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Lessons on direct seeding to restore Neotropical savanna

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OPINION ARTICLE

Tailoring restoration interventions to the grassland-savanna-forest complex in central Brazil

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Defining the reference system for restoration projects in regions characterized by complex vegetation mosaics is challenging. Here we use the Cerrado region of Brazil as an example of the importance of clearly defining multiple natural and anthropogenically altered states in grassland-savanna-forest mosaics. We define three main, natural vegetation types–grassland, savanna, and scleromorphic (*cerradão*) forest–to (1) distinguish between original and degraded states and (2) set appropriate targets for and guide restoration. We contend that the differences in Cerrado vegetation composition originally were driven by soil conditions and secondarily by fire frequency and precipitation patterns that differ from the core to the edge of the Cerrado region. Grasslands are found on the shallowest, least fertile soils and/or in waterlogged soils; scleromorphic forests are generally located on deeper, more fertile soils; and savannas occupy an intermediate position. In recent decades, this biophysical template has been overlain by a range of human land-use intensities that strongly affect resilience, resulting in alternative anthropogenic states. For example, areas that were originally scleromorphic forest are likely to regenerate naturally following low- or medium-intensity land use due to extensive resprouting of woody plants, whereas grassland restoration requires reintroduction of grass and forb species that do not tolerate soil disturbance and exotic grass competition. Planting trees into historic grasslands results in inappropriate restoration targets and often restoration failure. Correctly identifying original vegetation types is critical to most effectively allocate scarce restoration funding.

Key words: Brazilian savanna, Cerrado, natural regeneration, resilience, resprouting, woody encroachment

Implications for Practice

- Land managers and scientists should collaborate to identify the range of natural and anthropogenic states in grassland-savanna-forest mosaics to choose appropriate targets for restoration.
- Identifying natural and anthropogenic factors influencing these vegetation types and their degraded states can help guide selection of the most suitable and cost-effective restoration techniques.
- The resprouting ability of woody species allows for high resilience under low-intensity disturbance regimes; however, herbaceous native species rarely recover naturally following extensive soil disturbance and exotic grass invasion.
- There is an urgent need to improve evidence-based restoration techniques in the Cerrado grassland-savanna-forest complex, especially how to control invasive grasses, reestablish soil conditions, and manage fire, since techniques applicable at a large scale are necessary to achieve restoration commitments and targets.

Introduction

Restoration ecologists have long recognized that few degraded ecosystems follow a linear recovery trajectory toward a reference ecosystem (Trowbridge 2007; Matthews et al. 2009). Vegetation models that incorporate multiple endpoints or states with thresholds between them better describe the dynamics of many ecosystem types (Westoby et al. 1989; Suding et al. 2004; Bestelmeyer et al. 2017). Identifying alternative natural vegetation types and isolating the factors driving the transitions between them and degraded areas are essential to select and implement compatible management and restoration efforts. Yet, there are still few examples where the environmental drivers of transitions have been clearly identified and used to guide restoration (Suding et al. 2004). Briske et al. (2005) highlight the utility of this approach; they describe drivers that influence the transitions between grassland and woodland ecosystems in North American rangelands, pinpointing ecological features

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that should be considered to plan and implement management and restoration actions.

This need to distinguish among multiple states or vegetation types is especially true in savanna regions, where a complex mosaic of ecosystems naturally coexists across the landscape, influenced by soil properties, topography, rainfall patterns, natural disturbances, and human activities (Lehmann et al. 2011). Anthropogenic disturbances interact with natural drivers and ecosystem resilience, shaping ecosystem structure and community composition. In these complex ecosystem mosaics, it can be challenging to identify the level of ecosystem degradation and determine restoration targets. In such systems, vegetation types are commonly classified according to the current vegetation structure, which can lead to misinterpretations that jeopardize conservation and restoration (Veldman 2016). Old-growth savannas and grasslands (i.e. natural ancient ecosystems with a continuous herbaceous layer, and in the case of savannas, where grassy and woody species coexist, sensu Veldman et al. 2015), are threatened when they are seen as degraded forests and targeted for forest restoration or carbon-sequestration initiatives (Veldman 2016). On the flip side, degraded forests may structurally resemble savannas or grasslands and be misidentified as old-growth savannas or grasslands. These misidentifications of reference systems can lead to misguided conservation policies (Abreu et al. 2017) and the selection of inappropriate restoration targets and methods, leading to restoration failure (Suding 2011). For example, some state laws in Brazil require planting trees regardless of the original vegetation and do not consider nontree species in revegetation requirements (e.g. Brazil DF Laws 14.783/1993; 23.585/2003). This leads to the planting of fast-growing forest trees in areas that were originally grasslands and savannas, resulting in high tree seedling mortality (commonly > 60% in the first few years) and/or nonrecruiting tree stands (Sousa & Vieira, in review), as described in other systems (Suding 2011; Veldman et al. 2015).

Environmental laws and international commitments set a target for Brazil to restore approximately 12 million hectares of natural habitat of which 5 million hectares are within the Cerrado region (Federal Decree 8952/2017). To achieve such commitments, we need restoration methods that are cost-effective and practical at a large scale. Globally, grassland and savanna restoration methods are much less developed than forest restoration methods and are still incipient in the Cerrado (Pellizzaro et al. 2017; Coutinho et al. 2018). Given that barriers to grassland and savanna restoration differ from those in forest ecosystems, they need to be restored in distinct ways (Hedberg & Kotowski 2010).

Here, we use the natural complex mosaic of grasslands, savannas and forest systems characteristic of the Cerrado region in Brazil (Ribeiro & Walter 2008), as an example of how a clear understanding of natural and anthropogenic states can help guide restoration efforts. Our specific goals are to: (1) characterize natural versus degraded vegetation states, resulting from the most common human interventions; (2) identify the main controlling variable influencing transitions between those states; and (3) pinpoint the most effective restoration interventions based on the transition controlling variable and natural regeneration mechanisms.

Cerrado Vegetation Types

The Brazilian Cerrado is a mosaic of grasslands, savannas, and forests that originally occupied 2 million km^2, mainly in central Brazil (Fig. S1, Supporting Information; Ribeiro & Walter 2008; MMA 2015). We followed the Cerrado sensu lato concept of Coutinho (1978), that is a gradient of vegetation types of the *campo limpo* (a grassland) to *cerradão* (scleromorphic forest). It is a mesic savanna region, with a seasonal rainfall pattern varying from 600 to 2,000 mm/year (Sano et al. 2019), 90% of the rainfall occurs between October and April with 2 to 5 months of the year with no precipitation (Agência Nacional de Águas 2019).

The Cerrado is the most biodiverse savanna worldwide (>12,730 plant species) with high endemism rates (approximately 40% plant endemics) and ancient flora (Simon et al. 2009; Brazil 2018). Savannas and grasslands originally covered >75% of the Cerrado region (Eiten 1972; Ab'sáber 1981). In these old-growth savannas, graminoids, forbs, and woody species coexist with crown cover ranging from <5–20% open savanna-grasslands (regionally called *cerrado ralo*), to 20–50% in typical savannas (*cerrado típico*), to 50–70% canopy cover in closed savannas (*cerrado denso)*. Herbaceous and shrub species form a continuous layer and represent 60–80% of the species richness (Ribeiro & Walter 2008; Amaral et al. 2017). Shallow and sandy soils are covered by old-growth grasslands with no woody species (*campo limpo*) or with few shrub and tree species (*campo sujo*), whereas in deeper, mesic, and/or clay soils, tree canopy can cover 70–90%, forming scleromorphic forest (hereafter referred to as *cerradão*) with a sparse herbaceous layer (Ribeiro & Walter 2008). Several studies link the occurrence of *cerradão* to deep, fertile soils with a high proportion of clay, percent organic matter, C, N, and K availability, and pH compared to areas of typical cerrado (Furley et al. 1988; Furley & Ratter 1988; Haridasan 1992). The occurrence of *cerradão* on soils currently with low fertility is a possible consequence of past soil conditions maintained over time by nutrient cycling (Haridasan 1985, 2000).

Determinants of Grassland-Savanna-Forest Complex in Cerrado and Their Importance for Restoration

In the Cerrado region, as in other savannas worldwide, most authors recognize that a combination of soil conditions, rainfall seasonality, and fire regime drives the mosaic of vegetation (Mistry 2000; Moreira 2000; Ribeiro & Walter 2008; Lehmann et al. 2011; Pivello 2011; Bueno et al. 2013). However, many articles apply a linear successional trajectory, assuming that the exclusion of natural fire and anthropogenic disturbances (e.g. increased fire frequency and cattle) may result in encroachment and then transitions from grasslands into savannas and savannas to *cerradão* (Rizzini & Heringer 1962; Henriques 2005). Other

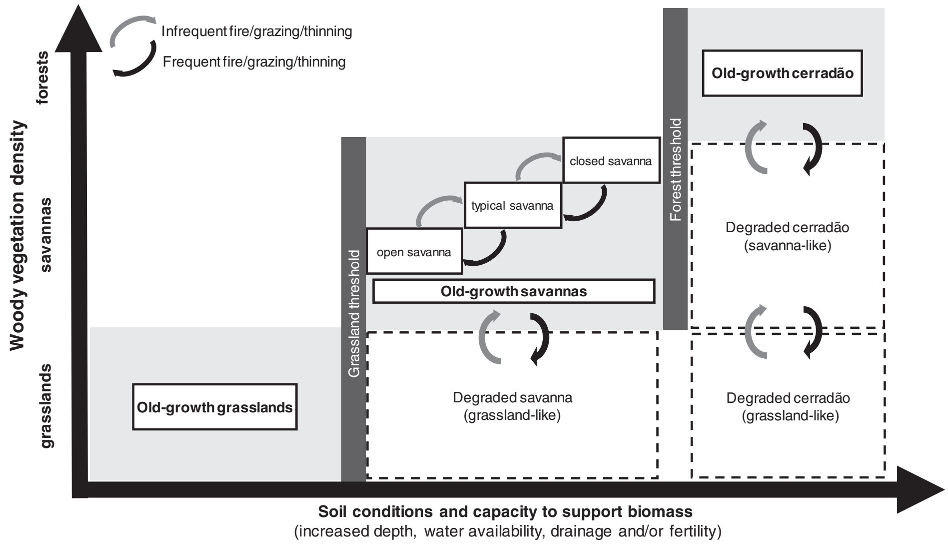

Figure 1. A conceptual model of the ecological factors and historical disturbances driving natural and anthropogenic vegetation types within the grassland-savanna-forest complex in central Brazil. Natural transitions between grasslands, savannas, and forests (cerradão) are mostly limited by soil conditions. Low-intensity land use such as changes in fire regime, wood harvesting, and light grazing by domestic livestock on native vegetation may cause transitions (black arrows) from which they often can naturally recover when disturbances are interrupted (gray arrows). After medium- or high-intensity land uses, other restorations interventions may be needed (Table 1), depending on the resilience of the original vegetation type.

studies indicate that with no human intervention, each of these Cerrado vegetation types tends to maintain some stability over ecological time scales (decades to centuries), even though the boundaries of these vegetation types can naturally expand and retract across the landscape in response to biotic and abiotic factors (Eiten 1972; Coutinho 1978; Ribeiro & Walter 2008). In addition, over geological time (thousands to millions of years), there may be transitions between vegetation types (Prado & Gibbs 1993; Oliveira-Filho & Ratter 1995).

We propose a conceptual model of the ecological factors and disturbances driving natural and anthropogenic vegetation states within the grassland-savanna-forest complex in central Brazil that (1) highlights soil as an important threshold and determinant of vegetation type and (2) incorporates degraded and alternative land-use states to guide restoration. We propose that, within the Cerrado region, grasslands, savannas, and *cerradão* represent three main natural vegetation types that should be considered as restoration targets (Figs. 1 and S1). Savannas can transition between open, typical, and closed vegetation subtypes with changes to the fire and grazing regime.

Soil conditions are major determinants of vegetation type in African, Australian, and South American mesic savannas. Generally, the rate of woody growth and canopy closure increase with soil fertility; this shades out C4 grasses rapidly, providing less opportunity for fire or grazing disturbance, thus maintaining a forest structure (Lloyd et al. 2008; Lehmann et al. 2011). In the core Cerrado region, soil conditions are the primary factor determining vegetation type, whereas annual precipitation patterns and fire play a secondary role (Fig. 1; Furley & Ratter 1988; Furley 1996; Villalobos-Vega et al. 2014). Woody species from tropical savannas have deep roots (approximately 15 m; Canadell et al. 1996) so shallow soils prevent colonization by most woody species, especially trees (Ribeiro & Walter 2008; Amaral et al. 2017; Buisson et al. 2018), acting as a barrier to most grassland-savanna transitions.

In the core Cerrado region, where soils are mostly acidic and infertile (Sano et al. 2019) and the dry season lasts from 3 to 5 months (Agência Nacional de Águas 2019), the transitions between open and closed savannas may be triggered by changes in fire frequency, with frequent fires favoring herbaceous species (Miranda et al. 2009). These savanna ecosystems evolved with lightning-strike fires mostly during early rainy season, the frequency of which is not well documented, but is hypothesized to be between 1 and 9 years (Ramos-Neto & Pivello 2000; França et al. 2007; Miranda 2010). What is clear is that humans have increased the frequency and changed the fire season with most anthropogenic fires concentrated in the late-dry season, which has negative effects, especially for woody species. For example, frequent (annual to triennial) late-dry season anthropogenic fires are common, even in protected areas (Schmidt et al. 2018). Frequent late-dry season fires kill trees and promote topkill (loss of aboveground plant structures) favoring open vegetation forms and transforming trees to a shrub-like morphology (Hoffmann 1999; Miranda et al. 2009). Such fire regimes may promote the shift from *cerradão* and old-growth savannas to anthropogenically derived savannas or grasslands (Fig. 1; Sato 2003; Miranda et al. 2009). Woody encroachment happens slowly and results in a low increase in basal area from the growth of stems in areas protected from natural and anthropogenic fires (Moreira 2000; Sato 2003; Souza 2010; Eugênio et al. 2011; Almeida et al. 2014). For example, after 18 years of fire protection, Moreira (2000) describes an increase in woody stem densities compared to areas burned biennially, but the change reported does not characterize the transition between a savanna and a forest physiognomy. The same author hypothesizes that fire protection for sufficiently long periods

Table 1. Restoration actions tailored to the original vegetation type and disturbance intensity. Resilience refers to the ability of the system to return to its original vegetation structure under passive restoration when anthropogenic disturbances cease.

	Restoration Actions Required According to Vegetation Type		
Anthropogenic Disturbance	*Grassland*	*Savanna (open, typical, or closed)*	*Cerradão*
Low-intensity land uses: increased fire frequency, low-intensity cattle grazing, wood harvesting, no invasive grasses	High resilience: reduce disturbance frequency to allow for natural regeneration through graminoid and forb resprouting	High resilience: reduce disturbance frequency, including anthropogenic fires, to allow for natural regeneration through graminoid, forb, and woody species resprouting	High resilience: reduce disturbance frequency, including anthropogenic fires, to allow for natural regeneration through woody species resprouting
Medium-intensity land uses: low technified pasture or silviculture: infrequent plowing, tilling, liming and soil fertilization, invasive grasses	Low resilience: control invasive grasses and reintroduce graminoids, forbs, and shrubs	Medium resilience: control invasive grasses, reduce anthropogenic fires, allow woody species resprouting, and reintroduce graminoids, forbs, and woody species	High resilience: control invasive grasses, reduce anthropogenic fires and allow woody species resprouting
High-intensity land uses: highly technified pasture, silviculture, or agriculture: underground structures removed, frequent plowing, tilling, liming and soil fertilization, invasive grasses	Low resilience: control invasive grasses, promote changes in soil properties, reintroduce graminoids and forbs	Low resilience: control invasive grasses, avoid anthropogenic fires, promote changes in soil properties, reintroduce graminoids, forbs, and woody species	Low resilience: control invasive grasses, avoid anthropogenic fires and reintroduce woody species
Very high-intensity land uses: mining or soil removal: vegetation and topsoil and/or subsoil removal	Very low: reintroduce soil, graminoids, and forbs, avoid anthropogenic fires	Very low: reintroduce soil, graminoids, forbs and woody species, avoid anthropogenic fires	Very low: reintroduce soil and woody species, avoid anthropogenic fires

of time could lead to more wooded physiognomies (Moreira 2000), but lacks data to support this statement. Our observations suggest that grasslands on infertile or shallow soils in the core Cerrado region do not transition to forests when protected from fire for up to three decades. We note that longer-term data are needed to fully clarify the relative importance of fire and soil in maintaining old growth grasslands and savannas.

In contrast, at the edges where the Cerrado borders humid tropical forest biomes (Amazon and Atlantic forest, Fig. S1), the dry season tends to be shorter and mesotrophic soils are more common (Sano et al. 2019). There, fire and cattle exclusion may result in the regeneration of derived-grasslands and derived-savannas into *cerradão* in a few decades (Durigan & Ratter 2006) and in savanna-forest transitions (e.g. Abreu et al. 2017) that have not been documented in the Cerrado core region.

For thousands of years, the Cerrado region has been subjected to low-intensity anthropogenic disturbances, such as occasional burning and wood harvesting (Pivello 2011). In the past few decades, however, large-scale intensive agriculture, pastureland, afforestation, and mining have become common, threatening the Cerrado (Klink & Machado 2005; Durigan & Ratter 2016). These activities limit natural regeneration potential much more strongly than historical disturbance regimes (Table 1). At least 30% of Cerrado has been converted to pastures and 12% to industrial agriculture (MMA 2015), where repeated plowing decreases native vegetation resprouting. Fertilizers and agricultural limestone are commonly added to enrich soil and neutralize acidity, frequently favoring invasions by exotic grasses (Bustamante et al. 2012). Pastures are typically seeded with highly competitive exotic grass species, which rapidly spread into agricultural fields and degraded areas, increasing fire frequency (Pivello et al. 1999), outcompeting native species, and decreasing the resilience of the herbaceous layer (Cava et al. 2017; Silva & Vieira 2017; Coutinho et al. 2018).

Identifying Restoration Targets and Barriers

In most cases, detailed historical disturbance and management information including fire regime, cattle grazing, and wood harvesting are unavailable for degraded areas. Even so, recognizing the original vegetation types as grassland, savanna, or *cerradão* and establishing it as a target is necessary to select the appropriate restoration methods and evaluate success. These three categories establish a reference system that respects the original structure and function of the vegetation, while recognizing the common transition between savanna types with low-intensity disturbances (Fig. 1). Based on our observations and studies, we propose that grasslands, savannas, and *cerradão* require different restoration approaches. Degraded grasslands should be restored with the focus on the herbaceous layers, whereas the coexistence between grasses and trees should be the target of restoring savanna ecosystems. Restoration of degraded *cerradão* should aim to establish a tree layer (Table 1).

Vegetation recovery rates vary with the intensity of past land use and vegetation type (Vesk & Westoby 2004). As in other ecosystems with an extended dry season and periodic natural fires, the resilience and the potential for natural regeneration in

Cerrado are related in large part to plants' resprouting ability (Abreu et al. 2017; Pausas et al. 2017). Many Cerrado species have low natural recruitment rates, due to low seed viability and dispersal, and/or high seed predation (Salazar et al. 2012; Aires et al. 2014), with natural populations persisting for decades through clonal reproduction and resprouting after fire, herbivory, and plowing (Moreira 2000).

Under low-intensity disturbance regimes, grasslands, savannas, and *cerradão* often show high resilience or regeneration potential, so interrupting anthropogenic disturbances may be enough for these areas to recover (Table 1). Perennial subshrubs, shrubs, and trees may persist in degraded savanna and *cerradão* if stem or even root structures have not been depleted by stump removal, frequent plowing, or repeated herbicide application (Ferreira et al. 2017). However, grasses, short-lived herbs, and shrubs have shallower roots and bud bank organs, making these species less resilient to anthropogenic soil disturbances (e.g. Castro & Kauffman 1998; Pausas et al. 2017). *Cerradão*, which naturally has a less diverse and abundant native herbaceous layer, may be more resilient and prone to natural regeneration after medium-intensity disturbances (Table 1) allowing for faster natural regeneration than savannas and grasslands (e.g. Durigan et al. 1997; Durigan et al. 1998). When underground structures are eliminated in *cerradão* through high-intensity land use, natural regeneration is constrained. In these cases, restoration may be achieved through control of invasive grasses, which act as barriers to native species recruitment and reintroduction of woody species (Table 1), as in other forested systems (Holl 2012). Since *cerradão* trees generally grow more slowly than humid forest trees (Vourlitis et al. 2001), invasive grass control is required for longer periods.

Grasslands and savannas that have been subjected to medium- or high-intensity disturbance have low resilience (Table 1), and restoration of the herbaceous layer is challenging because tree canopy shade cannot be used to reduce invasive grass cover. Improved techniques to restore soil properties, control invasive grasses, and re-introduce native herbaceous species are essential. Direct seeding can be an effective technique for increasing native cover (Pellizzaro et al. 2017), since planting seedlings of herbaceous species is logistically cost prohibitive at the scale and density required.

When soil is removed for mining or road construction, very low natural regeneration potential remains for any of the Cerrado vegetation types (Table 1). Intensive efforts to recreate soil structure and fertility and reintroduce plants are needed to restore the system (Corrêa 2009), and may or may not succeed. Translocating topsoil and underground structures from native habitats slated for conversion may be a feasible restoration approach (Ferreira et al. 2015, 2017; Pilon et al. 2018).

Fire should be used carefully as a restoration tool, and the fire regime needs to be managed considering natural fire frequency and the management context of specific vegetation types (Mistry et al. 2018; Schmidt et al. 2018). Frequent anthropogenic fires may alter the structure of *cerradão* and savannas to derived-savannas or derived-grasslands, due to tree mortality and topkill (Sato 2003; Miranda et al. 2009); therefore, in these systems, decreasing rather than increasing fire frequency may be the most appropriate restoration approach (Table 1). Such disturbed systems maintain high resilience and transition back to the original vegetation type if frequent burning ceases, although some fire-sensitive species may be eliminated (Hoffmann 1999) and need to be reintroduced as part of restoration efforts. Fire historically shifted the savanna ecosystem between closed and open vegetation types and hence may be an appropriate management tool in savannas (Fig. 1). Burning may also be useful when combined with mechanical and/or chemical control of invasive grasses (Martins et al. 2011; Coutinho et al. 2018). But most invasive grass species are from other fire-adapted systems so burning alone is unlikely to control these grasses (D'Antonio & Vitousek 1992). Fire management programs have only recently been implemented in Cerrado with the main goals of avoiding frequent large wildfires and protecting fire-sensitive vegetation (Schmidt et al. 2018).

Further research is needed on the effects of different fire frequencies and intensities on vegetation composition of the three vegetation types. In particular, quantitative data are needed on long-unburned sites to resolve debates about the relative importance of soil and fire in maintaining different vegetation types.

Conclusions

Restoring the millions of hectares of degraded grasslands-savanna-forest mosaics in the Cerrado region and in other continents is a daunting task, particularly in open canopy ecosystems where invasive grasses pose a formidable obstacle to recovery (Coutinho et al. 2018; Sampaio et al. in review). This highlights the importance of slowing the rapid ongoing conversion rate of Cerrado (Klink & Machado 2005) and grassy biomes worldwide (Veldman et al. 2015), as conserving old-growth grassland and savanna ecosystems is the best option. Efforts to protect these ecosystems are particularly urgent since the environmentally damaging industrial agribusiness model implemented in central Brazil in the past decades is under expansion, promoting land-use change in African savannas and other tropical systems (Castro 2013; Phalan et al. 2013).

Moving from the small-scale Cerrado restoration efforts currently underway toward the large scale necessary to restore grassland-savanna-woodland mosaics in Brazil and worldwide (Mistry 2000) requires two key steps. First, it is essential to identify both natural and anthropogenic states based on soil conditions, precipitation patterns, prior land use, fire history, and other factors to set appropriate restoration targets (Mistry 2000). Examples of misidentifying reference ecosystems in old-growth grassland and savanna ecosystems are widespread (Veldman 2016), which leads to a waste of scarce restoration funding on projects that are ecologically unsound and unlikely to succeed. After setting the target vegetation type, a second critical step is to assess the natural regeneration potential and barriers to recovery for each vegetation type. This will help in selecting the most ecologically appropriate and cost-effective restoration techniques and enhance restoration success. Finally, there is an urgent need to promote more experimentation to improve restoration techniques in the Cerrado grassland-savanna-forest complex.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Map of Brazilian biomes. The Cerrado region (light green) is in central Brazil and borders four different biomes.
Figure S2. Photos of the three main Cerrado vegetation types: (A) grassland; (B) savanna, and (C) *cerradão* (scleromorphic forest). Photos: Bruno M. T. Walter.

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