Challenges and directions for open ecosystems biodiversity restoration: An overview of the techniques applied for Cerrado

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Abstract

1. Ecological restoration of tropical open ecosystems remains challenging for both science and practice. Over the last decade, innovative techniques have been developed, but whether they have been successful or not remains to be demonstrated. Assessing the outcomes of these initiatives is crucial to drive the following steps to improve tropical grasslands and savanna restoration.

2. Analyzing 82 data sets from the literature and primary data collection, we assessed the effectiveness of passive and active restoration techniques applied in Cerrado open ecosystems. We used plant diversity variables (species and growth forms) as indicators, considering ruderals and exotics as non-target species. Specifically, we aimed to answer: (i) How does the diversity of target species change through time in areas subject to passive restoration? (ii) Are active and passive restoration techniques effective in restoring the proportion of target species found in old-growth reference ecosystems? (iii) Have the current techniques been successful in recovering the proportions of growth forms of reference ecosystems?

3. We found that target species proportions do not increase with time, suggesting limitations of typical species to colonize degraded sites. Hence, passive restoration will promote the conservation of a limited and constant number of target species. This number will depend on the magnitude of degradation and previous land use.

4. The restoration techniques currently applied to restore the biodiversity of Cerrado open ecosystems are not reaching the reference standards, with distinct techniques driving plant communities to different sets of growth forms. Active restoration based on propagules obtained from pristine donor sites (topsoil translocation, plant material transplant, and seeding) performed better than passive restoration for most of the growth forms analyzed.

5. *Synthesis and Applications*: Different growth forms have different roles in determining the structure and functioning of Cerrado vegetation. A mix of techniques can better approximate plant diversity and the proportionality of target species of pristine ecosystems. Singular restoration approaches are insufficient for restoring Cerrado open ecosystem biodiversity. Mixed efforts encompassing various techniques are required instead. Furthermore, it is likely restoration success can be improved with greater investment in improving our understanding of, and developing existing restoration techniques.

Resumo

1. A restauração de ecossistemas abertos tropicais é um grande desafio prático e científico. Nas últimas décadas, novas técnicas foram desenvolvidas, porém a eficácia destas ainda não foi amplamente demonstrada. Portanto, avaliar os resultados dessas iniciativas é crucial para conduzir as próximas etapas e aprimorar a restauração de campos e savanas tropicais.

2. Analisando 82 conjuntos de dados (literatura e dados primários), avaliamos a eficácia de técnicas de restauração passiva e ativa aplicadas em ecossistemas abertos do Cerrado. Usamos como indicadores espécies típicas (espécies-alvo) separadas em formas de crescimento. Consideramos com espécies não-alvo as ruderais e exóticas. Especificamente, buscamos responder: (i) Como a diversidade de espécies-alvo muda ao longo do tempo em áreas sujeitas a restauração passiva? (ii) As técnicas de restauração ativa e passiva são eficazes na recuperação da proporção de espécies-alvo encontradas em ecossistemas de referência? (iii) As técnicas atuais têm obtido sucesso na recuperação da proporção das diferentes formas de crescimento encontradas nos ecossistemas de referência?

3. A proporção de espécies-alvo não aumentou com o tempo, sugerindo que as espécies típicas possuem limitações para colonizar áreas degradadas. Assim, a restauração passiva promoverá a conservação de um número limitado e constante de espécies-alvo. Esse número dependerá da magnitude da degradação e do uso anterior da terra.

4. As técnicas de restauração, visando recuperar a biodiversidade dos ecossistemas abertos do Cerrado, não estão atingindo os valores encontrados no ecossistema de referência. Técnicas distintas conduzem as comunidades vegetais a diferentes conjuntos de formas de crescimento. Encontramos que restauração ativa, baseada em propágulos obtidos de áreas fonte conservadas (translocação de topsoil, transplante de material vegetal e semeadura), resultou em melhor desempenho do que a restauração passiva para a maioria das formas de crescimento analisadas.

5. *Síntese e Aplicações:* Diferentes formas de crescimento apresentam diferentes papéis na determinação da estrutura e funcionamento da vegetação do Cerrado. Vimos que técnicas isoladas são insuficientes em recuperar a diversidade encontrada em áreas conservadas. Portanto, a combinação de diferentes abordagens de restauração pode levar a uma comunidade com riqueza e proporção de espécies típicas mais próxima ao ecossistema de referência.

Keywords: savanna restoration, grassland restoration, recovery debt, growth forms, tropical grasslands, restoration practices, reference ecosystems

Introduction

The urgent need to mitigate the effects of climate change has raised the conservation and restoration of ecosystems to a high level of importance on a global scale (Suding et al., 2015; Temperton et al., 2019). Several restoration initiatives have been launched in the last few decades with global and ambitious goals. The global "Bonn Challenge" initiative has an ambitious goal of reforesting 350 million hectares of degraded areas by 2030 (GPFLR, 2019), the AFR100 – "African Forest Landscape Restoration Initiative" aiming to restore 100 million hectares or, in Brazil, the "Pact for the Restoration of the Atlantic Forest" which aims to restore 15 million hectares by the year 2050 (Crouzeilles et al., 2019). Despite the importance of these initiatives, only forest ecosystems have been considered, with grasslands and savannas being repeatedly neglected (Buisson et al., 2019; Temperton et al., 2019; Veldman et al., 2015), even within the United Nations (UN) Decade on Ecosystem Restoration (Dudley et al., 2020; Silveira et al., 2021). Consequently, there are no protocols to restore these ecosystems, nor is there a systematic evaluation of the techniques currently being used to restore them.

Restoring open ecosystems, especially in the tropics, is a significant practical and scientific challenge. Projects to restore grasslands and savannas have been implemented using several techniques, such as hay transposition (Le Stradic et al., 2014; Pilon et al., 2018), transposition of topsoil and plant material (Ferreira et al., 2015; Le Stradic et al., 2016; Pilon et al., 2018, 2019), direct seeding (Pellizzaro et al., 2017), driving natural regeneration (Cava et al., 2018; Zaloumis & Bond, 2011) or exotic grasses control (Assis et al., 2020). However, most of these techniques were applied pioneeringly, adapting strategies used to restore temperate grasslands. Although these techniques often represent the best techniques practitioners can access, they are applied in the context of an ongoing deficiency in our understanding of the ecological functioning and biodiversity in these tropical grasslands and savannas relative to temperate grasslands or tropical forests. Thus, they can often lack the potential to fully restore the different tropical open ecosystems' growth forms and functioning (Buisson et al., 2019).

To successfully assess restoration outcomes, it is necessary to evaluate how much of the biodiversity, ecosystem services, structure, and functioning have been recovered compared to well-conserved reference areas (Marchand et al., 2021). Critically, we must assess whether the restoration techniques applied are resulting in ecosystems closer to old-growth reference ecosystems or closer to degraded areas (anthropogenic grasslands or derived savannas) (Benayas et al., 2009; Marchand et al., 2021). For old-growth grasslands and savannas, each component embedded in their rich ground layer has a vital role in the ecosystem's functioning and resilience. For example, C4-grasses promote fire feedback which controls woody species density, maintaining the ecosystem in an open state (Bond, 2021). Shrubs and subshrubs quickly resprout and colonize after natural disturbances and are highly resilient to anthropogenic perturbations (Faleiro et al., 2022; Pilon et al., 2021); this component also stores a substantial proportion of its total carbon stocks underground, where they are permanently protected (Pausas et al., 2018). The diversity of forb species and their flowers regulate pollinator dynamics, maintaining their populations in the landscape (Oliveira & Gibbs, 2002), *e.g.*, providing resources for bees to forage throughout the year, due to the diversity of phenological patterns. Successful restoration aiming to recover biodiversity or ecosystem services must consider the reintroduction of all growth forms found in old-growth grasslands and savannas. If this simple indicator (i.e., diversity of growth forms of target species) works as a surrogate for a plethora of ecosystem functions and services, this relationship should be further considered in restoration actions and monitoring.

Restoration initiatives aimed at recovering Cerrado open ecosystems have increased exponentially (*e.g.*, Assis et al., 2020; Ferreira et al., 2015; Pellizzaro et al., 2017). Such initiatives represent a significant advance in the science of restoration for tropical open ecosystems. Knowledge about the ecology of these ecosystems, although incipient, has also progressed substantially in the last decade (e.g., Buisson et al., 2019; Lira-Martins et al., 2022; Pausas et al., 2018). Cerrado is a global hotspot for biodiversity conservation and should be considered a high priority in the UN Decade on Ecosystem Restoration, alongside other tropical grasslands and savannas (Dudley et al., 2020; Myers et al., 2000). Hence, a critical assessment of the effectiveness of the current restoration techniques is the next step to advance Cerrado restoration, guide future research, and improve existing restoration techniques.

In this study, we aimed to assess the success of restoration techniques applied in Cerrado open ecosystems to recover plant diversity. By analyzing 82 data sets obtained from published articles, theses, and field collection, we evaluated how different restoration techniques have succeeded in bringing back typical species from Cerrado open ecosystems. As the biodiversity of target species may increase with time, the age of the restoration intervention might be an issue in the analyses. To check this assumption, we first analyzed two chronosequences representing two common land uses in the Cerrado after abandonment (eucalypt plantation and pastures with exotic grasses). So, specifically, we intended to answer: (i) How biodiversity of target species changes through time in areas subject to passive restoration? (ii) Are active and passive restoration techniques efficient in restoring the proportion of target species found in old-growth reference ecosystems? (iii) Have the current techniques been successful in bringing back the main growth forms found in cerrado open ecosystems? We defined target species as those with preferential habitat being old-growth native ecosystems (i.e., sun-loving and shade-intolerant species, usually not found in anthropogenic ecosystems), not including exotics or ruderal species (i.e., plant species of broad geographic distribution, and, importantly, which occupy and proliferate particularly in human-modified environments) (Aronson et al., 2011). Passive restoration was defined as spontaneous natural regeneration of a degraded or human-modified ecosystem after ceasing economic land use without deliberate human intervention (management or species introduction), and active restoration as a set of techniques to introduce propagules in areas under restoration (Aronson et al., 2011).

Materials and Methods

We conducted a quantitative synthesis of the restoration treatments usually applied to degraded Cerrado open ecosystems, as well as a characterization of conserved reference ecosystems, based upon extensive literature search, supported by equally extensive data collection in the field. Combined, the literature search and field data collection constituted 82 data sets (37 from literature and 45 from field collection) (see Table S1). Among the restoration techniques analyzed were direct seeding, plant-material transplanting, tree-seedlings planting, and passive restoration after use as pasture or afforestation with pine and eucalypt trees.

Literature review

We surveyed published articles and theses addressing different restoration techniques for open Cerrado vegetation in the databases available (Scopus, Web of Science, ScienceDirect, PubMed, Google Scholar). To be incorporated into our database, the following criteria were applied: (i) restoration was performed in areas that were open ecosystems (cerrado grasslands or open savannas) before land conversion or degradation occurred, (ii) the study presents at least a list of species introduced, and (iii) describes the site history and the restoration technique in sufficient detail. Techniques were excluded from the analysis if they were not applied in at least three separate study areas. Sites originally occupied by rupestrian and wet grasslands were also not included. Several studies collected data in the same restoration area, therefore, we did not consider more than one publication about the same restoration initiative. Details for each data set considered here are presented in Table S1. A lack of standardized sampling procedures among studies turned impossible to compare changes in plant community structure (e.g. ground cover, biomass or even species richness). Instead, we analyzed community composition in terms of species and growth forms, which could be obtained from a majority of the studies and is a good surrogate for vegetation structure and diversity.

Data collection in the field

Studies presenting data from reference ecosystems or control plots were rare. Consequently, to assess restoration success relative to a reference ecosystem for these studies we sampled several pristine Cerrado open ecosystems representing the regions where the restoration interventions were implemented (see Figure S1). We, therefore, assumed that the proportions of target species and growth forms follow standards for conserved open ecosystems in the Cerrado and would provide a reliable comparison.

Data collection for the 13 conserved areas was performed in four Brazilian States (São Paulo, Paraná, Mato Grosso do Sul and Goiás) across the Cerrado ecoregion (Figure S1 and Table S1) (authorization for data collection according to Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio, Sisbio numbers: 77272-3 and 53328-2). We selected natural remnants free from exotic species and other sources of degradation; all areas were characterized as cerrado grassland (*campo cerrado*) - dominated by a rich herbaceous ground layer with few scattered shrubs and trees, with < 20% canopy cover. We focused on areas with < 20% canopy cover because these ecosystems are the most threatened and the hardest to recover (Durigan & Ratter 2006; Pilon et al., 2018, 2019).

For the restoration techniques to be sampled in the field, we selected: (i) two areas subject to direct seeding in 2016 and 2018 in the National Park of Chapada dos Veadeiros (PNCV, at Goías state); (ii) one area restored by grass tussock transplanting at Santa Ecological Station (EEcSB, at São Paulo state); and (iii) two areas where passive restoration has been conducted after eradication of former pine plantation at EEcSB and Ecological Station of Itirapina (also in São Paulo state) (Table S1). In each area, restoration sites and in undisturbed open ecosystems in the Cerrado, we performed a floristic characterization following the "quick survey" method. This method consists in carrying out at least three walks in a straight line across the vegetation 500 m apart from each other, sampling during regular time intervals the floristic composition (see details Walter & Guarino 2006). The walks were performed in homogeneous vegetation patches, and in our sites, up to three straight-line walks were necessary. In each straight line, sampling stopped when less than five species were added in two consecutive intervals of 15 minutes.

The species lists for areas in natural regeneration after eucalypt plantation were obtained from 19 former eucalypt stands, differing in the time lag since eucalypt clearcutting (unpublished data) (Table S1). In October 2019, permanent plots were established in each area (221 plots in total, of 25 m x 4 m), resulting in 19 lists of plant species (all growth forms included). In addition, three unpublished lists from abandoned pastures of different ages were also added to our data set, collected in 15-permanent plots of 25 m x 4 m (details Table S1).

Data analyses

The restoration interventions were classified as active restoration (direct seeding: 6 sites; transplant of plant material: 4 sites; topsoil transposition: 7 sites; and planting of tree seedlings - henceforth, tree planting: 5 sites), passive restoration (after cultivated pastures with exotic species: 25 sites, and after silviculture of eucalyptus or pine trees: 22 sites) and pristine sites (13 sites, old-growth reference ecosystems). From the 82 data sets, we extracted species lists to check the current nomenclature (Flora do Brasil 2020) and to verify the geographic distribution of the species, in search for possible identification inaccuracies (at Flora do Brasil 2020 and SpeciesLink 2022), resulting in 1232 species being identified (8% were not identified at species level). For each species, we searched for (i) growth form (forb, grass, shrub, subshrub, trees, and climbers), and if (ii) target or non-target for restoration. These classifications were based on field observations, specialized literature and data bases for species description and distribution (Sano et al., 2008; Durigan et al., 2018; Flora do Brasil, 2020; SpeciesLink, 2022) (see Table S2).

We calculated the proportion of target species for each restoration technique and pristine site. The option to work with proportions rather than total numbers of target versus non-target species at each site aimed to reduce the impact of different sampling efforts among studies, which directly affects the total number of species recorded. Thus, the proportion of target species represents a standardized metric of restoration success in terms of how much a technique can recover the proportion of typical species in general and in terms of growth form considering the values registered in the pristine sites.

To answer our first question, we modeled the proportion of target species through time: (i) 19 sites of former eucalypt plantations, ranging from 7 to 13 years after clearcutting and posterior abandonment, and (ii) 21 sites used as pasture with exotic species, ranging from 2 to 27 years after abandonment. Using beta regression models, by *betareg* package (Cribari-Neto & Zeileis, 2010), we tested for tendencies of increases or decreases in the proportions of target species, considering (i) only silviculture and (ii) only pastures.

For the second and third questions, effect-size analyses were performed to compare the restoration techniques with the reference values (conserved areas) (Hedges et al., 1999). Comparisons were made using the log response ratio, considering the following formula: ln (Restoration/X). Where X represents average values found in conserved ecosystems (ln (Restoration/Reference)) or average values of the passive restoration (ln (Active restoration/Passive restoration)) (Benayas et al., 2009). Effect size analyses were made using the R package *metafor* version 3.0-2 (Viechtbauer, 2010) using the *escalc* function weighting the average values by both sample size and variance, considering all species, and then separately by growth forms. Negative values denoted an inferior outcome in the reported restoration efforts compared to the reference values, and positive values represent an increase in the outcome regarding the reference values. To be similar to the reference, confidence intervals should comprise zero. All analyses were performed R version 4.1.1 environment (R Core Team, 2021).

Results

Chronosequence of passive restoration after different land uses

Target species proportions do not increase with time, suggesting limitations to typical species colonizing the degraded sites (Fig. 1). Areas previously used as eucalypt plantation have fewer proportion of target species (26% on average, Fig. 1a) than areas used as pasture with exotic grass species (43% on average, Fig. 1b). However, no restoration site reached the proportion of target species found in reference sites (82%), except for one abandoned pasture where the proportion of target species reached the reference values 12 years after the abandonment (82% of target species, Fig. 1b).

Plant diversity recovery by different restoration techniques

A broad view of the results showed a total of 712 species recorded in reference ecosystems, from which 338 were not sampled in any restoration site (47%). Of these, 85% were target species. Conversely, 520 species were recorded exclusively in restoration sites (68% non-target species), being absent in reference sites.

When comparing the effectiveness of different techniques in bringing back the proportion of target species found in the reference ecosystems (82% ± 10% SD), despite the significant variance in the dataset (Fig. 2a), we found that only the transplant technique was successful (63% ± 18% SD). Comparing the active techniques with passive restoration (proportion of target species 38% ± 19% SD), the introduction of seed (63% ± 17% SD) and transplant of plant material both improved the restoration outcomes (Fig. 2b).

Different restoration techniques have different effects on the recovery of the proportion of target species. However, no single technique could restore all growth forms. Considering typical forbs, only the transposition of topsoil (13% ± 11% SD) and transplant of plant material (10% ± 7% SD) were able to approximately reach reference values (18% ± 10% SD) (Fig. 2c). The proportion of target grasses did not significantly differ from the reference (18% ± 5% SD) for direct seeding (15% ± 12% SD), topsoil translocation (15% ± 10% SD), and transplant techniques (20% ± 9% SD) (Fig. 2d). However, in areas subject to tree planting, no target grasses were reported in the studies analyzed. For shrubs, the proportion was similar to the reference (14% ± 4% SD) in most techniques analyzed, except for topsoil translocation (5%± 6% SD) and tree planting (7% ± 3% SD) (Fig. 2e). For subshrubs, only the transplanting technique (15% ± 10% SD) could restore target species at the proportions found in pristine ecosystems (24% ± 8% SD) (Fig. 2f). The ratio of trees was greater than in the reference ecosystems in most restoration interventions analyzed. Topsoil translocation (5% ± 9% SD) and transplant (8% ± 4%SD) techniques did not differ from the reference for this growth form (6% ± 4% SD), despite showing high variability (Fig. 2g). For climbers, only pasture (0.8% ± 1% SD) and silviculture (0.2% ± 0.3% SD) presented target climber species, with pasture not differing from the reference (0.7% ± 0.7% SD) (Fig. 2h).

Discussion

Several techniques to restore Cerrado vegetation have been developed in the last decades. Here we present an assessment of how much these techniques can help recover plant species and functional composition (*i.e.*, growth forms) of open ecosystems. We found that the restoration techniques currently applied to recover biodiversity of Cerrado open ecosystems are not reaching the reference standards regarding growth forms and taxonomic composition, resulting in recovery debts considering pristine sites as a reference. Almost half the species recorded in reference ecosystems – mostly target species – have not been successfully introduced to restoration sites. The low potential for natural regeneration after land conversion or limitations in seed germination and dispersal, seedlings production and survival in the field are major constraints to be overcome in the restoration of Cerrado open ecosystems. It is also worrisome that almost half the species recorded in restoration sites were not observed in reference ecosystems, most of them being ruderals or exotics. Each technique brings a different set of growth forms, but no single technique is able to restore all growth forms. The different growth forms have different roles in determining the structure, functioning, and resilience to anthropogenic and natural disturbances of the cerrado open ecosystems (Pilon et al., 2021; Teixeira et al., 2021). Thus, a mix of techniques can better recover the target species proportions found in conserved areas.

Chronosequence after two different land uses

Target species proportions do not increase with time, suggesting limitations to typical species colonizing the degraded sites. There are three important findings from the models performed. Firstly, passive restoration supports a limited and constant number of target species (Fig. 1). The number of target species will depend on the magnitude of degradation and potential for natural regeneration via bud banks (Cava et al., 2018; Haddad et al., 2021; Marchand et al., 2021). Eucalypt plantation requires soil ploughing, liming and fertilization, besides creating a shaded environment, leading to a much lower proportion of target species (Fig. 1a), compared to abandoned pastures, where light is abundant and traditional soil management does not involve soil tillage, preserving typical woody Cerrado species (Cava et al., 2018; Haddad et al., 2021). Secondly, time will not favor the entry of typical native species (Fig. 1c). Therefore, active restoration techniques are necessary if there is no natural regeneration potential or if increasing the number of target species is desirable. Several studies have shown that species from tropical grasslands and savannas have a slow assembly (Nerlekar and Veldman, 2020). Without intervention, these ecosystems cannot recover the biodiversity, structure, and consequently the functioning of pristine areas (*e.g.*, fire resilience, species interactions, carbon and nutrient cycling, and rain infiltration). Only woody species with deep and complex underground storage organs can resist the land use practices for pastures with exotic species and silviculture, especially if they are intensive (Fig. 2e and g) (Cava et al., 2018; Faleiro et al., 2022; Haddad et al., 2021). Lastly, if target species fail to arrive, the desired final composition of the system undergoing restoration depends on their active introduction. In other words, we shouldn't expect cerrado open ecosystems to have a directional ecological succession as predicted for forest ecosystems (Silveira et al., 2020; Zaloumis & Bond, 2011).

Success of different restoration techniques

Transplant of plant material was the best technique to recover the proportion of target species in Cerrado grasslands. This technique is based on transplanting underground structures (typically alongside soil) and entire plants from a conserved area to the area undergoing restoration. Usually, whole communities are transplanted when the donor site (conserved area) is going to be converted to another land use (Ferreira et al. 2015, Pilon et al. 2019). Although perhaps unfeasible for large-scale restoration (i.e., one would need to convert a lot of land to restore a lot of land), there is scope to develop techniques to enable sustainable harvesting from native areas, to supplement other restoration techniques, since the donor ecosystems can quickly recover after the extraction (Pilon et al. 2019). Contrary to existing mainstream understanding on restoration, tree planting was the worst restoration technique, because the planting approach usually replicates forest restoration techniques, with no attempt to introduce growth forms other than trees. Despite how obvious this point may seem, tree planting is still widely used and proposed as a restoration technique across tropical grassy biomes (Veldman et al. 2015). The outcomes are even worse because trees have been planted at much higher density than they naturally occur in open reference ecosystems, resulting in higher-than-expected woody biomass and canopy cover (Haddad et al. 2021). Furthermore, we found trees exceeding the reference proportion for this growth form in almost all techniques assessed, except for topsoil translocation and transplant. This may be caused by ongoing woody encroachment in areas under passive restoration, even considering only target species in the analyses. In the absence of fire, even the typical tree species from savanna ecosystems can be a starting point for the woody encroachment process (see Abreu et al., 2021). Also, introducing a large proportion of tree species in direct seeding and tree seedlings planting can be a factor behind the high proportion of trees found. And finally, our reference sites were Cerrado grasslands and savannas with few scattered trees. If we select denser savannas as the reference, the results would be different, being the proportion of target tree diversity depending on the restoration goal. Furthermore, it is important to highlight that if trees and shrubs can recover through natural regeneration, then it is not necessary to introduce them (Cava et al., 2018). Resources can be optimized by introducing species that will not colonize the area under restoration (*i.e.*, grasses, forbs, subshrubs). The same applies to target climbers found only in passive restoration techniques. Of course, this decision will depend upon a careful assessment of the potential for natural regeneration of the degraded site, which will be case-dependent.

Different techniques provide distinct outcomes in the recovery of target species from different growth forms. Forbs benefited from topsoil transposition, highlighting the importance of soil seed banks for these species. Despite the soil seed bank being considered transient and species-poor in Cerrado (Buisson et al., 2019), we demonstrated that it could bring back key target species. It can also inoculate endemic microorganisms that can help native species to establish in degraded sites (D'Angioli et al., 2022; Martins et al., 1999). Furthermore, the transplant technique could bring subshrubs diversity, approximating the growth forms proportionality to that of reference ecosystems. This is an essential outcome expected for grasslands and savannas restoration since subshrubs are correlated with resilience after disturbance and underground carbon stocks (Bombo et al., 2022; Pausas et al., 2018; Pilon et al., 2021).

Future directions

Our findings showed that we are still far from restoring tropical grasslands and savannas in the stricter sense of the word "restoration" (Buisson et al., 2019; Zaloumis & Bond, 2011). Here, we could only analyze biodiversity in terms of the proportion of target species and their growth forms. We believe that the results could show much more about the recovery debt if we could directly assess data on community structure and richness (for some examples, see: Cava et al., 2018; Haddad et al., 2021; Zaloumis & Bond, 2011). Given this, we summarize some directions to guide future tropical grasslands and savannas restoration studies and actions, especially in the UN Decade on Ecosystem Restoration:

(i) *If the desirable species do not spontaneously arrive, we must introduce them.* The most successful techniques all depend on availability of well-conserved areas (source ecosystems) to provide material such as transplants, topsoil, seeds. A mix of techniques sounds like a promising solution to increase the diversity of growth forms reintroduced and, consequently, re-establish the functioning and

resilience of tropical open ecosystems. However, reducing the dependence and pressure on the few conserved remnants is necessary. Using them as donor sites for propagules (transplant or topsoil) is an alternative only for restoring sites inside protected areas or when a pristine ecosystem is going to be converted (which should be avoided at all costs). So, alternatives shall be created, such as farms specialized in producing seeds, native seedlings, and underground structures, increasing the available native seedlings production in commercial nurseries for all growth forms of target species (Oliveira et al., 2020).

(ii) *Provide guidelines on which plant species to introduce and in which proportions*. Considering the strong limitations for propagation of most target species (Buisson et al, 2021), planting all of them is not a feasible goal. Selecting species, therefore, requires criteria. Ideally, we should use the proportions of the target species and growth forms found in appropriate reference ecosystems (*i.e.*, considering the vegetation structure, soil properties, and natural disturbance dynamics). We are focusing on proportion because it is better to have a few target species representing each growth form of the pristine sites, than several ruderal and generalist species. Growth forms and their associated diversity of underground structures and responses after disturbance can help to restore resilient ecosystems (Bombo et al., 2022; Pilon et al., 2021). Here, we presented the proportion in terms of species richness, but ecological indicators of community structure are needed (e.g., species abundance, vegetation height, species/m^2) (Buisson et al., 2019; Dudley et al., 2020).

(iii) *Long-term monitoring restoration interventions and cost assessment.* Future studies assessing the structure, functioning and ecosystem services provided by restored open ecosystems based on standardized indicators would be welcome.

That includes the necessary assessment of plant invasion, one of the major obstacles to restore and conserve open ecosystems in the tropics. Cost: effectiveness analyses are also desirable to inform restoration planning and the decision-making process regarding neglected open ecosystems.

(iv) *Reference and control matters.* “If you don’t know where you want to go, then it doesn’t matter which path you take” (Lewis Carrol, Alice’s Adventures in Wonderland, 1865). Even if restoring ecosystems to what they were before degradation is an unfeasible target, pristine ecosystems are the basis for learning how to bring back resilient ecosystems. Having clear goals to advance restoration ecology in a world subjected to rapid and unpredictable environmental changes is crucial. Although we may not ever fully recover the historical reference ecosystem, their descriptors allow us to assess how far we are from the pre-existing biodiversity, ecosystem services and functioning. Even the restoration actions that aim to deliver ecosystem services must be based at least on some attributes found in reference sites (*e.g.*, vegetation structure, species interactions, nutrient cycling). Also, we can only truly assess the restoration outcome by establishing control areas (without any active intervention). Otherwise, it is impossible to know if “doing nothing is better than any intervention” or if the intervention shifts the ecosystems to another degraded state. During the literature review, we realized that the importance of reference and control sites/treatments has been neglected or misunderstood, with several studies lacking completely these important components (Guerra et al., 2020).

Conclusion

Here we showed whether the current restoration techniques can recover the proportion of target species of open cerrado ecosystems by considering pristine areas as reference sites. We acknowledged all the limitations of the comparisons but also realized that this assessment provided us clear directions to plan the next steps in tropical open ecosystems restoration. We cannot disregard that investing resources for conserving those tropical open ecosystems still remaining will always be preferable to bargaining their destruction by restoration elsewhere. We have much to learn about the diversity and functioning of these ecosystems and restoring what has been lost needs pristine sites as models and as propagule sources. Second, active restoration is necessary, but no technique alone can bring all the diversity and functioning of Cerrado open ecosystems. It is time to mix efforts and techniques to optimize the outcomes of open ecosystems restoration instead of searching for a panacea.

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Conflict of Interest Statement

The authors declare no conflict of interest. Also, Dr. Isabel Schmidt is an Associate Editor of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper

Author Contributions

Natashi A. L. Pilon and Rafael S. Oliveira conceived and designed the research. Natashi A. L. Pilon, Bruna Helena Campos, Giselda Durigan, and Mário G. B. Cava collected the data. Natashi A. L. Pilon analyzed the data and wrote the paper. Giselda Durigan, Rafael S. Oliveira, Lucy Rowland, Isabel Schmidt, and Alexandre Sampaio contributed to the interpretation of data and revised the paper critically. All authors revised the paper and gave final approval for publication.

Data accessibility

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.05qfttf6v (Pilon et al., 2023).

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Figure 1. Temporal trajectories of the proportion of target species of Cerrado open ecosystems being recovered through passive restoration after different land uses. (a) Eucalypt silviculture (Pseudo-R^2 = 0.002, Z = -0.19, P = 0.85), and (b) Pastures (Pseudo-R^2 = 0.01, Z= -0.49, P = 0.71). Redlines represent average values for pristine areas (reference sites, 82% of target species) and dashed gray lines represent 95% confidence intervals.

Figure 2. Effect size of different restoration techniques in recovering the target species proportions of open cerrado vegetation. (a) All species were compared to the reference values, (b) All species were compared to the passive restoration values. Following are different growth forms compared with reference values: (c) forb species, (d) grass, (e) shrub, (f) subshrub, (g) tree, and (h) climber. Boxes represent the mean effect size with 95% confidence intervals for each variable (the mean and confidence interval values on the right side), and different box sizes are related to the data variance. Vertical dashed line represents the conserved areas, except in figure (b), which is the passive restoration

values. RE (Random Effect) model: Diamond represents the pooled effect size and 95% confidence intervals (Plant symbols source: Integration and Application Network ian.umces.edu/media-library).

Supporting information:

Figure S1: Sites distribution across cerrado ecoregion. Due to proximity, some points were hidden, but the total areas for each technique are described in the legend. The up-left map are showing the Cerrado distribution and the red rectangle represents the bigger area where sites are located.

Table S1: Restoration techniques and reference sites' information. Time in years represents the age since abandonment for passive restoration after cessing land use.

Table S2: Species occurrence in the restoration techniques and reference, classified in target and non-target species and growth forms.