A research agenda for the restoration of tropical and subtropical grasslands and savannas

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Running title (3 to 6 words): **Research agenda for tropical grassland restoration**

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Abstract

Despite growing recognition of the conservation value of grassy biomes, our understanding of how to restore biodiverse tropical and subtropical grassy biomes (grasslands and savannas; TGB) remains limited. Several tools have recently been identified for TGB restoration including prescribed fires, appropriate management of livestock and wild herbivores, tree cutting and shrub removal, invasive species control and the reintroduction of native grasses and forbs via seeding or transplants. However, additional research for improved TGB restoration is needed. This paper aims to identify ecological research priorities for TGB restoration. The following points are crucial to scale up TGB restoration and meet the challenges of the UN Restoration Decade. Research should focus on: disentangling the reasons why TGB are often undervalued and misunderstood; mapping TGB restoration opportunities; identifying regions where TGB and other biomes naturally exist as alternative stable states; recognizing areas with natural regeneration potential to avoid unnecessary intervention; restoring soil conditions; disentangling factors driving low seed quality, determining germination requirements and developing vegetative propagation techniques for TGB species; disentangling the limiting factors and key ecological processes underlying seedling establishment and community assembly; improving and validating long-term management to mimic natural disturbance regimes; setting the minimum

attributes of desirable TGB in terms of structure, composition, functioning and resilience; and improving monitoring of restoration outcomes. Such research has the potential to advance theory, policy and practice in TGB restoration, ultimately resulting in long-term benefits for people and nature in some of the more neglected ecosystems of our planet.

Keywords: grassy biomes; old-growth grasslands; tropical old-growth grassy biomes; grasslands; savannas; woodlands

Conceptual implications

- TGB restoration cannot be upscaled if these ecosystems remain poorly known and undervalued, if their ecosystem services are not perceived or realized, and if the representation of restoration opportunities remains misleading.
- Low seed quality, germination and plant establishment must be investigated and overcome using innovative technologies to enhance restoration practice.
- Plant propagation techniques must be developed to facilitate the reintroduction of the large proportion of TGB species whose populations do not readily regenerate from the seed bank or seed rain.
- Critical research also includes finding the best practices for site preparation to preserve/recover soil properties in sustainable TGB restoration.

- Monitoring should be evidence-based to assess whether desirable structure, composition, functioning and especially resilience of a TGB have been recovered.

Introduction

International incentives in the last decade have brought ecological restoration to the forefront of proposed solutions to mitigate the impact of ecosystem degradation worldwide (Temperton et al. 2019). Ten years ago, the UN Convention on Biological Diversity proposed that 15% of degraded ecosystems be restored by 2020 (CBD 2011), whereas the Bonn Challenge aimed specifically at “restoring” (i.e., reforesting) 150 million hectares of the world’s deforested and degraded land by 2020, and 350 million hectares by 2030 (IUCN-DC 2011). These initiatives were subsequently endorsed by the New York Declaration on Forests at the 2014 UN Climate Summit (Climate Summit 2014) and by the UN Sustainable Development Goals (IRP 2019). Recently, the UN Environment Program declared 2021 – 2030 to be the “*UN Decade on Ecosystem Restoration*” (UN-Environment Programme 2019). Unfortunately, such policies are strongly forest- and tree-oriented, overestimate the potential of tree planting as a means of climate mitigation (Veldman et al. 2019), and do not fully acknowledge limits linked to forest stability and important ecological and climate-related risks (Anderegg et al. 2020). The intense pressure to afforest has even been identified as a major threat to non-forest ecosystems and human livelihoods (Johansson et al. 2020, Tölgyesi et al. 2020; Fagan 2020), and provides a compelling reason for establishing a detailed research agenda for the restoration of overlooked and misinterpreted open ecosystems (Temperton et al. 2019), including tropical grassy biomes.

Upscaling restoration, however, is challenging as it requires knowledge of natural ecosystems and their socio-economic context, and solid links between science and practice

(Miller et al. 2017; Cooke et al. 2019; Gann et al. 2019). Major hurdles limiting appropriate restoration and management of old-growth tropical and subtropical grasslands and savannas (TGB i.e. Tropical Grassy Biomes) have been recently identified (Buisson et al. 2019), yet it is unclear how to achieve the deeper scientific knowledge necessary to overcome such hurdles. TGB are megadiverse, ancient ecosystems with a continuous herbaceous cover composed of graminoids and forbs, with or without scattered shrubs and trees (Veldman et al. 2015). TGB are largely threatened by agricultural conversion, opencast mining, anthropogenic increases in or suppression of fires, mismanaged livestock, wood extraction, invasive species, and afforestation (Veldman et al. 2015). Such threats compromise biodiversity, ecosystem functioning, and human livelihoods. Owing to large knowledge gaps and widespread misconceptions concerning their basic ecology (Silveira et al. online early; Bond 2019), large-scale restoration in these key ecosystems is not yet feasible, despite their rich biodiversity, provision of ecosystem services and direct support of human livelihoods. Clearly, international agreements should recognize and endorse the fact that forests are not the only ecosystems in need of restoration, to make funding and government incentives available for the restoration of open ecosystems. Additionally, limited knowledge of the ecology and restoration of TGB reinforces the need for prioritization of research efforts to support and foster practices aimed at accelerating TGB restoration.

Here we propose a research agenda to guide research priorities for TGB restoration. We identify emerging issues across broad themes in restoration to structure questions aimed at optimizing practical restoration outcomes (Miller et al. 2017; Figure 1). Our focus is on the ecological dimensions of restoration ecology, but we also recognize the need for similar efforts towards socio-ecological dimensions of restoration (*sensu* Perring et al. 2015). Most of the questions we identify are from the perspective of the vegetation, but we also address some priority issues concerning herbivores in tropical grassy biomes.

Changing perceptions on Tropical Grassy Biomes (TGB)

Misunderstandings and misconceptions concerning the ecology of open ecosystems (Bond 2019, Fagan 2020) have led to pristine TGB being confused with degraded or secondary grasslands (e.g. TGB transformed to pastures) or with derived grasslands and savannas (e.g. grasslands derived from the degradation of forests), with subsequent recommendations for restoration directed at tree planting (Silveira et al. online early; Schmidt et al. 2019a; Figure 2). TGB are often thought to be by-products of forest degradation, despite clear criteria for identifying TGB being available (Veldman et al. 2015). Such misidentification of TGB results in ill-conceived restoration policies, including afforestation (Veldman 2016; Bond 2019). TGB have been demonstrated to be slow to recover if degraded by exogenous disturbances (Nerlekar & Veldman 2020).

Disentangling the reasons why TGB are often undervalued and misunderstood (Parr et al. 2014; Veldman et al. 2017) is a major research question which cannot be tackled by restoration ecologists alone, but calls for integration with environmental sociology. This research is likely to provide conditions to change the historical prejudice against open ecosystems (Bond 2019) that will promote best restoration practices and policy. Such a changed perspective can also be supported by better communication of the high benefit-cost ratios of TGB restoration (De Groot et al. 2013) and by the plethora of ecosystem services provided by restored ecosystems (Morecroft et al. 2019). Restoration benefits and costs should be identified regionally to provide support for practical decisions in TGB restoration. Socio-ecological research is needed to demonstrate the value and importance of the ecosystem services provided by TGB (Bengtsson et al. 2019), which can include, but should not be limited to carbon sequestration, which is the standard approach used in forested landscape restoration initiatives.

Defining TGB restoration opportunities and targets

Restoration opportunities

Identifying restoration opportunities for TGB requires: 1) information on the distribution of TGB, as well as degraded and derived grasslands at different scales, 2) finer-scale information on the distribution of TGB and 3) potential socio-economic constraints to feasibility, all of which can be mapped. Setting restoration priorities entails valuation of restoration benefits to society and using scientific evidence to make appropriate, informed and transparent prioritization decisions.

1) A critical step to adequately plan restoration is to have reliable information on the distribution of different grassland types, information that is not readily available in many tropical and subtropical regions. Ideally, mapping the global and regional distribution of grasslands should be aligned with mapping the distribution of forests, thus avoiding the kinds of overlap pointed out by Veldman et al. (2015). Careful planning for TGB restoration includes proper identification of: i) pristine TGB as reference ecosystems; ii) degraded TGB which constitute restoration targets; and iii) degraded forests converted to derived grasslands and savannas which constitute reforestation targets. Mapping these three ecosystem-types using remote sensing data derived from satellites should provide important information for regional and global analyses. However, because of their temporal and spatial resolution limitations, remote sensing techniques may not be precise enough and fail to distinguish TGB from degraded and derived grasslands (Veldman & Putz 2011). The recent GEDI - Global Ecosystem Dynamics Investigation - provides a powerful option to identify the complexity of TGB. First, it uses a high-resolution laser that allows quantification of the vertical distribution of vegetation and estimates variables including surface topography, canopy height and cover metrics, and vertical structure metrics (Dubayah et al. 2020). Second, GEDI-derived data can be downloaded for free. The feasibility of using both vertical and horizontal information to facilitate floristic differentiation and allow the separation of TGB from degraded and derived grasslands needs to be empirically tested. Remote sensing assessments should be coupled with *in situ* biodiversity assessments to calibrate the models and produce a reliable global map of TGB restoration opportunities. Large-scale mapping should also

incorporate spatial autocorrelation and spatial structure data to improve the predictive ability of mapping opportunities for restoration at the global scale (Ploton et al. 2020).

2) In many regions, TGB are composed of multiple grass-dominated ecosystems found in mosaics including woody vegetation types (Sankaran et al. 2005): i) forming a continuum from grassland and savanna to closed-canopy woodland and forests; ii) representing mosaics of natural alternative stable states in the landscape (Bond 2019); and iii) characterizing patterns due to edaphic factors or disturbance (Buisson et al. 2019; Le Stradic et al. 2015a; Figure 3). Each grassland type should be restored where it belongs, recreating mosaics to restore biodiversity and services at the landscape-scale, and maintained using management or natural disturbances.

3) Restoration opportunities are often constrained by environmental legislation, social will and available resources to implement restoration. Therefore, socio-ecological benefits should also be mapped and integrated in the definition of restoration opportunities (Brancalion et al. 2019). Funds for landscape-scale restoration have increased more rapidly for forest than for non-forest ecosystems (Veldman et al. 2015; Overbeck et al. 2015). Since fund availability changes quickly in space and time in unpredictable ways, frequent updating of this information is required.

Setting restoration targets

Identifying pristine ecosystems as references is challenging for TGB restoration because i) they are old-growth ecosystems and their restoration is often unachievable on human timescales (Veldman et al. 2015); ii) pristine ecosystems of a particular region may no longer exist; and iii) the highly dynamic nature of ecosystems (Higgs et al. 2018), particularly in response to periodic disturbance, hinder simple restoration targets. Nonetheless, identifying a reference ecosystem (or preferably a regional range) is critical in restoration planning. In many situations, finding a reference ecosystem is challenging where alternative stable states naturally exist, opening the possibility of restoring any of a range of savanna-forest transition states in the landscape (Bond 2019). Setting restoration goals for a particular project also requires discernment between what is desirable and what is possible under the local constraints and the needs of local communities (Ehrenfeld 2000). Ideally, restored ecosystems should be structurally similar to the reference ecosystem, be composed by a subset of species from the regional pool, and have sufficient functional diversity to sustain ecosystem functioning. It is crucial for these restored TGB ecosystems to be resilient to endogenous disturbances (i.e. disturbances that are part of the evolutionary history and internal dynamics of a system). Optimizing goal-setting for TGB restoration relies on multidisciplinary research aimed at: i) identifying the pre-existing vegetation type under the same climatic conditions; ii) recognizing potential alternative stable states and disrupting internal feedbacks to allow the transitions from degraded to the desirable states (Suding et al. 2004); iii) diagnosing the potential for natural regeneration before deciding to intervene (Zahawi et al. 2015; Meli et al. 2017) given the unclear relative (cost-)effectiveness of passive *versus* active restoration in TGB; and iv) defining fundamental attributes for the TGB to be restored.

Developing techniques to restore soil conditions

When degradation entails total or partial loss of desirable soil characteristics, earthwork may constitute the first restoration step, as in cases of post-mining restoration. While re-profiling mine sites is often done (Figure 4), restoring hydrological processes (including restoring soil infiltration capacity or reducing surface runoff), soil structure (the degree of aggregate stability), chemical properties and microbial ecology (decomposition and nutrient cycling) are poorly studied for TGB.

Soil aggregation is the result of soil biota and their organic products, and a driver of soil water movement and retention, erosion, crusting, nutrient recycling, root penetration and productivity (Bronick & Lal 2005). Soil aggregate stability is often degraded by management or restoration interventions, such as soil tillage (Plante & McGill 2002), so understanding how to restore soil aggregation in TGB, aiming at preserving both soil biota and hydrological processes, is key to improve restoration success.

For less extreme degradations, soil preparation may be the first step in restoration. Tilling may efficiently break sealed soil surfaces (Kinyua et al. 2010; Figure 5) and topsoil removal may reduce the seed bank of undesirable species (Pilon et al. 2018; Sampaio et al. 2019). Creating microtopography can contribute to reduced soil erosion and increase the capture of soil and seeds from the surrounding landscape (Kimiti et al. 2017). Overall, however, benefits and potential negative consequences of soil preparation have seldom been studied in TGB. Little is known about the effect of these practices on biological soil crusts. Techniques should be tested more widely, diversified (e.g. soil inversion), and compared. Many TGB species have a bud bank or underground storage organs that confer resilience to aboveground endogenous disturbances such as fire and herbivory (Figure 6). Therefore, disrupting the soil is advised only if the degradation has already largely eliminated the underground component of the vegetation (Buisson et al. 2019). If the soil has not been disturbed or compacted, soil preparation is likely to be inappropriate, as it will hamper recovery from the seed and bud bank. Fertilization degrades many TGB on nutrient-poor soils (Harpole et al. 2016) and techniques to reduce soil nutrients, such as mowing and exporting biomass, carbon amendment, and grazing (Sitters et al. 2020) warrant further exploration. In sum, restoring the physical and chemical properties of soils may be the key first step to restore an important ecological filter that impacts community assembly and desired restoration goals such as resilience and ecosystem functioning (Figure 5).

Reintroducing native species from seed

Extensive knowledge gaps in basic seed biology of TGB species severely limit our capacity to use seed-based restoration strategies. Landscape-scale restoration requires large quantities of seeds, but many TGB herbaceous species have traits that limit seed sourcing, including: i) small populations, individual rarity, and irregular fruiting phenology (Dayrell et al. 2016); ii) low resource allocation to reproduction (Bond & Midgley 2001); iii) recalcitrant seeds in forbs that impede seed storage; iv) high seed dormancy that inhibits germination (Rusdy 2017); v) low seed quality (low viability, high percentage of empty seeds, Dairel & Fidelis online early; Kolb et al. 2016; Dayrell et al. 2017); and vi) fire-dependent flowering, seed release, or germination (Bond 2019). Seed germination of herbaceous species is often low, slow, and asynchronous. Therefore determining germination requirements (including fire-related cues), dormancy classes for TGB species, and methods to overcome dormancy, will be useful to optimize seedling establishment and decrease costs, increase the number of herbaceous species included in restoration programs (Ladouceur et al. 2018), and avoid scenarios where shorter-lived species are preferred over long-lived perennials because of a shortage of viable seeds with known germination techniques.

Putative causes driving low seed quality in TGB species include nutrient-limitation (Fujita et al. 2014), pollen quality (Rosbakh et al. 2018), higher genetic load due to accumulation of deleterious somatic mutations over many disturbance cycles (Lamont & Wiens 2003), harvesting constraints when faced with irregular fruiting phenology, and a combination of these factors. It also remains to be tested to what extent managing fire regimes would create opportunities to improve sourcing seeds from native TGB species where fire-stimulated flowering typically results in higher and more synchronous seed production and higher seed quality (Young 2004; Le Stradic et al. 2015b; Wagenius et al. 2020).

Direct seeding for large-scale ecosystem restoration can be a cost-effective technique to reintroduce functionally diverse plant communities (Figure 7). However, it has rarely been implemented in TGB because of the overall low seed quality mentioned above and because native (local) seeds are not available in sufficient quantities. Two pioneering studies tested direct seeding for TGB restoration, but used relatively few grass and forb species compared to local diversity (13 grass species in Waters et al. 2001; 11 grass and three forb species in Sampaio et al. 2019). While these studies are necessary steps towards efficient seeding, more research on seed ecology is urgently needed. Conversely, the high demand for seeds may have positive impacts, including i) involvement of local communities, generating income and the support of livelihoods through the sustainable use of native biodiversity; ii) protection of native ecosystems as seed sources; iii) decreasing conflict between environmental agencies, local communities and companies that need to perform restoration projects (Schmidt et al. 2019b); and iv) greater cost-effectiveness associated with greater market demand. Because seeds are currently sourced from wild populations, thresholds of seed collection need to also be determined. Seed provision/supply chains must be supported and regulated, for which preliminary law and market analysis research are necessary (Urzedo et al. 2019). Although harvesting seeds from perennial species tends to have low impacts on adult plants and populations (Franco & Silvertown 2004), clear harvesting guidelines are needed to avoid or minimize negative impacts to plant populations, especially when these are conservation targets. Economic stimulus for the development of seed farming production can alleviate shortfalls in seed supply, improving the reliability and cost of seeds available for restoration and attenuating the potential for overharvesting of wild plant populations. Seed farming should address evolutionary selection and loss of genetic diversity (Broadhurst et al. 2008, 2015; Nevill et al. 2016). However, this also implies in the development of Seed Transfer Zones, as already developed for some temperate regions, e.g. in Germany (Durka et al. 2017). Given the large knowledge gaps on TGB composition and regional differentiation, the development of ecologically meaningful transfer zones will still require considerable research efforts for most regions.

Reintroducing native species by vegetative propagation and container stock

A large proportion of plant species from TGB have at least one of the above- mentioned traits that limit propagation from seeds. Therefore, the opportunities for their reintroduction and propagation *via* seed sowing, soil transfer, and hay transfer, are currently often limited for restoring TGB biodiversity (Le Stradic et al. 2015b; Kolb et al. 2016; Dayrell et al. 2016; Pilon et al. 2018). To be reintroduced, such species may depend mainly on vegetative propagation. Cerrado grassland restoration has proven to be successful at a small scale by transplanting grass tussocks when there are sources available (Pilon et al. 2019). However, for most TGB the transplantation of forbs, subshrubs and shrubs, sometimes even grasses (Le Stradic 2012), is not a promising technique. Alternative techniques must then be developed or applied, such as: transplantation of individual tillers grown in pots from fragmented tufts (du Toit 2009), transplantation of seed-germinated pot-grown grasses (Oliveira et al. 2020), cuttings (du Toit 2009; Martins et al. 2015), propagation from bulbs (S. Le Stradic, Technische Universität München, Germany) or roots (Silva et al. 2011), and micropropagation (Biondo et al. 2007; Oliveira et al. 2011; Souza et al. 2015), among others (Figure 8).

While vegetative propagation has been widely used for forestry and orcharding worldwide, it has rarely been mentioned in the context of ecological restoration, and its application at large scales relies on research and technological development, while assuring high genetic variability. Protocols for the reintroduction of TGB species from direct rescue transplantation, or plug production from cuttings, division, scarce seed quantities, or by micropropagation are needed (Koch 2007). Development of propagation protocols should take advantage of the underground storage organs and bud banks which are reliable sources of regeneration in TGB species (Fidelis et al. 2014), and which hold the promise of simultaneously increasing vegetation resilience and providing ecosystem services (Pausas et al. 2018). Most likely, solutions for successful TGB restoration will be based on a mix of different approaches including vegetative propagation, direct seeding and container stock. Examining the costs and benefits of each approach will depend on restoration goals and the socio-ecological context of each grassland.

Maximizing plant establishment and ecosystem sustainability

Poor seedling establishment in TGB is often related to seed quality (see above), competition from undesirable species, severe environmental filters acting upon seedling survival, or a combination of these. Research needs to focus on improving i) restoration treatments to maximize species establishment; and ii) subsequent long-term management promoting ecosystem functioning and sustainability.

Maximizing target species establishment

Controlling invasive herbaceous species (including intentionally introduced forage species), and invasive or native tree and shrub encroachment is a major restoration step to reduce competition from undesirable species. Numerous techniques are available including cutting, removal, grazing, prescribed fires (Figure 9), herbicide application, or, as mentioned in section "Developing techniques to restore soil conditions", deep plowing or topsoil removal if the site is already highly degraded (Buisson et al. 2019). The most suitable combination of treatments is, however, yet to be determined for each TGB type and for each invasive species.

Many TGB are maintained by specific fire regimes and grazing (Veldman et al. 2015). While reintroduction of fire or grazing regimes too early may hamper the establishment of reintroduced species, excluding them for excessive periods decreases diversity, promotes woody encroachment and biological invasion, and increases the danger of wildfire occurrence, all of which damage the system (Stevens et al. 2017; Alvarado et al. 2018; Fidelis et al. 2018). Therefore, the appropriate disturbance regime and optimum treatments to keep a balance between the establishment of native and invasive species is yet to be determined through long-term field experiments in both disturbance-dependent and edaphic TGB (*sensu* Buisson et al. 2019).

Community assembly in old-growth grasslands occurs at large temporal scales (Nerlekar & Veldman 2020), so pioneer or faster-growing species which are typically used in the early stages of forest or temperate grassland restoration (Silveira et al. online early) are either unknown, or are unsuitable for TGB restoration. Some studies identify and employ faster-growing, short-lived species to cover the ground and later allow the establishment of long-lived perennial species (e.g. Coutinho et al. 2019). However, these species might not guarantee the resilience of the system because they may actually inhibit the subsequent establishment of perennial species (Nerlekar & Veldman 2020). While introducing pioneer species could be useful in areas where invasive species and soil erosion are major issues, the ability of this practice to promote high biodiversity in the long-term remains to be demonstrated. Alternatively, restoring small, slow-growing species to facilitate colonization by other native species, and to thus increase native species richness can be a feasible strategy (Fynn et al. 2009). TGB restoration may benefit from trait-based approaches for grasses and forbs to address the functional role of herbaceous species in promoting community re-assembly (Silveira et al. online early).

We also need a better understanding of feedbacks between vegetation, fauna, soil microbiota and soil properties (Suding et al. 2004). Mycorrhiza, soil microbes (Lugo & Pagano 2019), ants (Parr et al. 2016), large herbivores, including livestock (Veblen 2012; Hempson et al. 2015; Fritz 2017), and nurse plants (Gómez-Aparicio 2009) have been shown to play important roles in enhancing target species establishment and persistence, but we still lack proper identification of key ecological engineers with the potential to maximize plant establishment in most TGB. Examining the role of microorganisms in the establishment of TGB species is worthy given recent evidence that restoration outcomes can be improved by reintroducing mycorrhizal fungi from the native plant microbiome in temperate grassy ecosystems (Koziol et al. 2018).

Maximizing ecosystem sustainability (long-term management)

When restoration goals include achieving a sustainable ecosystem, this means ensuring that i) degradation forces remain excluded; ii) introduced plants persist in the long-term; iii) additional native species can establish and successfully reproduce; and iv) restored ecological processes maintain ecosystem functioning (Miller et al. 2017). In disturbance-dependent TGB, wildfires and large herbivores play underappreciated roles not only in restoration (see section "*Maximize* *species establishment*"), but also in maintaining long-term sustainability and resilience (Asner et al. 2009; Burkepile et al. 2013; Riginos et al. 2018).

Maintaining an appropriate level of herbivory may entail either of two very different groups of large mammalian herbivores: native herbivores and domestic livestock (Figure 10). Native herbivores (and perhaps livestock, see below) not only have an important role in shaping TGB vegetation species composition and structural diversity via their foraging, but also for distributing and maintaining nutrient inputs via dung deposits (Fornara & Du Toit 2008; Asner et al. 2009; Sitters et al. 2020). Thus, addressing restoration of diverse native herbivore assemblages (refaunation; Seddon et al. 2014) to target sites may be critical to achieving sustainable TGB goals.

Domestic livestock in TGB are represented by a diverse set of species (cattle, sheep, goats, camels, donkeys) that, like wildlife, differ in dietary preferences and ecosystem impacts. Livestock is often the underlying cause of ecosystem degradation, through inappropriately high stocking densities. However, at moderate densities, it may effectively replace native diverse herbivore communities (Veblen et al. 2016; Sitters et al. 2020). This may be especially important in TGB where the native megafauna has been lost and cannot be reintroduced or where prescribed fires are not permitted. Yet, the social and economic forces that led to overgrazing are often still in place, and not easy to shift (Kimiti et al. 2017). Specific studies thus need to determine appropriate overall grazing rates, and spatial and temporal patterns that allow the maintenance of habitat heterogeneity and biodiversity. Studying which levels or combinations of domestic and wild native herbivore grazing are appropriate is an essential issue to allow restoration and sustainable use of TGB (Riginos et al. 2012).

Many TGB are maintained by fire (Bond 2019), suggesting that fire management may be needed for restoration (but see edaphic grasslands; Buisson et al. 2019). However, understanding natural fire regimes is challenging because of entrenched anthropogenic fire regimes often preventing an accurate assessment of natural fire frequency, timing, and patterns (Archibald et al. 2013; Johansson et al. 2020; Figure 11). Maintaining a mosaic of diverse fire regimes may be a way to maintain landscape heterogeneity and diversity, but application of specific fire regimes in support of restoration should be further studied (Bond 2019). Fires have declined worldwide in recent decades (Andela et al. 2017), but intentional fires for grassland management are still common in parts of South America (Eloy et al. 2019; Schmidt & Eloy 2020) and Madagascar (Alvarado et al. 2018) and eastern and southern Africa (Archibald 2016). Even there, increased grazing and bush encroachment (both of which reduce grass fuels) have locally decreased burning (Archibald 2016). In Kenya, grassland fires have become rare (Archibald 2016) both because of heavy grazing in communal rangelands and because private range managers are increasingly disinclined to burn livestock forage (R. Sensenig, Goshen College, IN, personal communication). In the latter case, fire reintroduction may require stakeholder outreach or environmental sociology studies. The strong synergistic effects of fire and herbivory, which can make the combination a far more powerful force than either alone (Midgley et al. 2010; Werner et al. in press) have been investigated for woody plants (Staver *et al*. 2009; Pringle et al. 2015), but remain understudied for the herbaceous component of TGB (but see Burkepile et al. 2016; Smith et al. 2016).

Monitoring

Monitoring is essential to evaluate restoration success and is particularly important for restored disturbance-dependent ecosystems that require long-term adaptive management (Holl & Cairns 2002). While monitoring indicators such as tree cover, aboveground biomass and species richness may be appropriate for forest restoration, this alone is not sufficient to determine TGB health (Silveira et al. online early). The suite of indicators to be monitored depends on the restoration goals (Holl & Cairns. 2002) and on clear definitions of the expected attributes of the desirable ecosystem. This should be better explored for TGB. Candidate indicators for TGB monitoring can be general, such as ground cover or species richness, above and belowground biomass, proportion between different life-forms, fidelity to reference community, abundance of indicator species, among others, but should also include indicators specific to degradation and resilience to disturbance, such as recovery after fire, drought or herbivory, presence and cover by ruderals and exotic species, soil erosion rates, soil compaction or woody encroachment.

Ecosystem functioning is easily affected by changes in the suite of functional traits present. Monitoring native TGB species richness alone may infer that a TGB has been restored adequately, although functional richness, and hence redundancy, may have collapsed, which will negatively affect the resilience of the restored ecosystem over time. Monitoring of functional diversity in TGB is therefore imperative to properly evaluate restoration success, providing that the traits to be assessed have been shown to be relevant to TGB functioning and their ecosystem services. Research aimed at developing indicators of TGB functioning should identify easy-to-measure surrogates for ecosystem attributes and processes that are difficult to assess (Dale & Beyeler 2001; Prach et al. 2019). Because a number of ecological processes (e.g. regeneration, succession and landscape-level connectivity) operate differently in open ecosystems than they do in forests (Bond 2019, Silveira et al. online early), monitoring TGB restoration is likely to span comparatively larger time frames than in forest restoration. This assumption remains to be tested across a range of TGB.

Conclusion

The rate of land-use conversion outpaces the rate of scientific knowledge production, posing a great threat to the long-term persistence of TGB and thus calling for collaborative research prioritization. Further, this escalating transformation makes the need for effective restoration initiatives all the more pressing. Here, we have identified emerging questions on ecological dimensions of restoration ecology (Perring et al. 2015) that need to be answered in order to scale up restoration of TGB to meet the challenges of the UN Restoration Decade. Achieving restoration targets for TGB by 2030 seems unlikely because these megadiverse ecosystems do not even have a collective name to describe their ecology (Bond 2019), let alone sufficient knowledge to restore them. The set of priorities discussed here are not without bias, but has been assembled by a team of experts facing challenges during TGB restoration for more than two decades. They constitute a first step towards a comprehensive effort to improve the success of TGB restoration worldwide (Figure 1). Providing answers to these questions has the potential to advance theory, practice and policy in TGB restoration (but see Dey et al. 2020), ultimately resulting in long-term benefits to people and nature in some of the most neglected ecosystems of our planet.

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Figure 1. We identified emerging questions across broad themes in restoration (left of the figure) to structure questions aimed at optimizing practical restoration outcomes for TGB (Tropical Grassy Biomes, i.e. old-growth tropical and subtropical grasslands and savannas). Research should focus on: disentangling the reasons why TGB are often undervalued and misunderstood; mapping TGB restoration opportunities; identifying and recognizing regions where alternative stable states exist (a – Suding et al. 2004) and recognizing areas with natural regeneration potential to avoid unnecessary intervention; restoring abiotic conditions; disentangling factors driving low seed quality; determining germination requirements and developing vegetative propagation techniques for TGB species; disentangling the limiting factors and key ecological processes underlying seedling establishment and community assembly; improving and validating long-term management to mimic natural disturbance regimes, and improving monitoring.

Figure 2. Pristine TGB are sometimes confused with degraded grasslands: (a) Open savannas in the Cerrado, Parque Estadual do Jalapão, Northern Brazil, composed of a continuous species-rich herbaceous layer and scattered shrubs and small trees; the photo also shows two rhea (*Rhea americana*), a bird native to these ecosystems (photo credit AF); (b) A former *Pinus* spp. plantation in the Cerrado after removal of the trees. *Melinis minutiflora* (purple inflorescence), an African grass, has invaded the system, outcompeting native grasses and forbs (photo credit AF); (c) Native grassland in Serra dos Carajás, Pará, Brazil (photo credit AJA); (d) Derived grassland replacing former forest in Carajás National Forest, Pará, Brazil (photo credit AJA); (e)

Open Acacia savanna, with a continuous herbaceous layer and scattered trees and shrubs, during the wet season in Kruger National Park, South Africa; the photo also shows ostriches (*Struthio camelus*), which are native to these systems (photo credit DT); (f) Open Acacia savanna during the dry season, Kruger National Park, South Africa (photo credit DT).

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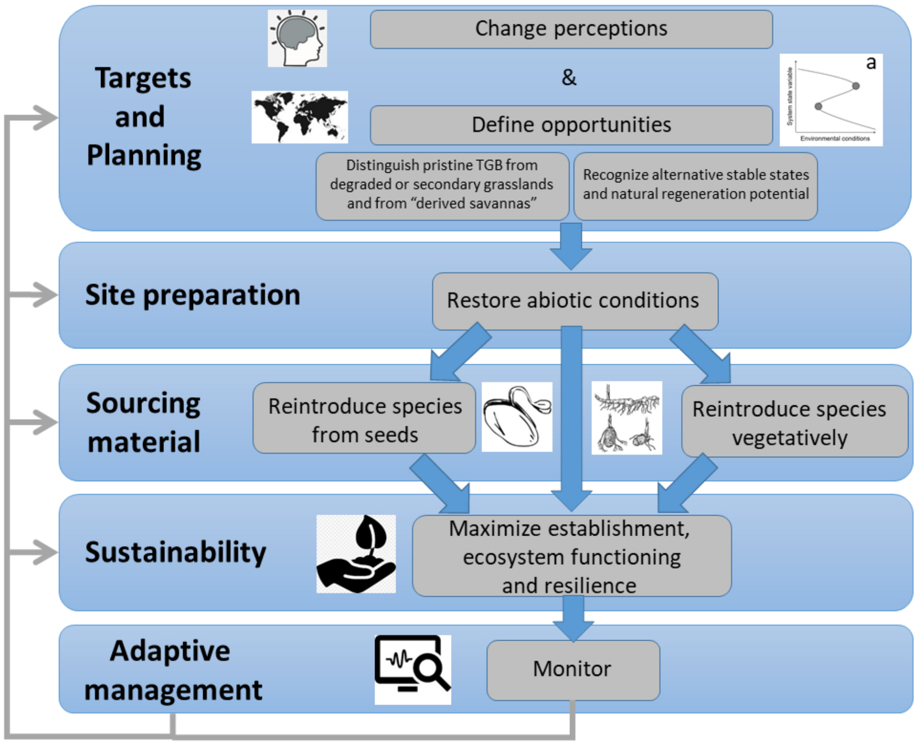
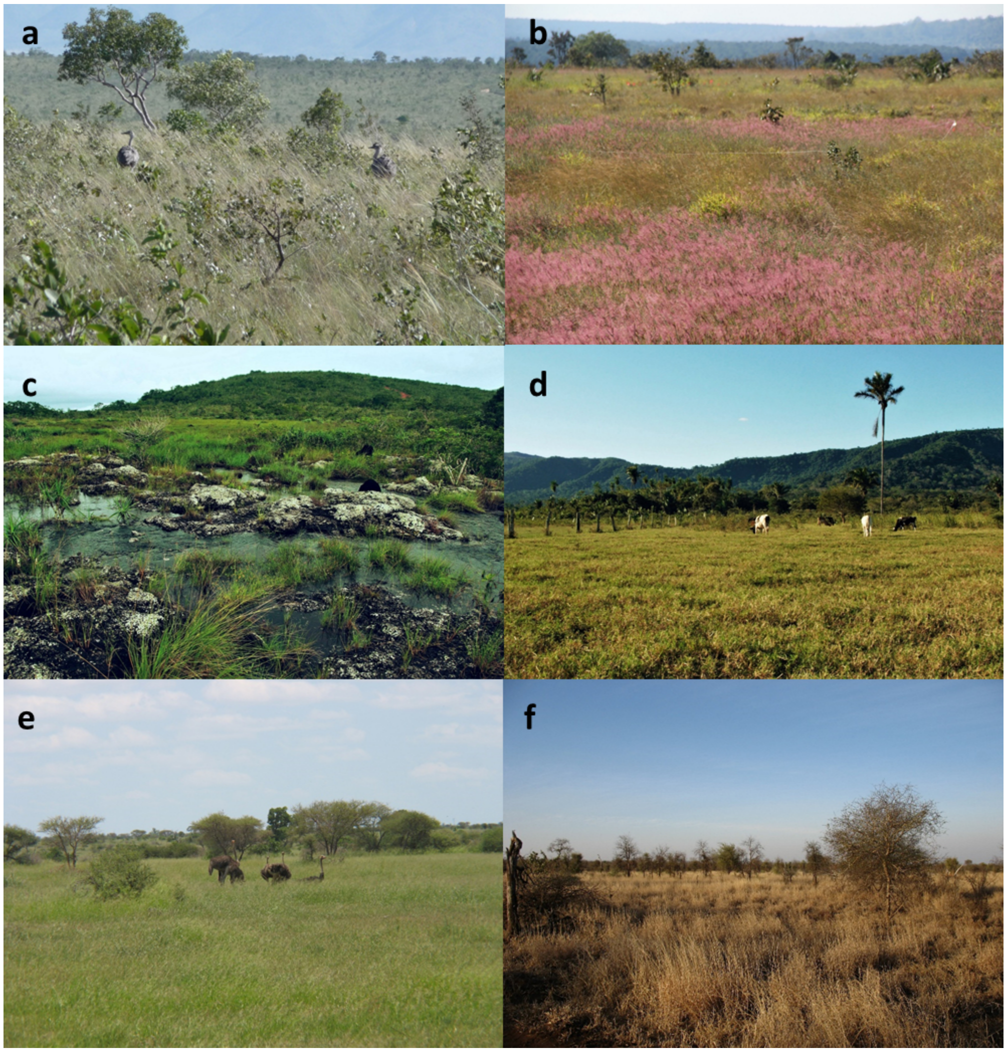


Figure 1. We identified emerging questions across broad themes in restoration (left of the figure) to structure questions aimed at optimizing practical restoration outcomes for TGB (Tropical Grassy Biomes, i.e. old-growth tropical and subtropical grasslands and savannas). Research should focus on: disentangling the reasons why TGB are often undervalued and misunderstood; mapping TGB restoration opportunities; identifying and recognizing regions where alternative stable states exist (a – Suding et al. 2004) and recognizing areas with natural regeneration potential to avoid unnecessary intervention; restoring abiotic conditions; disentangling factors driving low seed quality; determining germination requirements and developing vegetative propagation techniques for TGB species; disentangling the limiting factors and key ecological processes underlying seedling establishment and community assembly; improving and validating long-term management to mimic natural disturbance regimes, and improving monitoring.

277x239mm (96 x 96 DPI)



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263x274mm (96 x 96 DPI)

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263x297mm (96 x 96 DPI)

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355x266mm (96 x 96 DPI)

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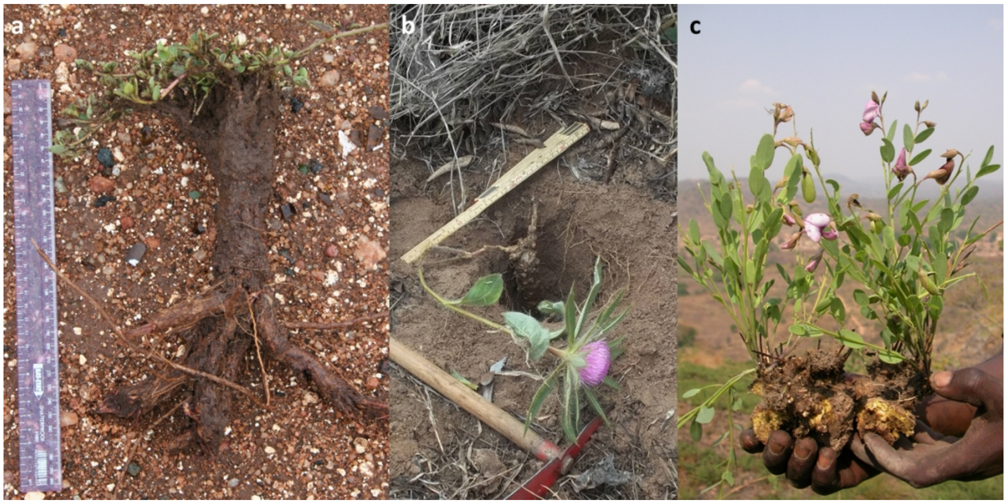
353x209mm (96 x 96 DPI)



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354x176mm (96 x 96 DPI)

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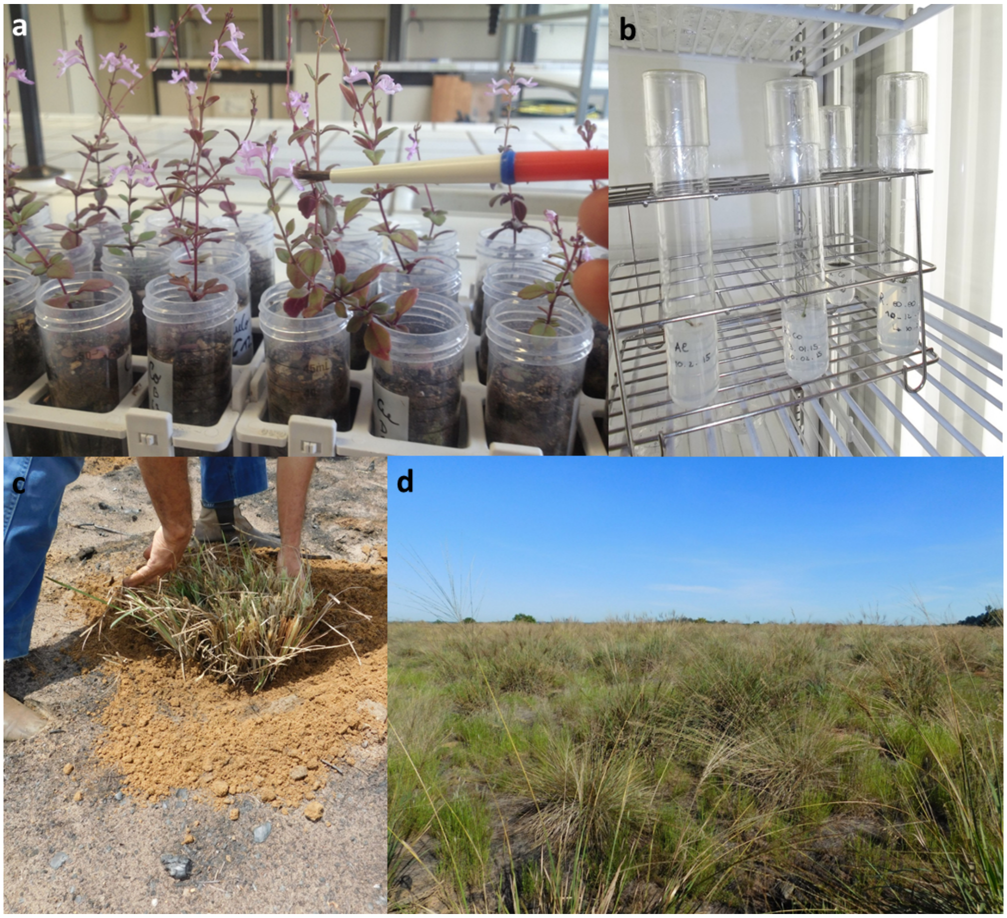
346x228mm (96 x 96 DPI)



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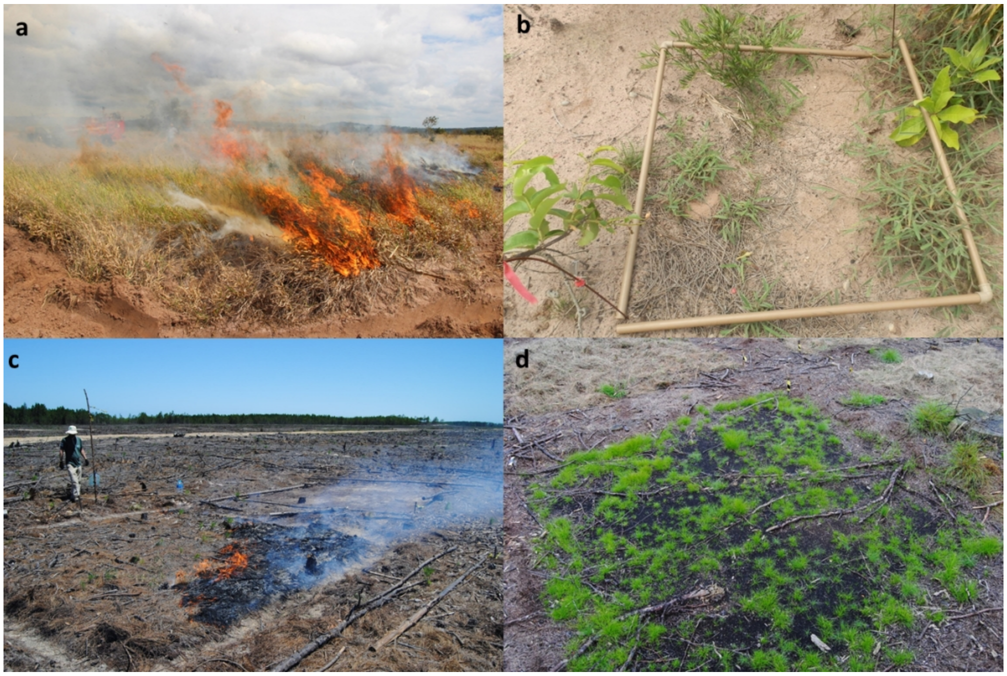
286x260mm (96 x 96 DPI)



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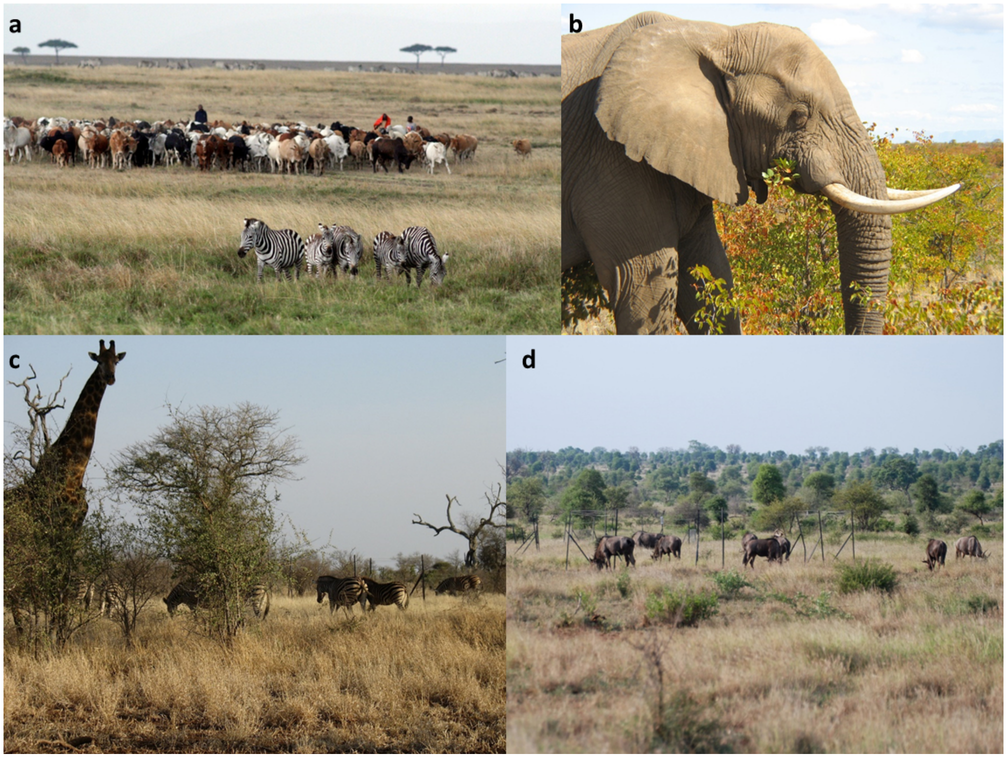
354x236mm (96 x 96 DPI)



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302x227mm (96 x 96 DPI)

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265x353mm (96 x 96 DPI)

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355x266mm (96 x 96 DPI)