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Toward an old-growth concept for grasslands, savannas, and woodlands

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We expand the concept of "old growth" to encompass the distinct ecologies and conservation values of the world's ancient grass-dominated biomes. Biologically rich grasslands, savannas, and open-canopy woodlands suffer from an image problem among scientists, policy makers, land managers, and the general public, that fosters alarming rates of ecosystem destruction and degradation. These biomes have for too long been misrepresented as the result of deforestation followed by arrested succession. We now know that grassy biomes originated millions of years ago, long before humans began deforesting. We present a consensus view from diverse geographic regions on the ecological characteristics needed to identify old-growth grasslands and to distinguish them from recently formed anthropogenic vegetation. If widely adopted, the old-growth grassland concept has the potential to improve scientific understanding, conservation policies, and ecosystem management.

Many of the world's grasslands are ancient ecosystems composed of communities that require centuries to assemble and perennial plants capable of living for decades to millennia. These ecosystems are being lost to agriculture, tree plantations, mining, and urban sprawl; they are also being degraded by invasive species, poorly managed domestic livestock, altered fire regimes, elevated atmospheric carbon dioxide, and nitrogen deposition (Parr *et al.* 2014). Meanwhile, other types of herbaceous and grass-dominated vegetation (eg old fields and derived savannas) are expanding (Veldman and Putz

In a nutshell:

- Old-growth grasslands are ancient ecosystems characterized by high herbaceous species richness, high endemism, and unique species compositions
- Biodiversity in old-growth grasslands is maintained by frequent fires, herbivores, and soil characteristics that limit tree growth
- To survive fires and grazing, many grassland herbs, forbs, and shrubs have developed specialized underground organs that enable them to resprout repeatedly; evidence of grassland plant longevity and ecosystem carbon storage is often belowground
- Old-growth grasslands are threatened by agricultural conversion, fire exclusion, invasive species, surface mining, poorly managed livestock, and misinformed afforestation projects
- Initiatives to identify, conserve, and restore old-growth grasslands are urgently needed

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2011). Confusion over the substantive differences between natural grassland ecosystems and their novel, anthropogenic counterparts has contributed to a lack of concern over the impacts of environmental change on biodiversity in natural grasslands. This confusion persists in large part because we currently lack a framework for conceptualizing the role of long periods of time in the development of biodiverse grasslands.

To promote the recognition and conservation of natural grasslands, we extend the concept of "old growth" to grasslands (Panel 1) and suggest that old growth is not limited to forests. The ideas we present are drawn from recent advances in grassland ecology and are motivated by the threats of human-caused environmental change. The old-growth grassland concept will help distinguish ecosystems with high conservation values and unique ecological attributes from vegetation that forms over short timescales in response to human land uses. The concept will also help us evaluate the ecological and economic costs associated with the loss or degradation of grassland ecosystems, and determine the rates at which such transitions occur. Finally, questions evoked by the old-growth grassland concept will help identify promising areas of fundamental ecological research.

We define grasslands broadly as ecosystems in which graminoids (ie grasses and grass-like plants), forbs, and shrubs form a relatively continuous "herbaceous layer" of vegetation. This classification includes grasslands without trees, as well as savannas and woodlands that support a range of tree densities (ie "grassy biomes"; Parr *et al.* 2014). We emphasize the ecology of the herbaceous layer, in recognition that herbaceous species account for the majority of plant diversity in these systems and are critical to ecosystem processes. Trees are important to the ecology of savannas and woodlands (eg

Ratnam *et al.* 2011), but the vast ecological differences between trees and herbaceous plants warrant explicit consideration of these plant communities in conceptualizing old-growth grasslands (Kirkman and Mitchell 2006).

Grasslands occur across a huge range of environmental conditions, from the tropics to the Arctic, from sea level to mountain tops, from arid to humid areas, from sites with long hydroperiods to well-drained sites, and from shallow rocky soils to deep clay soils (Brown and Makings 2014). Given the global diversity of grasslands, our intention is not to define old growth for any one place. Instead, we provide an overview of the common characteristics of old-growth grasslands in hopes of improving their fates.

■ Concept development

Descriptions of old-growth grasslands are scattered throughout the literature but to our knowledge have not previously been consolidated into a single framework. Feller and Brown (2000) argued that an old-growth concept for grasslands, similar to that for forests, was urgently needed to provide greater protection for natural grasslands of native species in the western US. Their article has gone largely unnoticed by ecologists, and "old growth" is still rarely used in the context of grasslands. Nonetheless, old-growth themes and descriptions of grasslands with old-growth characteristics do appear in the ecology and conservation literature (eg Noss 2013), as well as in literature on old-growth "forests" in the US – maintained by frequent fires – that many ecologists would consider to be savannas (Ratnam *et al.* 2011). For example, in ecosystems dominated by ponderosa pine (*Pinus ponderosa*) and longleaf pine (*Pinus palustris*), frequent fires and high herbaceous species diversity characterize old growth (Laughlin *et al.* 2004; Kirkman and Mitchell 2006).

A list of old-growth grassland characteristics based on observations of and literature about ecosystems in Africa, Australia, Europe, and the Americas is presented in Panel 1. We acknowledge a bias toward lowland to mid-elevational, tropical, and temperate ecosystems, and hope that experts in high-latitude and high-elevation grasslands will expand on our ideas. These general characteristics should serve as a guide for developing ecosystem-specific definitions of old growth.

Fire and herbivores

Recognition of antiquity in old-growth grasslands requires an appreciation for the roles of fire and herbivores in grassland plant evolution (Figure 1). Grasslands composed of C_3 plant species and grazed by ungulates developed by 20–30 million years ago (MYA; Jacobs *et al.* 1999). Grasslands composed of C_4 species, and that burned frequently, have been prominent in the tropics

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Panel 1. Characteristics of many old-growth grasslands, savannas, and woodlands

Ecosystem-level characteristics	**Life-history and functional characteristics of old-growth indicator plant species**
Species assemblages that do not occur in young, secondary grasslands	Slow growing
High herbaceous-layer plant species diversity	Long-lived
High small-scale (eg 1 m²) species richness	Strong resprouting capacity
Presence of endemic species	Low success at establishing from seed
Transient seed banks	Poor colonization ability
Persistent bud banks	Investment in underground storage organs
High ratio of herbaceous species to tree species	Clonal growth
High belowground biomass	High root:shoot ratio
Little accumulation of litter or duff	Fire-enhanced or fire-dependent flowering and fruiting
Open, discontinuous tree canopies	Fire-tolerant (thick-barked) trees
Factors that maintain biodiversity	**Causes of degradation**
Frequent surface fires	Fire suppression/exclusion
Herbivory by native megafauna	Overgrazing and poorly managed domestic livestock
Soil disturbance by digging animals	Declines in native megafaunal herbivores
Low-intensity domestic livestock grazing	Woody encroachment
Shallow soils; nutrient-poor soils	Invasive species
Seasonal water deficits; seasonal flooding	Atmospheric nitrogen deposition
High (toxic) concentrations of soil metals	Elevated atmospheric CO_2 concentrations
	Anthropogenic soil disturbances
Land uses incompatible with old growth	**Land uses potentially compatible with old growth**
Surface mining or quarrying	Low-intensity domestic livestock grazing
Tillage agriculture	Timber or fuelwood extraction
Plantation forestry	
Intensive pasture management (eg use of exotic forage grasses and fertilizers)	
Prolonged high-intensity grazing	
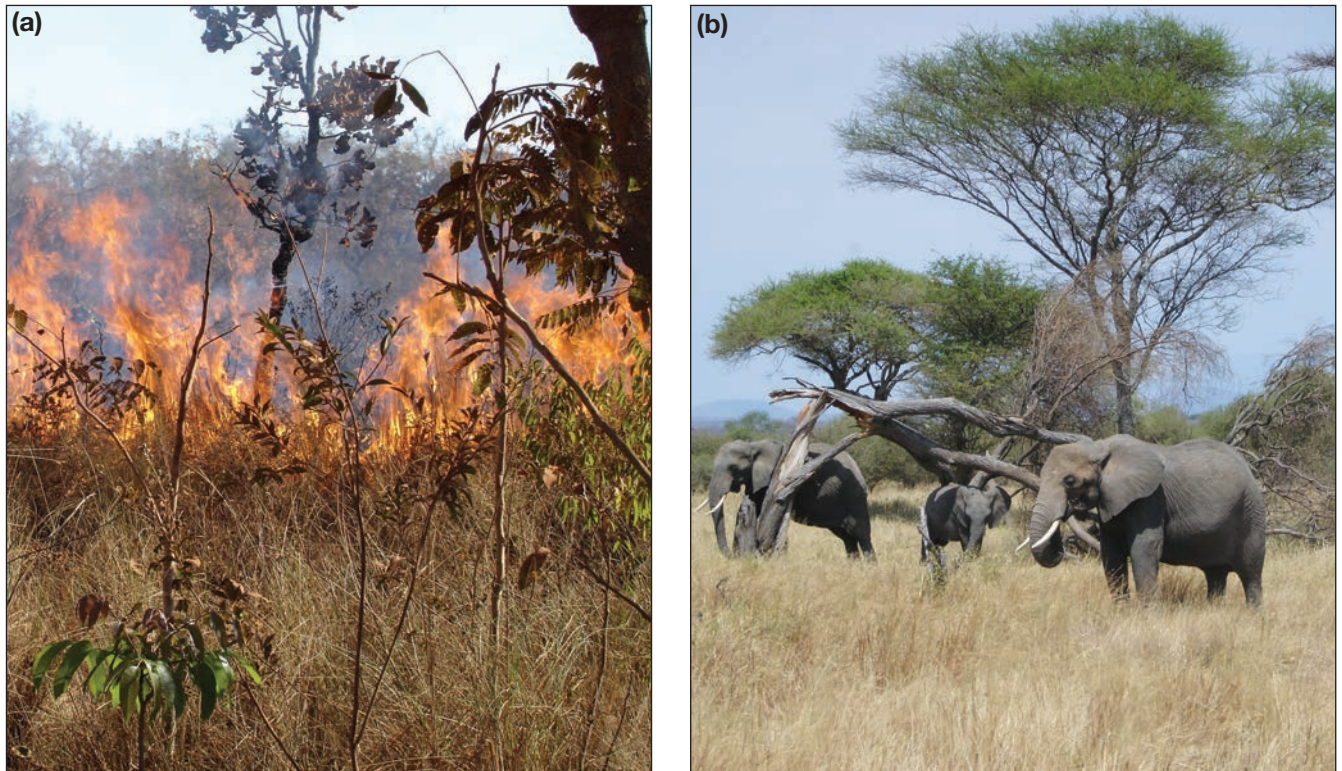
Figure 1. *Intact disturbance regimes: (a) a surface fire in a Bolivian savanna; (b) megafaunal herbivores in eastern Africa.*

and subtropics since 3–8 MYA (Cerling *et al.* 1997; Edwards *et al.* 2010). Millions of years of frequent disturbances in grasslands, which intermittently reduced aboveground biomass, selected for plant morphological characteristics and life-history strategies that are fundamentally different from those of forest species (eg Simon *et al.* 2009; Ratnam *et al.* 2011; Maurin *et al.* 2014).

Plant longevity in grassland environments requires that the parts of the plant where growth occurs (ie meristematic tissues, including buds and vascular cambia) are insulated from high temperatures and protected from herbivores, and that photosynthetic tissues can be rapidly regenerated following disturbances. For most perennial graminoids and forbs, the principal growth regions are located near or below the soil surface, where temperatures remain low during fires (Figure 2). In most savanna trees (and some herbs; Figure 3), fire-resistant stems with insulated buds permit a substantial portion of a plant's aboveground biomass to be retained through fires (Ratnam *et al.* 2011). To permit resprouting, many woody plants and perennial forbs invest in underground organs that store starch and water (Figure 2; Simon *et al.* 2009; Maurin *et al.* 2014). Clonal growth (eg via rhizomes, stolons, or tillers) is common, and allows plants to regenerate after disturbance and to colonize their local area. The prevalence of clonal growth likely reflects the many hurdles to establishment from seed (eg water stress and seed predation), and apparent life-history trade-offs between persistence and sexual reproduction (Benson and Hartnett 2006; Lamont *et al.* 2011). In sum, because disturbance regimes and plant characteristics are dramatically differ-

ent in grasslands than in forests, many signs of antiquity in old-growth forests (eg large diameter trees, accumulated woody debris; Franklin and Spies 1991) are inapplicable to grasslands.

Frequent fires and herbivory are essential to the persistence of most old-growth grasslands, especially where precipitation and soil nutrient availability are sufficient to permit forest development (Bond and Keeley 2005). Fire exclusion or removal of herbivores in these mesic grasslands can result in rapid transitions from grassland to forest or shrubland, with associated losses of herbaceous plant diversity. Grasslands also occur where tree growth is limited by shallow soils, low soil moisture availability, seasonal flooding, or high concentrations of toxic metals. Because these "edaphic" (influenced by soil properties) grasslands are less dependent on frequent disturbances than are mesic grasslands, they are often the only representatives of old growth in severely fire-excluded landscapes (Noss 2013). Climate-determined grasslands occur in regions where tree cover is limited by some aspect of climate, often low precipitation in the tropics (Staver *et al.* 2011) or low temperatures at high latitudes or elevations. While the distinctions between mesic, edaphic, and climate-determined grasslands are useful for identifying their primary environmental determinants (ie factors that limit trees), the importance of fire and herbivory to most old-growth grasslands cannot be overstated. Across a wide range of climatic and soil conditions, frequent fires and herbivores limit the abundance of trees and shrubs, promote herbaceous productivity, consume dead plant material, return nutrients to

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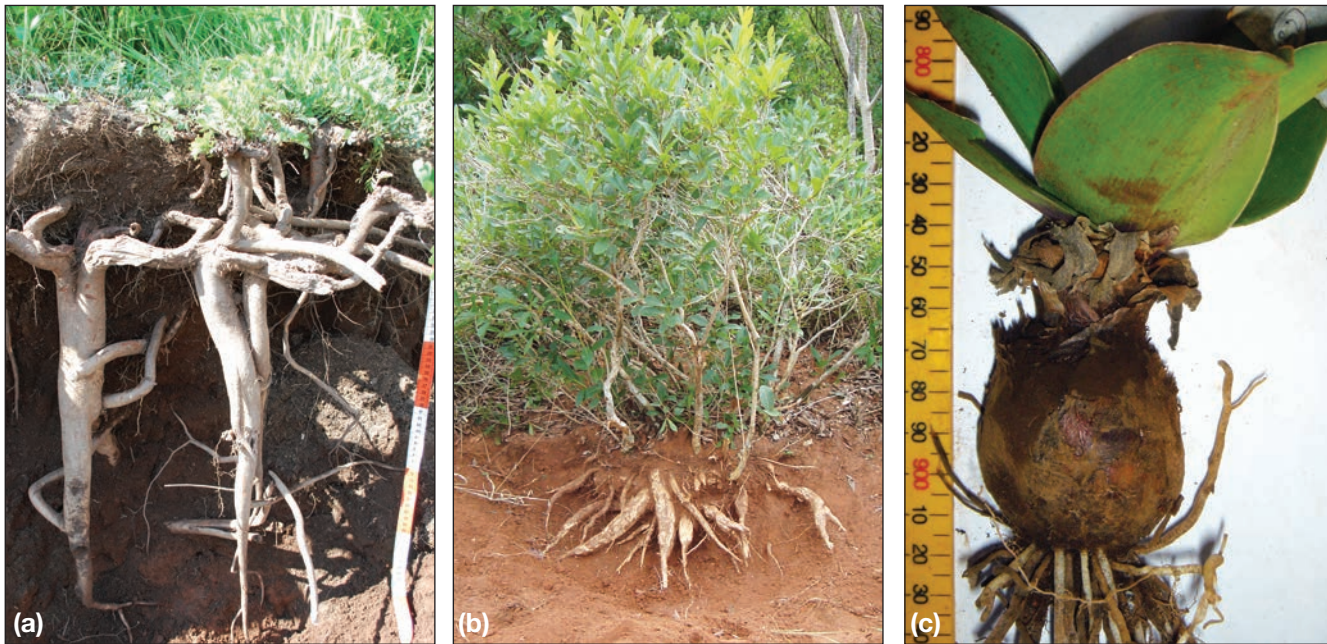
Figure 2. *(a) Storage taproots and rhizomes of a grassland forb* (Cryptosepalum maraviense) *in central Africa; (b) root tubers of a shrub* (Campomanesia adamantium) *in a Brazilian savanna; (c) basal rosette and bulb of a grassland herb* (Ledebouria stenophylla) *from southern Africa; (d) storage taproot (~1.1 m deep) of a savanna forb* (Eriogonum tomentosum) *in the southeastern US.*

the soil, stimulate reproduction, and maintain plant diversity (eg Platt *et al.* 1988; Lehmann *et al.* 2014; Nayak *et al.* 2014; Veldman *et al.* 2014).

Time, degradation, and recovery

How we perceive and conceptualize time has an enormous influence on how we study and seek to conserve organisms and their environments. Questions of time are critical; in a single day, a large tractor can plow up and convert a hectare or more of old-growth grassland into an agricultural field. If that field is abandoned, even if propagule sources are nearby and establishment conditions are favorable, it will require a century or longer for a comparable grassland to form (Baer *et al.* 2010; Redhead *et al.* 2014). Where invasive grass species are present or biophysical conditions are severely altered, ecosystems may never return to an old-growth state (Stromberg and Griffin 1996). Indeed, a number of studies of severely degraded grasslands conclude that old-growth indicator species are very slow to re-establish and that grasslands on former agricultural land are ecologically distinct from old growth (Stromberg and Griffin 1996; Kirkman *et al.* 2004; Zaloumis and Bond 2011; Le

Stradic *et al.* 2014; Redhead *et al.* 2014). Therefore, we suggest the term "secondary grassland" be used to describe young ecosystems on land that historically supported old-growth grasslands (eg Zaloumis and Bond 2011), and that old growth be used as the reference to develop definitions of grassland degradation and to guide restoration (Laughlin *et al.* 2004).

■ Promoting conservation

Cultural resonance

The old-growth grassland concept is a necessary precursor to public support for grassland conservation. Similar concepts that draw from both scientific theory and beliefs about nature have bolstered previous conservation efforts and achieved lasting relevance; for example, the development and promotion of the charismatic, culturally resonant concepts of "biodiversity" and – in the context of forests – "old growth" continue to serve popular conservation movements (Takacs 1996; Proctor 2009). The ideals embodied in these concepts are more than just tools to guide conservation research and advocacy. For the public, they evocatively capture the value of certain aspects of the natural world, including antiquity, diversity, and beauty, which some may even express in terms of sacredness (Taylor 2010).

If old-growth grasslands are to be conserved, they need to be conceptualized in a culturally resonant manner because their biodiversity is not always evident to the untrained eye. Even if ecologists recognize their value, most lay observers are not yet accustomed to seeking
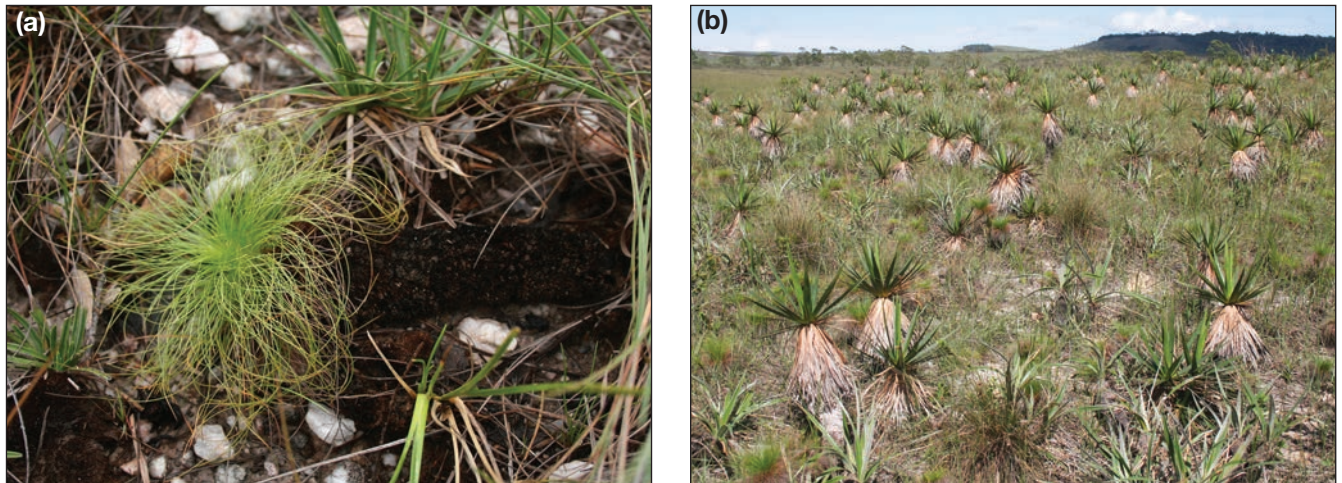
Figure 3. *(a) Persistent charred stem of a graminoid* (Bulbostylis paradoxa) *and (b) old stems of* Vellozia variabilis *in highland grasslands in Brazil.*

"Nature" – much less appreciating antiquity – in grasslands, where signs of old growth and associated conservation values are subtle, if not subterranean. Recognition of grassland conservation values is further complicated by the dependence of grasslands on disturbances that some consider "unnatural" or "undesirable" but that must be maintained, often through active management (Panel 2). Given this cultural context, we suggest that the old-growth concept can help scientists and the public to recognize the value of grasslands and to advocate for their conservation.

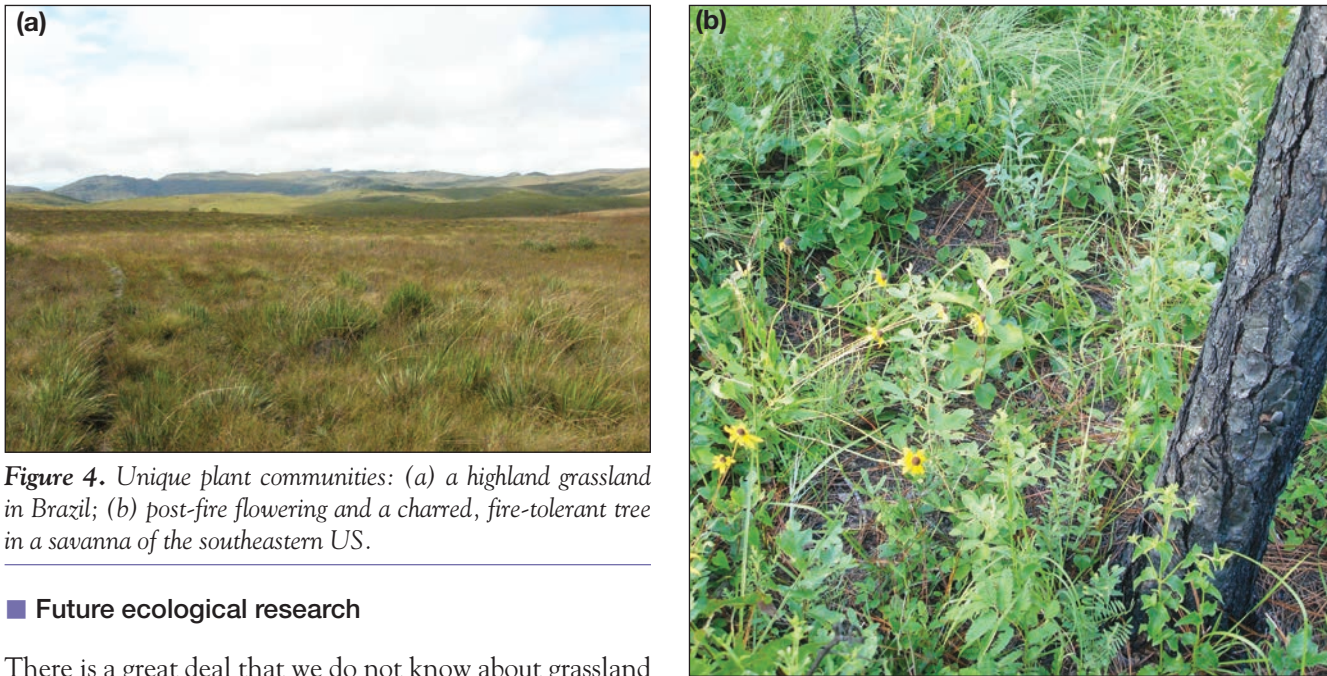### Carbon, conservation, and old growth

There is growing recognition that natural grasslands composed of native species are at risk from policies

> **Panel 2. The cattle conundrum**
>
> A challenge to conceptualizing old-growth grasslands is determining their compatibility with livestock grazing (Nayak *et al.* 2014). The idea of domestic livestock in an old-growth ecosystem may seem counterintuitive given the role of cattle ranching as a global driver of ecosystem degradation. Indeed, poor rangeland management (eg high stocking densities, sowing exotic grasses) can irreparably change natural grasslands (Feller and Brown 2000). Nevertheless, livestock grazing at appropriate densities and intervals appears to be compatible with, or even beneficial to, grassland biodiversity in some systems. This is the case in southern Brazil, where cattle exclusion leads to forest succession and declines in old-growth grassland plant diversity (Overbeck *et al.* 2007). Cattle may also provide opportunities to maintain or restore grasslands that would otherwise be converted to mechanized agriculture or other land uses (Miller *et al.* 2012). In grasslands highly suited to agriculture, livestock grazing is perhaps the only land use that provides economic returns while maintaining many old-growth grassland characteristics. In sum, livestock represent both perils and opportunities for grassland conservation. We need to determine where livestock are compatible with biodiversity and use the old-growth concept to move beyond production-focused grassland management (Feller and Brown 2000).

designed to sequester carbon (C) to mitigate climate change (Putz and Redford 2010; Parr *et al.* 2014). In particular, C payment schemes under development by the United Nations Framework Convention on Climate Change (UNFCCC) and the program for Reducing Emissions from Deforestation and Forest Degradation (REDD+), as well as the definitions of "forest" used by the United Nations Food and Agriculture Organization, put grasslands at risk from afforestation projects and agricultural conversion. Grasslands are a target for C sequestration projects because fire suppression and tree planting are straightforward means of dramatically increasing aboveground biomass, at least in the short term (Canadell and Raupach 2008). We are also concerned that a lack of international policies recognizing natural grasslands and including mechanisms to slow their loss will incentivize the conversion of old-growth grasslands to agricultural uses.

The old-growth grassland concept addresses these conservation concerns in several ways. First, by emphasizing the long periods of time required for species-diverse grasslands of native species to assemble, this concept will raise awareness of the long-term biodiversity costs associated with a narrow focus on C and forests. Second, by emphasizing the roles of time and disturbances in grassland formation, the old-growth concept requires that we consider the permanence of sequestered C in climate mitigation projects. With C stored in belowground plant organs, accumulated soil organic matter, and the wood of fire-tolerant savanna trees (eg Miranda *et al.* 2014), old-growth grasslands may securely store C for long periods of time in fire- and drought-prone landscapes. Third, advancement of the concept depends on ecologists developing ecosystem-specific definitions of old growth. Once established, these definitions should help reconcile conflicts between global agreements on C and biodiversity conservation priorities at the national level (Sasaki and Putz 2009).

Figure 4. Unique plant communities: (a) a highland grassland in Brazil; (b) post-fire flowering and a charred, fire-tolerant tree in a savanna of the southeastern US.

■ Future ecological research

There is a great deal that we do not know about grassland plant longevity, the time required for old-growth communities to assemble, and the rates at which other old-growth attributes develop (eg soil C storage). The old-growth concept challenges us to investigate basic questions about grassland natural history, potentially improving our ability to answer fundamental ecological questions (Panel 3).

The few estimates of grassland plant longevity that are available are based on anecdotal accounts of plant size, longitudinal studies of individual plants, and modeling of clonal plant demographics and growth. Accounts from Brazilian grasslands, for example, suggest that *Vellozia* spp require 100 years to reach reproductive maturity and can live for over 500 years (Alves and Kolbek 1994). Longitudinal studies provide reliable age estimates, but are limited in their time and spatial scales. On the basis of 39 years of observations in a grassland in central North America, Lauenroth and Adler (2008) found that forbs are typically short-lived (≤ 18 years) and that most grasses can live for at least 20 years, with individuals of two species known to be ≥ 39 years old. Previously, Lauenroth *et al.* (1994) used demographic data to estimate that blue grama (*Bouteloua gracilis*), a C_4 bunchgrass, can live for 450 years. Indeed, clonal species (including bunch-grasses) are likely to be the oldest grassland plants, with the potential to live for decades to millennia (de Witte and Stöcklin 2010). A variety of modeling techniques have been used to estimate the ages of both genets (colonies of genetically identical individuals) and ramets (individual clones). For example, matrix modeling of pale pitcher plants (*Sarracenia alata*) in wet savannas of the southern US suggests that ramets typically live 59 years (Brewer 2001), and genets can presumably be much older. Takahashi *et al.* (2011) combined molecular genetics and modeling approaches to estimate that genets of the fire-adapted saw palmetto, *Serenoa repens*, which is endemic

to the southeastern US, may live for 10 000 years. In sum, the maximum ages of old-growth grassland plants may range widely, depending on growth form, disturbance regimes, and historical climate stability (Panel 4). More research is needed on the ages and demographics of long-lived grassland plants, but short-lived species deserve consideration as well.

Short-lived grasses and forbs, in combination with long-lived perennials, can be indicators of old growth, particularly in grasslands of the arid tropics and temperate steppes (Coiffait-Gombault *et al.* 2012). Annual, biennial, and short-lived perennial species are often among the early colonists of sites disturbed by digging animals (Platt 1975) or locally intense grazing (Mack and Thompson 1982) and are thus an important part of dynamic, old-growth grasslands. But where abundant, annuals can indicate severe degradation associated with altered disturbance regimes, biological invasions, and declines in native perennial populations (Mack and Thompson 1982; Feller and Brown 2000). Whether as indicators of old growth or as signs of degradation it will be important to determine the role of short-lived plants in ecosystem-specific definitions of old-growth grasslands.

Although plant community composition is an indicator of grassland maturity (Panel 1; Figure 4), we lack firm estimates of the time required for species-diverse grasslands that include rare and endemic species to form. Our best estimates are based on studies of secondary grasslands following abandonment of agriculture, plantation forestry, and surface mining (Kirkman *et al.* 2004; Zaloumis and Bond 2011; Le Stradic *et al.* 2014; Redhead *et al.* 2014). These studies clearly demonstrate that old-growth grassland communities require many decades, and probably several centuries, to assemble. Rates of grassland formation are likely influenced by interactions between a

Panel 3. Relevance of old-growth grasslands to ecology

Adler *et al.* (2011) assessed the relationship between productivity and species richness in a global dataset of herbaceous plant communities; the majority of their study sites were grasslands of various forms and origins, and these were grouped together for their analyses. Although the authors did not specifically distinguish old-growth grasslands from others, they did describe a subset of sites as "anthropogenic". They concluded that there was no consistent pattern in the data, and thus productivity alone was a poor predictor of species richness.

We reclassified the sites used by Adler *et al.* (2011) into two groups (Figure 5): (1) those likely to be old-growth grasslands (ie sites with no known history of cultivation, intact disturbance regimes, and native plant communities; $n = 13$), and (2) secondary grasslands and derived savannas (ie previously cultivated sites and those classified by Adler *et al.* [2011] as anthropogenic; $n = 16$); sites with insufficient information remained unclassified ($n = 19$). We found a strong positive linear relationship between productivity and diversity for old-growth sites ($r^2 = 0.40$, $P = 0.02$), and no apparent relationship for secondary grasslands and derived savannas. We suggest that this is one example of how distinguishing old-growth grasslands from other ecosystem states may lead to fundamental insights.
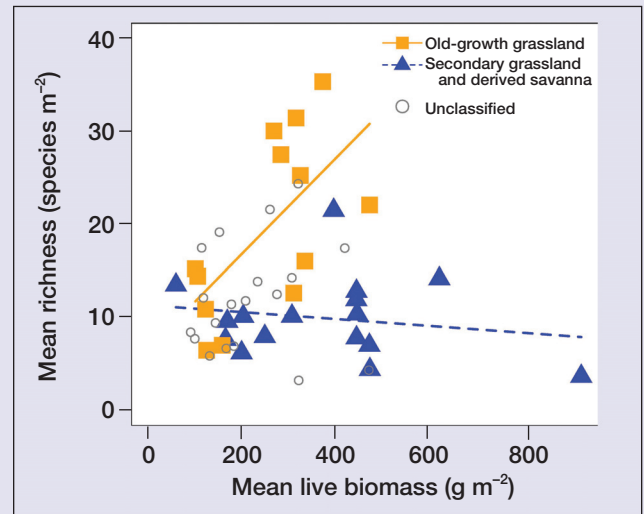
Figure 5. The productivity–diversity relationship in old-growth grasslands compared to secondary grasslands and derived savannas. Modified from Adler et al. (2011).

host of factors, including soil biophysical characteristics. At grassland restoration sites on former agricultural land in central North America, soil microbial communities are estimated to require 30–60 years, and soil C and nitrogen 140 years, to recover to levels found in old-growth grasslands (Bach *et al.* 2010; Baer *et al.* 2010). In these studies, soil recovery varied with soil texture, suggesting that rates of grassland soil development can be quite different, even within the same ecosystem. Additional studies are needed to improve our understanding of the role of time in the development of old-growth grassland soils, as well as the assembly of plant and animal communities.

■ Conclusions

Having presented the ecological basis and conservation motivations for the old-growth grassland concept, we suggest that much work remains. Ecologists should establish ecosystem-specific definitions of old growth and work to identify and map these grasslands at local, regional, and continental scales. Land managers should learn to recognize old-growth characteristics and prioritize the maintenance of disturbance regimes through prescribed fire, wildfire, native herbivores, and, in certain cases, domestic livestock. Conservation advocacy groups should seek legal protection for old-growth grasslands and support educational outreach to raise awareness of these imperiled biomes.

Policies designed to promote afforestation for any of a variety of reasons, including climate-change mitigation, should explicitly acknowledge the conservation values of old-growth grasslands. Specifically, these policies should recognize destruction of natural grasslands for agriculture to be a form of "agricultural conversion" with negative environmental consequences similar to those that occur from deforestation. Likewise, policies that promote fire suppression or planting exotic forage grasses should be re-evaluated in regions that support old-growth grasslands; non-native invasive species should be recognized as a serious threat to old-growth grassland biodiversity and a major hurdle to restoration. Finally, financial mechanisms (eg payments for ecosystem services) should be developed that promote the protection and maintenance of biodiverse ancient

Panel 4. Latitudinal trends in old-growth grasslands

There are likely to be profound differences between grasslands in regions that were transformed during Pleistocene glaciations (2.6–0.12 MYA) and grasslands of tropical and subtropical regions with relatively stable climates (Kirkman *et al.* 2014). Post-glacial grasslands (eg in temperate North America, Europe, and Asia) have assembled during the past 12 000 years through dispersal from refugia where grasslands persisted during glaciations. In contrast, many tropical and subtropical grasslands have existed for >2 million years in more or less the same locations. These trends in paleoclimatic stability have likely resulted in latitudinal trends in grassland plant life-history characteristics. In particular, we hypothesize that in post-glacial grasslands, perennial plants are shorter-lived (ie years to decades; Lauenroth and Adler 2008) and have higher dispersal and colonization potentials than in climate-stable grasslands, where perennial plants can be extremely long-lived (centuries to millennia; Alves and Kolbek 1994; Takahashi *et al.* 2011) and are usually poor colonizers. In looking for old-growth grasslands, we should expect that, as in old-growth forests (Outcalt 1997; Devall 1998), the time required for these grasslands to form – and the ages of old-growth plants – may vary by at least an order of magnitude, from ~100 years (Redhead *et al.* 2014) to perhaps >1000 years. In many cases, these differences may be attributable to latitudinal trends in climate stability.

grasslands. It is our hope that if our proposed concept is widely adopted by ecologists, policy makers and others will follow suit, thereby improving the prospects for conservation of the world's old-growth grasslands, savannas, and woodlands.

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