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POLICY ARTICLE

Myth-busting tropical grassy biome restoration

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The historical focus in research and policy on forest restoration and temperate ecosystems has created misunderstandings for the restoration of tropical and subtropical old-growth grassy biomes (TGB). Such misconceptions have detrimental consequences for biodiversity, ecosystem services, and human livelihoods in woodlands, savannas, and grasslands worldwide. Here, we demystify TGB restoration myths to promote a positive agenda to increase the likelihood of success of ambitious landscape-scale restoration goals of nonforest ecosystems. The 10 TGB restoration myths are: (1) grasslands originate from degraded forests, (2) tree cover is a reliable indicator of habitat quality, (3) planting trees is always good for biodiversity and ecosystem services, (4) grasslands are biodiversity-poor and provide few ecosystem services, (5) enhancing plant nutrition is needed in restoration, (6) disturbance is detrimental, (7) techniques used to restore temperate grasslands also work for TGB, (8) grasslands represent early stages of forest succession, (9) grassland restoration is only about grasses, and (10) grassland restoration is fast. By demystifying TGB restoration, we hope that policymakers, scientists, and restorationists come to understand and embrace the value of these ecosystems and are motivated to establish policies, standards, indicators, and techniques that enhance the success of TGB restoration. We must abandon misperceptions and misunderstandings of TGB ecology that result in ill-conceived policies and build an informed and compelling global ecosystem restoration agenda that maintains and improves the well-being of all inhabitants of grassy biomes.

Key words: afforestation, Bonn challenge, forest landscape restoration, grassland, savanna

Implications for Practice

- The lack of knowledge on the ecology of tropical old-growth grassy biomes (TGB; grasslands, savannas, and woodlands) has resulted in profound misunderstandings concerning their restoration.
- We must abandon the misperceptions that TGB are less valuable for biodiversity, ecosystem services and human livelihoods compared to forest ecosystems.
- Likewise, we must abandon TGB restoration myths that mainly stem from forest restoration, and shift theory and practice toward policy, standards, indicators, and techniques tailored for TGB.
- There is an urgent need for a positive agenda for global ecosystem restoration that integrates grassy biomes to benefit both people and nature.

Introduction

We are at the dawn of the UN Decade on Ecosystem Restoration, with the aim to restore 350 million hectares by 2030. Yet, restoration of tropical and subtropical old-growth grassy biomes (TGB) is overlooked because researchers and policymakers have largely focused on forest restoration. TGBs comprise the world's ancient open biomes: woodlands, savannas, and grasslands (Fig. 1; Veldman et al. 2015*a*) that are dominated by herbaceous species and have typically low tree cover. Many

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biodiversity hotspots are covered extensively by significant areas of TGB (Myers et al. 2000). TGB have been historically misunderstood and undervalued, compromising biodiversity, ecosystem services, and human livelihoods worldwide (Parr et al. 2014). Indeed, the Bonn Challenge website (https://www.bonnchallenge.org/), a highly visible initiative to advance ecological restoration, does not include a single reference to woodlands, savannas, and grasslands, while providing a flawed, outdated opportunity-for-restoration map that considers extensive TGB areas as degraded forests and, consequently, targets for tree planting or afforestation (Veldman et al. 2015*a*).

A number of ecological concepts and processes (e.g. regeneration dynamics, succession trajectories, and landscape-level connectivity) are widely accepted as the foundation in tropical forest restoration (Norden et al. 2015; Poorter et al. 2016; Arroyo-Rodríguez et al. 2017). In contrast, TGB restoration is, so far, less supported by long-term ecological research. Broader application of techniques is still at an initial stage, in contrast to semi-natural temperate grasslands of cultural landscapes where concepts, principles, and techniques of restoration are well developed (e.g. Walker et al. 2004; Kiehl et al. 2010). Here, we focus only on tropical and subtropical old-growth grassy biomes, while recognizing the value of protecting and restoring temperate old-growth grassy biomes.

Misconceptions on the basic ecology and biogeography of TGB and indiscriminate application of principles of forest or temperate semi-natural grassland restoration to TGB can actually be detrimental to these biodiverse ecosystems. Here, we

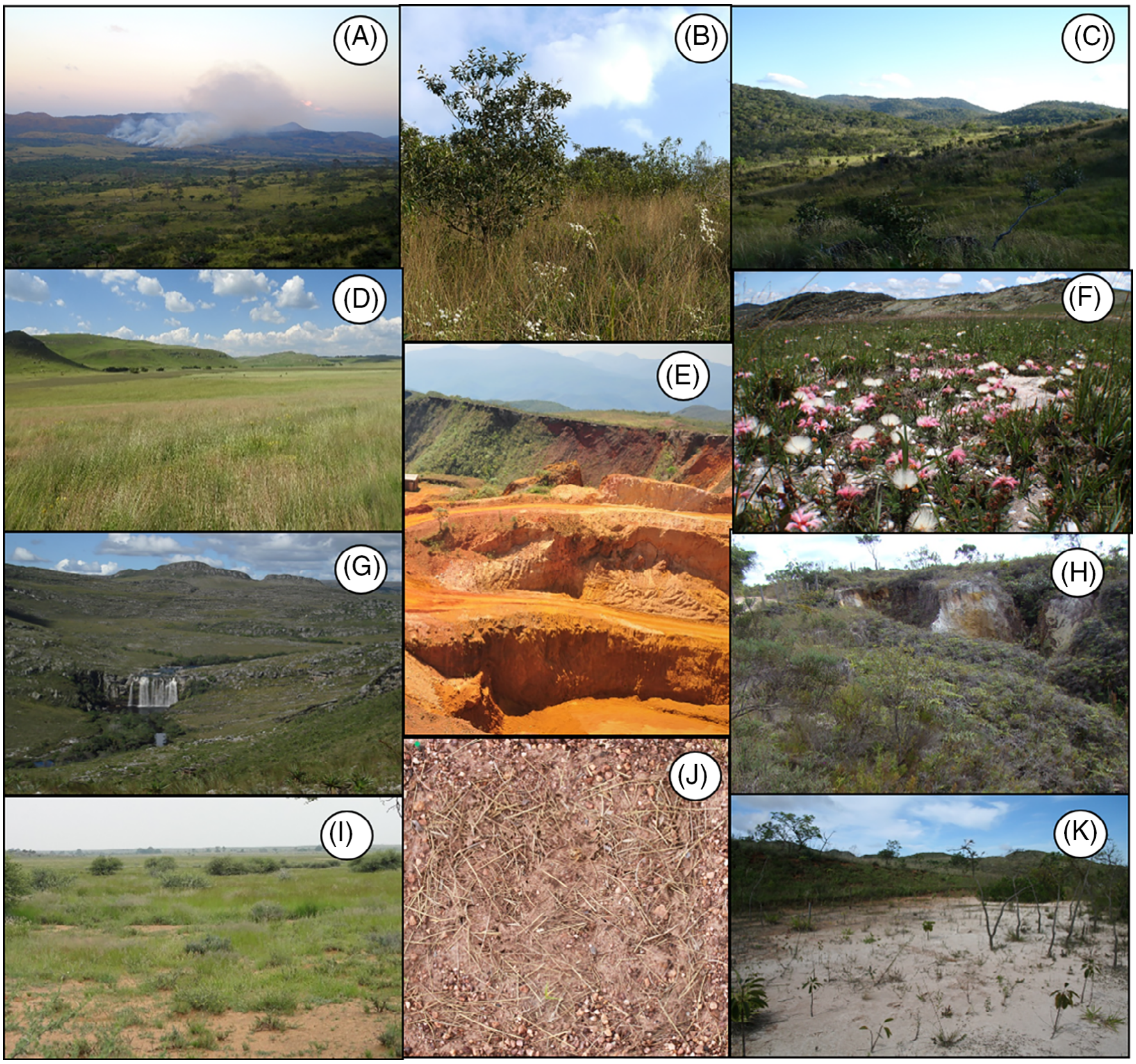

Figure 1. Examples of tropical and subtropical old-growth grassy biome (TGB) restoration myths. Forest degradation (A) often results in derived-savannas (B) that should be targeted for landscape forest restoration. Pristine grasslands (campo rupestre) in Brazil (C) and subtropical mesic in South Africa (D) are mostly treeless ecosystems threatened by mining (E). TGB are fire-prone ecosystems (post-fire flowering in *Calliandra linearis* (F) that provide key ecosystem services, such as water recharge (G), but their restoration is challenging. Invasive and ruderal species (H), but not forbs, the bulk of diversity in TGB (I) often colonize degraded areas, decreasing biodiversity. Vegetation survey in 40 cm × 40 cm quadrats showed no germination of native species after hay transfer in a subtropical TGB (J) and attempts to plant trees often result in catastrophic losses of TGB species (K).

aim to correct 10 common myths that impede successful restoration of TGB at a global scale. By myths, we mean ideas or techniques that were developed for other ecosystems, but which are a poor fit to TGB restoration.

Myth 1. Grasslands Originate From Degraded Forests

The idea that TGB are the result of forest degradation, and therefore are in need of restoration, probably originated from an historical and widespread misunderstanding of savanna and grassland ecology (Noss et al. 2015). This perception is perpetuated by a highly biased economic valuation of forests and lumber combined with a highly visible and widespread transition of forests to grassland following deforestation, particularly in developed countries. Mounting evidence suggest that some TGB evolved in the Miocene and Pliocene (Bond 2016), predating humans by millions of years. Many of them have long been maintained by fire and herbivores. A high proportion of grassland endemics also provide a key clue to the antiquity of TGB (Bond 2016). In contrast, derived secondary grasslands are recent, and can emerge from deforestation and anthropogenic fire (Sansevero et al. 2020). Because the latter have similar structure and spectral signatures with TGB, it is extremely difficult to use remote sensing to distinguish between them (Veldman & Putz 2011). Failure to distinguish between these two vegetation types results in misidentification of suitable areas for restoration (Bastin et al. 2019). TGB are by definition not the result of human-caused fires and deforestation, and therefore we must abandon the idea that they are degraded ecosystems.

Myth 2. Tree Cover Is a Reliable Indicator of Habitat Quality

TGBs are open ecosystems dominated by an herbaceous component which makes up the bulk of plant diversity (Siebert & Dreber 2019). The Food and Agriculture Organization (FAO) uses tree cover and height to classify forests worldwide (FAO 2000), but tree cover is not useful as an indicator of habitat quality in TGB. The application of the FAO definition misclassifies many tropical regions as forests that are in fact TGB (Griffith et al. 2017; Veldman et al. 2019; Kumar et al. 2020), and ignores the profound functional differences between open ecosystems with a highly flammable grassy understory and closed, fire-sensitive forests (Ratnam et al. 2011; Bond 2016). Low tree cover in TGB does not necessarily mean habitat degradation, and should not be used as a criterion to identify priority restoration targets.

Myth 3. Planting Trees Is Always Good for Biodiversity and Ecosystem Services

Since TGB are open, biodiverse ecosystems, carbon-focused tree planting over TGB, as suggested by the Bonn Challenge "Atlas of Forest and Landscape Restoration Opportunities" (https://www.wri.org/applications/maps/flr-atlas/), makes little to no ecological sense and may actually degrade TGB. It has been independently shown that species diversity decreases with increasing tree cover in TGB (Veldman 2016; Abreu et al. 2017). Therefore, it is critical to distinguish reforestation from afforestation. Reforestation, that is, planting trees after deforestation, is laudable, and needed to mitigate climate change, secure ecosystem services, and protect biodiversity. In turn, afforestation, planting trees where they historically did not occur, has been repeatedly shown to be detrimental to both plant and animal life, ecosystem services, and to climate change mitigation (Jackson et al. 2005; Veldman et al. 2015*b*, 2019).

Myth 4. Grasslands Are Biodiversity-Poor and Provide Few Ecosystem Services

Tropical forests are often seen as the world's most relevant biomes in terms of biodiversity and ecosystem services. However, many of the world's TGB as well as ancient semi-natural grasslands are also extremely rich in terms of taxonomic, phylogenetic, and functional diversity (especially on small scales), as well as species endemism (Bond & Parr 2010; Wilson et al. 2012; Parr et al. 2014). They provide a number of essential ecosystem services, and are highly threatened (Overbeck et al. 2015). For example, Brazilian savannas harbor comparable plant species richness to the Brazilian Amazon, even though savannas occupy half of the area covered by the Amazon (Filardi et al. 2018).

TGB provide ecosystem services including provisioning of forage resources for livestock in natural grasslands habitat and for agriculturally important pollinators (Öckinger & Smith 2007), and nontimber products for local populations, such as medicinal and ornamental plants (Dzerefos & Witkowski 2001; Resende et al. 2013). Some TGB also provide important attraction for tourism and regional economy systems, via support for many species of large mammalian herbivores (e.g. Kruger and Serengeti national parks).

TGB play key roles in regulating water and carbon cycles. A considerably larger proportion of rainfall reaches the ground of TGB than in forests, where more rainfall is intercepted by the canopy and evaporates (Honda & Durigan 2016). Consequently, afforestation causes reduction of infiltration and streamflow threatening down-stream water supply in seasonal climates where water is scarce (Jackson et al. 2005). TGB also have a high potential for belowground carbon storage (Wiesmeier et al. 2015; Wigley et al. 2020), sometimes higher than forests (Dass et al. 2018), but this potential is usually underestimated because assessments of belowground carbon are more difficult and error-prone than of aboveground carbon (Sanderman et al. 2017). Belowground carbon storage is very stable in TGB, and is relatively unaffected by fire or grazing, while forest carbon storage aboveground is more vulnerable to loss by fire (Veldman et al. 2019). Therefore, restoration of TGB results in benefits to people and nature, beyond climate change mitigation.

Myth 5. Enhancing Plant Nutrition Is Needed in Restoration

Deforestation frequently leads to soil impoverishment, and reforestation often employs fertilizers and mycorrhizae inoculation to improve seedling establishment. Many TGB native species are adapted to nutrient-poor soils and are unresponsive to nutrient addition (Negreiros et al. 2009; Silva et al. 2015). In addition, species from extremely nutrient-impoverished grasslands have root specializations as an alternative to mycorrhizae, and lack the need for fungi inoculation (Abrahão et al. 2019). In nutrient-poor ecosystems, fertilization facilitates biological invasion (Zefferman et al. 2015), increases the risk of pathogen infection (Lambers et al. 2018), decreases fitness of target species (Williams et al. 2019), changes the microbiota, and favors rapidly growing taller species, decreasing taxonomic and functional diversity (Harpole et al. 2016). Therefore, care should be taken when designing site-preparation strategies for TGB restoration to maximize cost–benefit effectiveness. Restoration of TGB in soils that have been previously fertilized or limed for agriculture should involve strategies to restore the soil back to its original nutrient-poor state to maximize the recovery of slow-growing species and biodiverse species assemblages (Sampaio et al. 2019).

Myth 6. Disturbance Is Detrimental

This myth poses that disturbances are anthropogenic (and therefore unnatural), and have negative impacts on vegetation. Indeed "degradation" in the WRI Atlas is defined as any reduction in tree cover due to, for example, fire and herbivores. Consequently, major African protected areas, such as the Serengeti and Kruger national parks, are mapped as degraded. However, most TGB are not only resilient to, but often dependent on one or more types of endogenous disturbances such as fire, herbivory, and trampling (Buisson et al. 2019). Fire likely promoted the Miocene expansion of tropical grasslands and savannas and shaped open ecosystems. TGB, particularly under relatively high rainfall (Sankaran et al. 2005), are maintained in an open stable state by various disturbances (Staver et al. 2011). The continuous herbaceous layer of TGB forms the main fuel for recurrent fire events and forage for herbivores. Both can create spatial and temporal heterogeneity, an important driver of grassland diversity (Ricketts & Sandercock 2016).

In contrast to grazing animals, fires are less selective, and their spread depends on plant traits, fuel loads, environmental conditions, and topographic features. TGB species regenerate after disturbance by seeding or resprouting, and some show fire-related germination cues and fire-induced flowering (Buisson et al. 2019). Many other species resprout, mostly from bud banks located in underground storage organs that store carbohydrates and water for resprouting after disturbance (Pausas et al. 2018).

Herbivores both create and are dependent on open ecosystems, and interact with fire and precipitation to maintain TGB. In African TGB, grazing and browsing often occur by both native and domestic animals (Du Toit 2003; Smith et al. 2016), and browsers such as elephants help prevent bush encroachment (Scogings & Gowda 2020). In many TGB, domestic livestock replaced native herbivores (Overbeck et al. 2007). In such systems, grazing intensity remains important, although overgrazing has negative effects on biodiversity (Herrero-Juregui & Oesterheld 2018) and can lead to biological invasion (Andrade et al. 2015), including woody encroachment (Belayneh & Tessema 2017). Managing the intensity of grazing, fire, or a combination of both should be incorporated in the maintenance and restoration of TGB. Without fire or sufficient browsing in some areas (Schmidt et al. 2019), woody encroachment and a biome shift from open to forested vegetation can lead to biodiversity losses, especially for endemic species (Abreu et al. 2017; Stevens et al. 2017).

Myth 7. Techniques Used to Restore Temperate Grasslands Also Work for TGB

Transferring seed-containing hay or soil are common and successfully applied techniques to overcome regeneration constraints for a high proportion of target plant species in restoration of semi-natural temperate grasslands (Kiehl et al. 2010; Blakesley & Buckley 2016; Török et al. 2018). In contrast to these examples, hay transfer in two TGB types in Brazil did not lead to the establishment of any native species (Le Stradic et al. 2014; Pilon et al. 2018). Seed quantity and quality are poor in some TGB (Dayrell et al. 2017), with very variable reproduction from seed, even for widespread keystone species (Snyman et al. 2013).

Topsoil transfers are particularly important for post-mining rehabilitation and restoration. Although outcomes vary depending on seed bank quality (Le Stradic et al. 2018), soil depth (Le Stradic et al. 2016), and transfer dates (Pilon et al. 2018), topsoil transfers to restore TGB seem more successful than hay transfers (Ferreira et al. 2015). Because TGB are often fire-prone ecosystems, many species rely on underground storage organs for regeneration, more than in semi-natural temperate grasslands (Veldman et al. 2015*a*), and soil seed banks with short-lived seed bank may explain failures of topsoil transfers.

Testing techniques developed for the restoration of semi-natural temperate grasslands in tropical and subtropical TGB is valuable, but careful analysis and appropriate adaptation that addresses the specific ecology of these TGB is advisable.

Myth 8. Grasslands Represent Early Stages of Forest Succession

Ecological succession theories predict changes in plant-community structure and composition over time, eventually reaching a relatively stable condition—the "climax" (Wilson 2011), which is invariably expected to have a higher plant biomass. Even if the idea of a single deterministic climax has been largely abandoned, especially in nonforest ecosystems, the idea of fast-growing, r-strategist pioneers colonizing a disturbed site and eventually being replaced by the arrival and establishment of late-successional, shade-tolerant, k-strategists persists (Pickett et al. 2011). Herbaceous vegetation thus is often misperceived as an initial state of forest succession, and disturbances that interfere in this trajectory are seemingly negative. Evidence does not support this view in TGB, where disturbances are important drivers of ecosystem structure and diversity. For example, woody species remain absent from some TGB even after 25 years of fire exclusion (Le Stradic et al. 2018).

The secondary-succession theory has been successfully applied in tropical forest restoration (Lamb et al. 2005). It is, however, a poor fit to TGB restoration (Walker & Reddell 2007). First, because continuous woody biomass increase is not a desirable outcome in disturbance-driven and light-demanding ecosystems. Second, because the functional traits defining pioneer, secondary, or late-successional species in tropical forests (Swaine & Whitmore 1988) are far from adequate to categorize plant species colonizing, covering the ground, and persisting in grassland ecosystems (Dayrell et al. 2018). To be applied in grassland restoration, plant functional group classification should be clearly defined according to their precise role in grassland reassembly instead of borrowing forest terms and definitions. Most importantly, TGB are often maintained by natural disturbance regimes, which can be mistaken for simply being early-successional states of a woodier "climax" community.

Myth 9. Grassland Restoration Is Only About Grasses

Grassland restoration often involves the restoration of high-quality forage resources and dominant species through the reintroduction of palatable perennial or tall grasses. Consequently, forbs have often been ignored in restoration, and may even be perceived as indicators of degradation (Siebert & Dreber 2019). The focus on dominant grasses (Kinyua et al. 2010) or forage grasses is subject to pitfalls. First, dominant grasses represent only a small proportion of species richness, and forb species richness can be 6-fold higher than grasses (Siebert 2011). Forbs provide services, such as nitrogen-fixing, nutritious seasonal food source for browsers, mixed feeders, and particularly for cattle (Odadi et al. 2007; O'Connor et al. 2010), invertebrates (Botha et al. 2017), and medicinal sources for human livelihoods (Dzerefos & Witkowski 2001).

Second, planting dominant grasses alone can hinder forb establishment (Werner et al. 2016). There is a general perception that forbs do well under conditions of high disturbance. However, only a small proportion of grassland forb species have evolved ruderality (Botha et al. 2017; Dayrell et al. 2018), and most have evolved with long histories of fire, herbivory, and frost (Bond & Zaloumis 2016), which renders them particularly vulnerable to disturbances that remove their underground storage organs (Fidelis et al. 2014). Restoring forbs with underground storage organs is therefore important for restoring grassland functionality (Morris & Scott-Shaw 2019).

Myth 10. Grassland Restoration Is Fast

How long does an ecosystem take to be restored? The answer to this question has practical implications and interest to decision makers. However, the speed to return to the pre-disturbance state depends on disturbance frequency and intensity, as well as the ecosystem type (Jones et al. 2018). TGB are resilient to endogenous disturbance (Fynn et al. 2016), which appears to suggest that their restoration is fast. TGB subjected to exogenous disturbance, however, show impoverished communities with low similarity to reference TGB (Andrade et al. 2015; Veldman 2016). TGB were not able to recover composition and functional diversity even 40 years after plantation forestry (Bond & Zaloumis 2016) or 60 years after mining or quarrying (Ilunga wa Ilunga et al. 2015). This pattern also proved true for TGB subjected to agriculture land use (Kirkman et al. 2004; Fensham et al. 2016). In contrast, secondary tropical forests take a median time of two decades to recover 80% of species richness (Rozendaal et al. 2019), and a median time of 66 years to recover up to 90% of the biomass of old-growth forests (Poorter et al. 2016). Relatively slow regeneration of tropical TGB compared to forests (Arroyo-Rodríguez et al. 2017) after exogenous disturbance is mostly related to slow plant growth rate, seed and dispersal limitation (Veldman et al. 2015*a*; Dayrell et al. 2017, 2018).

Conclusions

The UN Decade on Ecosystem Restoration aims to massively scale up ecological restoration to mitigate climate change, support biodiversity and secure food, and provide essential resources to human populations. Misperceptions and misunderstandings of TGB ecology and misapplication of principles used in other ecosystems will likely result in ill-conceived policies that preclude achieving these ambitious goals. By demystifying TGB restoration, we hope that policymakers, scientists, and restorationists fully embrace the characteristics of these valuable ecosystems with the ultimate goal of generating policy, standards, indicators, and techniques that enhance TGB restoration. A positive agenda for global ecosystem restoration needs to integrate the ecology of TGB that will benefit both people and nature.

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