REVIEW

Ancient grasslands guide ambitious goals in grassland restoration

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Grasslands, which constitute almost 40% of the terrestrial biosphere, provide habitat for a great diversity of animals and plants and contribute to the livelihoods of more than 1 billion people worldwide. Whereas the destruction and degradation of grasslands can occur rapidly, recent work indicates that complete recovery of biodiversity and essential functions occurs slowly or not at all. Grassland restoration—interventions to speed or guide this recovery—has received less attention than restoration of forested ecosystems, often due to the prevailing assumption that grasslands are recently formed habitats that can reassemble quickly. Viewing grassland restoration as long-term assembly toward old-growth endpoints, with appreciation of feedbacks and threshold shifts, will be crucial for recognizing when and how restoration can guide recovery of this globally important ecosystem.

Grasslands are essential components of Earth's system, supporting a biodiverse array of plants, birds, insects, and other animals and providing important ecosystem services such as pasture forage, water regulation and freshwater supply, erosion control, pollinator health, and carbon sequestration (*1*, *2*). Yet high rates of land cover conversion for intensive agriculture and silviculture, combined with woody encroachment and species invasion driven by altered fire and grazing regimes, threaten these systems (*3*, *4*). For instance, the Cerrado has been extensively cleared for agriculture, with more than half lost in the past 50 years, exceeding the rate of forest loss in the Brazilian Amazon (*5*). The Great Plains of North America has also lost more than half its original grasslands and continues to lose 2% each year (*6*).

As we enter the United Nations Decade on Ecosystem Restoration, much of the emphasis has been on the restoration of forests (*7*). Ironically, this emphasis presents an additional threat to grasslands: Careless or poorly planned tree-planting efforts in the name of restoration can establish forests in natural grassland and savannah ecosystems. For instance, almost 1 million km^2 of Africa's grassy biomes have been targeted for tree planting by 2030 (*8*). This practice ignores the value of protecting and restoring grasslands.

The conversion and degradation of grasslands can occur rapidly, yet restoring lost ecosystem services and diversity is often a discounted or underestimated challenge. Until recently, grassland assembly was assumed to be a relatively straightforward—albeit difficult—process (*9*): Allow herbaceous species to recolonize, at times augmenting with seed of native species; reestablish appropriate grazing and fire disturbance regimes; and control ruderal, exotic, or woody species. Because many herbaceous species reach reproductive maturity in a few years, it was also assumed that this assembly process was relatively quick, achieving desired diversity and function within several years to a decade. We now know that this view of grassland restoration does not adequately acknowledge the difficulty of restoring biodiversity and functions or the time and interventions needed to restore grasslands (*10*). Here, we review recent developments that widen the view of grassland restoration to include grassland age and development, describe how this lens identifies important but overlooked restoration interventions, and highlight several key unknowns for grassland restoration into the future.

Refining the reference: The old-growth concept for grasslands

Grasslands occur in a range of biogeographical contexts (Fig. 1) including the tropical and subtropical savannas in Africa, Australia, Asia, and South America; the boreal, temperate, and southern prairies in North America; and the steppes in Eurasia. Grasslands have a continuous herbaceous layer of graminoids and herbaceous dicots, either without trees or, in the case of savannas, supporting a range of tree densities with a continuous grassy understory (*3*) (Fig. 2). The processes creating and maintaining grasslands vary across locations (*11*); these include edaphic or climatic conditions and disturbances (i.e., herbivore grazing or fire), all of which can limit the establishment of woody species (Fig. 3).

The reference condition is a cornerstone concept in ecological restoration; it encapsulates a set of desired characteristics and provides guidance for how to evaluate project success, even if a restored system is rarely able to completely reach reference conditions (*12*). In grasslands structured by edaphic or climatic conditions, with soils, low temperatures, or low precipitation constraining tree establishment, grassland is generally acknowledged to be the desired reference state for restoration. In cases where climate is suitable for forests but herbivore grazing or fire maintain them in an open state (*10*) (Fig. 3), more debate and uncertainty surrounds the reference designation. These disturbance-dependent grasslands are often assumed to be a result of deforestation (i.e., derived grasslands; grass-dominated vegetation resulting from human-caused deforestation) in an early successional stage on a forest trajectory (Fig. 4). However, climate suitability for tree growth does not preclude the likelihood that old-growth grasslands exist (or used to exist) in the region (*13*).

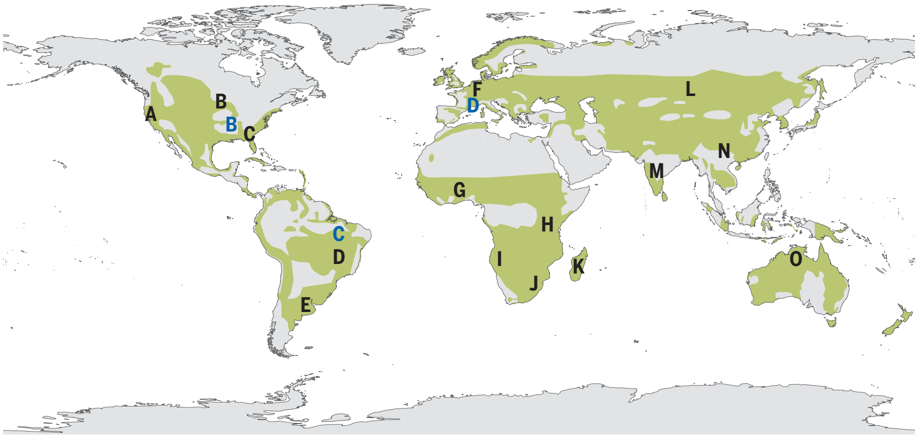

Fig. 1. The distribution of grasslands spans temperate and tropical regions of the globe. Green areas estimate the extent of grassland distribution. We note, however, that all maps of grasslands should be considered imprecise: Grasslands occur mixed within landscapes with other vegetation types and are often disturbed to an extent that masks historic distributions. Letters in black are grasslands represented in Fig. 2; letters in blue are grasslands represented in Fig. 3.

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Moreover, these disturbance-dependent grasslands are often at risk from factors driving woody invasion, rearranging landscape mosaics and shifting grass-forest boundaries (*14*). If afforestation policies under the guise of restoration disregard these dynamics, irreversible damage will occur (*7*).

In forest ecosystems, old-growth forests are often used as references for restoration. These are mature forests composed of large and old trees, large snags, and a diverse tree community with structural complexity, all of which require long time periods to develop. Recent work has made it abundantly clear that the "old growth" concept is not limited to forests (*4*, *11*): Old-growth grasslands, also called ancient or pristine grasslands, assemble over centuries and contain high species diversity, long-lived perennial plants, and a substantial proportion of well-developed belowground structure from which species can resprout after natural disturbance. Old-growth grasslands are unique in their underground structures and biodiversity: They store carbon and reallocate resources aboveground after disturbances and drought. All biogeographic contexts where grasslands are present (Fig. 1) support ancient old-growth grasslands that have persisted for millennia.

As with old-growth forests, there should be little expectation that restored grasslands will ever completely recover to resemble old-growth grasslands. Even so, old-growth grasslands provide a suite of characteristics that can be the aim in restoration: long-lived perennial plants; a complex diversity of belowground structures that enable resprouting after aboveground disturbances such as fire and grazing; and substantial belowground carbon stores. Traditional management can usefully target these old-growth characteristics even in cultural landscapes where grasslands are created and maintained by human activity, and regardless of historical analogs (*15*).

With maps of grasslands contested and overlapping those of forests (*8*, *13*), it can be challenging to determine whether a grassland is one that formed after the degradation of an old-growth grassland (i.e., a secondary grassland; grass-dominated vegetation resulting from the degradation of old-growth grasslands) or a derived grassland formed after deforestation. Paleoenvironmental methods, considering

Fig. 2. The incredible diversity of old-growth grasslands. See Fig. 1 for locations. Whether these grasslands are maintained by disturbance (such as grazing or fire) or are environmentally constrained (EC, edaphic or climatic; see Fig. 3 for details) is indicated within brackets. (**A**) California coastal grasslands on Mount Tamalpais, USA (disturbance). (**B**) Curtis Tallgrass Prairie Restoration, Wisconsin, USA (disturbance). (**C**) Longleaf pine (*Pinus palustris*) savanna, North Carolina, USA (disturbance). (**D**) Grassland in the Espinhaço mountain range, Minas Gerais, Brazil (EC, edaphic + disturbance). (**E**) Subtropical grasslands in Rio Grande do Sul, southern Brazil (disturbance). (**F**) Alpine meadow in the Alps, Vanoise National Park, France (EC, climatic). (**G**) A high-rainfall grassy savanna in Mole National Park, Ghana (disturbance). (**H**) The Serengeti ecosystem in Tanzania (EC, edaphic + disturbance). (**I**) The grasslands in the Kavango Catchment, Angola (EC, edaphic and climatic + disturbance). (**J**) Grassland in the Drakensberg, South Africa (disturbance). (**K**) Grassland and tapia savannas on Ibity mountain, Madagascar (disturbance). (**L**) Petrophytic steppe in Khakassky Zapovednik State Nature Reserve, Russia (EC, climatic). (**M**) Eravikulam Shola grasslands, India (EC, climatic + disturbance). (**N**) Oak savanna in South Yunnan, YuanJiang region, China (disturbance). (**O**) Mesic savanna in the Northern Territory, Australia (disturbance). These grasslands vary widely in composition and structure yet share key characteristics that can guide restoration: high belowground allocation, complex resprouting structures, and unique functional and taxonomic diversity.

PHOTOS: (A, B, D, K) ELISE BUISSON, (C, G, H, I, J, O) SALLY ARCHIBALD, (E) ALESSANDRA FIDELIS, (F, L) RENAUD JAUNATRE, (M) AATHIRA PERINCHERY, (N) TRISTAN CHARLES-DOMINIQUE

lengthy records of pollen, phytoliths, charcoal, and *Sporormiella* fungi specific to herbivore guts, can provide evidence for past grasslands and their disturbance history (*16*). Species composition and functional diversity (e.g., of belowground structures), as well as phylogenetic studies dating the origins of endemic grassland species, can also indicate antiquity and conservation value (*17*, *18*). There are also contexts where grasslands are the desired ecosystem state for cultural or social reasons despite being created or maintained by humans.

Pathways and thresholds of grassland degradation

Grasslands are increasingly degraded by land-use change and altered disturbance regimes, which can fundamentally alter their structure and functioning (Fig. 4). Such degradation increases the need for grassland protection and restoration but can also decrease the capacity of restoring old-growth grassland characteristics.

Grazing and fire are dominant aboveground disturbances that have coevolved with grassland plants, maintaining diversity and function in grasslands (*4*). Changes to these disturbance regimes can gradually alter grasslands. Although this results in the loss of biodiversity and simplification in composition, structure, and functioning, altered grassland often maintains some belowground structures (Fig. 4). Lack of grazers (or of particular suites of grazing species) can homogenize grasslands and increase fire occurrence. On the other hand, overgrazing, particularly in grasslands with no evolutionary history of grazing, can result in loss of basal cover, soil compaction, and increased erosion (*19*). Defining the degradation point in these circumstances is difficult; for instance, naturally occurring "grazing lawns" have many of the biophysical characteristics associated with degradation (low aboveground biomass, soil compaction, sometimes even increased bare ground) even though their unique biodiversity and ecological importance is now increasingly recognized. Fire regimes can also become too frequent or infrequent or occur during the wrong season. The longer these altered disturbance regimes persist, the more risk to belowground structure (e.g., bud banks) that speed recovery. Altered disturbance regimes can also facilitate exotic grass invasion and woody encroachment (*20*), which can compound impacts to belowground structure over time.

The most detrimental disturbances are those that rapidly destroy belowground structure, such as tillage agriculture, mining, and afforestation (*10*, *21*). For instance, 50 years of pine plantation completely eliminated the viable bud bank in a once-open savannah (*22*). Several decades after cultivation or mining, the composition of secondary grassland plant communities remains very different from that of nearby old-growth grasslands, lacking species with poor dispersal abilities and species regenerating from belowground organs (*10*, *23*). Belowground degradation can therefore cause grasslands to cross a hard-to-reverse threshold where restoration may be difficult or impossible within decades of these disturbances. Given the apparent existence of this threshold, it is vital that remaining old-growth grasslands are protected, particularly from the threats that affect belowground processes and structure, as we cannot rely on restoration to guide complete recovery after such degradation.

Interventions toward old-growth characteristics

In contrast to the early successional view of derived grasslands as a stage on their way to forests, restoring old-growth characteristics to altered or secondary grasslands requires attention to the development of a complex belowground structure akin to the aboveground complexity in an old-growth forest (*24*). A synthesis of 31 studies, including 92 time points on six continents, indicates that secondary grasslands may typically require at least a century, and more often millennia, to recover their former species richness (*23*). Even as their richness increases over decades to centuries, these grasslands still lack many characteristic old-growth grassland species and instead support more short-lived, early successional species than their old-growth counterparts. We know less about the timeline for belowground soil and structure development, but it likely corresponds with the timeline

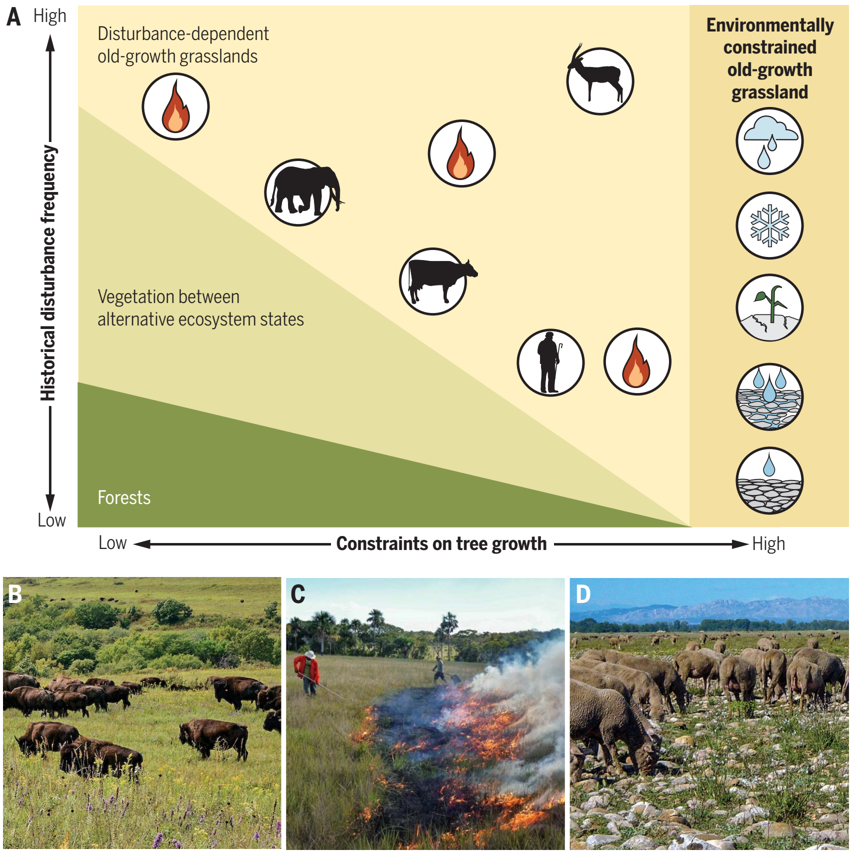

Fig. 3. Interactions among climate, soils, disturbance, and vegetation are key considerations for understanding old-growth grasslands as well as recovery trajectories in secondary grasslands. (**A**) On most soil types, the existence of disturbance-dependent grasslands (in light rose-color) is determined by interactions between soils and endogenous disturbances (fire, herbivory). Tree recruitment is limited by these disturbances. In environmentally constrained grasslands (in light brown), poor drainage (seasonally saturated or inundated soils), extremely low moisture-holding capacity (shallow, rocky soils), exceptionally low soil fertility, cold temperature, or low precipitation preclude dense tree cover, even in the absence of frequent disturbances. Disturbances and abiotic factors (circles, in no set order) that could result in exclusion of trees are placed as examples in each of the far left zones, respectively. In forests (dark green), dense tree cover constrains fire frequency and grazer abundance by limiting herbaceous plant productivity. The light green state space between disturbance-dependent old-growth grasslands and forests represents unstable vegetation (fire-excluded, tree-encroached grassland) in transition between alternative ecosystem states; old-growth grasslands and forests often co-occur in mosaics in such landscapes. (**B** to **D**) Examples of grasslands structured by different interactions. (B) Bison grazing in Konza prairie, where fire is needed to suppress woody encroachment. (C) Water saturation of the soil prevents tree establishment and fire maintains diversity in this wet grassland in Jalapão, Northern Brazil. (D) Sheep grazing in a Mediterranean grassland in Southern France, where pastoralism has coevolved with the system in a grassy state since the Holocene.

MODIFIED FROM (*10*); PHOTOS: (B) BARB VAN SLYKE; (C) ALESSANDRA FIDELIS; (D) ELISE BUISSON

of these compositional dynamics (*25*). The increased appreciation of the temporal dimension of grassland assembly emphasizes the need of restoration to accelerate this trajectory and challenges the view that one initial period of active restoration will be sufficient to guide development. We highlight three advances driven by this increased appreciation below.

Focus interventions on disturbance-vegetation feedbacks

In cases where degradation has not had a catastrophic impact on belowground structure, it may be possible to reestablish broken feedbacks that then can guide recovery (*26*). Feedbacks among disturbance, vegetation, and belowground soil development have structured grasslands for millennia (*4*, *27*). Disturbance regimes select for functional traits of the vegetation, which then provide feedback to affect the intensity, frequency, and impact of disturbances (*28*). For instance, fire regimes vary in flammability depending on plant properties, and herbivore pressure varies depending on the quantity and quality of forage and habitat suitability for predator avoidance (*27*). The response of vegetation to these disturbances varies based on plant traits such as resprout ability, clonal growth, and seed recruitment (*26*, *28*). Feedbacks also extend to soils and soil organisms, as soils determine plant growth but are also products of the plants that grow on them (*29*).

As feedbacks in degraded grasslands differ in their nature and strength from those with more old-growth characteristics, reestablishing a disturbance regime in degraded grasslands may not result in expected effects of the disturbance or in the intended vegetation responses to the disturbance. Interventions simultaneously addressing disturbance and biota may be the best option to break the feedbacks that constrain recovery. For instance, there are examples of creative use of prescribed fire as a tool to recreate grazing habitat (*30*), and livestock can be managed in such a way as to initiate grazing habitat that supports large mammalian herbivores (*31*). Amendments such as biochar and mycorrhizal inoculum can shift the soil environment to be more suitable for native species, characteristics which can be maintained by slow growth and resource cycling of the vegetation (*32*, *33*). As the system recovers, these interventions also need to shift depending how the recovering biota affects disturbance dynamics and vice versa.

Breaking the cycle of invasion: Vegetation change that constrains recovery

Restoration in areas where an altered disturbance regime has resulted in woody encroachment or exotic herbaceous species invasion demonstrate the importance of viewing restoration as a set of interventions that iteratively move the system to a new system state (*10*, *34*).

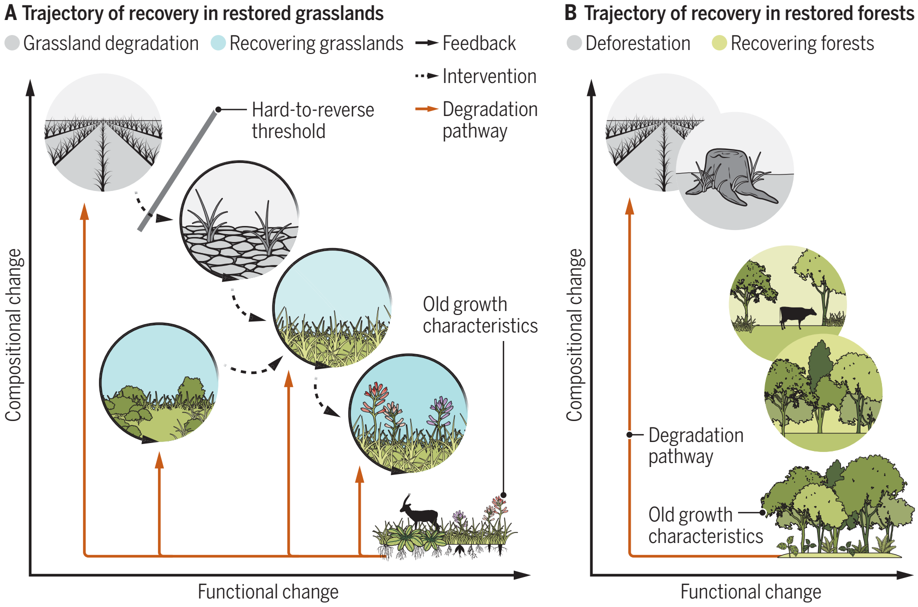

Fig. 4. Degradation pathways can result in differential loss of ecosystem function and diversity to old-growth grasslands, and the recovery of "old-growth" characteristics is dependent on the degree of functional change. Axes of functional and compositional change depict divergence from the reference characteristics [modified from (*51*)]. (**A**) The trajectory of recovery in restored grasslands (blue spheres) toward old-growth characteristics (lower right) is dependent on the degradation pathways (red arrows, ranging right to left from altered disturbance regimes to land use conversion) as well as vegetation-soil-disturbance feedbacks (black arrows) at each stage of recovery. Substantial belowground disturbance (e.g., tilling) may cause the system to cross a hard-to-reverse threshold (gray line) and woody encroachment shifts feedbacks and can lead to alternative trajectories. Iterative restoration interventions (dashed black arrows) that consider these feedbacks can result in progression back toward old-growth characteristics. (**B**) Forests show similar dynamics, where recovery to old-growth characteristics after deforestation may be hard if not impossible. An early recovery stage after deforestation may be a grassy stage (which we term a derived grassland), yet the recovery trajectory is toward forest. Restoration interventions may accelerate recovery.

A. MASTIN/*SCIENCE* BASED ON E. BUISSON *ET AL.*

Woody species can strongly influence disturbance regimes, and land managers have resorted to cutting, herbicides, and even plowing to remove trees—with striking consequences for the remaining biodiversity. Extreme fires (firestorms) have been applied in heavily encroached areas using spiral ignitions or extreme weather days to try to reverse the woody cover and reinitiate ecologically relevant feedbacks (*35*). Once the grassy understory has been reduced to the point that it cannot carry a fire or support grazers, woody encroachment becomes more difficult to reverse (*36*), requiring the replanting of herbaceous vegetation alongside the initiation of disturbance regime for recovery feedbacks.

When invasive species are grasses, they can often maintain disturbance regimes that benefit short-lived ruderal life histories, preventing transitions to the belowground complexity and allocation that characterize old-growth grasslands (*37*). High accumulation of litter and standing dead biomass changes local fire behavior, and a dependence on seed recruitment often confers advantage for invasives under this disturbance regime (*38*). Dominance in the seed bank and difficulty reestablishing long-lived natives can make this feedback particularly difficult to address. One strategy is to enhance the ability for natives to recruit by seed via seed enhancement technology (e.g., seed coating or pelleting aimed at mitigating the conditions that limit establishment) (*20*), potentially addressing priority effects (i.e., the order in which plants are reintroduced) that influence species dominance in early stages of restoration (*39*).

Overlooked old-growth grassland species

One important restoration question is how to accelerate or facilitate species turnover toward old-growth species composition and associated belowground function. Worldwide, grasslands are often restored by sowing seeds (*40*). However, as many species have developed colonization and survival strategies that are based on belowground buds and clonal growth (*23*, *41*) rather than on seeds, additional techniques may be needed to restore old-growth characteristics. Seeding fast-growing species can impede long-term restoration success by creating communities with low resilience to natural disturbance, such as fire, and excluding the longer-lived species from restoration (*42*). In fact, there may be many grasslands where seeded species maintain dominance long after restoration, spurring reconsideration of whether actions are achieving the desired old-growth structure (*43*).

Although bud-bearing belowground organs can persist in the absence of disturbance for some time in a degraded grassland (*44*), how long is still unclear. Once these belowground structures are gone, we have little understanding of how to reintroduce this component of the vegetation (*24*). Topsoil transfer has shown some success in broadening the type of species that restoration can reintroduce (*45*), yet even this technique favors species with high seed bank allocation. Vegetative propagation—such as micropropagation, transplantation of seedlings, and individual tillers—is often needed (*24*) but is hard to conduct at scale, with open questions about protocols, spatial configuration of planting, and genetic sourcing. Techniques aimed at speeding the establishment of bud banks and belowground organs in a restoration have shown promise but are just in their infancy (*24*, *41*).

Global change as a challenge and opportunity

Global climate change frames the emerging perspective of long-term assembly toward old-growth characteristics in grassland restoration. Climate controls the distribution of grasslands in some regions, influences the feedbacks and threshold shifts that determines where grasslands persist, and, in virtually all regions, can have a strong influence on the interventions needed to restore feedbacks (*14*, *46*). Depending on the degree to which climate influences these processes, it may also affect the historical approach to the determination of grassland types and disturbance regimes (*12*). For instance, changes such as elevated atmospheric CO_2, which exacerbates invasion of woody species, would require novel disturbance regimes to aim for a grassy state.

Given the strong feedbacks between composition and disturbances in grassland recovery, shifts in climate may exert large influences on the assembly process. In some cases, it may be important to let climate effects shift restoration trajectories, as climate can guide species composition or characteristics to those most able to tolerate future conditions (*47*). Restoration efforts under a climate change scenario may thus target not only which species should be present at a given site, but also functional diversity, soil structure, and the belowground component. In this way, the system may be able to recover from an extreme event, as the presence of a viable bud bank and underground storage organs ensures the resilience of the system (*48*). However, letting climate effects shift restoration trajectories might also be undesirable if it endangers fundamental feedbacks in the trajectory of the system toward old-growth functional characteristics (*46*) by, for instance, selecting for species with greater aboveground allocation characteristics. As belowground complexity is a characteristic that develops over long time horizons, understanding how climate influences priority effects and feedbacks that affect recovery trajectories is critical.

Climate change will add difficulty to the already difficult challenge of restoring old-growth grasslands that resemble specific reference sites, as these ancient grassland references developed in a different time, disturbance regime, and climate. Yet we expect that restoring old-growth characteristics in these situations, prioritizing processes such as belowground complexity and functional diversity (*49*), should enable resilience and facilitate adaptation to future change while still maintaining character, functions, and services that embody these globally important systems.

Outlook

As we enter the United Nations Decade on Ecosystem Restoration, advances in restoration science and practice in grasslands are critical if we are to combat the loss of old-growth grasslands and the decline of biodiversity (*50*). However, in the rush to provide nature-based solutions to tackle climate change, tree planting in grasslands has become synonymous with restoration in many regions (*13*). At the same time, the high demand for arable land continues to spur conversion to agriculture. These are irreversible actions, ignoring the belowground soil-locked carbon storage in these old-growth grasslands as well as the hard road to restore their belowground complexity and their biodiversity once they are lost.

Although there are many challenges ahead, viewing grassland restoration as assembly toward old-growth characteristics with unique biota and belowground complexity will enable us to achieve ambitious restoration goals for Earth's grassy ecosystems. Given that grassland recovery involves strong feedbacks among vegetation, disturbance, and soils, as well as the lengthy time horizon for recovery, future progress depends on creative interventions that focus on iterative management, taking into account changes in grassland assembly over time. Techniques to reestablish species characteristic of old-growth grasslands, given their belowground structure and limited recruitment by seed, will require looking beyond or augmenting traditional seeding techniques. Metrics of belowground complexity and functional diversity will be critical guideposts to track trajectories in development and assess success. We urge conservation initiatives to safeguard against the conversion of old-growth grasslands for tree planting or tillage agriculture, to maintain our ancient biodiverse grasslands with appropriate disturbance regimes, and to emphasize the long-term restoration of grasslands in efforts to restore Earth's biodiversity.

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