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Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands

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ABSTRACT

Despite growing recognition of the conservation values of grassy biomes, our understanding of how to maintain and restore biodiverse tropical grasslands (including savannas and open-canopy grassy woodlands) remains limited. To incorporate grasslands into large-scale restoration efforts, we synthesised existing ecological knowledge of tropical grassland resilience and approaches to plant community restoration. Tropical grassland plant communities are resilient to, and often dependent on, the endogenous disturbances with which they evolved – frequent fires and native megafaunal herbivory. In stark contrast, tropical grasslands are extremely vulnerable to human-caused exogenous disturbances, particularly those that alter soils and destroy belowground biomass (e.g. tillage agriculture, surface mining); tropical grassland restoration after severe soil disturbances is expensive and rarely achieves management targets. Where grasslands have been degraded by altered disturbance regimes (e.g. fire exclusion), exotic plant invasions, or afforestation, restoration efforts can recreate vegetation structure (i.e. historical tree density and herbaceous ground cover), but species-diverse plant communities, including endemic species, are slow to recover. Complicating plant-community restoration efforts, many tropical grassland species, particularly those that invest in underground storage organs, are difficult to propagate and re-establish. To guide restoration decisions, we draw on the old-growth grassland concept, the novel ecosystem concept, and theory regarding tree cover along resource gradients in savannas to propose a conceptual framework that classifies tropical grasslands into three broad ecosystem states. These states are: (1) old-growth grasslands (i.e. ancient, biodiverse grassy ecosystems), where management should focus on the maintenance

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of disturbance regimes; (2) hybrid grasslands, where restoration should emphasise a return towards the old-growth state; and (3) novel ecosystems, where the magnitude of environmental change (i.e. a shift to an alternative ecosystem state) or the socioecological context preclude a return to historical conditions.

Key words: forest and landscape restoration, invasive species, prescribed fire, rangeland management, secondary grassland, tropical grassy biomes, woody encroachment.

CONTENTS

I. INTRODUCTION

Grasslands, broadly defined, including savannas with scattered trees and open-canopy grassy woodlands, cover approximately 52 million km^2, approximately 40% of global land surface (White, Murray & Rohweder, 2000; Gibson, 2009; Dixon *et al.*, 2014), and approximately 20% of the tropics (Parr *et al.*, 2014; Bond, 2016). Across the globe, and particularly in the humid tropics and subtropics, ancient and biodiverse grassland ecosystems have long been misinterpreted as early successional vegetation, formed by human-caused deforestation (Bond & Parr, 2010; Joshi, Sankaran & Ratnam, 2018). In light of such misinterpretations, it is increasingly clear that to achieve biodiversity conservation goals, ecologists, environmental policymakers, and ecosystem managers should clearly distinguish old-growth grasslands (Veldman *et al.*, 2015*a*) from the low-diversity grass-dominated vegetation that is created by humans (i.e. planted pastures, derived savannas; Veldman, 2016).

Old-growth grasslands are ancient grassy ecosystems characterised by species-diverse herbaceous plant communities that are maintained by frequent fires, megafaunal herbivores, and edaphic factors that limit tree growth (Veldman *et al.*, 2015*a*). Old-growth grasslands occur worldwide, but those that occur in the humid tropics and subtropics (henceforth 'tropical old-growth grasslands') warrant particular conservation attention (Parr *et al.*, 2014). Tropical old-growth grasslands exhibit exceptional biodiversity, including high species richness and endemism, and provide important ecosystem services, including belowground carbon storage, soil stabilisation, ground and surface water recharge, forage production for domestic livestock and native game animals, and habitat for native charismatic and endangered animals [e.g. elephant, *Loxodonta africana* and bison, *Bison bison* (Fuhlendorf *et al.*, 2009; Resende, Fernandes & Coelho, 2013; Parr *et al.*, 2014; Hempson, Archibald & Bond, 2015; Veldman *et al.*, 2015*a*,*b*; Bond, 2016; Abreu *et al.*, 2017)].

During the past century, while the global area of human-created grass-dominated vegetation increased (due to forest clearing), the world's old-growth grasslands dramatically declined due to land-use change. The decline in old-growth grasslands has been caused by widespread agricultural conversion, afforestation, and forest expansion, as well as mining and urbanisation (White *et al.*, 2000; Nosetto, Jobbagy & Paruelo, 2005; Lark, Salmon & Gibbs, 2015; Noss *et al.*, 2015; Veldman *et al.*, 2015*b*). Moreover, many remaining old-growth grasslands are being degraded by altered fire regimes (i.e. changes to the historical frequency, intensity, and seasonality of fire), invasive species, overgrazing, loss of native megafauna, liming, nitrogen deposition, and elevated atmospheric carbon dioxide, which

promotes grassland encroachment by woody plants (White *et al.*, 2000; Weigl & Knowles, 2014; Bond, 2016; Stevens *et al.*, 2016).

Our knowledge of tropical old-growth grassland resilience (i.e. resistance to degradation and capacity for recovery; Hodgson, McDonald & Hosken, 2015) and restoration (i.e. intentional activities that initiate or accelerate the recovery of an ecosystem; SER Working Group, 2004) remains limited relative to our knowledge of temperate grasslands. In many temperate regions, grassland conservation values are well recognised (Leopold, 1949; Packard, Mutel & Jordan, 2005; Silva *et al.*, 2008; Bond & Parr, 2010), grassland resilience has been extensively studied (Grime *et al.*, 2000; Jentsch *et al.*, 2011), and grassland restoration efforts are widely promoted (Gibson, 2009). Consequently, many effective techniques to restore temperate grasslands have been developed (Perrow & Davy, 2002; Jordan, 2005; Kiehl *et al.*, 2010; Freudenberger & Gibson-Roy, 2011; Török *et al.*, 2011; Aronson, 2013; Marshall, Williams & Morgan, 2015). By contrast, recognition of the conservation values of tropical old-growth grasslands has only emerged recently (Overbeck *et al.*, 2007, 2013, 2015; Bond & Parr, 2010; Laurance *et al.*, 2011; Parr *et al.*, 2014; Fernandes, 2016; Lehmann & Parr, 2016; Ratnam *et al.*, 2016; Silveira *et al.*, 2016), or where concern has existed, conservation emphasis has been placed on the management of populations of charismatic animals (African megafauna) or agricultural conversion (e.g. Ratter, Ribeiro & Bridgewater, 1997), rather than ecosystem restoration (but see Fernandes, 2016; Strassburg *et al.*, 2017).

Further contributing to a lack of grassland restoration research, conservation agendas for the tropics have largely focused on forests (Overbeck *et al.*, 2015; Searchinger *et al.*, 2015; Bond, 2016; Veldman, 2016). Indeed, a key motivation for this review is to clarify, in light of the Forest and Landscape Restoration movement (e.g. Chazdon *et al.*, 2017), that ecological restoration of tropical grasslands rarely involves planting trees, suppressing fire, excluding large herbivores, or applying soil fertilizers – i.e. the suite of forest-restoration strategies that are commonly misapplied to tropical old-growth grasslands (Ratnam *et al.*, 2016; e.g. Gonçalves *et al.*, 2013; Reis *et al.*, 2016). We specifically aim to provide policymakers and practitioners with basic information on the kinds of activities (e.g. prescribed fire, tree cutting) that should be incorporated into large-scale restoration planning, as a means to conserve and restore biodiverse tropical grasslands.

To demonstrate the need for such information, in August 2017, we searched *Restoration Ecology*, the primary international ecology journal focused on restoration research [using the search function of Wiley Online Library (Wiley, 2017)] for the terms "tropical grassland", "subtropical grassland", and savannah AND tropic* in the title, key words, or abstract of articles published from 1993 to 2017. The search returned 14 articles, of which only eight were relevant to grassland restoration (see online Appendix S1, Table S1 in File S1). The same search using the term "tropical forest" yielded 109 articles. As further evidence that tropical grassland restoration research is lacking, the Global Partnership on Forest and Landscape Restoration (GPFLR, 2016), perhaps the most influential consortium of institutions promoting large-scale restoration in the tropics, offers very little information on restoration strategies for savannas and grasslands. Clearly, there is a great need to better integrate theoretical knowledge of tropical grassland ecology with management practice to conserve and restore these ecosystems.

This is not to say that conservationists have completely ignored tropical grasslands, indeed some tropical old-growth grasslands are recognised for their biodiversity and have elicited conservation concern (Strassburg *et al.*, 2017). For example, the grasslands of the Cerrado (Brazil), tropical Andes, and mountains of eastern Africa are recognised as biodiversity hotspots – i.e. regions of high conservation priority, based on high diversity and endemism as well as a high proportion of land conversion (Mittermeier *et al.*, 2011). Still, many other diverse and threatened tropical grasslands are not classified as biodiversity hotspots and receive little conservation attention. Examples of under-recognised grasslands include: Southern African Montane Grasslands, Guianan Lowland Grasslands and Savannas (Mittermeier *et al.*, 2011; Dixon *et al.*, 2014), Southern Central Africa edaphic grasslands (Faucon *et al.*, 2016), subtropical grasslands of southern Brazil (Overbeck *et al.*, 2007), subtropical savannas of North America (Noss *et al.*, 2015), and savannas of India and southeast Asia (Ratnam *et al.*, 2016). Unfortunately, even with better recognition, we should not expect classification of more grasslands as biodiversity hotspots to halt conversion for agriculture (Machado *et al.*, 2004; Carvalho, De Marco & Ferreira, 2009) or prevent forest expansion (e.g. Durigan & Ratter, 2016). As more tropical old-growth grasslands are lost, grassland restoration should increase in importance as part of efforts to maintain biodiversity and ecosystem services (Resende *et al.*, 2013; Parr *et al.*, 2014; Bond, 2016; Fernandes, 2016).

Herein, we review current research and identify knowledge gaps that must be filled to improve our understanding of the resilience of tropical old-growth grasslands and to improve our ability to restore tropical grassland biodiversity (Mace, 2014; Oliver *et al.*, 2015). Indeed, a key part of restoration planning is to consider the resilience of ecosystem states to environmental change and management interventions (Hobbs & Norton, 1996; Mitchell *et al.*, 2000; Hirst *et al.*, 2003; Belyea, 2004; Lockwood & Samuels, 2004; Suding, Gross & Houseman, 2004; White & Jentsch, 2004; Hobbs, Jentsch & Temperton, 2007; Briske *et al.*, 2008; Hobbs & Suding, 2013). We restrict our review to grasslands of the humid tropics and subtropics ($<35^{\circ}$ latitude) that receive >750 mm mean annual precipitation (Fig. 1 and see online Fig. S1); these are regions where climate can permit the development of both grasslands and forests (Hirota *et al.*, 2011; Lehmann *et al.*, 2011; Staver, Archibald & Levin, 2011). Whereas the herbaceous plant community of arid tropical grasslands tend to be composed of annual and

Fig. 1. Images of tropical and subtropical old-growth grasslands, savannas, and grassy woodlands with numbers on the images corresponding to the numbered geographical locations shown in online Appendix S2 in File S1, Fig. S1). (1) Subtropical grasslands (*campos sulinos*) in Rio Grande do Sul, Brazil. (2) *Cerrado* moist grasslands in São Paulo, Brazil. (3) *Cangas* grasslands, on ironstone outcrops in the Iron Quadrangle, Brazil. (4) *Campo rupestre* grasslands, southeastern Brazil. (5) *Campo rupestre* grasslands a few months after fire, southeastern Brazil. (6) *Cerrado* grasslands in Tocantins (*vereda*), Brazil. (7, 8) *Cerrado* in Goiás (*campo sujo*), Brazil. (9) *Cerrado* grasslands in Tocantins (*campo sujo and vereda*), Brazil. (10) *Cerrado* in eastern lowland Bolivia. (11) Cattle in grassland-forest mosaic Bolivia. (12) Prescribed fire in a subtropical pine savanna, southern USA. (13) Miombo, *Uapaca kirkina* savanna, Congo. (14) Katanga copper outcrops, Congo. (15) Savanna in Kenya. (16–18) Savanna in Kruger National Park, South Africa. (19) Montane grasslands, South Africa. (20) Coastal grasslands South Africa. (21) Tapia (*Uapaca bojeri*) savanna and quartzic grasslands on Ibity mountain, Madagascar. (22, 23) *Pandanus*, cycads and *Eucalyptus* savanna, Northern Territory, Australia. (24) High-elevation savanna, southwest China; also see Ratnam *et al.* (2016) for Asia.

short-lived perennial species, old-growth grasslands of the humid tropics are typically composed of long-lived perennial grasses and forbs (Bond & Zaloumis, 2016); for this reason, our review focuses primarily on the ecology of perennial grassland plants.

Unlike arid grasslands, where climate severely constrains woody plant growth, the ecological characteristics and biodiversity of humid tropical grasslands are maintained through interactions among disturbances (i.e. fire and herbivory) and soil characteristics (i.e. hydrology, soil depth, toxic concentrations of heavy metals, Fig. 2; Langan *et al.*, 2017). In Figure 2, we depict how disturbance frequency and edaphic constraints on tree growth interact to determine where tropical old-growth grasslands occur. Of particular note, this model (Fig. 2) highlights the continuum from edaphic old-growth grasslands (i.e. on soils that preclude the development of dense tree cover) to disturbance-dependent old-growth grasslands (i.e. on soils that can support either grassland or forest depending on fire and herbivory). Disturbance-dependent grasslands are of critical conservation and restoration importance because of their susceptibility to exclusion of fire and herbivores (Noss *et al.*, 2015; Durigan & Ratter, 2016), as well as their suitability for agriculture (i.e. on fertile soils and with ample precipitation; Searchinger *et al.*, 2015) or for mining (i.e. metal-rich soils; Pena *et al.*, 2017).

To offer a schematic representation of our findings, we produced a conceptual model (Fig. 3) that integrates ecological theory (depicted in Fig. 2) with restoration activities for tropical grasslands. In Figure 3, we adapted conceptual models of the novel ecosystem concept from Hobbs *et al.* (2009) to tropical grasslands. The novel ecosystem concept provides a framework for understanding ecological resilience and alternative stable state theory in

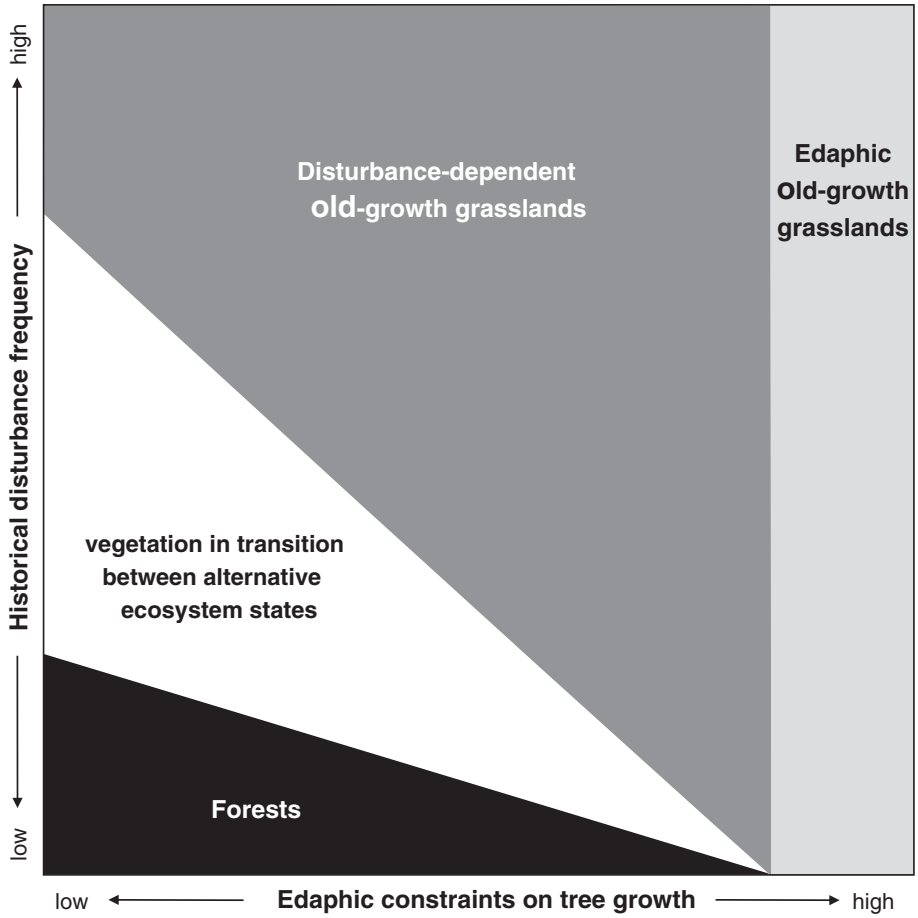

Fig. 2. Ecosystem state space occupied by tropical old-growth grasslands in regions where precipitation is sufficient for the development of forests (Bond, Woodward & Midgley, 2005; Hirota *et al.*, 2011; Staver *et al.*, 2011). On most soil types, the existence of disturbance-dependent grasslands is determined by interactions between soils and endogenous disturbances, especially fire (Hoffmann *et al.*, 2012; Murphy & Bowman, 2012; Noss, 2013; Lehmann *et al.*, 2014; Hempson *et al.*, 2015; Dantas *et al.*, 2016; Langan, Higgins & Scheiter, 2017). In edaphic grasslands, poor drainage (seasonally saturated or inundated soils), extremely low moisture-holding capacity (shallow, rocky soils), or exceptionally low soil fertility preclude dense tree cover, even in the absence of frequent disturbances (Noss, 2013; Le Stradic *et al.*, 2018*b*). In forests, dense tree cover constrains fire frequency and grazer abundance by limiting herbaceous plant productivity. The unlabelled state space between disturbance-dependent old-growth grasslands and forests represents unstable vegetation (fire excluded, tree-encroached grassland) in transition between alternative ecosystem states (Van Langevelde *et al.*, 2003).

the context of restoration (Suding *et al.*, 2004), with potential to inform management decisions (Hulvey *et al.*, 2013). In this model, we also incorporated the old-growth grassland concept to refer to the historical or reference ecosystems that should guide tropical grassland restoration (Veldman *et al.*, 2015*a*). To support these conceptual models, below we discuss the ecology of tropical old-growth grasslands, divided into two sections on resilience and restoration.

II. RESILIENCE

(1) Endogenous disturbances and plant resprouting

Most tropical old-growth grasslands are highly resilient to, and even dependent on, frequent fires and/or native megafaunal herbivores, which maintain grassland plant diversity and vegetation structure [i.e. low tree cover (Coutinho, 1990; Bond & Keeley, 2005; Cingolani, Noy-Meir & Díaz, 2005; Veldman *et al.*, 2015*a*; Bond, 2016)]. These endogenous disturbances (*sensu* McIntyre & Hobbs, 1999) are part of the evolutionary history and internal dynamics of tropical grasslands and should not be confused with the sorts of exogenous disturbances – often imposed by humans – that cause shifts to alternative ecosystem states (e.g. Fig. 3A, B).

Vegetation–fire and vegetation–herbivore feedbacks are key to understanding endogenous disturbances in tropical grasslands (e.g. Dantas & Pausas, 2013; Fill *et al.*, 2015; Hempson *et al.*, 2015). Herbaceous plants, grasses in particular (e.g. Simpson *et al.*, 2016), produce the fine fuel that promotes grassland flammability and provides

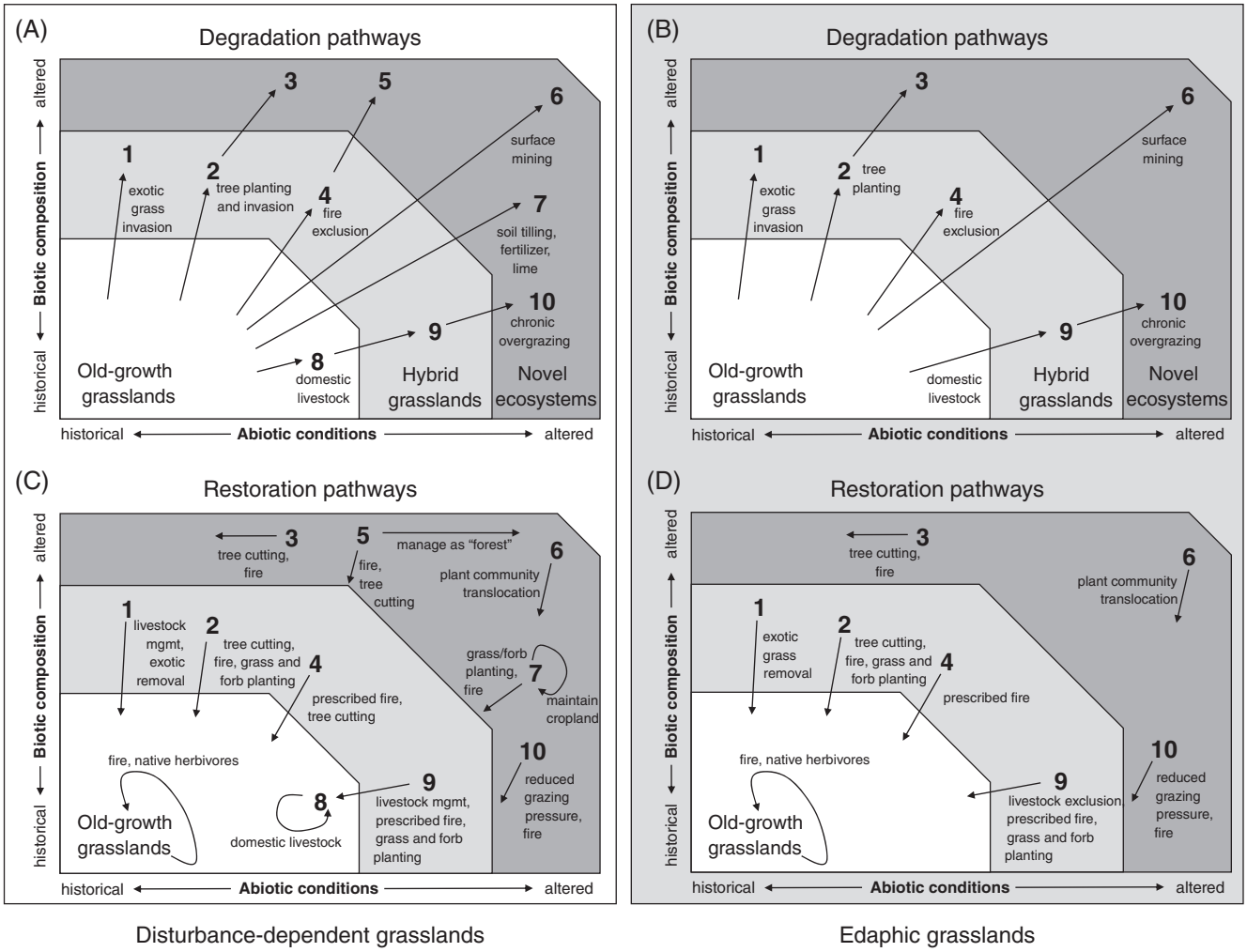

Fig. 3. (A, B) Common ecosystem state transitions (i.e. degradation pathways), and (C, D) management interventions (i.e. potential restoration pathways), for tropical grasslands. Disturbance-dependent grasslands (A, C, white box) and edaphic grasslands (B, D, grey box) are depicted separately, due to differences in resilience and restoration potential (see Fig. 2). Numbers represent the qualitative position of ecosystem states in relation to historical abiotic and biotic variables. Novel ecosystem states face strong biotic, abiotic and/or socioeconomic barriers to restoration. Hybrid ecosystems may be restored toward the reference (old-growth grassland) state, although full recovery likely requires many decades to centuries. Old-growth grasslands, the reference (historical) ecosystem states (Veldman *et al.*, 2015*a*), typically require frequent fire and/or domestic or native herbivores to maintain biotic composition and abiotic conditions. We adapted these diagrams to tropical grasslands from Hobbs, Higgs & Harris (2009).

forage for grazing herbivores; in some savannas, highly flammable tree litter (e.g. *Pinus* spp.; Platt *et al.*, 2016) is also critical to ecosystem flammability. In turn, fire and herbivores interact to restrict tree cover and woody encroachment that can otherwise limit the productivity of the herbaceous plant community (e.g. Veldman, Mattingly & Brudvig, 2013; Fig. 1). Many, if not most, tropical old-growth grassland plants have evolved to endure disturbances that remove aboveground biomass, including recurrent fires and herbivory (Bond & Keeley, 2005; Veldman *et al.*, 2015*a*; Bond, 2016; Pausas, 2017) by investing in underground storage organs (USOs; Simon *et al.*, 2009; Maurin *et al.*, 2014; Pausas *et al.*, 2018) and bud banks (near or below the soil surface) that allow resprouting after loss of aboveground biomass (Coutinho, 1990; Brewer & Platt, 1994*a*,*b*; Appezzato-da-Glória *et al.*, 2008; Fidelis, Lyra & Pivello, 2013).

Appreciation for herbaceous plant regeneration strategies is critical to understanding tropical old-growth grassland resilience to endogenous *versus* exogenous disturbances. Resprouting – i.e. vegetative regeneration of aboveground organs from roots, stems, or persistent bud banks – not seeding, is the principal manner by which grasslands regenerate from fire and herbivory (Coutinho, 1990; Bond & Midgley, 2001; Clarke *et al.*, 2013). By contrast, severe human-caused soil disturbances (e.g. tilling, surface mining) destroy belowground plant organs, thus killing whole plants and eliminating the possibility of resprouting (Kirkman

et al., 2004; Ostertag & Robertson, 2007; Brudvig *et al.*, 2013; Zaloumis, 2013; Ilunga wa Ilunga *et al.*, 2015; Vieira *et al.*, 2015). Reproduction from seed clearly plays a role in old-growth grassland plant population dynamics (Keeley & Fotheringham, 2000; Medina & Fernandes, 2007), but few old-growth tropical grassland plant populations rely on persistent seed banks for post-fire regeneration (Duvigneaud & Denaeyer-De Smet, 1963; Overbeck *et al.*, 2005; Overbeck & Pfadenhauer, 2007; Kolbek & Alves, 2008; Lamont & Downes, 2011; Fidelis *et al.*, 2012). Instead, many species flower profusely (Conceição *et al.*, 2013; Fidelis & Blanco, 2014) after resprouting from bud banks, and then produce seeds, most of which never establish (Overbeck *et al.*, 2006; Dayamba *et al.*, 2008, 2010; Neves & Conceição, 2010; Fichino *et al.*, 2012, 2016; Le Stradic *et al.*, 2015; Delhaye *et al.*, 2016; Fidelis, Daibes & Martins, 2016).

Low rates of seedling establishment among tropical old-growth grassland plants, even after fire, is perplexing, given that fire-stimulated flowering likely evolved as a means to focus investment in reproduction during post-fire periods (Brewer *et al.*, 2009), periods when otherwise limiting nutrients are most available (e.g. phosphorus; Butler *et al.*, 2018) and conditions are most favourable for establishment from seed (e.g. due to reduced competition; Myers & Harms, 2011). Although poor establishment from seed may simply be due to severe environmental constraints on seedlings (e.g. water stress, in hot, sunny grasslands) or a trade-off between investment in plant persistence and seed production, studies among long-lived resprouting shrubs, in recurrent-fire Mediterranean-type ecosystems, point towards the accumulation of somatic mutations as a cause of low fecundity (Lamont & Wiens, 2003). This hypothesis, which remains to be tested in grasses and forbs of the humid tropics, posits that since most somatic mutations result in deleterious alleles, poor seed quality is an inherent cost of evolving the capacity to resprout repeatedly over long periods of time (Wiens & Slaton, 2012).

Whatever the reason for low seedling establishment, the reliance of long-lived tropical old-growth grassland plants on USOs and bud banks to survive fires and herbivory (Bond & Midgley, 2001; Pausas *et al.*, 2018), and their contrasting low resilience to human-induced soil disturbances, highlights the need to distinguish endogenous disturbances that occur above ground (e.g. fire) from exogenous disturbances that alter soil structure (e.g. tilling). Whereas numerous studies deal with tropical grassland resilience to endogenous disturbances (e.g. post-fire recovery), few address community resilience to exogenous disturbances. Keeping the endogenous *versus* exogenous distinction in mind, below we discuss tropical old-growth grassland resilience to various forms of environmental change.

(2) Fire and grazing regime

Endogenous disturbances (i.e. fire, herbivory) are thought to maintain tropical old-growth grassland plant diversity by limiting competitively dominant herbaceous species, preventing woody encroachment, stimulating reproduction, and creating recruitment opportunities (Beckage & Stout, 2000; Overbeck *et al.*, 2005; Brewer *et al.*, 2009; Myers & Harms, 2011; Fidelis *et al.*, 2012; Müller *et al.*, 2012; Scott *et al.*, 2012; Andrade *et al.*, 2015; Abreu *et al.*, 2017). The resilience of tropical old-growth grasslands to human-altered grazing and fire regimes is highly dependent on ecosystem type and site-specific conditions. In general, disturbance-dependent grasslands, with moderate to high soil water and nutrient availability, can tolerate more intense grazing for longer durations (Müller *et al.*, 2012; Fedrigo *et al.*, 2018) relative to edaphic grasslands, where soil conditions severely constrain plant productivity and regeneration (Kolbek & Alves, 2008; Fig. 3A, B). Similarly, the frequency of fire required to prevent woody encroachment (Hoffmann *et al.*, 2012) and maintain plant diversity (Veldman *et al.*, 2014) increases along resource availability gradients, from resource-poor (edaphic) grasslands to resource-rich (disturbance-dependent) grasslands (Fig. 2). Although the frequency of fire required for the maintenance of grasslands depends on soils and interactions with herbivores, both disturbance-dependent and edaphic old-growth tropical grasslands appear quite resilient to frequent fire (Andersen *et al.*, 2005). Indeed, Le Stradic *et al.* (2018*b*) found that plant community composition in two distinct edaphic grasslands did not differ with fire history, and that after fire, both grasslands rapidly recovered their aboveground biomass.

(3) Fire exclusion

Fire exclusion can eliminate many characteristic herbaceous plant species from old-growth tropical grassland communities due to litter accumulation or competitive exclusion by dominant grasses, shrubs, or trees (Uys, Bond & Everson, 2004; Overbeck *et al.*, 2005; Hiers *et al.*, 2007; Fidelis *et al.*, 2012, 2013; Scott *et al.*, 2012; Veldman *et al.*, 2013; Abreu *et al.*, 2017; Fig. 3A). In the short term, fire exclusion can lead to increased fire intensity, due to the accumulation of biomass that would have historically been consumed in more frequent, lower intensity fires (Batista *et al.*, 2018). Over longer time scales (i.e. many years to decades), fire exclusion results in forest expansion (i.e. woody encroachment leading to forest formation in former grassland; Oliveira & Pillar, 2004; Parr, Gray & Bond, 2012; Durigan & Ratter, 2016), the loss of herbaceous grassland species (Hiers *et al.*, 2007; Brooks, Setterfield & Douglas, 2010; Parr *et al.*, 2014; Abreu *et al.*, 2017; Fig. 3A, B), and reduced ecosystem flammability, as flammable grasses are replaced by fire-impeding forest tree species (Kane, Varner & Hiers, 2008; Kreye *et al.*, 2013; Veldman *et al.*, 2013; Fill *et al.*, 2015). Conversely, human-initiated fire management (implemented to increase visibility for hunting or to improve forage production), which is highly dependent on the local socio-cultural context (Alvarado *et al.*, 2015), can result in fires that are more frequent or intense compared to historical fire regimes [e.g. through a change from cool burning,

wet-season, lightning fires to hotter fires in the dry season (Ramos-Neto & Pivello, 2000; Rissi *et al.*, 2017; Alvarado, Silva & Archibald, 2018)]. Given the high rates of woody encroachment in grasslands globally, the high resprouting capacity of old-growth grassland plants, and the dependence of grassland biodiversity on fire, we contend that increased fire frequencies are of far less concern for tropical grassland resilience relative to fire exclusion (Andersen *et al.*, 2005; Parr *et al.*, 2014; Durigan & Ratter, 2016). That said, where altered fire regimes result in more-intense fires, they can threaten fire-sensitive components (e.g. small groves of trees) embedded in grassland landscapes (Trauernicht *et al.*, 2012; Coelho *et al.*, 2018). Studies on the resilience of tropical grasslands to these new fire regimes (Drewa, Platt & Moser, 2002; Andersen *et al.*, 2005; Ribeiro & Figueira, 2011; Alvarado *et al.*, 2012, 2014; Russell-Smith *et al.*, 2013; Fernandes, 2016) suggest that fire-management decisions should account for landscape-scale heterogeneity in vegetation and incorporate local knowledge to deliver maximum social and ecological benefits.

(4) Livestock grazing

Old-growth grasslands vary widely in their resilience to domestic livestock grazing (e.g. Cingolani *et al.*, 2005). Grasslands that occur on infertile soils and did not evolve with megafaunal herbivores appear to be the least resilient to domestic grazers (Fig. 3B) (Milchunas, Sala & Lauenroth, 1988; Cingolani *et al.*, 2005). The *campos rupestres* of Brazil are an example of such a system where shallow soils and shallow-rooted plants are very sensitive to trampling (Kolbek & Alves, 2008). In other grasslands, typically with higher soil fertility, domestic livestock may be important to the maintenance of biodiversity by functioning as a surrogate for fire or by mimicking the effects of native herbivores (Boldrini & Eggers, 1996; Blanco *et al.*, 2007; Overbeck *et al.*, 2007). Indeed, literature on grasslands that are resilient to moderate cattle grazing (Mcintyre, Heard & Martin, 2003; Fig. 3A, C) attribute this resilience to a long evolutionary history with either extant native megaherbivores (e.g. Africa) or recently extinct Pleistocene megafauna (Frost, 1993; Ratter *et al.*, 1997; Miller, 2005; Overbeck *et al.*, 2007; Noss, 2013). Where wild herbivores and livestock co-occur, management to minimise direct competition for forage can foster positive (facilitative) interactions between wild and domestic herbivores, while also maintaining grassland structural heterogeneity and associated biodiversity (Riginos *et al.*, 2012; Fynn *et al.*, 2016). Grazers can dramatically reduce aboveground grass biomass, thereby altering grassland fire spread and intensity (Trauernicht *et al.*, 2013), thus complicating the relationship between livestock and the maintenance of grassland ecosystem functioning. Given that elevated atmospheric carbon dioxide appears to be shifting the competitive balance between C_4 grasses and C_3 trees and shrubs (Collatz, Berry & Clark, 1998; Bond & Midgley, 2012), and that grazers further alter grass–tree interactions through effects on ecosystem flammability (Case & Staver, 2016), more research is needed on the contribution of livestock as a driver of woody encroachment in old-growth grasslands of the humid tropics and subtropics.

(5) Overgrazing

Overgrazing occurs when grazing intensity, frequency, and duration exceeds site-specific thresholds (i.e. shifting an old-growth or hybrid grassland to a novel ecosystem state; Fig. 3A, B). Such shifts are typically characterised by dramatic changes in both abiotic (e.g. soil compaction or erosion) and biotic (e.g. species composition) components of ecosystems (Fig. 3A, B). Among the most well-documented biotic consequences of mismanaged livestock on plant communities, overgrazing can cause exotic grazer-tolerant grasses or unpalatable native species to increase in abundance (Crowley & Garnett, 1998; Fensham, 1998; Andrade *et al.*, 2015).

Savanna tree cover, a common metric used in forestry and remote-sensing studies, responds very differently to grazing compared to the herbaceous plant community (Stevens *et al.*, 2016). As such, when planning grassland restorations, it is necessary to look to the herbaceous plant community, rather than just trees (Brudvig *et al.*, 2014; Veldman, 2016). Likewise, remote-sensing vegetation indices, such as normalised difference vegetation index (NDVI) and enhanced vegetation index (EVI), should be used with caution to detect ecosystem state changes in tropical grasslands, because these indices do not distinguish native from exotic grasses (but see Zlinszky *et al.*, 2015). That said, time-series remote-sensing data on tree and shrub cover at global and regional scales can be quite useful to monitor grazer-mediated woody encroachment, particularly where grassland fire regimes have been altered. Indeed, among key research needs, we must determine how best to manage domestic livestock in old-growth grasslands that occur where land-use policies restrict fire [e.g. *Cerrado* and subtropical grasslands (Ratter *et al.*, 1997; Overbeck *et al.*, 2007; Müller *et al.*, 2012] and determine better ways to use remote sensing to detect changes in grassland plant communities (e.g. through consideration of phenology; Wilsey, Martin & Kaul, 2018).

(6) Afforestation and invasive species

Afforestation, the establishment of tree plantations in grasslands (de Abreu *et al.*, 2011; Zaloumis & Bond, 2011, 2016; Veldman *et al.*, 2015*a*,*b*), and exotic tree invasions (de Abreu & Durigan, 2011) lead to the loss of herbaceous grassland species due to competition with trees for light and water as well as litter accumulation (Hiers *et al.*, 2007; Brooks *et al.*, 2010; Parr *et al.*, 2014; Fig. 3A, B). The magnitude of plant community change with afforestation can vary widely depending on tree density and whether or not fires are excluded (Veldman *et al.*, 2014). When tree density is high and fires are excluded for long periods of time, herbaceous plant communities decline substantially in diversity and cover (Brudvig *et al.*, 2014). Herbaceous plants can recolonise following tree removal (Harrington, 2011; Torchelsen, Cadenazzi & Overbeck, 2018), but post-afforestation grasslands remain compositionally different from old-growth

grasslands (Koch *et al.*, 2016; Zaloumis & Bond, 2016). These secondary grasslands, like those that form after agricultural abandonment, tend to be dominated by ruderal species that are either good dispersers or that emerge from persistent seed banks. Such ruderal plant traits are markedly different from the traits of species that are characteristic of tropical old-growth grasslands (e.g. USOs; Veldman *et al.*, 2015*a*).

Non-native grass invasion can represent a huge threat to tropical grasslands, due to the negative impact caused by exotic grasses on native grasses and forbs (e.g. Pivello, Shida & Meirelles, 1999; Damasceno *et al.*, in press; Dresseno *et al.*, in press). In addition to suppressing native species, invasive grasses can lead to a high biomass accumulation, with consequences for fire regimes, including increased fire intensity (Mistry & Berardi, 2005; Setterfield *et al.*, 2010; Gorgone-Barbosa *et al.*, 2015). Because invasive grasses can alter fire regimes and native plant community composition, they are one of the most challenging filters to overcome in restoration projects. Where fires are frequent, exotic grasses hamper native herbaceous plant establishment from seed and increase the mortality of woody species (Hoffmann & Haridasan, 2008; Mendonça *et al.*, 2015). Yet in the absence of fire, exotic-dominated tropical grasslands will become low-diversity forests. Indeed, across a chronosequence of abandoned pastures invaded by African grasses in Brazil, Cava *et al.* (2018) found that herbaceous savanna plants did not spontaneously regenerate and that fire exclusion promoted the formation of low-diversity forests, which lacked the historical old-growth savanna structure and species composition. Further complicating matters, exotic grass invasions can be promoted by cattle, which disperse seeds and influence apparent competition between native and invasive species (e.g. *via* soil compaction, selective grazing). Because cattle ranchers often intentionally sow seeds of non-native forage grasses in an attempt to increase grassland productivity (Parsons, 1972), restoration ecologists must consider both the biodiversity impacts of non-native species and the value attributed to them by pastoralists.

(7) Exogenous soil disturbance

Tropical grassland resilience to tillage agriculture and surface mining is extremely low, with plant community recovery ranging from slow and incomplete to non-existent. In subtropical Australia, Fensham *et al.* (2016) found, 60 years after cultivation, that secondary grassland plant communities had only 60% compositional similarity to nearby old-growth grasslands. In subtropical North America, Kirkman *et al.* (2004) found, 65 years after agriculture, that secondary pine savannas still lacked many grass and forb species typical of old-growth savanna. In South Africa, Zaloumis (2013) found, 20 years after cultivation, that secondary grasslands recovered only 25% of the species that occur in old-growth grasslands. In Brazil, Le Stradic, Fernandes & Buisson (2018*a*) found, 8 years after excavation for gravel, that quarry sites had almost no grassland species, suggesting severe recruitment limitation. In mined heavy-metal grasslands in central Africa, both Faucon *et al.* (2011) and Ilunga wa Ilunga *et al.* (2015) found, 60 years after mining for heavy metals, that despite the proximity of seed sources, vegetation on mining sites remained very different, both compositionally and functionally from old-growth grasslands. Such exogenous soil disturbances destroy both above- and belowground vegetation, thus eliminating the potential for plants to persist *via* resprouting (Fig. 3A, B). Because old-growth grassland plants have evolved strategies (e.g. underground storage organs) to survive repeated aboveground disturbances, apparently at the cost of colonisation potential (Silcock & Scattini, 2007; Veldman *et al.*, 2015*a*; Silveira *et al.*, 2016), grasslands on former agricultural land fail to recover their characteristic plant communities even after many decades (Kirkman *et al.*, 2004; Brudvig *et al.*, 2013; Vieira *et al.*, 2015). Whereas recolonisation of characteristic old-growth grassland species is extremely limited in secondary grasslands (Silcock & Scattini, 2007; Ilunga wa Ilunga *et al.*, 2015; Veldman *et al.*, 2015*a*; Silveira *et al.*, 2016), many non-native invasive and native weedy species are rapid colonisers of post-agricultural grasslands due to their higher germination and better ability to establish in disturbed environments (Brudvig *et al.*, 2014; Gorgone-Barbosa *et al.*, 2016*a*). These weedy species can limit the establishment of desired old-growth grassland species (Zaloumis, 2013; Gorgone-Barbosa, 2016; Le Stradic *et al.*, 2016), posing a huge hurdle to restoration (see also Section II.6).

In addition to killing plants, agriculture and mining can alter soil conditions to such a degree that they are no longer suitable for old-growth grassland plant communities. This can occur due to several factors, including: loss of topsoil; increased soil nutrient availability, a legacy of agricultural fertilizers that favours dominant competitors (Andrade *et al.*, 2015; Koch *et al.*, 2016); changes in soil heavy metal content [e.g. copper, cobalt (Leteinturier, Baker & Malaisse, 1999; Barbosa *et al.*, 2010; Faucon *et al.*, 2011)]; or depletion of soil microbial communities (Bach *et al.*, 2010). For all these reasons, the species composition of secondary grasslands that develops following agriculture or mining is very different from that of old-growth grasslands (Faucon *et al.*, 2011; Ilunga wa Ilunga *et al.*, 2015; Koch *et al.*, 2016; Le Stradic *et al.*, 2018*a*); full grassland community recovery in such circumstances will require many decades to several centuries (Veldman *et al.*, 2015*a*; Fernandes, 2016). Consequently, we suggest that in many cases, secondary grasslands that form after abandonment of row crop agriculture, afforestation, or mining operations qualify as novel ecosystems (Fig. 3A, B). Because such novel ecosystems, by definition, cannot be restored to their historical conditions, we further suggest that the conservation of existing old-growth tropical grasslands must be a top priority in restoration planning (Veldman *et al.*, 2015*a*).

III. RESTORATION

(1) Prescribed fire and tree cutting

Most knowledge on restoration of tropical grasslands using prescribed fire comes from studies in Australia (Scott *et al.*,

2012), Africa (e.g. Sawadogo, Tiveau & Nygård, 2005; Savadogo *et al.*, 2008, 2009; Dayamba *et al.*, 2010; Smit *et al.*, 2016) and the southeastern USA (Provencher *et al.*, 2001; Walker & Silletti, 2006). The application of prescribed fires can clearly contribute to the reduction of shrub or tree cover and re-creation of historical vegetation structure (i.e. scattered trees), but the role of fire in re-establishment and maintenance of native herbaceous plant communities is more complicated. For example, in Australia, reintroduction of fire can restore open savanna vegetation structure, but not the composition of the herbaceous layer (Scott *et al.*, 2012). Prescribed fires can also be combined with additional treatments, including cutting and herbicide application to trees to favour herbaceous groundcover, as well as seed additions to reintroduce herbaceous plant species (Walker & Silletti, 2006). In all cases, for fire to be effective in restoration, sufficient fuel must be present, a key challenge if the herbaceous plant community is sparse, or flammable tree litter is lacking.

In some fire-excluded savannas in the southeastern USA, tree cutting can be both unnecessary and expensive: in a restoration experiment by Provencher *et al.* (2001), positive effects on plant community recovery were due to the restoration of fire regime, not reduction in tree cover. Prescribed fires alone, if applied at the early stages of woody encroachment, also seem to be sufficient to restore grasslands of the North American Great Plains (Twidwell *et al.*, 2013) and the savannas of South Africa (Booysen & Tainton, 1984). In other cases, where tree cover is particularly dense, such as fire-excluded savanna invaded by pines, tree cutting (coupled with prescribed fire) is thought to be a prerequisite for re-establishment of savanna plant communities (de Abreu & Durigan, 2013). The extremely low recovery of Cerrado grassland plant communities after pine invasion, regardless of the restoration treatment applied (tree cutting, fire, litter removal or a combination), led de Abreu & Durigan (2013) to conclude that a combination of treatments to reduce tree cover and pine litter must be accompanied by native plant reintroduction, if there is to be any potential for plant community restoration. We suggest that plant community restoration efforts may additionally benefit from treatments such as inoculation with soil microbial communities from old-growth grasslands (Middleton & Bever, 2012), to restore plant–soil interactions.

While fire effects have been studied in the Cerrado (Hoffmann, 1996, 1998; Miranda, Bustamente & Miranda, 2002), fire management is only starting to be explored more widely (Durigan & Ratter, 2016; Rissi *et al.*, 2017; Schmidt *et al.*, 2017; Alvarado *et al.*, 2018; Schmidt *et al.*, 2018) and mostly with a focus on responses of woody plants (de Medeiros & Miranda, 2005). A particular gap in restoration research, little is known about the role of fire in the reproduction and establishment of savanna grassland plants. Initial studies on heat shock simulated in the laboratory suggest that fire does not break seed dormancy, stimulate germination, or kill the seeds (Le Stradic *et al.*, 2015; Fichino *et al.*, 2016; Zupo, Baeza & Fidelis, 2016), whereas in field experiments, although many seeds died, fire indirectly promoted germination of surviving seeds, by reducing vegetation cover, which increased soil surface temperature fluctuation (Daibes *et al.*, 2017). In a laboratory study of grasses of southern Africa, Ghebrehiwot *et al.* (2009) found that exposure to liquid smoke increased germination rates of five of six species; effects of elevated temperatures had differing effects on seedling growth, suggesting that elevated post-fire temperatures may favour establishment of some species over others. More research is needed to provide precise information on what constitutes optimal fire management in plant-community restoration in different local contexts, such as in the presence of invasive species or unique soils (Driscoll *et al.*, 2010). One aspect of fire management in restoration is clear: without fire, grasslands do not recover on abandoned agricultural lands. Instead, they develop into low-diversity forests (Veldman *et al.*, 2014; Abreu *et al.*, 2017; Cava *et al.*, 2018).

(2) Invasive plant removal

In small-scale experiments (1–100 m^2), controlling invasive species can be successful when numerous restoration techniques are combined, such as topsoil transfer, fire, and manual weeding (Fig. 3C, D, Brooks *et al.*, 2010; te Beest *et al.*, 2012; Castillioni, 2015; de Assis, 2017). Pilon, Buisson & Durigan (2018) showed that in exotic grass-invaded savanna, topsoil scraping combined with native topsoil transfer effectively eliminated invasive grasses and reintroduced herbaceous plants, including endemic species. Castillioni (2015) and de Assis (2017) showed that herbicides should be applied with great caution to control *Urochloa decumbens*, an African grass that is invasive in Brazil, because herbicides can impair native forbs and grasses. Moreover the use of herbicides to control invasive plant species is controversial because of toxicity to people and the environment (Wittenberg & Cock, 2001). De Assis (2017) showed that manual weeding can effectively control *Urochloa decumbens*; in the same experiment, fire reduced the cost of manual weeding, but fire alone was not sufficient to control grass invasion. In southern Brazil, Thomas (2017) showed that topsoil removal and herbicide application were effective in reducing cover of *Urochloa decumbens* from over 40% to less than 5% 1 year after treatment, but did not promote re-establishment of typical grassland species, even when combined with hay transfer. Establishment of an assemblage of competitive native species after eradication of invasive species is thought to be important to prevent reinvasion of restored sites (Cordero *et al.*, 2016). Unfortunately, despite successful invasive plant control in small plots in short-term experiments, over the longer term at larger spatial scales, restorations remain prone to reinvasion (Sampaio *et al.*, 2015).

Invasive grasses, such as *Imperata cilindrica* in the southern USA (Platt & Gottschalk, 2001) and *Andropogon gayanus* in Australia (Rossiter *et al.*, 2003) can increase the frequency, intensity, and spatial extent of grassland fires through production of large quantities of fine fuel. Other invasive species (e.g. *Urochloa brizantha*) can reduce ecosystem flammability relative to native-dominated grasslands, but this can

depend on the fire season (Gorgone-Barbosa *et al.*, 2015). Although fire can be effective at controlling fire-sensitive invasive species (Stevens & Beckage, 2009; te Beest *et al.*, 2012), fire can also promote invasive species that evolved with frequent fires (*Imperata cylindrica*; Lippincott, 2000) or indirectly promote invasive species by opening recruitment sites, suitable for germination (*Urochloa brizantha* and *Urochloa decumbens*; Gorgone-Barbosa *et al.*, 2016*a*,*b*). The fire ecology of invasive species should therefore be carefully considered as part of fire management (Gorgone-Barbosa, 2016) in tropical grassland restoration.

(3) Grazing management

In a review on the restoration of land degraded by overgrazing, Papanastasis (2009) highlighted appropriate livestock management as a vital tool for restoration of ecosystems composed of species that evolved with large herbivores. One cannot substitute native wildlife for livestock and expect to maintain the same ecological processes and plant communities; grazing and browsing patterns differ among species and may change fire regimes, woody plant cover, and biogeochemical cycling (Hempson, Archibald & Bond, 2017). Whereas livestock are incompatible with conservation of edaphic old-growth grasslands, in certain disturbance-dependent old-growth grasslands, native wildlife and/or livestock can be used to manage vegetation if manipulated adequately (Fuhlendorf & Engle, 2001; Joubert, Pryke & Samways, 2017; Fedrigo *et al.*, 2018). Further, where land-use policies restrict fire in disturbance-dependent grasslands, domestic livestock can, in some cases, serve as an imperfect surrogate for fire, by controlling the biomass of palatable dominant plants (both native or exotic) and preventing shrub and tree encroachment (Ratter *et al.*, 1997; Overbeck *et al.*, 2007; Müller *et al.*, 2012). Livestock can also create establishment sites for rare plant species and can enhance the diversity of habitats across landscapes (Lunt *et al.*, 2007). Appropriate use of livestock in tropical grassland restoration will require improved knowledge of the ecological factors that influence plant community responses to grazing and fire (Joubert *et al.*, 2017), as well as an understanding of the contribution of livestock to local livelihoods (cessation of grazing may not be feasible if alternative income sources are not available).

(4) Reintroduction of grasses and forbs

A common objective of grassland restoration is to reintroduce plant species that have become locally extinct or to increase the abundance of desirable plant species whose populations declined due to altered disturbance regimes. In temperate grassland restoration, the most common approach to plant propagation is to sow seeds, either collected from existing populations or cultivated specifically for restoration plantings (Kiehl *et al.*, 2010), or alternatively, to rely on seed dispersal by wind or animals, as was historically done by pastoralists (Poschlod *et al.*, 1998). Seeds can be directly sown or introduced *via* hay or soil transfers, accomplished by hand or machine. Hay transfers involve cutting and collecting the herbaceous layer of temperate grasslands at a time when seeds are mature but have yet to disperse. This cut hay, with attached seeds, is then spread at the restoration site. Soil transfers involve collecting temperate grassland topsoil and then spreading this soil, along with dormant seeds contained in the soil, onto the restoration site.

For restoration of tropical grasslands, knowledge is slowly increasing about the transfer (Le Stradic, Buisson & Fernandes, 2014*a*; Le Stradic *et al.*, 2016; Pilon *et al.*, 2018) and propagation of old-growth grassland species (Negreiros *et al.*, 2009; Oliveira *et al.*, 2012; Le Stradic *et al.*, 2014*b*; Gomes *et al.*, 2018), yet for most ecosystems such information remains scarce or non-existent, particularly for herbaceous species (Fernandes, 2016). Complicating matters, emerging research on species of the Cerrado, Katanga copper outcrops (Central Africa), and Queensland (Australia), suggests that many graminoids – a functional group that is critical to ecosystem flammability and livestock forage – produce few seeds, much of which is of low quality (Silcock & Scattini, 2007; Boisson *et al.*, 2015; Le Stradic *et al.*, 2015; Kolb *et al.*, 2016; Dayrell *et al.*, 2017). As such, the opportunities for reintroduction and propagation *via* seed sowing, soil transfer, and hay transfer, are often extremely limited (Le Stradic *et al.*, 2014*a*, 2016; but see Le Stradic *et al.*, 2014*b*; Sampaio *et al.*, 2015; Gomes *et al.*, 2018; Pilon *et al.*, 2018). When seeds are available, plant species introduction must often be combined with an appropriate set of treatments for them to establish (Wiseman *et al.*, 2002; Sampaio *et al.*, 2015; Pilon *et al.*, 2018). In sum, due to both knowledge gaps and ecological hurdles to establishment from seed, the reintroduction of tropical grassland species remains technically difficult and expensive (Dayrell *et al.*, 2016).

On a positive note, extensive research on the restoration of subtropical grasslands of Australia and the southeastern USA suggests that with significant investment in research and seed harvesting, reintroductions of seeds, particularly when coupled with other management techniques (e.g. prescribed fire and tree cutting, see Section III.1), can help restore grassland ecosystem services (e.g. livestock forage; Waters, Whalley & Huxtable, 2001) and improve plant diversity and community composition (Walker & Silletti, 2006). But, even in these well-studied grasslands, full plant community recovery to old-growth conditions cannot be achieved in short periods of time and there remain huge hurdles to the re-establishment of many species of conservation concern (Aschenbach, Foster & Imm, 2010). Clearly, much research on population ecology, especially the germination and establishment requirements of native species of tropical old-growth grasslands, is needed.

(5) Restoration after soil disturbance

Whereas for most temperate grasslands, common site preparation includes topsoil manipulation, such as ploughing, tilling, and soil transfer (Kiehl *et al.*, 2010), in tropical grasslands, even minor changes in soil structure are likely to hamper natural regeneration from USOs and buried buds. Soil preparation should therefore be used only on

sites where repeated soil disturbance has already destroyed the belowground bud bank. For example, Sampaio *et al.* (2015) showed that plowing areas of Cerrado that were previously cultivated or long-served as planted pastures can help reduce invasive species density and increase native species establishment. USOs are extremely difficult to uproot and transfer without damage (Zaloumis, 2013; Le Stradic *et al.*, 2016) and can require long periods of time to develop (Veldman *et al.*, 2015*a*). Given the importance of bud banks to the regeneration capacity of tropical grasslands (Fidelis *et al.*, 2014; Pausas *et al.*, 2018), determining if and how USOs may be transplanted is a key research need. Among human land uses that severely affect tropical grasslands, surface mining (including open-pit mining) has the most profound local ecological impact (Sonter *et al.*, 2014). As a consequence, in many countries, mining companies are highly encouraged, and often legally obligated, to restore the ecosystems they destroy. Drawing on substantial wealth, some mining companies plan ambitious and expensive restoration projects, including full community translocation (i.e. whole-turf translocation). Ideally, this technique involves removing old-growth grassland turf (i.e. the aboveground plant community and soil to a depth of *ca.* 40 cm), before mining, and then transferring the turf to a nearby site where the plant community and soil has been recently destroyed. At the experimental scale (translocations of 0.04–200 m^2), such translocations can be successful in grasslands with shallow soils (Le Stradic *et al.*, 2016), but not for grasslands with deeper soils; deeply rooted species and species with large USOs are not amenable to translocation (Fig. 3C, D; Le Stradic *et al.*, 2016). Translocation faces similar limitations as restoration following cultivation: deeply rooted species do not survive translocation (Fig. 3C; Zaloumis, 2013). Despite some success in an experimental context, the financial cost for full community translocation is prohibitively high and turf donor sites are destroyed in the process. Moreover, even if some species survive transplantation, they fail to colonise outside of transplanted plots (Le Stradic, 2012; Zaloumis, 2013). Such poor colonisation may be due to a combination of factors, including unsuitable soil conditions outside the turf plantation area (Kardol, Bezemer & Van Der Putten, 2009), low seed production, slow growth and recovery after transplant damage to USOs and roots (Fahselt, 2007), and bud dormancy induced by harsh transplant conditions (Le Stradic, 2012; Zaloumis, 2013).

In addition to killing plants that rely on USOs and buried buds, there are a variety of ways that soil-disturbing land uses create conditions that are unsuitable for tropical grassland plant communities. For example, fertilizers (N and P) which remain in the soil after cultivation can favour competitive or invasive species (Barbosa *et al.*, 2010; Andrade *et al.*, 2015) and metal content (e.g. copper, cobalt, aluminium) can be changed by mining (Leteinturier *et al.*, 1999; Faucon *et al.*, 2011). Such novel soil conditions may cause restoration plantings to fail, to take a very long time to establish, or to require additional treatments, such as liming (Shutcha *et al.*, 2010) or metal additions [e.g. to elevate copper concentration (Chipeng *et al.*, 2009; Faucon *et al.*, 2012)]. Clearly, some soil amendments, especially those containing expensive elements, cannot be economically applied in all grasslands (Barbosa *et al.*, 2010). Where heavy metal concentrations are too high, Leteinturier *et al.* (1999, 2001*a*,*b*), Shutcha *et al.* (2010), and Boisson *et al.* (2015) found that metals can be immobilised *via* phytostabilisation. Like many other promising restoration experiments, scaling up small plot-level studies of phytostabilisation to landscapes will require additional studies. In temperate grasslands, research has been carried out to try to reduce nutrients (N and P) in soils in order to favour a high diversity of native species. These N- and P-reduction techniques include: mowing and removing the cut biomass (Maron & Jefferies, 2001); carbon amendment to reduce N levels (Wilson & Gerry, 1995; Reever Morghan & Seastedt, 1999; Török *et al.*, 2000; Wilson, 2002); and topsoil removal as a restoration technique to reduce both competition from the exotic seed bank and soil N levels (Marrs, 2002; Wilson, 2002; Buisson *et al.*, 2006, 2008). More research on these potential techniques for tropical grassland restoration is needed.

IV. CONCLUSIONS

(1) Whereas the destruction and degradation of tropical and subtropical old-growth grasslands, including savannas and grassy woodlands, can occur very rapidly, recovery of their biodiverse plant communities occurs slowly, or not at all (Veldman *et al.*, 2015*a*). Overgrazing, fire exclusion, and woody encroachment can replace tropical old-growth grasslands with low-diversity swards of exotic grasses or dense tree cover in a matter of years to a few decades (e.g. Cava *et al.*, 2018). Grassland conversion for agriculture, plantation forestry, or mining not only destroys plant and animal communities, but also profoundly changes chemical and physical soil features (Brudvig *et al.*, 2013; Le Stradic *et al.*, 2018*a*). Our review of the restoration literature suggests that such human-induced environmental change often pushes tropical grasslands across ecological thresholds to alternative ecosystem states, from which recovery, where possible, requires huge efforts and many decades to centuries.

(2) Among key priorities for restoration practice and research, we must determine when state shifts in tropical grasslands qualify as novel ecosystems, from which recovery is ecologically impossible or socially impractical, as opposed to hybrid grasslands, which are amenable to restoration toward the old-growth state (Fig. 3; Hobbs *et al.*, 2009; Hulvey *et al.*, 2013). Given the paucity of tropical grassland restoration research, it is possible that some ecosystem states that we currently perceive to be novel will, after future research and technological innovation, prove capable of recovery towards the old-growth state (Murcia *et al.*, 2014). In the meantime we suggest that recognition of novel ecosystems and their different restoration scope (Fig. 3) can serve to highlight the irreplaceability of tropical old-growth grasslands (Hobbs, Higgs & Harris, 2014). Because ecological restoration is not

a panacea for the recovery of tropical grassland biodiversity, in the extensive areas where old-growth grasslands still exist, environmental policies and ecosystem management should prioritise grassland conservation, which must include prescribed fire, wildfire, and/or megafaunal herbivory.

(3) Most tropical old-growth grasslands require frequent endogenous disturbances (i.e. fire and herbivory) to maintain plant diversity and prevent state shifts to low-diversity forests (Fig. 2). Such disturbance-dependent grasslands, common throughout the humid tropics, differ from much rarer edaphic grasslands in key aspects of resilience and restoration (Fig. 3). Of particular note, whereas appropriate livestock management can be used to maintain or restore disturbance-dependent old-growth grasslands, livestock are typically incompatible with the conservation of edaphic old-growth grasslands. Another difference is that disturbance-dependent grasslands, on soils that are favourable to plant growth, are far more susceptible to conversion for agriculture than edaphic grasslands on infertile or poorly drained soils; as such, cultivation represents a far greater threat to disturbance-dependent grasslands (Searchinger *et al.*, 2015) relative to edaphic grasslands. A final notable difference is that because soil conditions in edaphic grasslands severely constrain tree growth, fire exclusion does not result in the same rapid, irreversible state shifts to forest that threaten disturbance-dependent grasslands (Fig. 3A, B; Durigan & Ratter, 2016). In sum, although disturbance-dependent and edaphic grasslands have many similarities (e.g. herbaceous communities of long-lived perennial plants), recognition of relationships between grassland disturbance regimes and edaphic conditions is critical to anticipating the outcomes of environmental change (Fig. 3A, B) and planning restoration for specific tropical grassland ecosystems (Fig. 3C, D).

(4) Unlike tropical forests, where cessation of human-induced disturbance is often sufficient for restoration (i.e. passive restoration; Meli *et al.*, 2017), restoration of most tropical grasslands (i.e. disturbance-dependent grasslands; Figs 2 and 3A, C) must include ongoing, active management to maintain endogenous disturbance regimes. Restoration planners, in their consideration of disturbances and degradation in the tropics, should acknowledge that tropical grassland species have evolved for millions of years with endogenous disturbances that do not regularly occur in forests (i.e. fire and grazing; Veldman, 2016); consequently, tropical grassland communities are highly resilient to disturbances that remove aboveground biomass, but not resilient to disturbances that alter soils and destroy underground organs (Bond, 2016; Fig. 3A, B). After repeated soil disturbance or afforestation, tropical grassland restoration is severely limited by the poor colonisation potential (e.g. low seed viability, limited dispersal) of plant species that are characteristic of old-growth grasslands (Veldman *et al.*, 2015*a*). Further complicating restoration, grassland species that rely on bud banks for persistence are not easily transplanted. Exotic forage grasses, which are commercially available and easy to establish, should never be sown as part of tropical grassland restoration.

(5) Although many of the techniques used to actively restore forests or temperate grasslands are ecologically inappropriate (e.g. fire exclusion; Ratnam *et al.*, 2011) or ineffective when applied to tropical grasslands (e.g. hay or topsoil transfer; Le Stradic *et al.*, 2014*a*, 2016; Pilon *et al.*, 2018), there are several management tools that do offer hope for ecosystem recovery where degradation is not irreversible (i.e. hybrid grasslands; Fig. 3C, D). Despite this hope, a great deal of confusion still exists over the activities that constitute ecological restoration (Suding *et al.*, 2015), particularly in the context of forest and landscape restoration (Brancalion & Chazdon, 2017) as applied to tropical savannas and grassland–forest mosaics (Veldman *et al.*, 2015*b*). Through this review, we have sought to reduce this confusion by offering clarity about the distinct conservation values and ecological attributes of tropical grasslands that require a set of restoration tools that are distinct from the tools applied for forest restoration. To summarise, the tools of tropical grassland restoration include: (1) prescribed fire; (2) appropriate management of livestock and wild herbivores; (3) tree cutting and shrub removal; (4) invasive species control; and (5) reintroduction of native grasses and forbs, *via* seeding or transplants. Finally, because most tropical old-growth grasslands are dependent on recurring endogenous disturbances, restoration efforts must plan for the long-term maintenance of fire regimes, megafauna herbivory, or both, to prevent woody encroachment from leading to forest expansion.

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VI. REFERENCES

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VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Literature search in *Restoration Ecology*.

Table S1. Results of literature search in *Restoration Ecology*.

Figure S1. Approximate distribution of disturbance-dependent tropical and subtropical old-growth grasslands, including savannas, open-canopy woodlands, and grassland–forest mosaics.

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