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Challenges and opportunities for grassland restoration: A global perspective of best practices in the era of climate change

Kelly G. Lyons^{a,1}, Péter Török^{b,c,d,2,*}, Julia-Maria Hermann^e, Kathrin Kiehl^{f,3}, Anita Kirmer^{g,4}, Johannes Kollmann^{e,5}, Gerhard E. Overbeck^{h,6}, Sabine Tischew^{g,7}, Edith B. Allen^{i,8}, Jonathan D. Bakker^{j,9}, Christy Brigham^k, Elise Buisson^{l,10}, Kerri Crawford^{m,11}, Peter Dunwiddie^{j,12}, Jennifer Firn^{n,13}, Devin Grobert^{o,p,14}, Karen Hickman^{q,15}, Soizig LE Stradic^{r,16}, Vicky M. Temperton^{s,17}

^a Trinity University, Department of Biology, San Antonio, TX, USA

^b University of Debrecen, Department of Ecology, 4032 Debrecen, Hungary

^c ELKH-DE Functional and Restoration Ecology Research Group, 4032 Debrecen, Hungary

^d Polish Academy of Sciences, Botanical Garden, Center for Biological Diversity Conservation in Powsin, Warszawa, Poland

^e Chair of Restoration Ecology, Technical University of Munich, 85354 Freising, Germany

^f Vegetation Ecology and Botany, Osnabrück University of Applied Sciences, 49009 Osnabrück, Germany

^g Chair of Vegetation Science and Landscape Ecology, Anhalt University of Applied Sciences, 06406 Bernburg, Germany

^h Department of Botany, Institute of Biociences, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

ⁱ Department of Botany and Plant Sciences, University of California, Riverside, USA

^j School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA

^k Resources Management & Science, Sequoia & Kings Canyon National Parks, USA National Parks Service, USA

^l IMBE – Institut Méditerranéen de Biodiversité et d'Ecologie, Avignon University, CNRS, IRD, Aix Marseille University, Avignon, France

^m Department of Biology and Biochemistry, University of Houston, Houston, TX, USA

ⁿ School of Biology and Environmental Studies, Queensland University of Technology, Brisbane, Queensland, Australia

^o Wildland Conservation Division, Austin Water, City of Austin, Austin, TX, USA

^p Department of Integrative Biology, University of Texas at Austin, Austin, TX, USA

^q Environmental Science Oklahoma State University, Stillwater, OK, USA

^r BIOGECO - Biodiversity, Genes and Communities, INRAE, University of Bordeaux, Pessac, France

^s Institute of Ecology, School of Sustainability, Leuphana University Lüneburg, 213335 Lüneburg, Germany

* Corresponding author at: University of Debrecen, Department of Ecology, 4032 Debrecen, Hungary.

E-mail address: molinia@gmail.com (P. Török).

¹ 0000-0002-3781-2040

² 0000-0002-4428-3327

³ 0000-0003-3931-187X

⁴ 0000-0002-2396-713X

⁵ 0000-0002-4990-3636

⁶ 0000-0002-8716-5136

⁷ 0000-0001-6995-5188

⁸ 0000-0003-4618-854X

⁹ 0000-0002-8973-2771

¹⁰ 0000-0002-3640-8134

¹¹ 0000-0003-4421-2243

¹² 0000-0002-7254-0423

¹³ 0000-0001-6026-8912

¹⁴ 0000-0002-8775-650X

¹⁵ 0000-0002-1937-6580

¹⁶ 0000-0003-2643-3544

¹⁷ 0000-0003-0543-4521

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ABSTRACT

Grasslands are ubiquitous globally, and their conservation and restoration are critical to combat both the biodiversity and climate crises. There is increasing interest in implementing effective multifunctional grassland restoration to restore biodiversity concomitant with above- and belowground carbon sequestration, delivery of carbon credits and/or integration with land dedicated to solar panels. Other common multifunctional restoration considerations include improved forage value, erosion control, water management, pollinator services, and wildlife habitat provisioning. In addition, many grasslands are global biodiversity hotspots. Nonetheless, relative to their impact, and as compared to forests, the importance of preservation, conservation, and restoration of grasslands has been widely overlooked due to their subtle physiognomy and underappreciated contributions to human and planetary well-being. Ultimately, the global success of carbon sequestration will depend on more complete and effective grassland ecosystem restoration. In this review, supported by examples from across the Western world, we call for more strenuous and unified development of best practices for grassland restoration in three areas of concern: initial site conditions and site preparation; implementation of restoration measures and management; and social context and sustainability. For each area, we identify the primary challenges to grassland restoration and highlight case studies with proven results to derive successful and generalizable solutions.

1. Introduction

Grassland restoration and maintenance are critical to address global issues such as conservation of biodiversity and climate change mitigation and adaptation. While mostly, and often mistakenly, seen as agricultural artifacts with little conservation value (Veldman et al., 2015), natural and semi-natural grasslands are dominant ecosystems in many regions and provide critical ecosystem services (Fig. 1; Le Provost et al., 2021) as well as essential habitat for a diversity of organisms. At small scales, grasslands are among the world's most diverse terrestrial ecosystems and support the largest biodiversity at higher food web levels among higher latitude ecosystems (Wilson et al., 2012). Furthermore, grasslands account for ca. 30% of global land area and are estimated to hold 12% of the planet's terrestrial carbon (Ojima et al., 1993), mainly belowground, with longer residence times than many forests (Carvalho et al., 2014).

In the fight to curb climate change, grasslands are an important complement to forests and other high carbon-storage ecosystems (Yang et al., 2019). For example, grasslands contribute to cooling through solar radiation albedo effects (Temperton et al., 2019) and are notably resilient and resistant to changing disturbance regimes, even in the face of extreme events (Dass et al., 2018). For restoration interventions to deliver the maximum benefit for climate mitigation factors such as resilience and resistance to extreme weather events, carbon sequestration potential and permanence must be considered.

In past centuries, grasslands were frequently converted to intensively managed agricultural lands, traffic infrastructure, or housing. In areas where these conversions occurred, many of the remaining are of low quality with limited recoverability (Buisson et al., 2019). Grassland conservation and restoration are legally mandated in many countries and international standards have been developed (McDonald et al., 2019), yet these actions remain undervalued and underfunded (Bond and Parr, 2010; Török et al., 2021; Tölgyesi et al., 2022a). Recent biodiversity research demonstrates that many of the plant species that have decreased in abundance in the last century require grassy biomes (Jandt et al., 2022), underlining the contribution of grasslands to maintaining healthy food webs and ecosystems. In spite of these advances, the potential of grassy biomes is widely untapped as contemporary best practices are still poorly developed and need unification, particularly in light of the highly idiosyncratic and localized nature of ecosystems.

In this review, we provide an overview of best practices for grassland restoration, drawing on expertise from across the world, with a lean towards European, New World, and Australian perspectives. To frame this work, we focus on the most pressing, common, and persistent challenges to grassland restoration. We first provide an overview of initial site conditions and site preparation. We then focus on implementation challenges related to seed availability and target species success, soils, invasive species, and microbes. Finally, we review aspects of the social context of restoration including challenges of valuation and financing, landscape multifunctionality and mixed use, and utilizing grasslands in the battle to combat climate change. We illustrate best practices through case studies based on the expertise of the authors, with emphasis on empirical studies.

2. Initial site conditions and site preparation

2.1. Nitrogen deposition and residual soil fertility

Nitrogen (N) deposition is a significant impediment to restoration globally. While the degree of damage is contingent on the ecosystem type and the amount of N deposited, eutrophication is associated with decreases in plant diversity (Stevens et al., 2010), increases in invasive species (Clark et al., 2019), and decreases in the diversity and effectiveness of mycorrhizal fungi (Pardo et al., 2011).

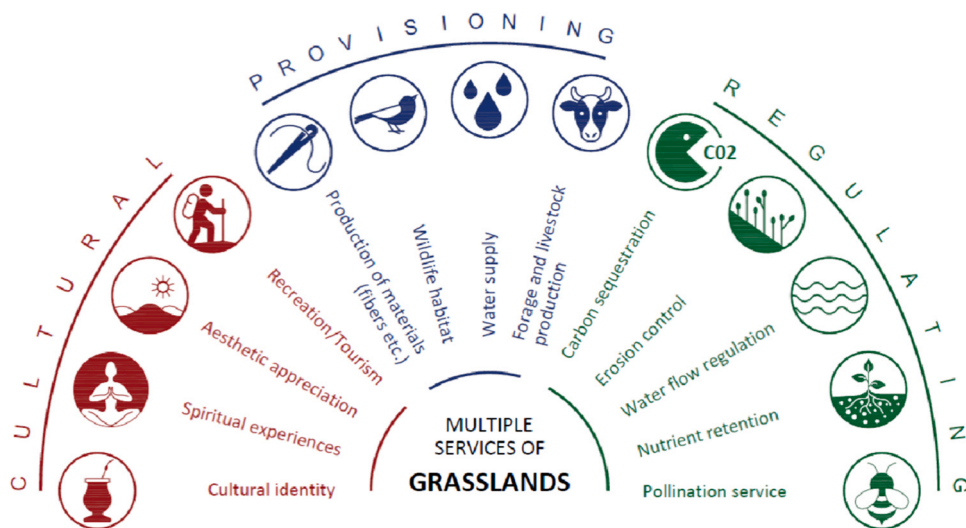


Fig. 1. Grasslands provide a broad range of critical services for human society, often simultaneously. This enhances the potential for multifunctionality in restoration.

The figure represents selected important services (adapted from list in Zhao et al., 2020).

As is the case for most pollutants, large-scale restoration of soil N dynamics requires a regional and/or international policy approach. While a substantial portion of nitrogen pollution is attributed to agricultural fertilization (Török et al., 2000) and nitrogen-fixing invasive plant species (Nsikani et al., 2018), recent conflicts following European Union and Dutch court-imposed controls on N-producing sectors of the Dutch economy (animal husbandry and types of construction) forecast probable continued clashes between environmental protection and profitable economic sectors (Stokstad, 2019). Nonetheless, clean air regulations have demonstrated effective reduction in N deposition in Europe and the United States (Koolen and Rothenburg, 2019; Clark et al., 2019; Stokstad, 2019; Table 1, Best Practice (BP) 1 A). Studies on cessation of mineral N fertilization designed to simulate reduction in atmospheric deposition demonstrate a concomitant decline in soil mineral N, although a lag effect is expected for vegetation recovery (Bowman et al., 2018). Thus, clean air regulations and agricultural reforms to reduce N inputs to ecosystems will be one of the most effective tools to reduce soil N in the long term.

Even more challenging for restoration is to reduce nutrients in eutrophic soils at the local scale. Topsoil removal, deep plowing, and soil inversion (burial of upper soil layers) can decrease residual soil fertility and the seed bank of weedy species (Kiehl et al., 2010; Jaunatre et al., 2014; Jones et al., 2010, Table 1, BPs 2A–C). These techniques promote target species establishment in nutrient-enriched temperate grasslands (Bakker et al., 2012; Table 1, BP 2D). Such techniques should, however, be considered with caution when (i) target species are still found in large proportion in the actual vegetation, seed, or bud banks (Buisson et al., 2019), and (ii) there is a risk of re-invasion of exotic species, particularly where invasive species removal is not followed by revegetation.

Soil nutrients can also be reduced by carbon amendment to immobilize N, or by vegetation removal through mowing, grazing, or fire (Török et al., 2000; Marrs et al., 2002; DiTomaso et al., 2006; Bakker et al., 2012; Table 1, BPs 2E–G). However, depending on microbial species metabolism and the rates of carbon and N cycling, application of carbon may have a short-lived N immobilization effect. Whether these measures are successful for N reduction depends on the relationship between yearly N output from a grassland (i. e., leaching, denitrification, and NH_3 or NO_x volatilization) and aerial N deposition (Bakker et al., 2012).

In contrast, soil nutrients may be depleted (Li et al., 2007) in tilled and/or highly eroded soils. Nitrogen depletion can occur because inorganic forms are mobile and readily lost from the soil. Options to restore productive grasslands on sites with low soil N include planting legumes or using inorganic fertilizers plus mulch with a relatively low C/N ratio (e.g., straw rather than wood chips) to immobilize N and thus conserve it in the soil (Weidlich et al., 2018; Török et al., 2000; Table 1, BPs 3A–B).

2.2. Seed bed and seed bank considerations

Regions with a higher proportion of extant natural vegetation generally have a more diverse species pool and harbor higher target species propagule resources than intensively used agricultural landscapes (Kirmer et al., 2008). The contribution of local species pools to re-colonization processes mostly depends on landscape connectivity and species dispersal abilities.

Soil seed and bud banks can be important propagule sources (Kiss et al., 2018) over short time scales (<5 years), particularly if the soil structure has not been altered (Buisson et al., 2019). The role of soil seed banks in vegetation recovery depends on factors such as site history, management type, degradation status, grassland type, altitude, and climate (Funk et al., 2019). Nevertheless, most target species form a short-lived seed bank (<5 years; de Souza Vieira and Overbeck, 2020) and the proportion of grassland target species in soil seed banks after degradation is often low. For example, the seed bank of most European grasslands is largely composed of species from early successional stages or of the most frequent species (Kiss et al., 2018). Across many ecosystems, but particularly in the New

Table 1
Best Practices (BP): Initial conditions and site preparation for grassland restoration.

BP	Problem	Solution	Example/References
Soil Nutrients: Nitrogen			
1	Elevated nutrients: Anthropogenic nitrogen deposition.	Policy approach to reduce anthropogenic N deposition.	A. Legislation to reduce air pollution emissions from ag. and internal combustion engines reduced N deposition (Koolen and Rothenberg, 2019; Clark et al., 2019; Stokstad, 2019). Europe, USA.
2	Elevated nutrients: Non-nitrogen.	Deturfing, deep plowing, soil inversion. Grow high-yield crops to deplete nutrients. Mulch (high C/N) to immobilize N. Fire to reduce N. Grazing, mowing, haying.	A. Establishment of species-rich grasslands most successful after tilling or topsoil removal in ex-arable fields (Kiehl et al., 2010). Germany. B. Topsoil removal restored soil conditions (reduced P and K) in Mediterranean grasslands (Jaunatre et al., 2014). France. C. pH and OM of soil surface layers became comparable to reference ecosystem after soil inversion in sand dunes (Jones et al., 2010). UK. D. Crops may need to be grown for several years before nutrients are depleted to former ambient levels (Bakker al, 2012). USA. E. Mulch immobilizes but does not remove soil mineral N in short term, often enabling establishment of target species (Török et al., 2000). Hungary. F. Fire typically has short-term impacts on depletion of soil N, if at all. Annual burning may be effective, but not appropriate for all grassland types (DiTomaso et al., 2006; Bakker et al., 2012). USA. G. Case studies of vegetation management typically show little depletion in soil nutrients (Marrs, 2002; Bakker et al., 2012). USA.
3	Depleted nitrogen in eroded or constructed soils.	N-fixing Legumes. Fertilize, Mulch (high C/N).	A. Legumes add organic N to soil, most efficient soil N restoration (Weidlich et al., 2018). Germany. B. Inorganic N fertilizers (nitrate, ammonium) are mobile in soil and readily leached. Mulching with low C/N mulch (hay, straw) adds N, reduces leaching through immobilization (Török et al., 2000). Hungary.
Seed bed and Seed bank Considerations			
4	Lack of "safe sites" for species establishment.	Seed bed preparation. Restore microtopographic features or stone cover. Establish nurse or engineer species first.	A. Tilling to break the crust in semi-arid grasslands tripled plant biomass of herbaceous forbs and annual grasses (Kinyua et al., 2010). Kenya. B. Topographic heterogeneity played an important role in improving the development of both temporal and spatial vegetation variability (Biederman and Whisenant, 2011). USA. C. Planting aloes improve the effectiveness of grass reseeding for arid rangeland restoration (King and Stanton, 2008). Kenya.
BP	Problem	Solution	Example/References
Fire, Grazing, Pyric-Herbivory			
5	Woody species encroachment in open and dry habitats.	Fire prevents additional woody encroachment or reverses prior woody encroachment.	A. High-intensity fires conducted during the growing season induced significant mortality among resprouting shrubs in the Great Plains, and high-intensity (but not as high as in the Great Plains) fires conducted in Kruger National Park during the dormant season did not induce significant mortality among resprouting shrubs (Scholtz et al., 2022). South Africa and USA. B. Higher than historic fire frequency maintained or decreased woody cover, approximately historic fire frequency maintained woody cover or facilitated woody encroachment, and low fire frequency facilitated woody encroachment. Fire effects on woody cover and encroachment interact with environmental factors including precipitation and soil type (Case and Staver, 2017). South Africa. C. Annual fire maintains low woody cover whereas 4 year and 20 year fire return intervals facilitate similar rates of shrub encroachment and cover (Ratajczak et al., 2014). USA. D. Woody cover in savannas declines with high fire frequency, especially with long-term fire regime (Pellegrini et al., 2021).
6	Non-native herbaceous species outcompetes native species and reduces biodiversity.	Fire applied under conditions when non-native invasive species are disproportionately vulnerable benefits native species.	A. Growing season fire reduces non-native invasive grass abundance while codominant native species respond neutrally or positively (Simmons et al., 2007). Fire during drought resulted in higher invasive C4 grass suppression (Havill et al., 2015) USA. B. Fire reduces the seed bank of the non-native invasive grass <i>Urochloa decumbens</i> in Cerrado grasslands, a complement to other control measures (Assis et al., 2021). Brazil. C. Fire can complement other methods in an integrated vegetation management program to reduce abundance of multiple noxious species with disparate life history strategies. Fire timing may be a particularly important variable (DiTomaso et al., 2006). USA.

(continued on next page)

Table 1 (continued)

BP	Problem	Solution	Example/References
7	Niche limitation in grass-dominated species-poor habitats.	Year-round grazing regime with large herbivores opens dense grass swards.	<p>A. Diversification of species-poor site, seasonal grazing by cattle, promote spread of target species from sown diversity hotspots (Kiss et al., 2021). Hungary.</p> <p>B. Dry calcareous site, year-round grazing, horses, supports dry grassland species, orchids, rare birds (Köhler et al., 2016). Germany.</p> <p>C. Dry sandy heathland, year-round grazing, horses/cattle, suppresses dominant grasses, supports target species (Henning et al., 2017). Germany.</p> <p>D. Tallgrass prairie site, year-round bison grazing suppresses dominant grasses, improves plant diversity and drought resilience (Ratajczak et al., 2022). USA.</p>
8	Woody species encroachment in open and dry habitats.	Intensive goat/cattle grazing in early season when palatability is highest reduces shrub cover.	<p>A. Rocky dry site, seasonal grazing, goats, supports highly endangered dry grassland species (Elias and Tischew, 2016). Germany.</p> <p>B. High stocking density applied over a short period (mob grazing) effective both in controlling the establishment and increasing the mortality of woody <i>Phillyrea angustifolia</i> individuals (Mesléard et al., 2017). France.</p>
9	Limited dispersal capacity.	Introduction of grazing animals as dispersal vectors.	<p>A. Silvopastoral savanna, managed herding, wild guanacos (Root-Bernstein et al., 2017). Central Chile.</p> <p>B. Floodplain and old-field/ancient grassland, integrated year-round grazing, horses/cattle (Mann and Tischew, 2010). Central Germany.</p>
10	Homogenous disturbance regime reduces patch contrast and therefore biodiversity.	Fire/herbivory interaction increases heterogeneity of vegetation structure, forage quality, and biodiversity.	<p>A. Pyric herbivory increases patch contrast and biodiversity on sites where fire drives grazing site selection (McGranahan et al., 2012). USA.</p> <p>B. Pyric herbivory increases vegetation structural and functional diversity and heterogeneity, with broader benefits for biodiversity considered likely (Donaldson et al., 2017). South Africa.</p>

World and Australia, seed banks contain undesirable weeds, highly competitive natives or non-natives species, that can hinder the establishment of desired species (see below). In many areas, failure to adequately control the germination and establishment of undesirable, non-target species is a common reason for restoration failure.

Seed bed preparation techniques can improve conditions for resident seedling re-establishment, including soil management methods to deplete soil nutrients as discussed above. Soil tillage is commonly used to open dense swards and reduce competition of unwanted species before introducing native target species in highly disturbed grasslands (Török et al., 2011). This process also breaks surface crusts in semiarid grasslands and can improve seed–soil contact (Kinyua et al., 2010; Table 1. BP 4 A).

Safe sites or regeneration gaps can be created to promote target species establishment and grassland diversity by introducing macroinvertebrates (e.g., earthworms; Forey et al., 2018); restoring microtopographic features, heterogeneity, and rock (Biederman and Whisenant, 2011); and re-introducing nurse species (King and Stanton, 2008; Table 1, BPs 4B–C). Naturally, appropriate action must be tailored to specific types of degradation. For example, an area being restored after use as a pine plantation may require burning to remove the residual layer of pine needles (Porto et al., 2023).

2.3. Fire, grazing, and pyric-herbivory

Target species absence in grassy biomes often occurs due to the loss of fire and cessation of natural and traditional grazing practices which result in woody plant encroachment or dominance of generalist herbaceous, often invasive, species (Stevens et al., 2017). Along with climate and CO₂ enrichment, and soil type, fire is one of the major predictors of the global grassland distribution (Staver et al., 2011), and the pattern of declining biodiversity with long-term fire suppression in fire prone ecosystems is globally robust. Restoring some approximation of historic fire and grazing regimes is often essential for grassland restoration and can mitigate further degradation. In some cases, restoring the fire and grazing may even facilitate recovery of biodiversity (Tölgyesi et al., 2022b).

Restoration of fire-prone ecosystems requires appropriate fire frequency and/or timing for species establishment and survival. Ongoing management of these ecosystems is simplified where dominant vegetation is flammable enough to maintain a stabilizing feedback loop between structure and process (Pausas and Bond, 2022). Reinstating a resilient feedback system may require post-fire seeding, translocating species with planting or with the transfer of belowground bud-bearing organs, or relying on vegetative propagation to establish target plant communities (Buisson et al., 2020; Valkó and Deák, 2021).

Grassland plant species generally respond either neutrally or positively to fire (Limb et al., 2016). Thus, using fire to alter plant community composition may be effective only where fire-sensitive undesirable species are the primary target for suppression. Fire can induce changes in relative abundance between functional classes, such as C3:C4, annual:perennial, grasses:forbs, or grasses:shrubs, but most compositional changes from fire among herbaceous plants and resprouting shrubs do not persist beyond the initial three years

post-fire (Limb et al., 2016). Fire can also be useful to remove excessive litter accumulation, reduce homogenizing species to make room for restoration, promote light availability at the soil surface, or to improve forage quality, however these responses are highly variable and can be short-lived (Valkó et al., 2014).

Fire can also be an effective tool to reduce soil nutrients and control invasive species, (e.g., DiTomaso et al., 2006; Table 2, BP 15D). Fire-adapted ecosystems where fire is used historically as an ecologically-based management tool are ripe for research on fire timing and frequency wherein studies take into consideration when invasive species are most vulnerable and desirable species favored (Sweet

Table 2

Best Practices (BP): Implementation of restoration measures and management of grasslands.

BP	Problem	Solution	Example/References
Plant Materials: Native Seed Supply, Markets, and Transfer			
11	Lack of suitable local donor sites for seed and plant material harvest.	Donor site register systems as suitable sites clearing house.	A. Web-based register of high nature value grasslands, information on best practice restoration/management (Hefter et al., 2010). Spenderflächenkataster, Germany. B. Web-based register of high nature value grasslands, information on best practice restoration/management (Müller, 2017). Regio Flora, Switzerland.
12	Genetic diversity of species and local adaptations.	Establishment of Seed Transfer Zones (STZs).	A. 22 STZs with 8 production areas from which propagation of populations from neighbouring seed source zones is permitted (Mainz and Wieden, 2019). Germany. B. 9 STZs with 1 production area from which propagation of populations of all STZs is permitted (Krautzer et al., 2020). Austria. C. Climate zones defined by min. winter temperature, aridity and ecoregions best explain variation in morphology, phenology, growth traits (Bower et al., 2014). Continental/Rocky Mountains, USA.
13	Documentation of wild seed quality, genetic integrity, suitable provenance.	Establishment of certification systems.	A. Certification system through which all stages of agricultural seed production are verified (collection method, origin of basic seed material, field propagation, yield, storage, sales quantity) (Krautzer et al., 2020; Mainz and Wieden, 2019). Germany.
14	Availability of wild provenances on the seed market.	Support for farmers in the procurement of basic seed material and technical guidance.	A. Great Basin Restoration Initiative: comprehensive government funding, guarantees seed purchase for seed-producing farmers (Oldfield et al., 2019). Great Basin, USA. B. Collaborative effort of government agencies and people from local communities to restore Cerrado savannas using seed-collection network, provides income for rural populations (Schmidt et al., 2019). Chapada de Veadeiros National Park, Brazil.
Target and unwanted species management			
15	Invasive species.	Topsoil removal. Grazing. Invasive plant removal. Fire.	A. Topsoil removal reduced the non-target seed bank in Mediterranean grasslands, southern France (Jaunatre et al., 2014). France. B. High stocking density over short period was effective both in controlling establishment and increasing mortality of <i>Phillyrea angustifolia</i> (Mesléard et al., 2017). France. C. The regeneration of grassland communities following the removal of conifers is possible if tree removal occurs early in the invasion process (Cuevas and Zalba, 2010). Argentina. D. Review on prescribed burning as a tool for invasive weed management (DiTomaso et al., 2006). USA.
16	Dominant ruderals/non-natives in soil seed bank after sowing target species.	Control through targeted biomass removal through cutting.	A. Mowing hay meadow 3, as compared to 1, significantly increased number of established target species, target species introduction improved with biomass removal (John et al., 2016). Wulfener, Germany.
Microbes			
17	Depleted soil fungal community.	Add AMF with inoculated nurse plants. Add native soil inocula.	A. Planting inoculated nurse plants helped aid recovery of mycorrhizal communities in restored prairies (Middleton and Bever, 2012; Koziol and Bever, 2017). USA. B. Native soil inoculant addition resulted in increased target species establishment and richness and diversity (Lubin et al., 2019; Koziol et al., 2020). USA.
18	Mismatch between plant communities and soil microbial communities.	Introduce native soil microbial communities.	A. Following topsoil removal, including soil microbes from existing desired communities increased similarity between reference and restored sites (Wubs et al., 2016 and 2019). The Netherlands.
19	Reduced native plant diversity/ evenness.	Introduce native soil microbial communities.	A. Introduction of native soil communities suppressed a dominant plant and increased plant species evenness (Crawford et al., 2019). USA.
20	Depleted soil microbes important for carbon sequestration/storage.	Apply substrates to facilitate microbes.	A. Cellulose additions during grassland restoration selected for microbes that benefit carbon storage (Docherty and Gutknecht, 2019). USA.
21	Microbial imbalance following plant invasion.	Apply treatments targeting specific soil microbes.	A. Application of fungicide to soils from invasive plants increased the performance of native plants (Perkins and Hatfield, 2016). USA.
22	Lack of AMF presence.	Plant facultative mycorrhizal species.	A. Planting facultative AMF species may promote fungal colonization, increasing fungi for more AMF dependent plant species (Koziol and Bever, 2019). USA.

et al., 2008; Havill et al., 2015). Used improperly, fire can promote invasion through a flush of nutrients or creation of an invasive plant-fire cycle, where increased biomass from invasive grasses fuels increasingly more frequent and intense fires (D'Antonio and Vitousek, 1992).

C3 woody species are increasing in many grassland ecosystems as a function of changes in disturbance regimes and atmospheric CO₂ enrichment. Restoration of a natural fire regime can prevent woody encroachment through high-energy or high-frequency fire and repeat burns with careful consideration of the length of the burn interval (Scholtz et al., 2022; Case and Staver, 2017; Ratajczak et al., 2014; Pellegrini et al., 2021; Table 1, BPs 5A-D). Fire can be used to target non-native invasive herbaceous species, particularly if temporal fire attributes can be manipulated to target invasives without harming co-occurring native species or if fire is used in conjunction with other weed management interventions (See also DiTomaso et al., 2006 and Table 2, BP 16D). Naturally, a common concern is that clonally-spreading invasive species may increase where fire is applied as a sole source of control (but see Table 1, BPs 6A-C).

Grazing also serves as an important restoration tool in some grasslands. The effect of grazing on plant diversity depends on the productivity of the ecosystem and whether grazing has been an important factor in the ecological history of the plant community (Price et al., 2022). Grazing intensity is also critical to consider; use of livestock is controversial in more arid ecosystems that have been subjected to long-term overgrazing where irreversible degradation is associated with soil loss or invasive species.

In other grassland ecosystems, reintroduction of natural or agricultural grazing regimes is used widely as a restoration tool and has resulted in an increase of desirable species (Köhler et al., 2023). Many studies demonstrate benefits of site-adapted, low-intensity livestock grazing and trampling to reduce litter layer and cover of dominant grasses, resulting in more open swards (Kiss et al., 2021; Köhler et al., 2016; Henning et al., 2017; Ratajczak et al., 2022; Table 1, BPs 7A-D). At appropriate levels, goat and cattle grazing can control woody species without damaging target species in temperate and Mediterranean grasslands (Elias and Tischew, 2016; Mesléard et al., 2017; Table 1, BPs 8A-B). In productive subtropical grasslands, periodic grazing deferment can help relieve effects of overgrazing in ecosystems where grazing at lower stocking rates is beneficial (Fedrigo et al., 2018). Finally, grazing animals can disperse seeds, and promote grassland regeneration (Root-Bernstein et al., 2017; Mann and Tischew, 2010; Table 1, BPs 9A-B).

Many grassland ecosystems evolved with multiple interacting disturbances that shape landscape heterogeneity and biodiversity. Combined disturbances from fire and herbivory (pyric-herbivory) alter patch-scale physiognomy, palatability, and flammability, which can then amplify the contrast between more and less disturbed sites and extend the gradient of successional conditions represented at larger scales. Naturally, the efficacy of grazing as a tool to increase diversity and to reduce issues of homogenization depend on the grazing species and the relative palatability of dominant plants that determines grazing intensity. In turn, grazing efficacy acts as a determinant of the efficacy of fire as a management tool (Fuhlendorf et al., 2009; McGranahan et al., 2012; Donaldson et al., 2017; Table 1, BP 10A-B). The evolutionary role of fire, herbivory, and their ecological interaction in maintaining biodiversity varies between grassland systems and deserves further intensive research consideration.

3. Implementation of restoration measures and management

3.1. Native seed supply, markets, and plant material transfer

Species reintroduction is necessary in many restoration projects. Given the dominance of relatively small herbaceous species at high densities within grasslands, species are often seeded rather than out planted as nursery stock. There are many ways to reintroduce species, including the direct transfer of seed-rich biomass harvested directly from donor sites by hand, mowing, threshing, brushing, or vacuuming, translocation of turf or topsoil, or direct sowing (Kiehl et al., 2010; Jaunatre et al., 2014; Broadhurst et al., 2017). These techniques can be complemented by planting propagated plugs in specific situations such as for particular species (Schmidt et al., 2019).

In Central Europe, where centuries of haymaking have synchronized grassland species' phenologies, it is possible to successfully transfer entire plant communities by means of seed-rich hay or threshed material (Kiehl et al., 2010). However, this approach can be problematic when there is low seed set or if there are invasive species within the donor site. For tropical and subtropical grasslands, the transfer of entire vegetation as turf or topsoil that is rich in seeds and buds has the potential to be more successful than hay transfer (Pilon et al., 2018) though these methods tend to omit deep-rooted species (Le Stradic et al., 2016). Issues associated with topsoil transfer include damage to the donor sites and resident species; the high cost and intense labor required to collect, move, and install turf; limitations on transport distances to maintain turf integrity; and the inevitable stress on plants during the transfer and planting process. Naturally, the success of turf transplantation will be higher where short transport distances are maintained; however, expectations must be managed as in some cases high mortality of transferred plants is expected (Török et al., 2011; Gerrits et al., 2023). So far, few studies are available on the topic for tropical, subtropical, or temperate regions, and generalizations should be made with caution.

Ultimately, the selection of the seeding approach depends on vegetation type, climate, available funds, machinery, donor sites, and markets. For example, for on-site seed harvesting of entire plant stands, donor sites may be limited or very small, contain unwanted species, or have variable seed production (Broadhurst et al., 2017). Donor site registers can track suitable grasslands for on-site harvesting, with coordination to avoid overharvesting (Hefter et al., 2010; Müller, 2017; Table 2, BPs 11A-B). In the tropics, the use of direct seed harvesting is still rather rare, but successful examples of community-based seed collection networks exist, with the additional benefit of providing economic profits for local populations (Schmidt et al., 2019).

Large quantities of native seed are now produced by native seed companies as small-scale agriculture (Tischew et al., 2011; Pedrini et al., 2020), primarily in temperate regions. Where practical and economically feasible, genetic diversity, ploidy levels, and adaptive

traits should be assessed and maintained within and among source populations of every target species intended for propagation and seeding (Leger et al., 2015; Durka et al., 2017), employing state-of-the-art genetic tests and common garden experiments (Nevill et al., 2018).

In countries with relatively strong native seed markets, Seed Transfer Zones (STZs) define areas with similar landscape and climate characteristics that are often assumed and sometimes proven (e.g., Bucharova et al., 2019 for Germany) as determinants of genetic and phenotypic differences among populations. Ideally, STZs are large enough to provide sufficient markets for the seed industry but small enough to provide locally adapted seed for restoration (Nevill et al., 2016). Ideally, STZs are also species-specific, reflecting genetic patterns within species (Listl et al., 2017). Native seed markets with emerging STZs are now thriving in the USA, Europe, and Australia, many combined with certification systems (Bower et al., 2014; Mainz and Wieden, 2019; Krautzer et al., 2020; Pedrini et al., 2020; Table 2, BPs 12A–C and BP 13 A). However, as climatic changes become increasingly manifest, STZs and legal framings will need to be adjusted accordingly, with greater attention paid to incorporating seed from zones appropriate to current and anticipated future climatic conditions. Indeed, flexibility in seed transfer rules will require consistent reconsideration in light of predicted clinal variation patterns and/or seed ecotype shortages.

Cultivars of native species are available in some regions of the world. Due to agricultural selection, cultivars are often more productive and competitive than natural ecotypes. They can quickly establish and may behave as local, wild-collected populations under disturbance in certain cases (Poelman et al., 2019), but may also prevent establishment of diverse native plant communities (Conrad and Tischew, 2011). Moreover, nearly all cultivars are phenotypically constrained (Leger and Baughman, 2015) with low levels of genetic diversity. They may therefore be less responsive to selection imposed by climate change or new disturbance regimes (Espeland et al., 2017). While there are instances where reliable cultivars are used, a major task for restoration practitioners of grasslands is to replace the use of narrowly selected cultivars with locally-adapted, native seed of high genetic diversity (Oldfield et al., 2019; Schmidt et al., 2019; Table 2, BPs 14A–B). This might be facilitated by tax concessions to invest in plant material centers responsible for research and development of native propagule collection, selection, propagation, processing, and handling procedures (Nevill et al., 2018). International standards have been developed that define principles for the application of native seeds in ecological restorations forming a basis for developing quality measures and guidance statements (Pedrini and Dixon, 2020). Finally, we note again that low commercial availability of native seed can strongly limit grassland restoration success in regions where these markets have not yet developed.

3.2. Target and unwanted species management

Highly competitive non-target species are often major impediments to successful establishment and/or subsequent survival of introduced target species (Pywell et al., 2002). These undesirable species can be native or invasive non-native, agricultural or not. In many cases, mixed perspectives about their utility exist among stakeholders (e.g., non-native pasture grasses).

Site-specific management must include on-going suppression of unwanted species, especially where seedbanks are large and persistent (Table 2, BP 15 A). Most successful control treatments reflect the biology, phenology, and ecology of the unwanted species. Treatments may include mowing, grazing, fire, or selective herbicides, now more often used in combination (Elias and Tischew, 2016; John et al., 2016; Buisson et al., 2019; Table 2, BP 16 A). For instance, mechanical measures or grazing with high stocking density are often used as initial restoration measures in abandoned semi-natural grasslands in Europe (Mesléard et al., 2017; Table 2, BP 15B) or to remove invasive trees (e.g., Cuevas and Zalba, 2010; Table 2, BP 15 C).

Restoration success is often foiled by invasive species re-establishment following management efforts and invasive species suppression is more effective when combined with restoration as part of a whole-system integrated weed-management approach (Bakker and Wilson, 2004; Vranjic et al., 2012); however, surprisingly, many invasive species removal campaigns fail to include active revegetation as part of a management plan (Kettenring and Adams, 2011). Restoration designed to sustain control of invasive species following removal must include species richness, diversity, and composition, as well as a strategy for temporal re-introduction. Diversity is an effective post-removal restoration tool as more diverse plant communities are less susceptible to invasive species re-establishment (e.g., Lyons and Schwartz, 2001; Dukes, 2002). At the same time, these goals must also be balanced with re-introduction of species and functional groups that readily establish, are competitive and persistent, and even suppressive (Fargione et al., 2003; Longo et al., 2013). Finally, many *priority effects* studies demonstrate the potential of strategic, coordinated introduction of native species to maximize overyielding and control invasive species ahead of re-invasion (Vaughn and Young, 2015; Delory et al., 2019) by providing native species a head-start during assembly. Early arriving species can significantly influence further assembly as well as ecosystem functions and services (Funk et al., 2008; Weidlich et al., 2021). Nonetheless, the persistence over time and utility of *priority effects* still needs further research (Hess et al., 2022; Byun et al., 2023).

3.3. Microbes

The extent to which microbes modulate traditionally plant-focused restoration outcomes is attracting increasing attention, as indicators of system-state drivers of plant community composition and structure, mediators of ecosystem processes, and facilitators (Harris, 2009). Grasslands are often dependent on mutualistic associations with arbuscular mycorrhizal fungi (AMF) and other symbionts which increase grassland productivity and diversity (Afkhami and Strauss, 2016) and help plants withstand environmental stress (Singh et al., 2011). While historically understudied, dark septate endophyte fungi are emerging as potentially critical players in mediation of abiotic plant stressors such as drought and metal tolerance (Santos et al., 2021). Microbes, in their many capacities as pathogens, mutualists, saprophytes, etc. can also influence biotic interactions (e.g., competition) that increase plant diversity by

promoting plant species coexistence. Indeed, pathogens have been shown to prevent species dominance through negative plant–soil feedbacks (Fitzsimons and Miller, 2010; Bever et al., 2015).

Finally, as one of the largest biomass pools in grassland soils, microbes have a large capacity for carbon storage (Bai and Cotrufo, 2022). Disturbed, degraded, and invaded grasslands often have compromised microbial community structure and function, producing negative soil legacies (Baer et al., 2002) that may impede restoration through altered plant–plant and plant–microbe interactions.

To combat undesired changes in microbial community structure and function, it may be necessary to inoculate with beneficial microbes. The addition of AMF to grasslands often enhances establishment of target species and increases plant productivity, especially in heavily disturbed soils (Neuenkamp et al., 2019). Native AMF inoculants tend to outperform commercial inoculants (Maltz and Treseder, 2015), and help minimize concerns of introducing nonnative AMF that may be present in many commercial inoculants (Koziol et al., 2018). Inoculated nurse plants can be a beneficial alternative to expensive, large-scale AMF applications. Likewise, inoculations with native soil, which contains many different microbes, can have large positive impacts on restoration outcomes (Middleton and Bever, 2012; Koziol and Bever, 2017; Lubin et al., 2019; Koziol et al., 2020; Wubs et al., 2016 and 2019; Crawford et al., 2019; Table 2. BPs 17A–B, 18 A and 19 A). Another method for changing microbial community composition is through the addition of soil substrates, such as cellulose additions (Docherty and Gutknecht, 2019; Table 2, BP 20 A).

There may also be utility in applying treatments (e.g., fungicides) to control certain groups of microbes (Perkins and Hatfield, 2016; Table 2, BP 21 A). The presence of grass fungal symbionts can determine the species composition and structure of a grassland by controlling whether grasslands remain grassy or transition to a woody habitat (Rudgers et al., 2010). The driver of this trend is likely that fungal endophytes confer a competitive anti-herbivore advantage to their grass host as native grass species hosting endophytes experience lower herbivore damage and negatively affect the performance of invertebrate herbivorous larvae (Crawford et al., 2010). When these strategies are not available, a simple approach is to plant facultative mycorrhizal species, such as early successional grasses, which promote natural colonization of AMF that can benefit future establishment of mycorrhizal-responsive plant species (Koziol and Bever, 2019; Table 2, BP 22 A).

Despite the promise of using microbes to aid grassland restorations, challenges remain. We know little about the impact of large-scale restoration interventions on the soil microbiome (e.g., Barto et al., 2012). Tracking changes in microbial structure and function following these treatments may lead to insights into how microbes benefit or impede grassland restoration.

Methods that manipulate microbial communities do not always produce the desired outcomes (Perkins and Bennett, 2018; Leonard and Lyons, 2015). One possible reason is that plant–microbe interactions can be highly context-dependent and dynamic over time. Unraveling this complexity will help improve the utility of microbes for restoration, including how microbes facilitate or constrain restorations in changing climates (Classen et al., 2015). Finally, little attention has been paid to the role of above-ground microbes, such as endophytes or pathogens despite their strong effects on herbivory, community composition, and ecosystem functioning (but see Rudgers et al., 2010).

4. Social context and sustainability

4.1. Valuation, funding, and financing

The cost of grassland restoration varies greatly and depends on site conditions, ecological context, and techniques employed. A simple change in management strategy can be inexpensive whereas interventions such as topsoil transfer and removal of pollutants are expensive. While costs are relatively easy to quantify (though limited data are published; Török et al., 2011; Knight and Overbeck, 2021), the benefits of restoration are much more difficult to quantify. For example, it is easier to assess economic returns (e.g., improved animal husbandry, pollination service) than improved environmental conditions that result in increased biodiversity (Orford et al., 2016; Bullock et al., 2007; Table 3, BPs 23A–B). Overall, however, restoration returns are especially high for grasslands. In an analysis of more than 200 studies, the cost-benefit ratio of ecological restoration was higher for grasslands than for forests, wetlands, or aquatic/marine systems, reaching 1:35 (De Groot et al., 2013).

Current funding schemes are insufficient to tackle the broad-scale restoration necessary to address biodiversity loss and climate mitigation (Richardson, 2016). When restoration is required after degradation or damage, it is important to identify responsible parties where possible (e.g., Holl and Howarth, 2000). Ideally, these parties would voluntarily financially support the cost of restoring damaged sites, though the externalities (hidden costs) of resource extraction (e.g., fracking, intensive agriculture) have often been passed to the public sector. As with restoration in general, successful outcomes in grassland restoration often require more extensive and on-going input from the private sector, either voluntarily or via policy initiatives (Löfquist and Ghazoul, 2019). In general, C sequestration is rapidly becoming marketable, with C offset programs developing in agricultural (cropping and grassland) as well as peatland and forest settings (e.g., the Southern Plains Carbon Offset Program or the Grassland Project Protocol in the USA, or the Gold Standard or Verra Offset Programs globally). Caution is needed here to ensure that offsetting does sequester additional C (here restoration is set to play a key role) rather than compensate for emissions that are offset by conserving a habitat (e.g., forest) and stating that the forest/grassland was in danger of being logged.

Though designed to support reforestation in developing countries, the REDD+ framework provides a potentially powerful model for future development of grassland restoration as well (Alexander et al., 2011), though it also involves risks and pitfalls that need to be addressed for effective implementation (Loft et al., 2017). Its focus on carbon sequestration through tree planting and forest restoration brings the risk that ecosystems such as grasslands are not sufficiently considered, even though they can provide equally important benefits, both in terms of carbon sequestration, climate cooling, and resilience to extreme weather (see Temperton et al., 2019). As mentioned above, grassland restoration contributes significantly and at a reasonable cost to long-term soil carbon storage (Ojima et al.,

Table 3
Best Practices (BP): Social context and sustainability of grassland restoration.

BP	Problem	Solution	Example/References
Valuation, Funding, Financing			
23	Little support for grassland restoration as restoration benefits are not recognized.	Evaluate and show benefits of restoration, including monetary benefits.	A. Modest increase in grassland diversity increases functional diversity of pollinator communities which can increase productivity in commercially important crops (Orford et al., 2016). UK. B. Restoration of biodiverse grasslands increases hay yields as compared to species-poor communities (Bullock et al., 2007). UK.
Carbon Sequestration			
24	Depleted soil carbon coupled with elevated atmospheric CO ₂ .	Increase grassland soil organic matter to sequester carbon by revegetation, controlled grazing, natural fire regimes, mulching, irrigation, fertilization.	A. Case studies, modeling and biogeochemical studies from grasslands around the world suggest that the most cost-effective way to ensure increased carbon sequestration of degraded grasslands over large scales is to revegetate and manage grazing intensity for increased productivity of adapted species (Petri et al., 2010).
Landscape Multifunctionality and/or Mixed Use			
25	Uniform treatments across restoration sites lead to homogenization of environmental conditions.	Underpin multifunctionality by more theoretical research.	A. Different plant functional groups (legumes, grasses, forbs) at different times significantly affected both below- and aboveground productivity in grasslands, with impacts on ecosystem services (Weidlich et al., 2018). Germany.
26	Distinct species require distinct restoration actions.	Development of management strategies tailored to requirements of target species, even if contrasting within one restoration project.	A. Rare plant and a rare butterfly species required contrasting restoration management approaches, but recovery of populations of both could be achieved (Dunwiddie et al., 2016). USA.
27	Uniform treatments across restoration sites lead to homogenization of environmental conditions.	Creating heterogeneity in restoration to achieve multifunctionality.	A. In many grassland systems, heterogeneity of vegetation increases habitat suitability for different groups of organisms. Variation in intensity or frequency of management actions, such as fire, can lead to such heterogeneity (Hill et al., 2017). USA.
28	Conflicting restoration goals.	Develop ways to reconcile biodiversity conservation and productions.	A. Low-input and high-diversity grasslands contributed higher biofuel and greater greenhouse gas reduction than biofuel monocultures, while also preserving biodiversity (Tilman et al., 2006). USA.

1993; Yang et al., 2019), a fact often overlooked in the global restoration debate (but see Temperton et al., 2019). Even more problematic is that misguided afforestation of grasslands causes considerable biodiversity decline and loss of valuable ecosystem services (e.g., groundwater provisioning or pollination) with immense societal costs (e.g., Lu et al., 2018; Veldman et al., 2019).

4.2. Carbon storage and sequestration

For depleted soils, carbon storage (current stocks) but particularly sequestration (additional C removed from the atmosphere) have been recognized as one of the major potential benefits and goals of restoration to improve soil nutrient storage conditions and offset rising anthropogenic C emissions (Kämpf et al., 2016). The net amount of C sequestered is a balance between inputs from primary producers (via roots) and litter or anthropogenic sources (e.g., mulch) and losses via decomposition, respiration, grazing, fire, harvesting, and erosion. A key study based on a long-term experiment in Sweden found that C input to soils from roots is 2.5 times larger than that from organic matter input from above ground litter (Kätterer et al., 2011). This underlines the need for future restoration aimed at enhancing C sequestration to focus more on belowground processes. Restoring a wide mix of plant species with diverse traits is a promising proposition for increasing C sequestration, as biodiversity experiments have found that restoring grassland plant diversity accelerates long-term C sequestration, with 200% greater C storage rates compared to free succession (non-sown plots), and 70% greater rates compared to monocultures (Yang et al., 2019). Restoration management to promote C sequestration includes revegetation with deep-rooted forbs and grasses (with underground storage organs where appropriate), low-intensity grazing regimes that increase carbon inputs from above-ground production and root development, and, where appropriate, reinstatement of fire regimes to promote nutrient cycling and grassland productivity (see Bai and Cotrufo, 2022). Increasing biodiversity can produce higher levels of primary production on par with nutrient addition, which could be an interesting means to sequester more C by restoring plant diversity in extensively managed mesic grasslands (see also Petri et al., 2010; Table 3, BP 24 and BPs 23A-B).

Management of grasslands can significantly alter C sequestration (Bai and Cotrufo, 2022). Variability in management effects is large, however, pointing to the need for additional research to improve our understanding of how management interacts with abiotic conditions. Altering the order of arrival of plant functional groups has been shown to influence root distribution at depth in loamy soils, whilst not altering plant diversity much (Weidlich et al., 2018). Roots in deeper soil layers are more long-lived, so adjusting the arrival order of species could also increase long-term carbon storage in deeper soil layers, whilst maintaining plant diversity. While potentially subtle in terms of diversity outcomes, priority effects can thus strongly affect ecosystem functions and services (Weidlich et al., 2018; Table 3, BP 25 A).

We recommend two priority areas for grassland restoration to maximize C storage. First, the highly organic soils of grasslands closely associated with peatlands (common at e.g., higher latitudes) can contain five times as much C as those of lower latitude less organic soils. As such, these grasslands have higher potential for C storage. Second, a clear positive linear correlation between diversity and net primary productivity suggests that restoration focused on species-rich grasslands is more likely to maintain and enhance belowground C compared to restoration of lower diversity grassland sites as well as tree plantings where increased frequency and severity of fires and drought can destroy gains through woody biomass and aboveground C increases (Dass et al., 2019). Thus, there seems to be much scope for increasing belowground C sequestration while also promoting grassland plant diversity.

4.3. Landscape multifunctionality and/or mixed use

While grasslands can provide a broad range of benefits, functions, and services (Fig. 1; see e.g., Zhao et al., 2020), tradeoffs exist among different ecosystem services (Le Clec'h et al., 2019; Teixeira et al., 2023) and restoration practitioners are required to balance multiple ecological and socioeconomic objectives (Cord et al., 2017). A multi-use approach inevitably promotes higher diversity and synergistic interactions between species and across spatial scales (Hautier et al., 2017; Conradi et al., 2017). At the landscape scale, patches can be restored and managed in different ways to achieve desired outcomes. Indeed, this approach has been tested in forest restoration for decades (Lamb et al., 2005) and is also used in grassland management for rare plants and animals with different habitat, refugia, or disturbance needs (e.g., fire) (Dunwiddie et al., 2016; Hill et al., 2017; Table 3, BPs 26 A and 27 A).

In many regions, species-rich grasslands can sustain long-term yields and be as productive in terms of nitrogen cycling – though without fertilization – as annual crops (Glover et al., 2010) or fertilized grasslands (Weigelt et al., 2009). Restoring extensively managed grasslands provides the best method to stimulate biodiversity and recreate essential habitat and resource availability for pollinators (Öckinger and Smith, 2006). Nonetheless, perennial, long-term managed species-rich grasslands are prime benchmarks for agricultural sustainability (Glover et al., 2010). These grasslands also have high potential for biofuel production (Tilman et al., 2006; Table 3. BP 28 A).

Indeed, climate change adaptation as well as mitigation need to be considered in multifunctional land use, when planning restoration interventions at landscape scale (Temperton et al., 2019). Many grasslands are fire-adapted and drought tolerant, and ongoing changes in disturbance regimes (fire frequency) suggest that grasslands deserve more attention as reliable, long-term carbon sinks compared to forests (Dass et al., 2018; Naidu et al., 2022). A system that accounts for resilience as well as carbon or albedo effect credits could be a feasible option for addressing multiple desired outcomes, since storing more C does not always lead to climate cooling and the ability to deal with increased disturbance is going to be a key trait of the habitats we need as climate change unfolds. Consciously creating multifunctional landscapes will contribute to current diversity and sustainability goals if we embrace the creation of knowledge through inter- and transdisciplinary teams of stakeholders, while aiming for best-practice governance during implementation (Weidlich et al., 2018; Table 3. BP 25 A).

5. Conclusions: challenges and opportunities

- **CHALLENGE:** Large knowledge gaps still exist across many of the topics addressed in this paper, especially for tropical and sub-tropical regions (e.g., the role of microbes or the potential role of management in carbon sequestration). **OPPORTUNITY:** Restoration ecologists will continue to be in high demand with international focus on carbon sequestration and the need for international integrated collaboration efforts.
- **CHALLENGE:** Designing restoration management of grasslands to address certain target species (e.g., endangered plants or animals including the pervasive problem of limiting nutrient input to stem biodiversity loss). **OPPORTUNITY:** Increase spatio-temporal heterogeneity of grasslands to enhance biodiversity at the site or landscape level. Coordinated international efforts will be designed to make policy changes to address nutrient input from agriculture and transport.
- **CHALLENGE:** Knowledge gaps regarding restoration of specific grassland functions and services (e.g., the potential to sequester belowground C with long turnover times, increases in albedo and hence climate cooling, and improved plant-soil interactions to facilitate water filtration). **OPPORTUNITY:** Interdisciplinary collaborations with experts in plant species functional ecology and plant-soil processes. In addition, there are growing opportunities for concerted assessments across large research consortia regarding biodiversity and belowground C sequestration and turnover. Likewise, there are consistently growing opportunities and interests in inclusion of C sequestration and storage in grassland restoration projects, including lucrative options for C-credit financing.
- **CHALLENGE:** A lack of knowledge on successful strategies and techniques continues to impede restoration, particularly understanding how to improve their spatial and temporal replicability. **OPPORTUNITY:** Integration of monitoring of sufficient duration into restoration practice will be fundamental to move forward, especially in regions where restoration proceeds with science and practice merged at the onset.
- **CHALLENGE:** Policy approaches addressing afforestation are important; however, these policies are often implemented with blind spots and negative side effects on grasslands. **OPPORTUNITY:** There is a great need for communication with the public and with policy makers regarding the benefits of grasslands, the value of grassland conservation and/or restoration and the risk of destroying or afforesting them, and the need to differentiate between extensively managed high-nature-value grasslands, intensive pastures, and fallow lands.

CRediT authorship contribution statement

KGL, VMT conceived of and organized the original symposium entitled “Limitations to grassland restoration: a cross continental comparison” at the 2013 SER World Conference in Madison, USA; KGL, VMT, WI, JMH, KK, AK, JK, GEO, and ST were consistently part of early and continued discussions; PT was instrumental in moving the paper toward publication; all authors contributed to sections of the manuscript related to their areas of expertise.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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