration of species functionality and conservation value. The underuse of native herbs and forbs may constrain the restoration of key ecological processes, including pollination and nutrient cycling. Addressing species propagation barriers and expanding nursery availability of open-ecosystem specialists are essential for functionally effective and compositionally accurate restoration.

While tree planting is widely promoted, alone, it cannot ensure biodiversity recovery, especially in open ecosystems. Effective restoration requires ecologically informed approaches that respect native vegetation structure, incorporate a broader diversity of growth forms aligned with reference ecosystems, and are supported by long-term monitoring and transparent data reporting. By addressing key knowledge gaps, this thesis provides actionable recommendations to improve restoration outcomes, and supports the development of more effective, evidence-based, restoration frameworks aligned with global targets, including those set by the UN Decade on Ecosystem Restoration:

- i) Clear and transparent data reporting with standardized implementation and reporting protocols
- ii) Promoting the integration of herbs and forbs in open ecosystem restoration
- iii) Prioritizing long-term monitoring in open ecosystem restoration using ecologically meaningful indicators
- iv) Avoid exotic monoculture plantations when enhancing biodiversity is a restoration target

v) Implementing adaptative management that favours native forbs important for pollinators

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APPENDIX A - List of systematic review on Tropical Grassy Biomes on-ground restoration experiments

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**APPENDIX B - List of the sources of degradation in 155 Tropical Grassy Biomes (TGB)
restoration research experiments**

One degradation cause (79)

- Mining (21)
- Livestock (16)
- Agriculture (13)
- Exotic species (9)
- Fire (9)
- Afforestation (6)
- Unknown (5)

Two degradation causes (54)

- Livestock and exotic species (39)
- Agriculture and urban development (4)
- Livestock and fire (4)
- Agriculture and fire (2)
- Agriculture and livestock (1)
- Afforestation and exotic species (1)
- Afforestation and fire exclusion (1)
- Livestock and chopping (1)
- Mining and exotic species (1)

Three degradation causes (9)

- Agriculture, livestock, and exotic species (7)
- Livestock, chopping and exotic species (1)

- Livestock, feral animals, and exotic species (1)

Other degradation causes (13)

- Road and tracks (4)
- Mechanical clearance (2)
- Absence of endogenous disturbance (grazing – 01)
- Oil spill (1)
- Urban development (1)
- Livestock, barren soil, drought, afforestation and encroachment (1)
- Livestock, mechanical soil disturbance, exploration of timber and small-scale mining (1)

APPENDIX C – Table of the sources of degradation in Tropical Grassy Biomes (TGB) restoration experiments. Some original papers reported more than one degradation as simultaneously happening or as occurring through time. In the second case, they were recorded separated by “+”

Degradation source categories	Degradation source standardized	Degradation sources as self-reported by the original paper
One cause	Agriculture	Cropland
	Agriculture	Agriculture
	Agriculture	Abandoned agriculture
	Agriculture	Agriculture (tillage and intense fertilization)
One cause	Exotic species	Invasive species
	Exotic species	Invasive grass
	Exotic species	Exotic species
One cause	Fire	Shift to intense fire regime (late dry season) experiment
	Fire	Fire
One cause	Livestock	Cattle stocking
	Livestock	Abandoned cattle ranch
	Livestock	Livestock grazing
	Livestock	Cattle grazing
	Livestock	Paddock cultivation (grazing) with fertilizer and herbicide
	Livestock	Livestock
	Livestock	Grazing
	Livestock	Paddock (overgrazing)
	Livestock	Pasture

One cause	Mining	Mining (uranium)
	Mining	Mining (bauxite)
	Mining	Mining (Cu-Co)
	Mining	Mining (metalliferous fallout - Cu)
	Mining	Mining (coal)
	Mining	Mining
	Mining	Mine site (compacted area with a water pond)
Others	Mining	Mining (gravel mine) / Quarrying
	Urban development	Clay pit for hydroelectric construction
	Oil spill	Oil spill
	Old tracks	Old tracks
	Road construction	Road construction
	Road construction	Soil extraction for road construction
	Road construction	Soil, sand and gravel extraction (vegetation and upper soil horizons were destroyed) for road construction
	Multiple	Cattle grazing + Mechanical activities that disturb soil + timber getting + small-scale mining (cattle grazing is the last one)
	Multiple	Barren soil + Grazing + Drought with barren soil + Grazing + Afforestation (encroachment of introduced invasive tree)
	Encroachment	Vegetation thickening (encroachment)
	Encroachment	Invasive woody encroachment
	Encroachment	Heavily encroached by woody plants
	Mechanical clearance	Aeromodelling activities (removal of vegetation and topsoil for flying airplane models)
	Mechanical clearance	Mechanical grader clearing - bare soil

Two causes	Afforestation + Fire exclusion Afforestation + Invasive grass	Afforestation + Fire exclusion Pine plantation + Invasive grass
Two causes	Agriculture + Fire Agriculture + Fire	Slash-and-burn agriculture Slash-and-burn farming
Two causes	Agriculture + Livestock	Agriculture and pasture (abandoned cultivation paddocks)
Two causes	Agriculture + Urban development	Agriculture and urban development
Two causes	Livestock + Chopping	Overgrazing with wood chopping
Two causes	Livestock + Fire Livestock + Fire	Cattle station + Fire Grazing + Fire
Two causes	Livestock + Exotic species	Grazing + Pine plantation
	Livestock + Exotic species	Abandoned pastures with <i>Eucalyptus</i> and <i>Pinus</i> plantation
	Livestock + Exotic species	Abandoned pasture with exotic grasses
	Livestock + Exotic species	Abandonment of cultivated pastures for cattle grazing with invasive grass
	Livestock + Exotic species	Grazing with invasive grass
	Livestock + Exotic species	Invasive species and pasture
	Livestock + Exotic species	Grazing + Exotic species
Two causes	Livestock + Exotic species	Livestock grazing with exotic grass
	Mining + Exotic species	Invasive species in a mining site (uranium)

	Agriculture + Livestock + Exotic species	Grazing with agriculture + Exotic species
	Agriculture + Livestock + Exotic species	Farming + Livestock + Invasive species
Three causes	Agriculture + Livestock + Exotic species	Agriculture + Livestock grazing + Exotic grass
	Agriculture + Livestock + Exotic species	Agriculture (plowed, fertilized, limed) + Grazing with invasive grass
	Agriculture + Livestock + Exotic species	Grazing with agriculture (tillage with liming or fertilizer) and seed sowing of exotic species
Three causes	Fire + Feral animals + Exotic species	Fire + Feral animals + Invasive plant species
Three causes	Livestock + Chopping + Exotic species	Roller chopping with cattle grazing and invasive grass

APPENDIX D - List of the restoration techniques in 155 Tropical Grassy Biomes (TGB) restoration research experiments. Some of the experiments applied more than one technique resulting in 218 interventions

One technique (161)

- Natural regeneration (49)
- Fire management (48)
- Physical intervention (22)
- Planting or seed sowing (20)
- Chemical intervention (10)
- Livestock removal (7)
- Translocation (3)
- Hay transfer (1)
- Topsoil spreading (1)

Two techniques (37)

- Chemical intervention with physical intervention (5)
- Physical intervention with planting or seed sowing (5)
- Chemical intervention with planting or seed sowing (4)
- Physical intervention with hay transfer (4)
- Fire management with livestock management (4)
- Physical intervention with topsoil translocation (3)
- Topsoil translocation with planting or seed sowing (2)
- Different chemical interventions (2)
- Different physical interventions (1)

- Different planting or seed sowing interventions (1)
- Fire management with herbicide (1)
- Fire management with planting or seed sowing (1)
- Fire management with sheltering (drier) (1)
- Physical intervention with fire management (1)
- Physical intervention with natural regeneration (1)
- Physical intervention with translocation (1)
- Translocation with mycorrhizal (1)

Three techniques (17)

- Chemical intervention with physical intervention and planting or seed sowing (7)
- Planting or seed sowing with different chemical interventions (2)
- Chemical intervention with physical intervention and fire management (1)
- Physical intervention with topsoil translocation and hay transfer (1)
- Physical intervention with topsoil translocation and planting or seed sowing (1)
- Physical intervention with translocation and fire management (1)
- Planting or seed sowing with topsoil translocation and fire management (1)
- Planting or seed sowing with plant translocation and fire management (1)
- Planting or seed sowing with different physical interventions (1)
- Translocation with different chemical interventions (1)

Multiple techniques (3)

- Burning with plowing, inversion tillage, and direct seed sowing (1)
- Turning substrate with plant biomass (litter) incorporation, topsoil translocation, and seed sowing with no covering (1)

- Plowing with direct seed sowing with different density of seeds, fire, plowing once more, tillage and direct seed sowing (1)

APPENDIX E – Table of restoration techniques applied in Tropical Grassy Biomes (TGB) restoration experiments

Restoration technique categories	Restoration technique standardized	Restoration technique as self-reported by the original paper
One technique	Chemical intervention	Chemical removing of invasive grass (herbicide)
	Chemical intervention	Clearance (chemical treatment with glyphosate)
	Chemical intervention	Compost application
	Chemical intervention	Fertilizer
	Chemical intervention	Herbicide + other chemicals (glyphosate + dalapon)
	Chemical intervention	Herbicide + other chemicals (glyphosate + flupropanate)
	Chemical intervention	Herbicide + other chemicals (glyphosate + sulfometuron)
	Chemical intervention	Herbicide + other chemicals (glyphosate + tebacil)
One technique	Chemical intervention	Limestone application
One technique	Livestock removal	Destocking progressively
	Livestock removal	Grazing removal
One technique	Fire management	Burning
	Fire management	Burning (single burning of entire tract + no grazing)
	Fire management	Change to a less intense fire regime (in the early dry season)
	Fire management	Clearance with fire treatment
	Fire management	Fire
	Fire management	Prescribed burns (early-dry)
	Fire management	Prescribed burns (late-dry)
	Fire management	Prescribed burns (mid-dry)
	Fire management	Prescribed fire
	Fire management	Removing of exotic species with fire
	Fire management	Natural regeneration with fire avoidance
	Fire management	Natural regeneration after fire to remove plantation (afforestation)

One technique	Hay transfer	Hay transfer
One technique	Natural regeneration	Natural regeneration
	Natural regeneration	Natural regeneration (enclosure)
	Natural regeneration	Natural regeneration after slash-and-burn
	Physical intervention	Addition of physical barriers (wooden logs)
	Physical intervention	Clear-cut
	Physical intervention	Clear-cutting
	Physical intervention	Grass clipped
	Physical intervention	Ground level cut removal of exotic grass (partial grass removal)
One technique	Physical intervention	Hand removal of exotic grass (complete grass removal)
	Physical intervention	Lopping
	Physical intervention	Mechanical removal
	Physical intervention	Mowing
	Physical intervention	Removing of exotic species (cutting)
	Physical intervention	Reworked substrate
	Physical intervention	Removal of needle layer (exposing bare soil)
	Physical intervention	Soil removal
	Physical intervention	Tilled
	Planting or seed sowing	Planting
	Planting or seed sowing	Planting native woody shrub species
	Planting or seed sowing	Planting seeds
One technique	Planting or seed sowing	Planting seeds and seedlings
	Planting or seed sowing	Reseeding native grasses
	Planting or seed sowing	Seeding
	Planting or seed sowing	Seeding (low diversity or one species)

One technique	Topsoil spreading	Topsoil spreading
One technique	Translocation	Transplantation
	Translocation	Transplantation of adult tussock species
	Translocation	Whole-turf translocation

Two techniques	Chemical intervention	+	Physical intervention	Herbicide with scarification (glyphosate with scarification)
	Chemical intervention	+	Physical intervention	Mowing with herbicide application
	Chemical intervention	+	Physical intervention	Established plants with herbicide application
	Chemical intervention	+	Physical intervention	Tilled with fertilizer
	Chemical intervention	+	Physical intervention	Weed control (herbicide with cutting)
	Chemical intervention	+	Physical intervention	Removing of exotic species by conventional clearing with herbicides and hand-pulling or slashing

Two techniques	Chemical intervention + Panting or seed sowing	Compost application with planting
	Chemical intervention + Panting or seed sowing	Limestone application with planting
	Chemical intervention + Panting or seed sowing	Planting of seeds with fertilizers usage
	Chemical intervention + Panting or seed sowing	Herbicide with seeding grass (glyphosate with biological treatment with black spear grass)
Two techniques	Different chemical interventions	Herbicide with litter (glyphosate with litter)
	Different Physical interventions	Mowing with topsoil removal
	Different Planting or seed sowing interventions	Planting seedlings with sown mixture of perennial species
Two techniques	Fire management + Herbicide	Fire with herbicide
	Fire management + Planting or seed sowing	Planting with burn

	Fire management + Sheltering (drier)	Burning with sheltering (drier)
	Fire management + Livestock management	Fire + destocking progressively
Two techniques	Fire management + Livestock management	Graze-and-burn (single burning of entire tract with free access by cattle)
		Patch-burn graze (annual burning of spatially distinct patches with free access by cattle)
	Fire management + Livestock management	
	Topsoil translocation + Planting or seed sowing	Topsoil translocation with seeding
Two techniques	Translocation + Mycorrhizal addition	Transplanting seedlings with mycorrhizal
	Physical intervention + Fire management	Clear-cut with fire
	Physical intervention + Planting or seed sowing	Mowing with planting
Two techniques	Physical intervention + Planting or seed sowing	Mowing with sowing native species

	Physical intervention + Planting or seed sowing	Plowed with direct seeding, direct seeding with different density of seeds
Two techniques	Physical intervention + Planting or seed sowing	Removal of needle layer (exposing bare soil) with direct seeding
	Physical intervention + Planting or seed sowing	Tilled with seeding
	Physical intervention + Translocation	Needle layer removal (exposing bare soil) with plant material transplantation
	Physical intervention + Topsoil translocation	Removal of needle layer with topsoil translocation
Two techniques	Physical intervention + Topsoil translocation	Scraping removing all aboveground biomass, superficial roots and seed bank with topsoil transfer at the end of dry season
	Physical intervention + Topsoil translocation	scraping removing all aboveground biomass, superficial roots and seed bank with topsoil transfer at the end of rainy season
Two techniques	Physical intervention + Natural regeneration	Scraping removing all aboveground biomass, superficial roots and seed bank with natural regeneration
Two techniques	Physical intervention + Hay transfer	Scraping removing all aboveground biomass, superficial roots and seed bank with hay transfer at the end of dry season

Two techniques	Physical intervention + Hay transfer	Mowing with hay transfer
Three techniques	Physical intervention + Topsoil translocation + Hay transfer	Scraping removing all aboveground biomass, superficial roots and seed bank with topsoil translocation and hay transfer at the end of dry season
Three techniques	Physical intervention + Topsoil translocation + Planting or seed sowing	Removal of needle layer with topsoil translocation and direct seeding
Three techniques	Plant translocation + Different chemical interventions	Transplanting saplings with dolomitic limestone and cattle manure
Three techniques	Planting or seed sowing + Plant translocation + Fire management	Planting and transplanting with prescribed burns
	Planting or seed sowing + Topsoil translocation + Fire management	Spreading fresh topsoil with seed mix native species and fire exclusion

Three techniques	Planting or seed sowing + Different physical interventions	Planting seedlings with pond removal and shaping surface with sprading material from adjacent area
	Planting or seed sowing + Different chemical interventions	Seeding with fertilizer and different plant cover treatments (no cover, crops, or green manure)
	Planting or seed sowing + Different chemical interventions	Sowed with fertilizer and liming
Three techniques	Chemical intervention + Fire management	Physical Removing of exotic species with fire and conventional clearing with herbicides and hand-pulling or slashing
Three techniques	Chemical intervention + Planting or seed sowing	Physical Clear-cut with plating and herbicide
	Chemical intervention + Planting or seed sowing	Physical Replaced soil with fertilisers and revegetation with mixture herbaceous species

Three techniques	Chemical intervention + Physical intervention + Planting or seed sowing	Tilled with fertilizer and seeding
	Chemical intervention + Planting or seed sowing	Physical Turning substrate with plant biomass (litter) incorporation and seeding covering with laterite
	Chemical intervention + Planting or seed sowing	Physical Turning substrate with plant biomass (litter) incorporation and seeding with no covering
	Chemical intervention + Planting or seed sowing	Physical turning substrate with plant biomass (litter) incorporation and seeding with topsoil covering
Three techniques	Chemical intervention + Planting or seed sowing	Physical Weed control (chemical + mechanical) with seeding

	Multiple techniques	Burning + Plowing + Inversion tillage + Direct seeding
Multiple techniques	Multiple techniques	Turning substrate + Plant biomass (litter) incorporation + Topsoil translocation + Seeding with no covering
	Multiple techniques	Plowing + Direct seeding with different density of seeds and fire management + Plowing + Tillage + Direct seeding

APPENDIX F – Table of Tropical Grassy Biomes (TGB) restoration research papers that mentioned fire as a degraded source in their experiments. The full information about each paper is available in Appendix A

Authors (year)	Degradation cause	Degradation self-reported data
Beringer <i>et al.</i> (2003)	Fire severity	Qualitative
Gomes <i>et al.</i> (2014)	Fire severity	Qualitative
Nunes <i>et al.</i> (2018)	Fire severity	Quantitative
Strydom <i>et al.</i> (2019)	Fire severity	Qualitative
Haddad <i>et al.</i> (2020)	Fire severity	Qualitative
Marques <i>et al.</i> (2022)	Fire severity	Qualitative
Legge <i>et al.</i> (2015)	Fire frequency; Fire severity	Quantitative
Cuenca <i>et al.</i> (1998)	Fire frequency	Qualitative
Townsend <i>et al.</i> (2004)	Fire seasonality	Qualitative
Williams <i>et al.</i> (2007)	Slash-burn	Qualitative
Anjos <i>et al.</i> (2015)	Fire frequency	Qualitative
Koch <i>et al.</i> (2016)	Fire frequency	Qualitative
Carlsen <i>et al.</i> (2017)	Fire frequency	Qualitative
Montfort <i>et al.</i> (2021)	Slash-burn	Quantitative
Questad <i>et al.</i> (2022)	Not clear	Quantitative

**APPENDIX G – Table of Tropical Grassy Biomes (TGB) restoration research papers
that mentioned livestock as a degraded source in their experiments. The full information
about each paper is available in Appendix A**

Authors (year)	Degradation cause	Degradation self-reported data
Kinyua <i>et al.</i> (2010)	Livestock	Quantitative
Legge <i>et al.</i> (2011)	Livestock	Quantitative
Kutt <i>et al.</i> (2012)	Livestock	Qualitative
Tessema <i>et al.</i> (2012)	Livestock	Qualitative
Kaiser <i>et al.</i> (2015)	Livestock	Qualitative
Ladouceur & Mayfield (2017)	Livestock	Quantitative
Chikorowondo <i>et al.</i> (2018)	Livestock	Qualitative
Oduor <i>et al.</i> (2018)	Livestock	Qualitative
Legge <i>et al.</i> (2019)	Livestock	Qualitative
Correa <i>et al.</i> (2020)	Livestock	Qualitative
Osazuwa <i>et al.</i> (2021)	Livestock	Qualitative
Correia <i>et al.</i> (2022)	Livestock	Qualitative
Pereira <i>et al.</i> (2013)	Livestock with Exotic species	Qualitative
Abom & Schwarzkopf (2016)	Livestock with Exotic species	Quantitative
Ferreia & Melo (2016)	Livestock with Exotic species	Qualitative
Cava <i>et al.</i> (2019)	Livestock with Exotic species	Qualitative
Giles <i>et al.</i> (2021a)	Livestock with Exotic species	Qualitative
D'Angioli <i>et al.</i> (2022)	Livestock with Exotic species	Qualitative
Legge <i>et al.</i> (2015)	Livestock with Fire	Quantitative
Koch <i>et al.</i> (2016)	Livestock with Fire	Qualitative
Li <i>et al.</i> (2007)	Livestock with Chopping	Qualitative
Stephens & Quintana-Ascencio (2015)	Livestock with Chopping and Exotic species	Qualitative
Fensham <i>et al.</i> (2016)	Agriculture with Livestock	Qualitative
Abom <i>et al.</i> (2016)	Agriculture with Livestock and Exotic species	Quantitative
Thomas <i>et al.</i> (2018)	Agriculture with Livestock and Exotic species	Qualitative
Sampaio <i>et al.</i> (2019)	Agriculture with Livestock and Exotic species	Quantitative
Ferreira <i>et al.</i> (2022)	Agriculture with Livestock and Exotic species	Quantitative

APPENDIX H – Multilingual guidelines to assist data reporting in TGB restoration (English version)



Project title: _____

☐ Novel ecosystem



Site information

Country: _____

Site name/id: _____

Site longitude: _____

Site latitude: _____

Reference ecosystem

• Grassland



• Shrubland



• Savanna



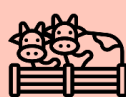
Habitat type: _____

Main restoration goal

- Biodiversity
- Ecosystem service
- Human livelihood
- Legal compliance
- Other: _____



Degradation history



NOTE: Evaluation of initial soil physical and chemical conditions as well as ecosystem biodiversity could provide a complete picture of the degradation status

Degradation source	Starting year	Cessation year	Degradation source	Starting year	Cessation year
• Cattle	_____	_____	• Encroachment	_____	_____
• Crop/Agriculture	_____	_____	• Afforestation	_____	_____
• Mining	_____	_____	• Altered fire regime	_____	_____
• Quarrying	_____	_____	• Altered grazing regime	_____	_____
• Urbanization	_____	_____	• Overharvesting	_____	_____
• Exotic species	_____	_____	• Erosion	_____	_____
Other(s): _____					



Restoration experiment



Experiment design

- ☐ Population level
- ☐ Community level
- ☐ Ecosystem level
- ☐ Landscape level

Sampling

Units (SU)

- ☐ Plot
- ☐ Transect
- ☐ Individual

Restoration and Experiment Controls

- ☐ Restoration negative control (degraded site)
- ☐ Restoration positive control (reference ecosystem)
- ☐ Experiment control

n° SU

size of SU

Restoration technique(s) and experiment treatment(s)

Technique

Application year(s)

Complementary information

- ☐ Passive restoration/natural regeneration
- ☐ Prescribed fire
- ☐ Seeding**
- ☐ Seedling planting**
- ☐ Chemical intervention
- ☐ Physical intervention
- ☐ Grazing/Destocking

burning season _____ frequency _____

n° tree species _____ n° herbaceous species _____

n° tree species _____ n° herbaceous species _____

specific technique(s) _____

specific technique(s) _____

initial stock density _____ target stock density _____

** Please provide the list of species planted/seeded

Additional information: _____



Restoration monitoring

<i>Indicator(s)</i>	<i>First assessment</i>	<i>Number of assessments</i>	<i>Assessment interval</i>	<i>Monitoring length</i>
Absence of threats				
Physical conditions				
Species composition				
Structural diversity				
Ecosystem function				
External exchanges				

APPENDIX I – List of the scientific papers included in the systematic review of seeded and planted species on tropical open ecosystems (Chapter 3)

- Adhikari, A., Yao, J., Sternberg, M., McDowell, K., & White, J. D. (2017). Aboveground biomass of naturally regenerated and replanted semi-tropical shrublands derived from aerial imagery. *Landscape and Ecological Engineering*, 13(1), 145–156. <https://doi.org/10.1007/s11355-016-0310-x>
- Andersen, A. N., Ludwig, J. A., Lowe, L. M., & Rentz, D. C. F. (2001). Grasshopper biodiversity and bioindicators in Australian tropical savannas: responses to disturbance in Kakadu National Park. *Austral Ecology*, 26(3), 213–222. <https://doi.org/https://doi.org/10.1046/j.1442-9993.2001.01106.x>
- Brady, C. J., & Noske, R. A. (2010). Succession in bird and plant communities over a 24-Year chronosequence of mine rehabilitation in the Australian monsoon tropics. *Restoration Ecology*, 18(6), 855–864. <https://doi.org/https://doi.org/10.1111/j.1526-100X.2008.00511.x>
- Carlsen, T. M., Espeland, E. K., Paterson, L. E., & MacQueen, D. H. (2017). Optimal prescribed burn frequency to manage foundation California perennial grass species and enhance native flora. *Biodiversity and Conservation*, 26(11), 2627–2656. <https://doi.org/10.1007/s10531-017-1376-y>
- Coelho, P. G. L., Antonini, Y., & da Costa, F. V. (2023). Soil disturbance impacts on ant-diaspore multilayer networks in a tropical savanna. *Ecological Entomology*, 48(3), 295–306. <https://doi.org/https://doi.org/10.1111/een.13221>
- Correia, M. R. de M., Ferreira, M. C., Alves, M., Consolaro, H. N., & Vieira, D. L. M. (2022). Less is more: Little seed processing required for direct seeding in seasonal tropics. *New Forests*, 53(4), 695–719. <https://doi.org/10.1007/s11056-021-09881-y>
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- D’Angioli, A. M., Giles, A. L., Costa, P. B., Wolfsdorf, G., Pecoral, L. L. F., Verona, L., Piccolo, F., Sampaio, A. B., Schmidt, I. B., Rowland, L., Lambers, H., Kandeler, E., Oliveira, R. S., & Abrahão, A. (2022). Abandoned pastures and restored savannas have distinct patterns of plant–soil feedback and nutrient cycling compared with native Brazilian savannas. *Journal of Applied Ecology*, 59(7), 1863–1873. <https://doi.org/https://doi.org/10.1111/1365-2664.14193>

- Ezeokoli, O. T., Mashigo, S. K., Maboeta, M. S., Bezuidenhout, C. C., Khasa, D. P., & Adeleke, R. A. (2020). Arbuscular mycorrhizal fungal community differentiation along a post-coal mining reclamation chronosequence in South Africa: A potential indicator of ecosystem recovery. *Applied Soil Ecology*, 147, 103429. <https://doi.org/https://doi.org/10.1016/j.apsoil.2019.103429>
- Ferreira, M. C., de Oliveira Cordeiro, A. O., Sampaio, A. B., Schmidt, I. B., & Vieira, D. L. M. (2023). Direct seeding versus seedling planting: survival, biomass, growth, and cost up to 6 years for four tropical seasonal tree species. *Restoration Ecology*, 31(4), e13807. <https://doi.org/https://doi.org/10.1111/rec.13807>
- Figueiredo, M., Messias, M. C., Leite, M., & Kozovits, A. (2021). Seed covering and dry periods in the rainy season interfere with direct seeding success in the restoration of post-mined grasslands. *Ecología Austral*, 31, 444–455. <https://doi.org/10.25260/EA.21.31.3.0.1446>
- Giles, A. L., Costa, P. de B., Rowland, L., Abrahão, A., Lobo, L., Verona, L., Silva, M. C., Monge, M., Wolfsdorf, G., Petroni, A., D'Angioli, A. M., Sampaio, A. B., Schimidt, I. B., & Oliveira, R. S. (2022). How effective is direct seeding to restore the functional composition of neotropical savannas? *Restoration Ecology*, 30(1), e13474. <https://doi.org/https://doi.org/10.1111/rec.13474>
- Haddad, M. T., A. G. Viani, R., G. B. Cava, M., Durigan, G., & W. Veldman, J. (2020). Savannas after afforestation: assessment of herbaceous community responses to wildfire versus native tree planting. *Biotropica*, 52(6), 1206–1216. <https://doi.org/https://doi.org/10.1111/btp.12827>
- Kinyua, D., McGeoch, L. E., Georgiadis, N., & Young, T. P. (2010). Short-term and long-term effects of soil ripping, seeding, and fertilization on the restoration of a tropical rangeland. *Restoration Ecology*, 18(s1), 226–233. <https://doi.org/https://doi.org/10.1111/j.1526-100X.2009.00594.x>
- Ladouceur, E., & Mayfield, M. M. (2017). The early response of subtropical tussock grasslands to restoration treatments. *Restoration Ecology*, 25(5), 689–695. <https://doi.org/https://doi.org/10.1111/rec.12491>
- Lovera, M., & Cuenca, G. (1996). Arbuscular mycorrhizal infection in Cyperaceae and Gramineae from natural, disturbed and restored savannas in La Gran Sabana, Venezuela. *Mycorrhiza*, 6(2), 111–118. <https://doi.org/10.1007/s005720050115>
- Luck, L., Bellairs, S. M., & Rossiter-Rachor, N. A. (2019). Residual herbicide treatments reduce *Andropogon gayanus* (Gamba Grass) recruitment for mine site restoration in northern Australia.

Ecological Management & Restoration, 20(3), 214–221.
<https://doi.org/https://doi.org/10.1111/emr.12376>

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- McKenna, P., Erskine, P. D., Glenn, V., & Doley, D. (2019). Response of open woodland and grassland mine site rehabilitation to fire disturbance on engineered landforms. *Ecological Engineering*, 133, 98–108. <https://doi.org/https://doi.org/10.1016/j.ecoleng.2019.04.013>
- Pereira, S. R., Laura, V. A., & Souza, A. L. T. (2013). Establishment of Fabaceae tree species in a tropical pasture: influence of seed size and weeding methods. *Restoration Ecology*, 21(1), 67–74. <https://doi.org/https://doi.org/10.1111/j.1526-100X.2011.00858.x>
- Pilon, N. A. L., Assis, G. B., Souza, F. M., & Durigan, G. (2019). Native remnants can be sources of plants and topsoil to restore dry and wet cerrado grasslands. *Restoration Ecology*, 27(3), 569–580. <https://doi.org/https://doi.org/10.1111/rec.12902>
- Questad, E., Uowolo, A., Brooks, S., & Cordell, S. (2022). Shifting Limitations to Restoration across Dryland Ecosystems in Hawai‘i. *Sustainability*, 14, 5421. <https://doi.org/10.3390/su14095421>
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- Schmidt, S., Stewart, G. R., & Ashwath, N. (1999). Monitoring plant physiological characteristics to evaluate mine site revegetation: a case study from the wet-dry tropics of northern Australia. *Plant and Soil*, 215(1), 73–84. <http://www.jstor.org/stable/42950563>
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APPENDIX J – List of the 220 plant species planted in Tropical Grassland Biome restoration experiments. Ecosystems: G = grassland, Sh = shrubland, Sa = savanna; IUCN status: DD = data deficient, EN = endangered, LC = Least Concern, NT = near threatened, VU = vulnerable.

Plant species	Country(ies)	Ecosystem(s)	Familly	Growth form	Life cycle	IUCN
<i>Acacia harpophylla</i> F.Muell. ex Benth.	Australia	G – As	Fabaceae	tree	perennial	LC
<i>Acacia holosericea</i> A.Cunn. ex G.Don	Australia	G – As	Fabaceae	shrub-tree	perennial	na
<i>Acacia salicina</i> Lindl.	Australia	G – As	Fabaceae	shrub-tree	perennial	LC
<i>Acacia saligna</i> (Labill.) H.L.Wendl.	Australia	G – As	Fabaceae	shrub-tree	perennial	LC
<i>Acacia stenophylla</i> A.Cunn. ex Benth.	Australia	G – As	Fabaceae	shrub-tree	perennial	LC
<i>Achyrocline saturejoides</i> (Lam.) DC.	Brazil	As	Asteraceae	subshrub	perennial	na
<i>Acisanthera alsinefolia</i> (DC.) Triana	Brazil	G	Melastomataceae	herb	na	na
<i>Acrocomia aculeata</i> (Jacq.) Sweet	Brazil	As	Arecaceae	tree	perennial	LC
<i>Aldama bracteata</i> (Gardner) E.E.Schill. & Panero	Brazil	Sa	Asteraceae	subshrub	perennial	na
<i>Alibertia edulis</i> (Rich.) A.Rich. ex DC.	Brazil	Sa	Rubiaceae	shrub-tree	perennial	LC
<i>Amburana cearensis</i> (Allemão) A.C.Sm.	Brazil	Sa	Fabaceae	tree	perennial	EN
<i>Amsinckia grandiflora</i> (A.Gray) Kleeb ex Greene	USA	G	Boraginaceae	na	annual	na
<i>Anacardium humile</i> A.St.-Hil.	Brazil	Sa	Anacardiaceae	tree	perennial	na
<i>Anacardium occidentale</i> L.	Brazil	Sa	Anacardiaceae	tree	perennial	LC
<i>Anadenanthera colubrina</i> (Vell.) Brenan	Brazil	Sa	Fabaceae	shrub-tree	perennial	LC
<i>Anatherum bicornis</i> (L.) P.Beauv.	Brazil	G - Sa	Poaceae	herb	perennial	na
<i>Anatherum leucostachyum</i> (Kunth) Voronts. & E.A.Kellogg	Brazil	G - Sa	Poaceae	herb	perennial	EN
<i>Andropogon</i> sp.	Brazil	As	Poaceae	herb	annual-perennial	na
<i>Andropogon virgatus</i> Desv.	Brazil	G	Poaceae	herb	perennial	na
<i>Annona crassiflora</i> Mart.	Brazil	Sa	Annonaceae	tree	perennial	LC
<i>Aristida cf. recurvata</i> Kunth	Brazil	Sa	Poaceae	herb	perennial	na
<i>Aristida gibbosa</i> (Nees) Kunth	Brazil	Sa	Poaceae	herb	perennial	na
<i>Aristida jubata</i> (Arechav.) Herter	Brazil	G	Poaceae	herb	perennial	na
<i>Aristida megapotamica</i> Spreng.	Brazil	G	Poaceae	herb	perennial	na

<i>Aristida riparia</i> Trin.	Brazil	Sa	Poaceae	herb	perennial	na
<i>Aristida</i> sp.	Brazil	Sa	Poaceae	herb	annual-perennial	na
<i>Aspidosperma macrocarpon</i> Mart.	Brazil	Sa	Apocynaceae	tree	perennial	LC
<i>Aspidosperma tomentosum</i> Mart.	Brazil	Sa	Apocynaceae	tree	perennial	LC
<i>Astronium fraxinifolium</i> Schott	Brazil	Sa	Anacardiaceae	tree	perennial	LC
<i>Axonopus aureus</i> P.Beauv.	Brazil	G - Sa	Poaceae	herb	perennial	na
<i>Axonopus brasiliensis</i> (Spreng.) Kuhlman.	Brazil	G	Poaceae	herb	perennial	na
<i>Axonopus fissifolius</i> (Raddi) Kuhlman.	Brazil	G	Poaceae	herb	annual-perennial	na
<i>Axonopus marginatus</i> (Trin.) Chase ex Hitchc.	Brazil	G	Poaceae	herb	perennial	na
<i>Axonopus pressus</i> (Nees ex Steud.) Parodi	Brazil	G	Poaceae	herb	perennial	na
<i>Axonopus siccus</i> (Nees) Kuhlman.	Brazil	G - Sa	Poaceae	herb	perennial	na
<i>Baccharis trimera</i> (Less.) DC.	Brazil	G	Asteraceae	subshrub	na	na
<i>Balduina angustifolia</i> B.L.Rob.	USA	Sh	Asteraceae	herb	na	na
<i>Barrosoa betoniciformis</i> (DC.) R.M.King & H.Rob.	Brazil	G	Asteraceae	herb	na	na
<i>Bauhinia dumosa</i> Benth.	Brazil	Sa	Fabaceae	shrub	perennial	na
<i>Bidens menziesii</i> Sherff	USA	Sh	Asteraceae	na	na	na
<i>Bothriochloa insculpta</i> (Hochst. ex A.Rich.) A.Camus	Australia	G - Sa	Poaceae	herb	perennial	na
<i>Bowdichia virgilioides</i> Kunth	Brazil	Sa	Fabaceae	shrub-tree	perennial	LC
<i>Brachychiton rupestris</i> (T.Mitch. ex Lindl.) K.Schum.	Australia	G - Sa	Malvaceae	tree	perennial	LC
<i>Brosimum gaudichaudii</i> Trécul	Brazil	Sa	Moraceae	shrub-tree	perennial	na
<i>Bulbostylis fimbriata</i> (Nees) C.B.Clarke	Brazil	G	Cyperaceae	herb	annual	na
<i>Bulbostylis juncooides</i> (Vahl) Kük. ex Herter	Brazil	G	Cyperaceae	herb	perennial	na
<i>Byrsonima crassifolia</i> (L.) Kunth	Brazil	Sa	Malpighiaceae	shrub-tree	perennial	LC
<i>Calopogonium</i> sp	Venezuela	Sa	Fabaceae	herb-climb-subshrub	na	na
<i>Caryocar brasiliense</i> A.St.-Hil.	Brazil	Sa	Caryocaraceae	shrub-tree	perennial	LC
<i>Cecropia pachystachya</i> Trécul	Brazil	G - Sa	Urticaceae	tree	perennial	LC
<i>Cenchrus ciliaris</i> L.	Australia, Kenya	G - Sh - Sa	Poaceae	herb	perennial	LC
<i>Centrosema coriaceum</i> Benth.	Brazil	G	Fabaceae	subshrub	perennial	na
<i>Chaetogastra gracilis</i> (Bonpl.) DC.	Brazil	G	Melastomataceae	herb-subshrub-shrub	na	LC

<i>Chamaecrista fasciculata</i> (Michx.) Greene	USA	Sh	Fabaceae	herb	annual	na
<i>Chamaecrista rotundifolia</i> (Pers.) Greene	Australia, Brazil	G - Sa	Fabaceae	subshrub	perennial	na
<i>Chenopodium oahuense</i> (Meyen) Aellen	USA	Sh	Amaranthaceae	shrub-tree	perennial	na
<i>Chloris gayana</i> Kunth	Australia, Kenya, South Africa	G - Sh - Sa	Poaceae	herb	perennial	na
<i>Chromolaena congesta</i> (Hook. & Arn.) R.M.King & H.Rob.	Brazil	G	Asteraceae	subshrub	perennial	na
<i>Chromolaena squalida</i> (DC.) R.M.King & H.Rob.	Brazil	G	Asteraceae	shrub	perennial	na
<i>Chrysolaena obovata</i> (Less.) Dematt	Brazil	G	Asteraceae	herb-subshrub	perennial	na
<i>Copaifera langsdorffii</i> Desf.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Brazil	Sa	Boraginaceae	shrub-tree	perennial	LC
<i>Cordia obtusa</i> (K.Schum.) Kuntze	Brazil	G	Rubiaceae	shrub-tree	perennial	na
<i>Corymbia citriodora</i> (Hook.) K.D.Hill & L.A.S.Johnson	Australia	G - Sa	Myrtaceae	tree	perennial	LC
<i>Couepia grandiflora</i> (Mart. & Zucc.) Benth. ex Hook.f.	Brazil	Sa	Chrysobalanaceae	tree	perennial	na
<i>Crotalaria balansae</i> Micheli	Brazil	G	Fabaceae	subshrub	perennial	na
<i>Croton glandulosus</i> L.	Brazil	G	Euphorbiaceae	herb-subshrub	annual	na
<i>Cuphea micrantha</i> Kunth	Brazil	G	Lythraceae	subshrub	perennial	na
<i>Cybistax antisiphilitica</i> (Mart.) Mart.	Brazil	Sa	Bignoniaceae	shrub-tree	perennial	LC
<i>Cymbopogon pospischilii</i> (K.Schum.) C.E.Hubb.	Kenya	G	Poaceae	herb	perennial	na
<i>Cynodon dactylon</i> (L.) Pers.	South Africa	G	Poaceae	herb	perennial	EN
<i>Cyperus aggregatus</i> (Willd.) Endl.	Brazil	G	Cyperaceae	herb-shrub	perennial	na
<i>Dalbergia miscolobium</i> Benth.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Davilla elliptica</i> A.St.-Hil.	Brazil	Sa	Dilleniaceae	shrub	perennial	na
<i>Desmoscelis villosa</i> (Aubl.) Naudin	Brazil	G	Melastomataceae	shrub	perennial	LC
<i>Dichanthium sericeum</i> (R.Br.) A.Camus	Australia	G	Poaceae	herb	annual-perennial	na
<i>Didymopanax macrocarpus</i> (Cham. & Schltdl.) Seem.	Brazil	Sa	Araliaceae	shrub-tree	perennial	LC
<i>Diectomis fastigiata</i> (Sw.) P.Beauv.	Brazil	Sa	Poaceae	herb	annual	na
<i>Digitaria eriantha</i> Steud.	South Africa	G	Poaceae	herb	perennial	na
<i>Dimorphandra mollis</i> Benth.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Diplusodon microphyllus</i> Pohl	Brazil	G	Lythraceae	subshrub-shrub	perennial	na

<i>Dipteryx alata</i> Vogel	Brazil	Sa	Fabaceae	tree	perennial	VU
<i>Dodonaea viscosa</i> Jacq.	USA	Sh	Sapindaceae	subshrub-shrub	perennial	LC
<i>Dubautia linearis</i> (Gaudich.) D.D.Keck	USA	Sh	Asteraceae	na	na	na
<i>Echinolaena inflexa</i> (Poir.) Chase	Brazil	Sa	Poaceae	herb	perennial	na
<i>Elionurus muticus</i> (Spreng.) Kuntze	Brazil	G	Poaceae	herb	perennial	na
<i>Emmotum nitens</i> (Benth.) Miers	Brazil	Sa	Metteniusaceae	tree	perennial	LC
<i>Enterolobium contortisiliquum</i> (Vell.) Morong	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Enterolobium gummiferum</i> (Mart.) J.F.Macbr.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Enteropogon macrostachyus</i> (Hochst. ex A.Rich.) Munro ex Benth.	Kenya	G	Poaceae	herb	perennial	na
<i>Eragrostis curvula</i> (Schrader.) Nees	South Africa	G	Poaceae	herb	perennial	na
<i>Eragrostis leucosticta</i> Nees ex Döll	Brazil	G	Poaceae	herb	perennial	na
<i>Eragrostis polytricha</i> Nees	Brazil	G	Poaceae	herb	perennial	na
<i>Eragrostis superba</i> Peyr	Kenya	G - Sh	Poaceae	herb	perennial	na
<i>Eragrostis tef</i> (Zuccagni) Trotter	South Africa	G	Poaceae	herb	annual	na
<i>Eremanthus erythropappus</i> (DC.) MacLeish	Brazil	G	Asteraceae	tree	perennial	LC
<i>Eremanthus glomerulatus</i> Less.	Brazil	Sa	Asteraceae	tree	perennial	LC
<i>Eremanthus uniflorus</i> MacLeish & H.Schumacher.	Brazil	Sa	Asteraceae	tree	perennial	LC
<i>Eriotheca pubescens</i> (Mart. & Zucc.) Schott & Endl.	Brazil	Sa	Malvaceae	tree	perennial	na
<i>Eucalyptus camaldulensis</i> Dehnh.	Australia	G - Sa	Myrtaceae	tree	perennial	NT
<i>Eucalyptus crebra</i> F.Muell.	Australia	G - Sa	Myrtaceae	tree	perennial	LC
<i>Eucalyptus populnea</i> F.Muell.	Australia	G - Sa	Myrtaceae	tree	perennial	VU
<i>Eucalyptus punctata</i> DC.	Australia	G - Sa	Myrtaceae	tree	perennial	LC
<i>Eucalyptus shirleyi</i> Maiden	Australia	G - Sa	Myrtaceae	tree	perennial	LC
<i>Eucalyptus tereticornis</i> Sm.	Australia	G - Sa	Myrtaceae	tree	perennial	LC
<i>Eugenia anomala</i> D.Legrand	Brazil	G	Myrtaceae	subshrub	perennial	na
<i>Eugenia dysenterica</i> DC.	Brazil	Sa	Myrtaceae	shrub-tree	perennial	LC
<i>Eustachys distichophylla</i> (Lag.) Nees	Brazil	G	Poaceae	herb	perennial	na
<i>Evolvulus sericeus</i> var. <i>sericeus</i>	Brazil	G	Convolvulaceae	herb	perennial	na
<i>Fimbristylis dichotoma</i> (L.) Vahl	Brazil	G	Cyperaceae	herb	annual-perennial	LC

<i>Froelichia procera</i> (Seub.) Pedersen	Brazil	G	Amaranthaceae	subshrub-shrub	perennial	na
<i>Genipa americana</i> L.	Brazil	Sa	Rubiaceae	tree	perennial	LC
<i>Guazuma ulmifolia</i> Lam.	Brazil	Sa	Malvaceae	tree	perennial	LC
<i>Gymnopogon spicatus</i> (Spreng.) Kuntze	Brazil	G	Poaceae	herb	perennial	na
<i>Hancornia speciosa</i> Gomes	Brazil	Sa	Apocynaceae	shrub-tree	perennial	LC
<i>Handroanthus ochraceus</i> (Cham.) Mattos	Brazil	Sa	Bignoniaceae	tree	perennial	LC
<i>Helia alata</i> (Aubl.) Kuntze	Brazil	G	Gentianaceae	herb	annual	na
<i>Heteropogon contortus</i> (L.) P.Beauv. ex Roem. & Schult.	Australia	G - Sa	Poaceae	herb	perennial	na
<i>Hymenaea courbaril</i> L.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Hymenaea stigonocarpa</i> Mart. ex Hayne	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Inga laurina</i> (Sw.) Willd.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Jacaranda brasiliana</i> (Lam.) J.St.-Hil.	Brazil	Sa	Bignoniaceae	tree	perennial	LC
<i>Jacaranda ulei</i> Bureau & K.Schum.	Brazil	Sa	Bignoniaceae	shrub	perennial	na
<i>Kielmeyera coriacea</i> Mart.	Brazil	Sa	Calophyllaceae	shrub-tree	perennial	na
<i>Kielmeyera lathrophyton</i> Saddi	Brazil	Sa	Calophyllaceae	tree	perennial	LC
<i>Lagenocarpus rigidus subsp. tenuifolius</i> (Boeckeler) T.Koyama & Maguire	Brazil	G	Cyperaceae	herb	perennial	na
<i>Laurembergia tetrandra</i> (Schott) Kanitz	Brazil	G	Haloragaceae	herb-subshrub	na	LC
<i>Lepidaploa aurea</i> (Mart. ex DC.) H.Rob.	Brazil	Sa	Asteraceae	herb	na	na
<i>Lippia lupulina</i> Cham.	Brazil	G	Verbenaceae	subshrub-shrub	perennial	na
<i>Loudetiopsis chrysothrix</i> (Nees) Conert	Brazil	G - Sa	Poaceae	herb	perennial	na
<i>Lycopodiella alopecuroides</i> (L.) Cranfill	Brazil	G	Lycopodiaceae	herb	na	na
<i>Machaerium opacum</i> Vogel	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Magonia pubescens</i> A.St.-Hil.	Brazil	Sa	Sapindaceae	tree	perennial	LC
<i>Megathyrsus maximus</i> (Jacq.) B.K.Simon & S.W.L.Jacobs	Australia	G - Sa	Poaceae	herb	perennial	na
<i>Melinis repens</i> (Willd.) Zizka	Brazil	G	Poaceae	herb	annual-perennial	na
<i>Metrosideros polymorpha</i> Gaudich.	USA	Sh	Myrtaceae	shrub-tree	perennial	VU
<i>Miconia ligustroides</i> (DC.) Naudin	Brazil	G	Melastomataceae	shrub-tree	perennial	LC
<i>Microchloa altera</i> (Rendle) Stapf	Congo	Sa	Poaceae	herb	perennial	na
<i>Microlicia serpyllifolia</i> D.Don	Brazil	G	Melastomataceae	shrub	perennial	na

<i>Mimosa caesalpiniiifolia</i> Benth.	Brazil	Sa	Fabaceae	shrub	perennial	VU
<i>Mimosa claussenii</i> Benth.	Brazil	Sa	Fabaceae	shrub	perennial	LC
<i>Mimosa</i> sp.	Brazil	Sa	Fabaceae	na	na	na
<i>Mitracarpus hirtus</i> (L.) DC.	Brazil	G	Rubiaceae	herb-subshrub	annual	na
<i>Myracrodruon urundeuva</i> Allemão	Brazil	Sa	Anacardiaceae	tree	perennial	DD
<i>Paepalanthus lundii</i> Körn.	Brazil	G	Eriocaulaceae	herb	perennial	na
<i>Parinari obtusifolia</i> Hook.f.	Brazil	Sa	Chrysobalanaceae	subshrub-shrub	perennial	na
<i>Paspalum ammodes</i> Trin.	Brazil	G	Poaceae	herb	perennial	na
<i>Paspalum cordatum</i> Hack.	Brazil	G	Poaceae	herb	perennial	na
<i>Paspalum flaccidum</i> Nees	Brazil	G	Poaceae	herb	perennial	na
<i>Paspalum guenoarum</i> Arechav.	Brazil	G	Poaceae	herb	perennial	na
<i>Paspalum hyalinum</i> Nees ex Trin.	Brazil	G	Poaceae	herb	perennial	na
<i>Paspalum notatum</i> Flüggé	Brazil	G	Poaceae	herb	perennial	na
<i>Paspalum scrobiculatum</i> L.	Brazil	G	Poaceae	herb	annual-perennial	LC
<i>Peltaea polymorpha</i> (A.St.-Hil.) Krapov. & Cristóbal	Brazil	G	Malvaceae	shrub	perennial	na
<i>Peltophorum dubium</i> (Spreng.) Taub.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Plathymenia reticulata</i> Benth.	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Platypodium elegans</i> Vogel	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Pleroma candolleanum</i> (DC.) Triana	Brazil	Sa	Melastomataceae	shrub	perennial	na
<i>Pleroma oleifolium</i> (DC.) R.Romero & Versiane	Brazil	Sa	Melastomataceae	subshrub-shrub	perennial	na
<i>Poa secunda</i> J.Presl	USA	G	Poaceae	herb	perennial	na
<i>Poaceae</i> sp.	Brazil	G	Poaceae	herb	na	na
<i>Polycarpaea corymbosa</i> (L.) Lam.	Brazil	G	Caryophyllaceae	herb	annual	na
<i>Pterogyne nitens</i> Tul.	Brazil	Sa	Fabaceae	tree	perennial	NT
<i>Pterolepis glomerata</i> (Rottb.) Miq.	Brazil	G	Melastomataceae	herb	na	na
<i>Qualea grandiflora</i> Mart.	Brazil	Sa	Vochysiaceae	tree	perennial	LC
<i>Rhynchospora albiceps</i> Kunth	Brazil	G	Cyperaceae	herb	perennial	na
<i>Rhynchospora tenuis</i> Link	Brazil	G	Cyperaceae	herb	perennial	na
<i>Ruellia geminiflora</i> Kunth	Brazil	G	Acanthaceae	herb-subshrub	na	na

<i>Sauvagesia racemosa</i> A.St.-Hil.	Brazil	G	Ochnaceae	subshrub	perennial	na
<i>Schinopsis brasiliensis</i> Engl.	Brazil	Sa	Anacardiaceae	tree	perennial	LC
<i>Schizachyrium sanguineum</i> (Retz.) Alston	Brazil	Sa	Poaceae	herb	perennial	na
<i>Scleria hirtella</i> Sw.	Brazil	G	Cyperaceae	herb	annual	LC
<i>Scoparia dulcis</i> L.	Brazil	G	Plantaginaceae	herb-subshrub	annual	na
<i>Sehima nervosa</i> (Rottler) Stapf	Kenya	G	Poaceae	herb	perennial	na
<i>Senega timoutoides</i> (Chodat) J.F.B.Pastore	Brazil	G	Polygalaceae	herb	perennial	na
<i>Senegalia polyphylla</i> (DC.) Britton & Rose	Brazil	Sa	Fabaceae	shrub-tree	perennial	LC
<i>Senna alata</i> (L.) Roxb.	Brazil	Sa	Fabaceae	shrub-tree	perennial	LC
<i>Senna reniformis</i> (G.Don) H.S.Irwin & Barneby	Brazil	G	Fabaceae	shrub	perennial	LC
<i>Setaria incrassata</i> (Hochst.) Hack.	Australia	G - Sa	Poaceae	herb	perennial	na
<i>Sida fallax</i> Walp.	USA	Sh	Malvaceae	subshrub-shrub	perennial	na
<i>Sipanea pratensis</i> Aubl.	Brazil	G	Rubiaceae	herb-subshrub	na	na
<i>Smilax fluminensis</i> Steud.	Brazil	G	Smilacaceae	climber	na	na
<i>Solanum lycocarpum</i> A.St.-Hil.	Brazil	Sa	Solanaceae	shrub	perennial	LC
<i>Sophora chrysophylla</i> (Salisb.) Seem.	USA	Sh	Fabaceae	shrub-tree	perennial	na
<i>Sorghastrum minarum</i> (Nees) Hitchc.	Brazil	G	Poaceae	herb	perennial	na
<i>Spermacoce multiflora</i> (DC.) Delprete	Brazil	G	Rubiaceae	subshrub	perennial	na
<i>Sporobolus metallicola</i> Longhi-Wagner & Boechat	Brazil	G	Poaceae	herb	perennial	na
<i>Stryphnodendron adstringens</i> (Mart.) Coville	Brazil	Sa	Fabaceae	shrub-tree	perennial	na
<i>Stryphnodendron rotundifolium</i> Mart.	Brazil	G	Fabaceae	shrub-tree	perennial	LC
<i>Stylosanthes capitata</i> Vogel	Brazil	Sa	Fabaceae	herb-subshrub	na	na
<i>Stylosanthes guianensis</i> (Aubl.) Sw.	Brazil	Sa	Fabaceae	herb-subshrub-shrub	perennial	na
<i>Stylosanthes hamata</i> (L.) Taub.	Australia	G - Sa	Fabaceae	herb-subshrub-shrub	annual-biennial	na
<i>Stylosanthes macrocephala</i> M.B.Ferreira & Sousa Costa	Brazil	Sa	Fabaceae	herb-subshrub	na	na
<i>Stylosanthes scabra</i> Vogel	Australia	G - Sa	Fabaceae	herb-subshrub-shrub	perennial	na
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Brazil	Sa	Arecaceae	tree	perennial	LC
<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	Brazil	Sa	Bignoniaceae	tree	perennial	LC
<i>Tachigali rubiginosa</i> (Mart. ex Tul.) Oliveira-Filho	Brazil	Sa	Fabaceae	tree	perennial	LC

<i>Tachigali vulgaris</i> L.F.Gomes da Silva & H.C.Lima	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Tapirira guianensis</i> Aubl. + mixture of <i>Stylosanthes capitata</i> Vogel	Brazil	Sa	Anacardiaceae	tree	perennial	LC
<i>Terminalia argentea</i> Mart.	Brazil	Sa	Combretaceae	shrub-tree	perennial	LC
<i>Terminalia corrugata</i> (Ducke) Gere & Boatwr.	Brazil	Sa	Combretaceae	tree	perennial	na
<i>Terminalia fagifolia</i> Mart.	Brazil	Sa	Combretaceae	shrub-tree	perennial	LC
<i>Terminalia</i> sp.	Brazil	Sa	Combretaceae	shrub-tree	perennial	na
<i>Tetrapogon roxburghiana</i> (Schult.) P.M.Peterson	Kenya	Sh	Poaceae	herb	perennial	na
<i>Thesium aphyllum</i> Mart. ex A.DC.	Brazil	G	Santalaceae	herb	perennial	na
<i>Trachypogon spicatus</i> (L.f.) Kuntze	Brazil	G - Sa	Poaceae	herb	perennial	na
<i>Trachypogon vestitus</i> Andersson	Brazil	G	Poaceae	herb	perennial	na
<i>Trichantheium parvifolium</i> (Lam.) Zuloaga & Morrone	Brazil	G	Poaceae	herb	perennial	LC
<i>Urochloa dictyoneura</i> (Fig. & De Not.) Veldkamp	Venezuela	Sa	Poaceae	herb	perennial	na
<i>Urochloa eminii</i> (Mez) Davidse	Venezuela	Sa	Poaceae	herb	annual-perennial	na
<i>Vatairea macrocarpa</i> (Benth.) Ducke	Brazil	Sa	Fabaceae	tree	perennial	LC
<i>Vernonanthura phosphorica</i> (Vell.) H.Rob.	Brazil	Sa	Asteraceae	shrub	perennial	na
<i>Vernonanthura polyanthes</i> (Spreng.) A.J.Vega & Dematt.	Brazil	Sa	Asteraceae	shrub	perennial	na
<i>Waltheria communis</i> A.St.-Hil.	Brazil	G	Malvaceae	subshrub	perennial	na
<i>Xyris jupicai</i> Rich.	Brazil	G	Xyridaceae	herb	annual-biennial	na
<i>Xyris savanensis</i> Miq.	Brazil	G	Xyridaceae	herb	annual	na
<i>Xyris tortula</i> Mart.	Brazil	G	Xyridaceae	herb	na	na
<i>Zanthoxylum rhoifolium</i> Lam.	Brazil	Sa	Rutaceae	tree	perennial	LC
<i>Zeyheria montana</i> Mart.	Brazil	Sa	Bignoniaceae	shrub-tree	perennial	na
<i>Zornia reticulata</i> Sm.	Brazil	G	Fabaceae	herb-shrub	perennial	Na

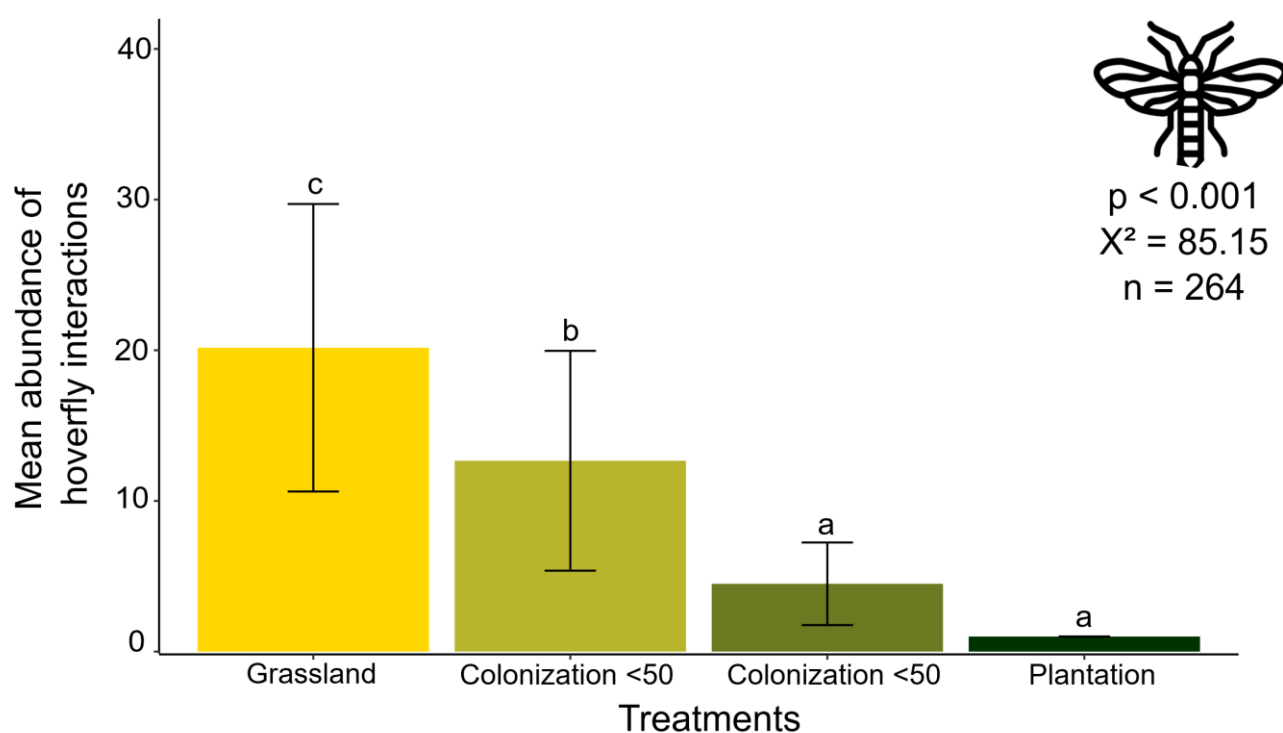
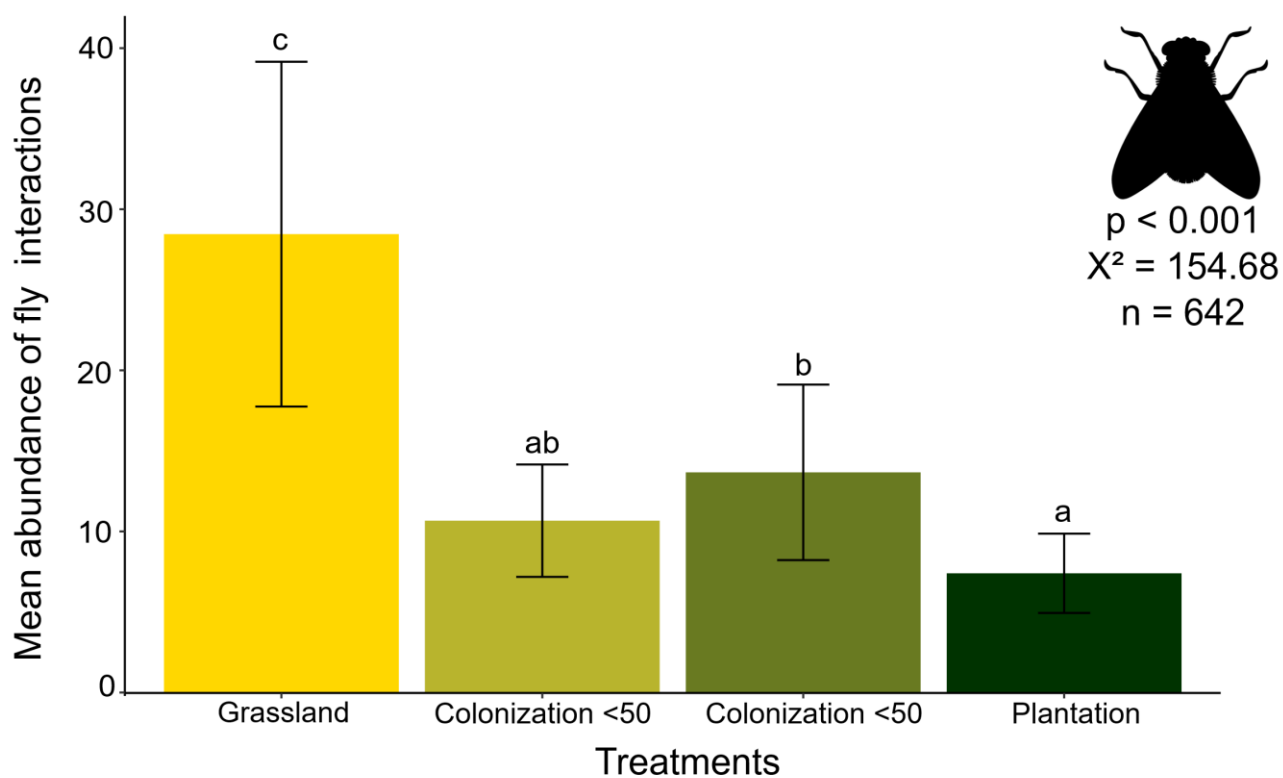
APPENDIX K – Table with the most important plant species in each network according to Centrality degree, which means the species more connected in the network (number of interactions of the species)

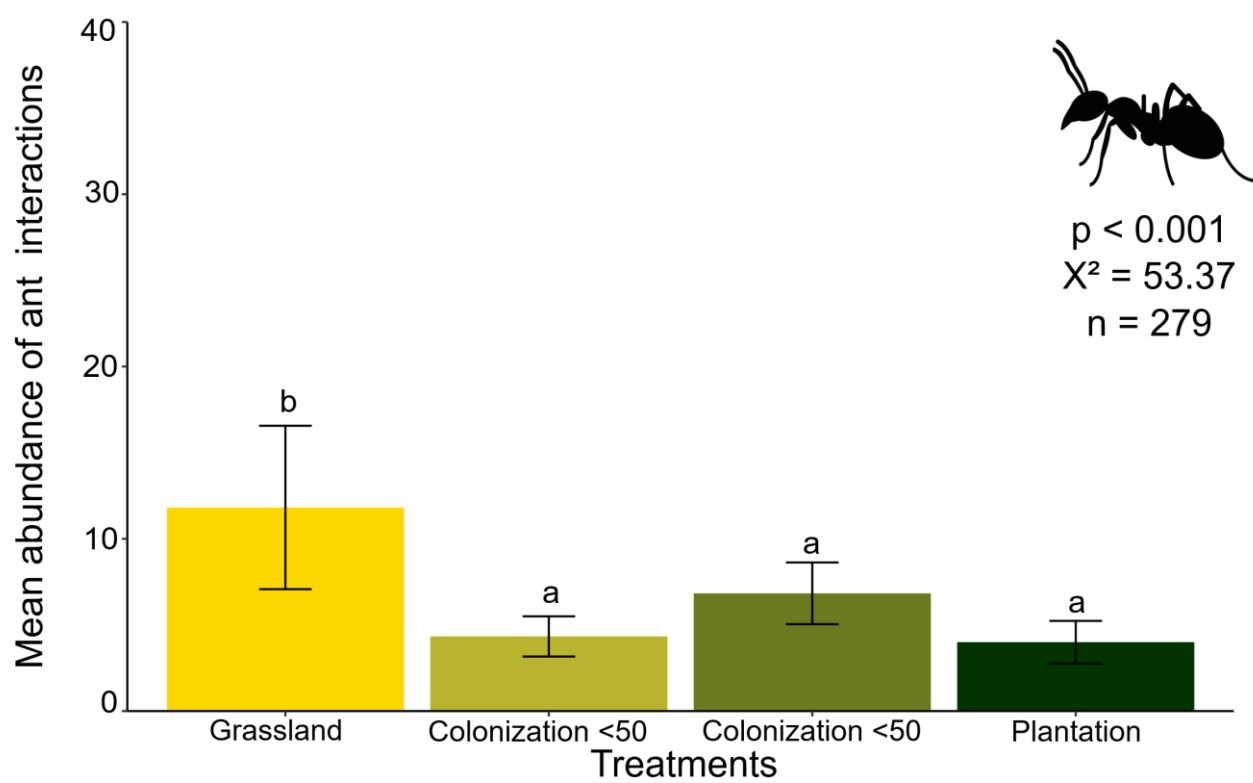
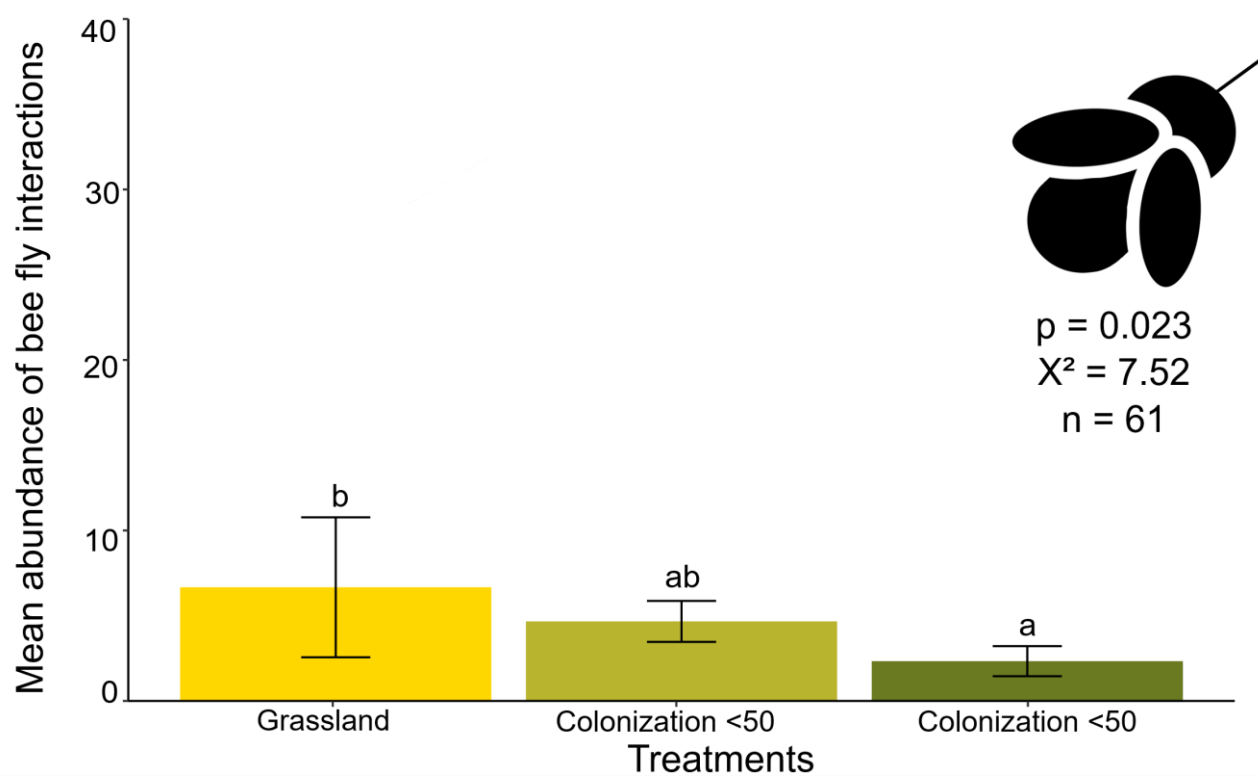
Plant species	Grassland	Colonization < 50	Colonization > 50	Plantation
1st	Euphorbia seguieriana (722)	Euphorbia duvalii (138)	Euphorbia seguieriana (176)	Helianthemum oelandicum (56)
2nd	Linum suffruticosum (236)	Anthyllis montana (124)	Aster alpinus (88)	Hieracium murorum (52)
3rd	Thymus serpyllum (174)	Euphorbia seguieriana (124)	Helianthemum oelandicum (74)	Fragaria viridis (40)
4th	Leucanthemum graminifolium (110)	Helianthemum oelandicum (94)	Coronilla minima (62)	Pyrola chlorantha (32)
5th	Helianthemum apenninum (76)	Linum suffruticosum (88)	Galium corradifolium (56)	Galium pumilum (26)

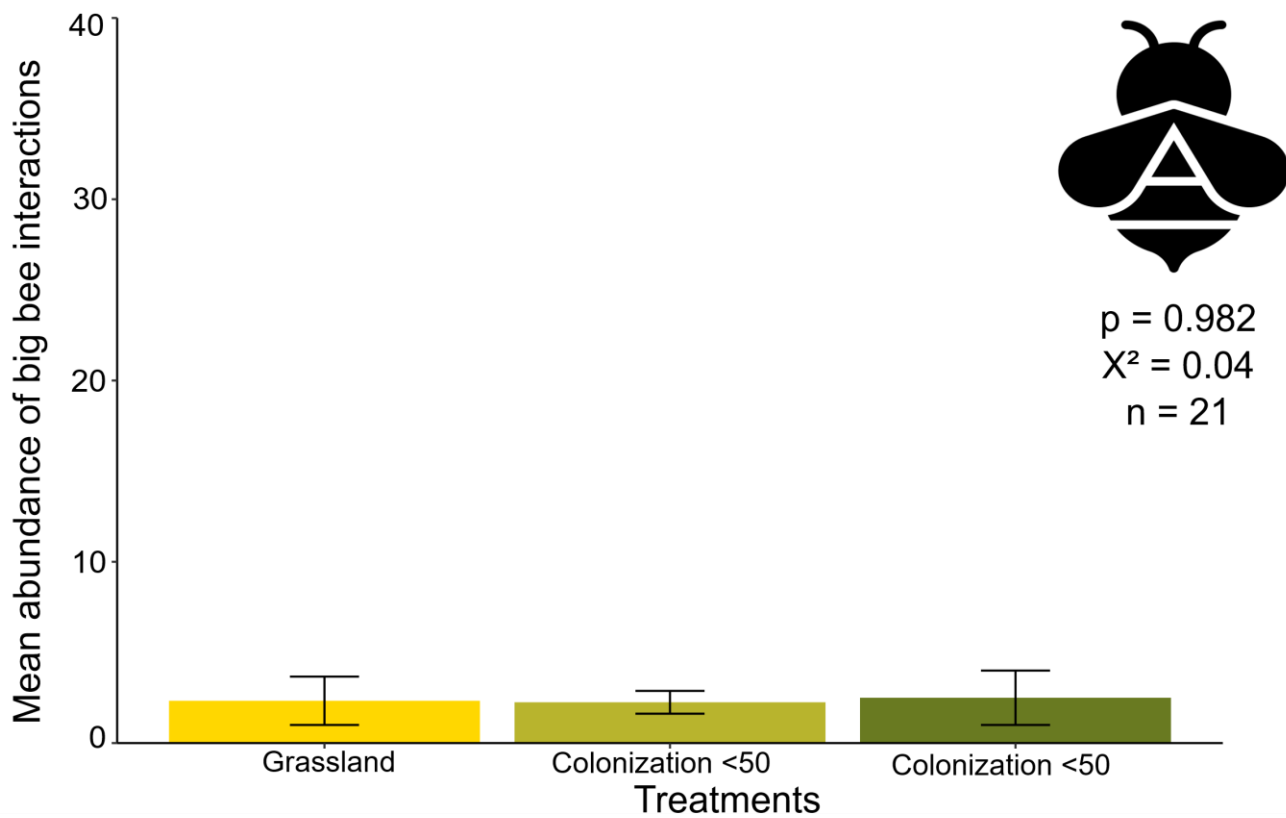
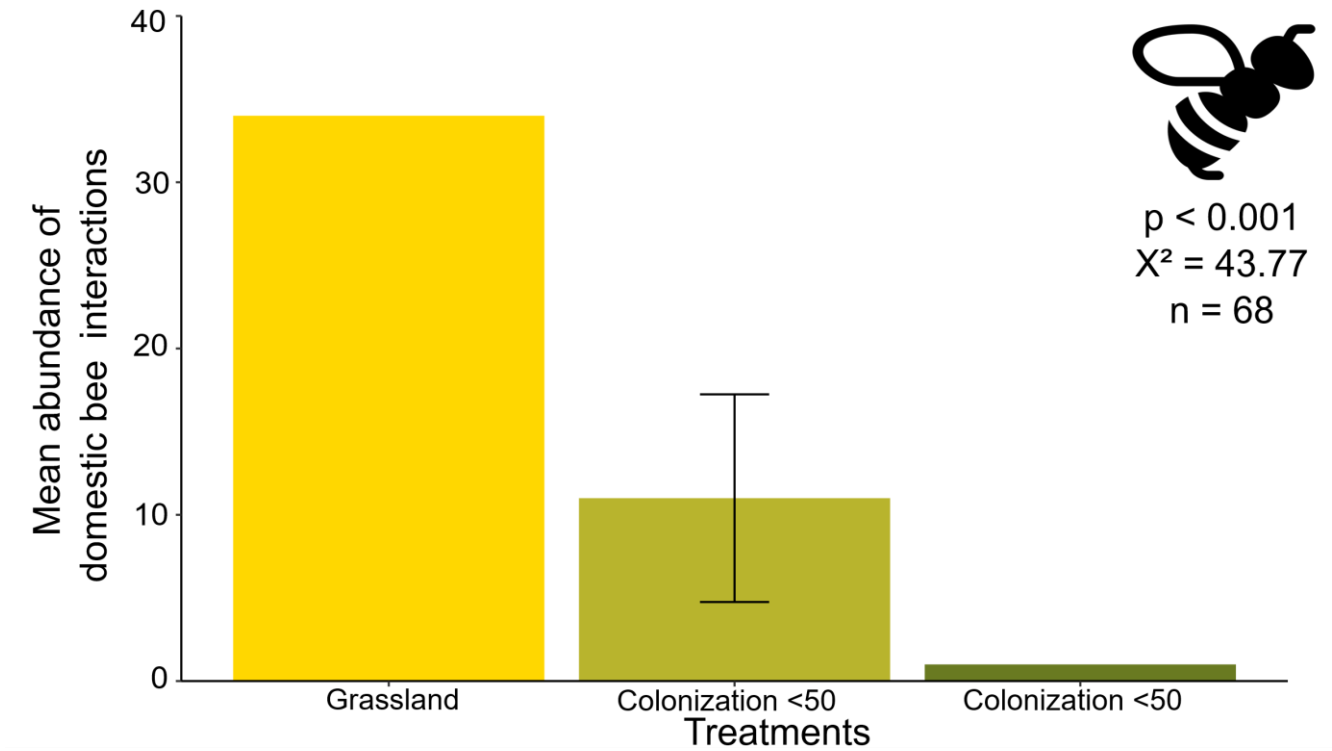
APPENDIX L – Table with the most important pollinator species in each network according to Centrality degree, which means the species more connected in the network (number of interactions of the species)

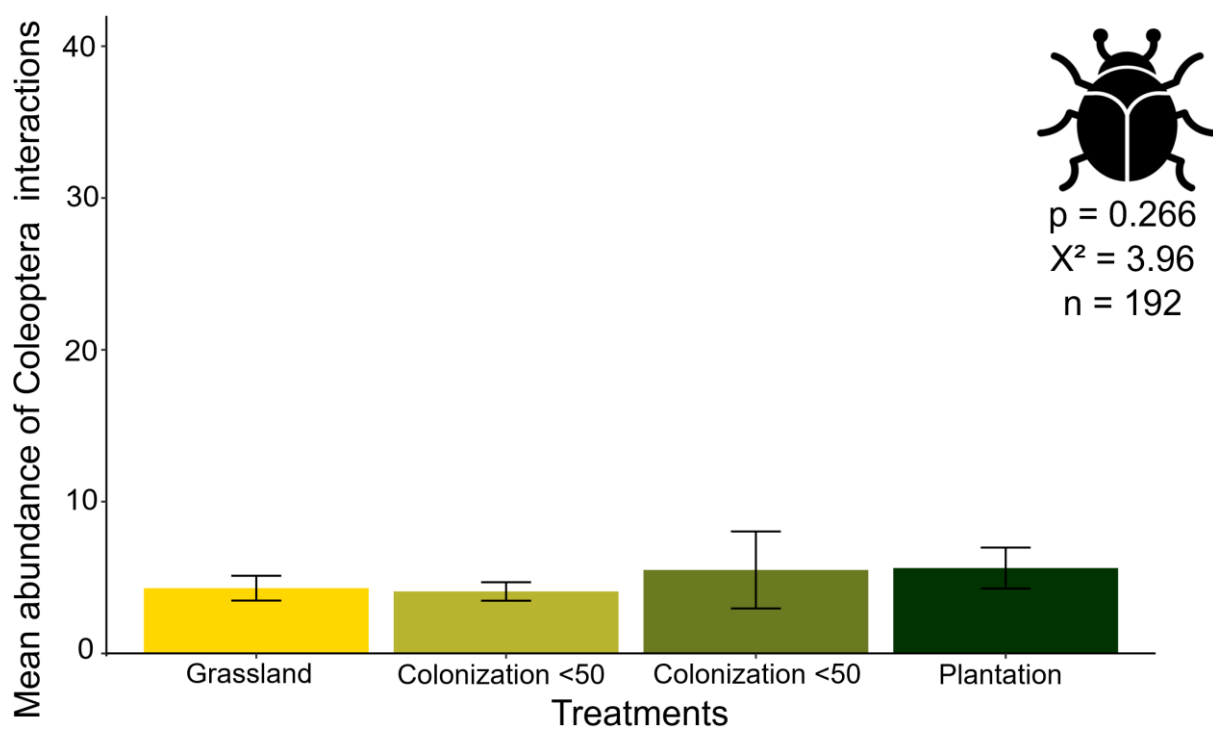
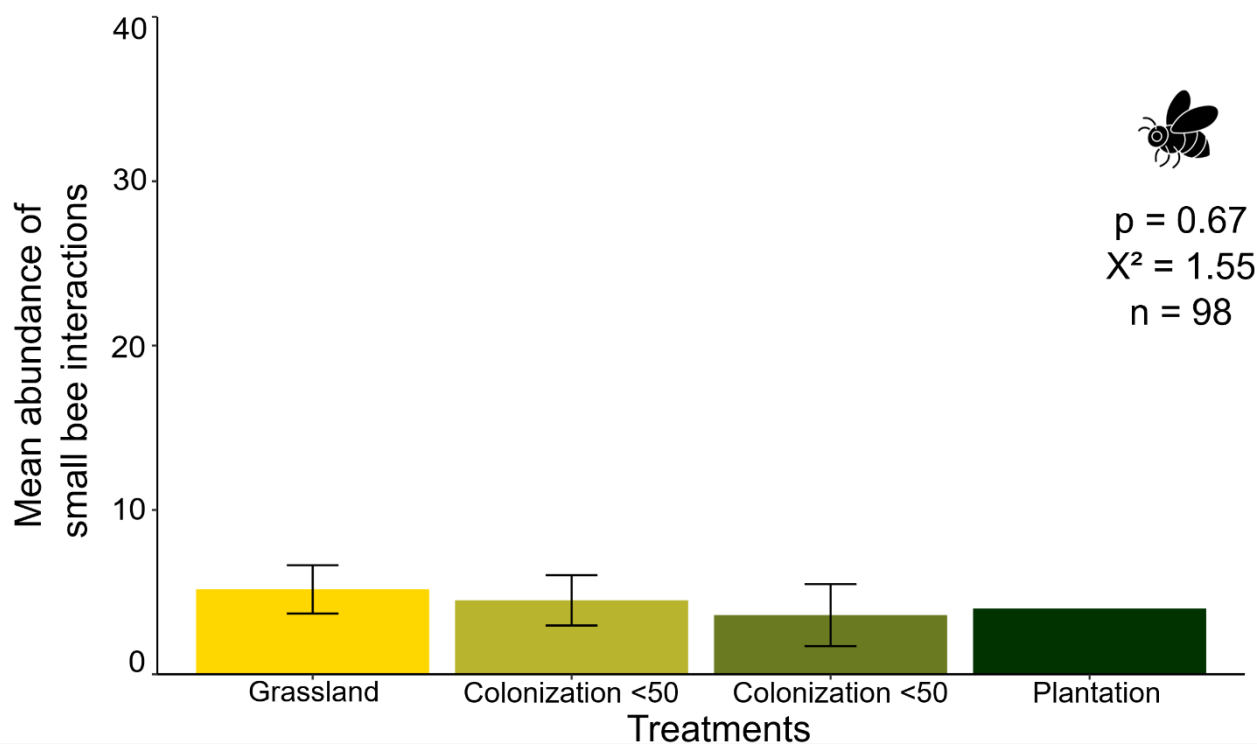
Pollinator species	Grassland	Colonization < 50	Colonization > 50	Plantation
1st	Diptera – fly (626)	Diptera - fly (256)	Diptera – fly (328)	Coleoptera (90)
2nd	Hymenoptera – ants (260)	Diptera - hoverfly (228)	Hymenoptera – ants (164)	Diptera – fly (74)
3rd	Diptera – hoverfly (242)	Coleoptera (98)	Coleoptera (110)	Hymenoptera – ants (56)
4th	Coleoptera (86)	Hymenoptera – small bee (90)	Diptera – hoverfly (54)	Hymenoptera – wasps (20)
5th	Diptera – bee fly (80)	Hymenoptera – ants (78)	Hymenoptera – small bee (36)	Hymenoptera – small bee (8)

APPENDIX M – Interaction abundance of different pollinator groups: A) Fly - Diptera; B) Hoverfly - Diptera; C) Bee fly – Diptera; D) Ant – Hymenoptera; E) Hymenoptera - Domestic bee; F) Hymenoptera - Big bee; G) Hymenoptera - Small bee; and H) Coleoptera

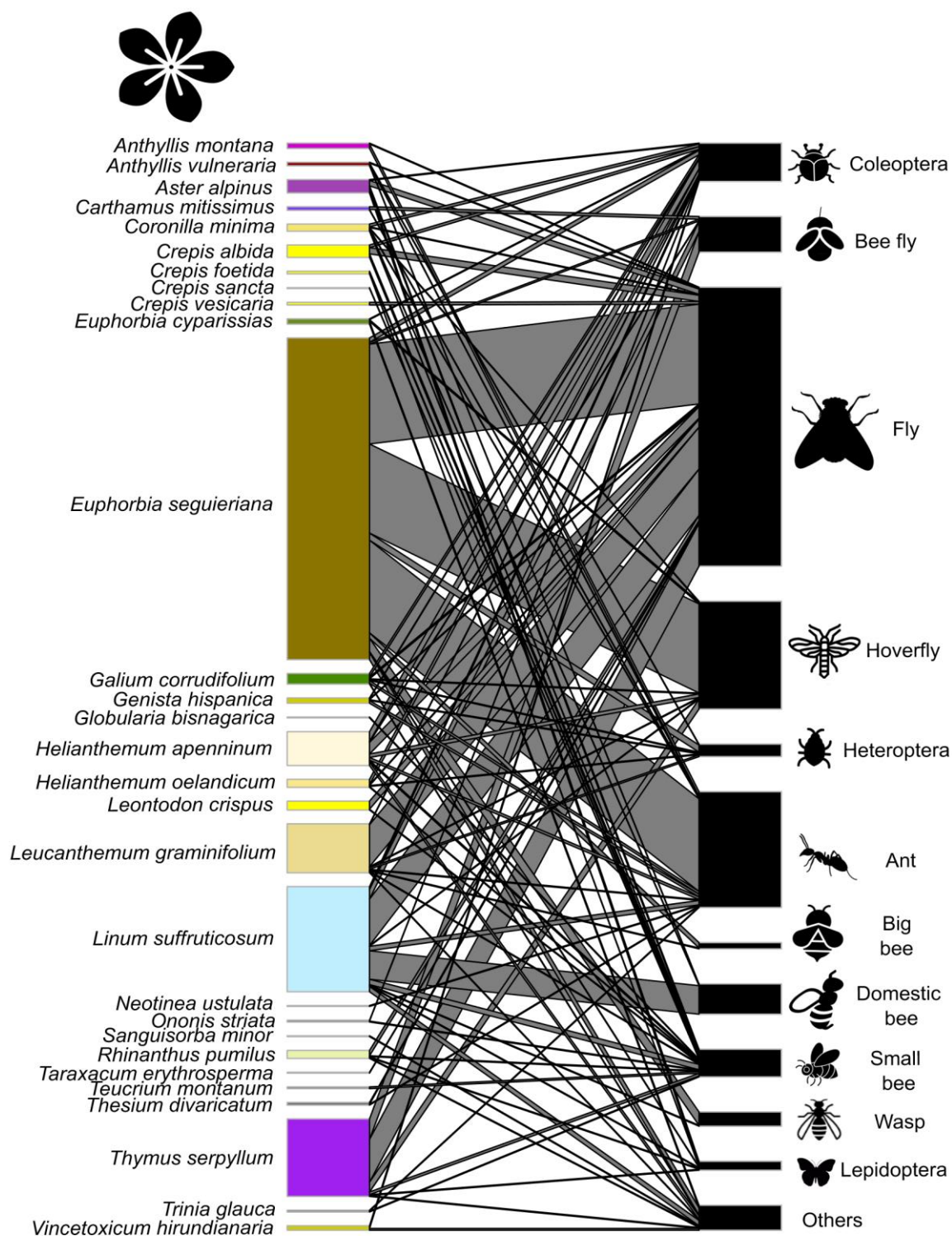




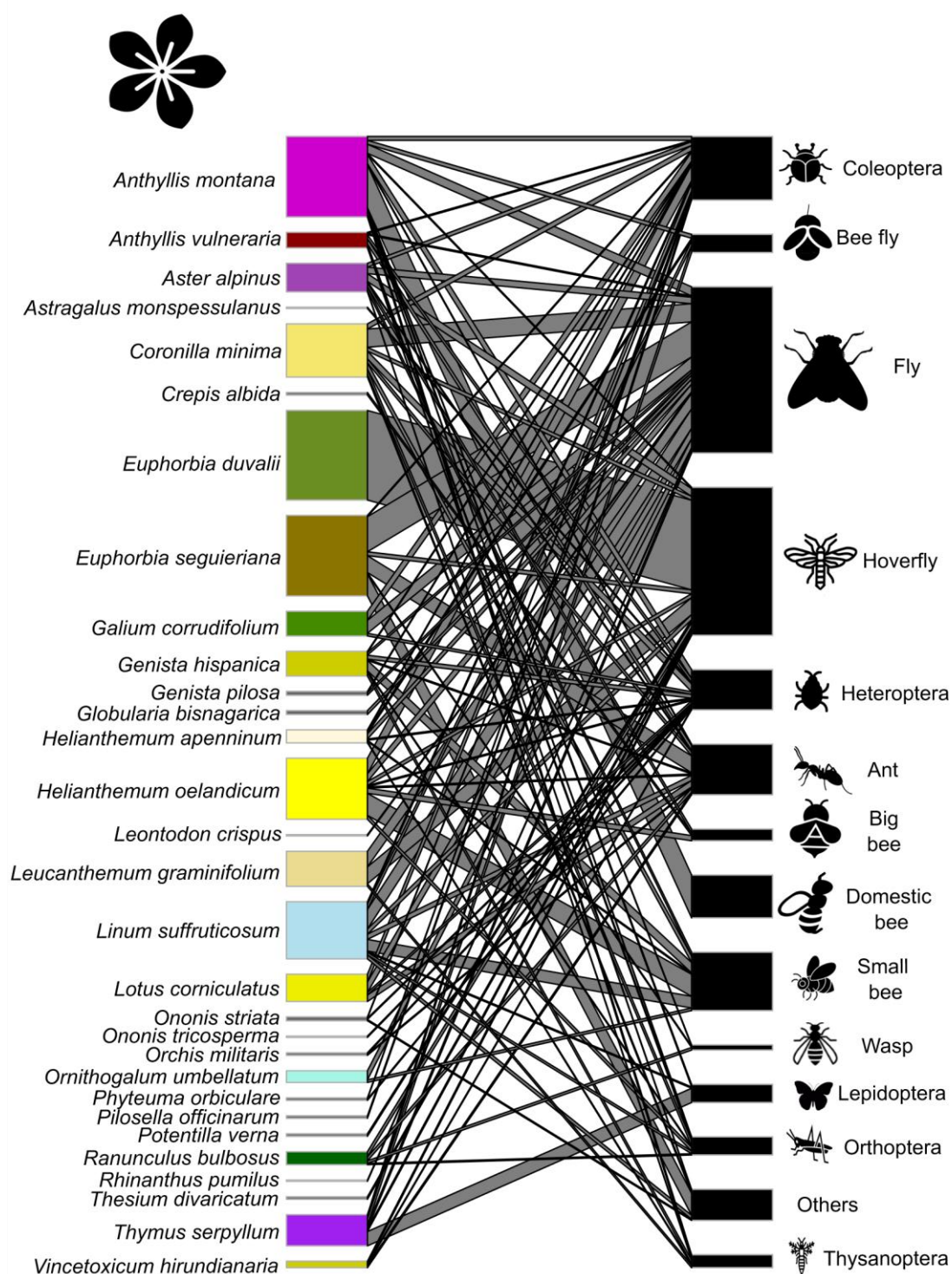




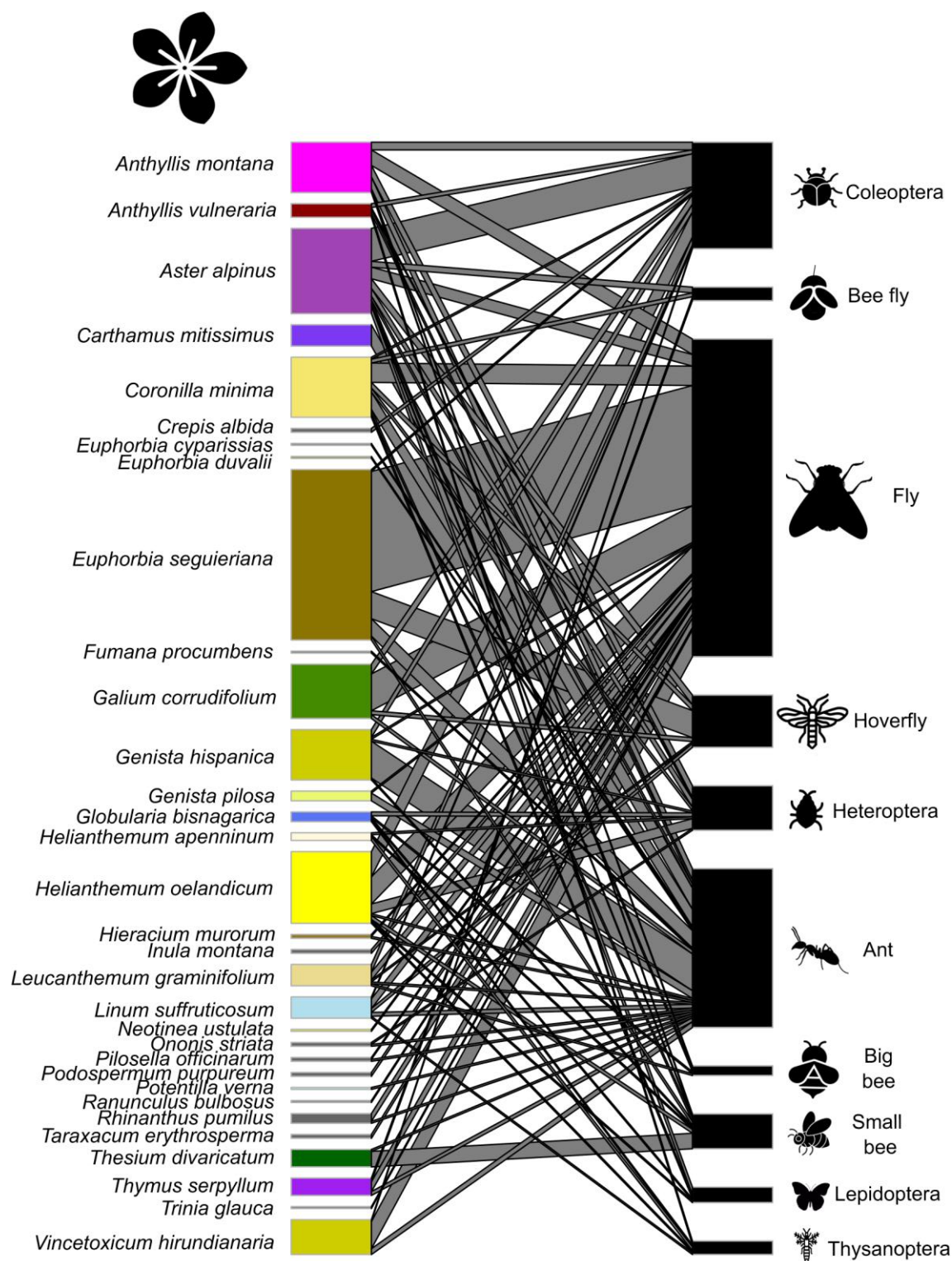
APPENDIX N – Plant-pollinator network for grassland treatment (12 plots). Plant species are on the left side of the graph and pollinators on the right side of the graph. The size of the links indicates how many interactions between each assigned plant-pollinator



APPENDIX O – Plant-pollinator network for colonization < 50 treatment (12 plots).
Plant species are on the left side of the graph and pollinators on the right side of the
graph. The size of the links indicates how many interactions between each assigned
plant-pollinator



APPENDIX P – Plant-pollinator network for colonization >50 treatment (12 plots). Plant species are on the left side of the graph and pollinators on the right side of the graph. The size of the links indicates how many interactions between each assigned plant-pollinator



APPENDIX Q – Plant-pollinator network for plantation treatment (12 plots). Plant species are on the left side of the graph and pollinators on the right side of the graph. The size of the links indicates how many interactions between each assigned plant-pollinator

