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Using a state-transition model of the grassland-savanna-forest complex in central Brazil to guide restoration

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Abstract

Developing state-transition models of complex vegetation mosaics and identifying the factors driving these transitions can help to guide restoration efforts. Misidentification of anthropogenically-degraded grasslands and savannas as natural states can lead to misguided restoration efforts and legislation. Here we describe multiple natural and anthropogenically-altered states in the grassland-savanna-forest mosaic in the Cerrado region of central Brazil. We contend that the varying vegetation composition was originally driven by soil types and secondarily by precipitation and fire frequency. Grasslands were found on the shallowest, least fertile soils and scleromorphic forests on the most fertile, with savannas occupying an intermediate position. In recent decades, this biophysical template has been overlain by a range of human land use intensities that strongly affect resilience of the different ecosystem types. In particular, planting and subsequent spread of invasive exotic pasture grasses and intensive tilling which damages the natural resprouting capacity of native species, reduce recovery rates. Hence, restoration efforts should start by carefully distinguishing between historically and anthropogenically degraded ecosystem states. Then it is important to evaluate the natural resilience in a given site to select the most appropriate method to facilitate recovery.

Introduction

Restoration ecologists have long recognized that few degraded ecosystems follow a linear recovery trajectory towards a reference ecosystem (Trowbridge 2007; Matthews et al. 2009). State-transition models that incorporate multiple endpoints with thresholds and feedbacks between them better describe the dynamics of many ecosystem types (Westoby et al. 1989; Suding et al. 2004). Identifying alternative natural states and isolating the factors driving the transitions between them are essential to select and implement compatible management and restoration efforts. Nonetheless, there are few examples where the triggers to transitions between alternative states have been clearly identified and used to guide restoration.

This need to distinguish multiple states is especially true in savannas where a complex mosaic of ecosystems coexists across the landscape, influenced by soil properties, topography, rainfall gradients, natural disturbances, and human activities (Lehmann et al. 2011). When these natural and anthropogenic drivers interact to shape ecosystem structure and community composition it is challenging to define ecosystem degradation levels and determine restoration targets. In such systems, vegetation types are commonly classified according to the current vegetation structure or physiognomy, which can lead to mistakes that jeopardize conservation and restoration (Veldman 2016). Old-growth savannas and grasslands are threatened when they are seen as degraded forests and targeted for forest restoration or carbon-sequestration initiatives (Veldman et al. 2015; 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 policies and selecting inappropriate restoration targets and methods, and in turn restoration failure (Suding 2011). For example, some state laws in Brazil require tree seedling planting regardless of the original vegetation and do not consider herbaceous species (DF Laws 14.783/1993; 23.585/2003). This leads to high seedling mortality (commonly >60% in the first few years) and/or non-recruiting tree stands.

Here we use the complex mosaic of grasslands, savannas and forest systems in central Brazil, hereafter called the Cerrado region, as an example of how a clear understanding of natural and anthropogenic states, as well as the factors affecting transitions among them, can help guide restoration efforts. We characterize natural and degraded vegetation states resulting from common human interventions, identify transitions between those states due to natural regeneration mechanisms, and pinpoint restoration interventions.

Cerrado vegetation types

The Brazilian Cerrado is a mosaic of grasslands, savannas and forests occupying 2 million km^2 mainly in Central Brazil. It is a humid savanna region, with a seasonal rainfall pattern varying from 750 to 2,000 mm/year, 90% of which falls between October and April. Rainfall is higher in the southeastern and northwestern portions at ecotones with the Atlantic and Amazonian tropical rain forests (Ribeiro & Walter 2008). The Cerrado is the most biodiverse (>10,000 plant species) savanna worldwide with high endemism rates (~44% plant endemics) and ancient flora [illegible] Open vegetation types originally covered >75% of Cerrado region. In these old-growth savannas, graminoids, forbs and woody species coexist with crown cover ranging from 10% in open savanna-grasslands (regionally called *campo sujo*), 10-50% in typical savannas (*cerrado sensu stricto*), to 50-70% crown cover in closed savannas (*cerrado denso).* Herbaceous and shrub species form a continuous layer and represent 60-80% of the species richness (Amaral et al. 2017). Shallow soils are covered by old-growth grasslands with no woody species (*campo limpo*), whereas in deeper, mesic soils, tree canopy can cover 70-90% forming scleromorphic forests (*cerradão*) with a sparse herbaceous layer (Ribeiro & Walter 2008). Each physiognomic type has a distinct flora, even though some woody species are abundant in most vegetation types throughout the region (Ratter et al. 2003; Amaral et al. 2017).

Many Cerrado species have low natural recruitment rates, due to low seed viability and dispersal, and high seed predation (Salazar et al. 2012; Aires et al. 2014), with natural populations persisting through clonal reproduction and resprouting after fire, herbivory, and plowing, like in many fire-prone ecosystems (Pausas et al. 2017). Underground storage organs allow woody species to persist in frequently plowed areas for decades (Moreira 2000), whereas the bud bank of graminoids and forbs is shallower (~20-cm), making these species less resilient to anthropogenic soil disturbances.

Vegetation determinants and state-transition model

In the Cerrado region, as in other savannas worldwide (Lehmann et al. 2011), most authors recognize that a combination of soil conditions, rainfall seasonality, and fire regime drive the mosaic of vegetation composition and structure (Pivello 2011). In contrast, some papers apply linear successional trajectory models and assume that fire-exclusion alone may result in transitions from grasslands into savannas and savannas to scleromorphic forests (Rizzini & Heringer 1962; Durigan & Ratter 2006). Even when authors propose alternative-state models, some describe successional transitions between grasslands, savannas and scleromorphic forests (Pivello & Coutinho 1996; Meirelles et al. 1997).

Factors affecting thresholds and transitions vary across savannas throughout the world. For example, herbivory plays a larger role in African savannas, where large herbivores prevent canopy closure (Sankaran et al. 2008). We argue that, in the Cerrado, soil characteristics are the primary factor determining vegetation type, whereas fire and precipitation play a secondary role. We propose a soil-driven framework to understand the state-transition models in the Cerrado region. Woody species from tropical savannas have deep roots (~15 m; Canadell et al. 1996) so shallow soils prevent colonization by most woody species (Ribeiro & Walter 2008), acting as a barrier to grassland-savanna transitions. The transitions between open and closed savannas may be trigged by changes in fire frequency, with frequent fires favoring herbaceous species (Miranda et al. 2009). In contrast, the transitions between savanna and scleromorphic forests are limited by soil conditions. In other words, the state transitions from grassland-to-savanna, grassland-to-scleromorphic forests, and savanna-to-scleromorphic forests start from degraded-grasslands or degraded-savannas and not from old-growth (natural) formations (Figure 1).

Woody encroachment that results in transitions from savannas into forests are mostly restricted to ecotone regions with higher precipitation and mesotrophic soils where the Cerrado borders humid tropical forests (Amazon and Atlantic forest). In these areas, fire exclusion may result in savanna-forest transitions (e.g. Abreu et al. 2017) that are not documented in the Cerrado core region (Moreira 2000).

Cerrado vegetation has been subjected to low intensity anthropogenic disturbances such as increased fire frequency and wood harvesting for thousands of years. In the past few decades, large-scale intensive agriculture, pastureland, afforestation and mining became common in the Cerrado (Klink & Machado 2005). These activities differentially affect natural regeneration potential (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. Pastures are typically seeded with highly competitive African grass species which rapidly spread into agricultural fields and degraded areas (Pivello et al. 1999), increasing fire frequency and outcompete native species (Silva et al. 2015).

Manipulating filters and thresholds to improve resilience and restore ecosystems

Environmental laws and international commitments set a target for Brazil to restore ~12 million hectares of natural habitat of which 5 million hectares are within the Cerrado region (Decree 8952/2017). To achieve such commitments, restoration techniques that are cost-effective and practical at a large scale are needed. 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). 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). We propose to use the state transition model to identify original vegetation states and then modify disturbance regimes and/or select restoration strategies to restore specific states.

The resilience and natural regeneration potential in Cerrado are directly related to plants' resprouting ability. Vegetation recovery rates vary along a gradient of soil fertility and intensity of past land use. Under low intensity disturbance regimes, grasslands, savannas and scleromorphic forests may show high resilience. However, the resilience of the herbaceous layer decreases rapidly due to soil disturbance and exotic grass invasion (Cava et al. 2017). In contrast, woody species (subsshrubs, shrubs and trees) may persist in degraded savanna and scleromorphic forests if root structures have not been removed by frequent plowing and repeated herbicide application (Ferreira et al. 2017).

Scleromorphic forests, which have a less diverse native herbaceous layer, may be more resilient to medium intensity disturbances (Table 1). This higher resilience allows for faster passive recovery transitions from degraded-grasslands or savannas into scleromorphic forests (e.g. Durigan & Ratter 2006; Cava et al. 2017). When underground structures are eliminated in scleromorphic forests, resilience is constrained and restoration may be achieved through control of invasive grasses and reintroduction of woody species (Table 1), as in other forested systems (Holl 2012). Since scleromorphic forest trees generally grow slower than humid forest trees (Vourlitis et al. 2001), invasive grass control is required for longer periods. In grasslands and savannas dominated by invasive grasses, 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 exotic grasses, and re-introduce native ground-cover herbaceous species are essential. Direct seeding may be an effective technique for increasing native cover (Pellizzaro et al. 2017), since planting seedlings of herbaceous species is cost prohibitive at the scale and density required.

When soil is removed for mining or road construction, very low natural regeneration potential remains (Table 1). Translocating topsoil and underground structures from native habitat slated for conversion may be a cost-effective restoration approach (Ferreira et al. 2015).

Restoring the millions of hectares of degraded grasslands, savannas, and forests in the Cerrado region is a daunting task, particularly in open canopy ecosystems where invasive grasses pose a formidable obstacle to recovery. This highlights the importance of slowing the rapid ongoing conversion rate of Cerrado ecosystems (Klink & Machado 2005) where conserving old-growth grassland and savanna ecosystems is the best option. That said, we reiterate that clearly identifying both natural and anthropogenic states based on soil type, precipitation, and prior land use, is a first step in setting appropriate restoration targets. This information, combined with an initial assessment of the natural resilience in a given location, will help to guide the selection of the most appropriate and cost-effective restoration techniques.

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Table 1. Restoration actions tailored to the original vegetation and land use intensity

	Restoration actions required according to vegetation type		
Anthropogenic disturbance	Grassland *(campo limpo)*	Savanna *(campo sujo to cerrado denso)*	Scleromorphic forests *(cerradão)*
Low intensity land uses: increased fire frequency, low intensity cattle grazing, wood harvesting, no exotic grasses	**High Resilience:** allow for natural regeneration through graminoid and forb resprouting	**High Resilience:** allow for natural regeneration through graminoid, forb, and woody species resprouting	**High Resilience:** allow for natural regeneration through woody species resprouting
Medium intensity land uses - low technified pasture or silviculture: infrequent plowing, tilling, liming and soil fertilization, exotic grasses	**Low resilience:** control exotic grasses and reintroduce graminoids and forbs by direct seeding	**Medium resilience**: control exotic grasses, allow woody species resprouting and reintroduce graminoids, forbs and woody species by direct seeding	**High resilience:** control exotic grasses 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, exotic grasses	**Low resilience:** control exotic grasses, promote changes in soil properties, reintroduce graminoids and forbs	**Low resilience:** control exotic grasses, promote changes in soil properties, reintroduce graminoids, forbs and woody species	**Low resilience:** control exotic grasses 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	**Very low**: reintroduce soil, graminoids and forbs	**Very low**: reintroduce soil and woody species

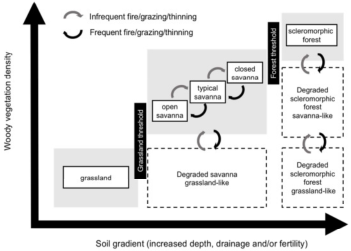

Figure 1. Natural states and transitions between Cerrado grasslands (*campo limpo*), savanna vegetation, open savanna (*campo sujo*), typical savanna (*cerrado sensu stricto*) and closed-savanna *(cerrado denso*), and scleromorphic forests (*cerradão)*. Soil conditions prevent most transitions between old-growth grasslands and savannas as well as between savanna and scleromorphic forest (thresholds). Transitions among these states only happen between previously degraded areas within the same soil type after low intensity land use such as changes in fire regime, wood harvesting and low intensity grazing by domestic livestock on native vegetation.