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Rewilding grasslands and rangelands

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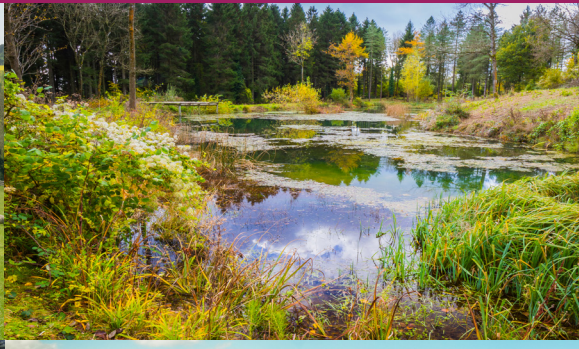

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1 Introduction

Both grasslands and rangelands support grasses and other herbaceous plants (Allen et al., 2011). Together, these lands cover about 40% of the Earth's area (Buisson et al., 2022; Bardgett et al., 2021). Grasslands include prairies, grassy shrublands, and savannas (Bardgett et al., 2021). They are typically found on relatively fertile soils in reasonably humid climates and therefore can produce more forage and support a higher livestock-carrying capacity than rangelands.

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Grasslands may be described as 'natural,' occupied primarily by native species, or 'tame' or 'improved,' primarily occupied by introduced species. Grasslands may be managed intensively for agricultural production, which arrests successional processes (Allen et al., 2011).

Rangelands usually support indigenous vegetation that is managed as a natural ecosystem to support grazing livestock and wildlife (Holechek et al., 2010; Stoddart et al., 1975). Grasslands may be described as tame, primarily occupied by introduced species, or natural, occupied primarily by native species. While grasslands have the potential to be managed intensively with irrigation and fertilization, rangelands are necessarily managed extensively as minimal-input natural ecosystems (Holechek et al., 2010). Hence, management intensity is a distinction between grasslands and rangelands. Relative to grasslands, rangelands typically have greater abiotic limitations than grasslands, e.g. low or erratic precipitation, rough or steep topography, poor or excessive drainage, extremely high or low temperatures, or saline or sandy soils (Briske, 2017; Holechek et al., 2010; Stoddart et al., 1975). Thus, rangelands display a high degree of spatial or temporal variability (Herrick and Whitford, 1995), while grasslands tend to be more uniform. While grasslands may be cultivated, most rangelands cannot sustain cultivation (Holechek et al., 2010). Rangelands may display a significant woody-plant component, shrubs and/or trees, while grasslands support primarily grasses and other herbaceous plants, with perhaps a small frequency of woody plants (Allen et al., 2011).

Since the agricultural revolution of the Neolithic Period, humans have expanded grasslands to support livestock agriculture (Slodowicz et al., 2023) through livestock management, controlled burns, and clearing and thinning timber (Staude et al., 2023). These ecosystems provide ecosystem services, including biodiversity, forage, water, erosion control, pollinator and wildlife habitat, carbon (C) sequestration, and meat, milk, and fiber products (Buisson et al., 2022). Relative to forests, grasslands and rangelands are especially valuable for theoretical and applied ecological studies due to small plant size, ease of manipulation, and short time scales (Wilsey, 2021).

Natural and seminatural grasslands, as well as rangelands, are disturbance-driven ecosystems (Török et al., 2021). Disturbance events curtail the growth of dominant species, thus facilitating light penetration that supports the growth of subordinate species (Sturchio et al., 2022). When these lands are abandoned, however, reversion to woody vegetation may ensue following cessation of grazing (Knapp and Seastedt, 1986), at least partly due to the expansion of scrub, i.e. shrub-dominated vegetation (Bardgett et al., 2021). The impacts of fire may be either favorable (e.g. suppression of woody vegetation, stimulation of growth and diversity) or unfavorable (e.g. altered fire regimes, providing a niche opening for invasive species, displacement by cropland, loss of soil C)

(Bardgett et al., 2021; Wagle and Gowda, 2018; Chambers et al., 2014; Rowe, 2010; Copeland et al., 2002).

Grasslands and rangelands are largely underappreciated and misunderstood by both the public and much of the scientific community, leading to limited recognition and priority in policy-making despite ongoing degradation (Staude et al., 2023; Bardgett et al., 2021). Tropical grasslands are ignored to an even greater extent than temperate grasslands (Buisson et al., 2021b). Misconceptions about grasslands include the presumptions that they are necessarily of recent origin, they may be reassembled quickly and easily, and they are merely early successional stages of forests (Buisson et al., 2022). In fact, ancient (i.e. 'old-growth') grasslands require centuries to assemble their high species and functional diversity. Their subterranean structure drives recovery from aboveground disturbances such as grazing and fire. However, once these lands are damaged below ground (Buisson et al., 2022), ecological thresholds may be crossed that are impractical to reverse, especially on a broad scale (Hobbs et al., 2009; Briske et al., 2006), though notable exceptions do exist (Gibson-Roy and McDonald, 2014).

The seven objectives for this chapter are as follows:

- Spotlight threats to the integrity of grasslands and rangelands worldwide;
- Delineate ecological principles that drive grasslands and rangeland functioning and upon which their rewilding is based;
- Highlight the diversity of best practices used to rewild grasslands and rangelands along with their supporting science. Such practices include those to restore biological soil crusts, apply prescribed fire, increase stand establishment and persistence, overcome soil limitations, rectify nutrient pollution, and sequester soil C;
- Describe concepts and emerging technologies with great potential to rewild grasslands and rangelands;
- Showcase the role of native seed industries in the USA, Europe, and Australia in supporting the rewilding of grasslands and rangelands;
- Provide numerous science-based examples from around the world supporting the above objectives; and
- Offer a case study of the restoration of sagebrush-steppe rangelands in the state of Utah (Intermountain West, USA), including the scientific documentation of the successes and limitations of these efforts.

2 Past and current threats to grasslands and rangelands

Grasslands and rangelands are vulnerable to conversion to cropland (tillage), mining, overgrazing by livestock, invasive species, and afforestation (Buisson et al., 2022; Bardgett et al., 2021). Because unprotected grasslands and rangelands are often considered expendable, land-use change is a major

cause of their loss. In Rio Grande do Sul, Brazil, grasslands are being lost due to afforestation and conversion to cropland for maize and soybean cultivation (Staude et al., 2023) as the agricultural frontier is extended into undeveloped areas (Rey Benayas and Bullock, 2012). Likewise, large expanses of temperate grasslands have been lost in southeastern Australia due to diversion to agriculture, leaving only small and largely disconnected relict areas (Williams and Morgan, 2015).

Iowa, USA, was opened for agricultural development in 1833, but once settlers arrived in a particular area, tallgrass prairie disappeared within 10–20 years (Smith, 1990). John Deere's moldboard plow was designed in 1837, and by 1857, his Iowa factory was manufacturing 10 000 plows annually. Large numbers of former Civil War soldiers moved to the state to farm after 1865, and beginning in 1888, large-scale tile drainage opened lands to cultivation that were previously inaccessible. By the end of the century, 97% of the vast Iowa tallgrass prairie was no more.

Semi-natural grasslands were once widespread throughout Europe (Ridding et al., 2015; Hedberg and Kotowski, 2010). They were primarily occupied by native flora without fertilizer or pesticide application. However, semi-natural grasslands were utilized for grazing and haying. An example is the Salisbury Plain of southern England, home of Stonehenge, once an extensive area of species-rich semi-natural grasslands (Wedin, 1992). These 'chalk grasslands' occurred on thin infertile soils over calcareous bedrock. They were maintained by sheep, whose diet includes woody species, for centuries. However, in the 1870s, sheep grazing declined for economic reasons, which led to an invasion of tree and shrub species, though grazing by wild rabbits continued.

During the Great War, much of the chalk grasslands was diverted into cropland, a process that continued through World War II (Wedin, 1992). Subsequently, these vast areas were largely compromised by the advent of technology that increased agricultural productivity but led to the demise of small-scale farming. These novel inputs included mineral fertilizers, herbicides, pesticides, and drainage infrastructure (Lawson et al., 2004). These, along with widespread seedings of perennial ryegrass (*Lolium perenne*), increased forage production but, at the same time, sharply curtailed species diversity due to N fertilizer-induced eutrophication (Wedin, 1992). In the Salisbury Plain, species composition and critical functional traits may take up to 100 years to reappear after the abandonment of arable agriculture, as many of the ancient grassland species are limited by low seed dispersal (Redhead et al., 2014).

Agricultural lands, particularly in Europe but more recently in developing countries, are being abandoned due to migration to urban areas (Rey Benayas and Bullock, 2012). In other cases, land is abandoned due to agricultural policy addressing commodity surpluses, water-quality problems, and biodiversity

losses (Wedin, 1992). Regardless, abandonment is followed by forest and scrub encroachment (Navarro and Pereira, 2015) and often an expansion of exotic plant populations, along with a concomitant decline in native plant biodiversity (Wedin, 1992). While fires and herbivores may function to check woody-plant invasions of grasslands (Staude et al., 2023), fire suppression and afforestation policies may lead to grassland and rangeland degradation (Bardgett et al., 2021).

Certain agricultural practices may also trigger degradation. Improperly timed or excessive livestock grazing primarily impacts herbaceous understory plants, but woody-plant expansion may be difficult to reverse once the grassy understory is insufficient to support grazing or fuel a fire (Buisson et al., 2022). Conversion to cropland, beginning with tillage, leads to a rapid loss of grassland biodiversity, a negative impact on wildlife, and dramatic losses in sequestered soil C (Bardgett et al., 2021). Intensification of agriculture typically reduces native-plant diversity (Bardgett et al., 2021, McIntyre and Lavorel, 1994; Wedin, 1992), though it often increases the diversity of exotic species (McIntyre and Lavorel, 1994).

Climate change has led to more frequent and intense fires and droughts (Bardgett et al., 2021). As 67% of the world's grasslands are found in semiarid, arid, or cold climates, climate change is expected to have a negative impact on their ability to sequester soil organic C (Bai and Cotrufo, 2022). In addition, desertification is expected to expand the ranges of drylands (Buisson et al., 2021a). Because of climate's overarching influence, it may be necessary to modify restoration plans to accommodate shifting restoration trajectories in response to labile future climates (Buisson et al., 2022).

3 Application of ecological models to restoration management

The traditional model of rangeland management was based on Clementsian succession, where vegetation moves along a trajectory toward a single climax state (Westoby et al., 1989). In this model, stocking rate and drought are presumed to work in a similar fashion, but in opposite directions. Therefore, rangeland management sought to balance the two opposing forces to maintain an equilibrium, such that animal weight gains could be achieved without damaging the rangeland. This equilibrium is maintained by reducing the stocking rate under conditions of drought and increasing the stocking rate in years of higher precipitation.

Despite the intuitive appeal of the Clementsian model, however, empirical evidence supported by accompanying theory has suggested that this model generally fails to hold, particularly in drier climates (Prach and Walker, 2020; Stringham et al., 2003; Westoby et al., 1989). For such

situations, state-and-transition models have been developed with multiple stable states, both desirable and undesirable. Stable states are separated by thresholds, either disturbances or management decisions, that trigger a non-reversible conversion to an alternate stable state. Within a stable state, multiple community phases may also be present. The difference between a stable state and a community phase is that the latter is reversible, while to former is not (Briske et al., 2008). Transitions between states often occur in patches, but as the process continues, patches may coalesce, consolidating the transition (Bestelmeyer et al., 2003).

Once a threshold has been crossed, management should focus on restoring the damaged ecological process rather than establishing a plant community that cannot be sustained in the new state (Stringham et al., 2003). In other words, for all practical purposes, restoration to the previous state may not be feasible (Monaco et al., 2012; Bestelmeyer et al., 2003). For example, using long-term vegetation-monitoring data, Bagchi et al. (2013) compared a higher-elevation wetter rangeland (1923–1973) to a lower-elevation drier rangeland (1950–2006), both in eastern Idaho. Monitoring occurred before and following invasion by downy brome (*Bromus tectorum*). When the sagebrush-perennial bunchgrass community of the higher-elevation rangeland crossesa threshold to a downy brome state, it may reverse itself, indicating a phase shift. However, when the same occurrs on the lower-elevation rangeland, the transition is irreversible, indicating a threshold.

Thresholds are central to the 'novel ecosystem' concept. Novel ecosystems are systems of 'abiotic, biotic and social components (and their interactions) that, by virtue of human influence, differ from those that prevailed historically, having a tendency to self-organize and manifest novel qualities without intensive human management' (Hobbs et al., 2013). Novel ecosystems are derived from natural historic ecosystems through a disturbance-induced threshold crossing. However, once the threshold is crossed, the novel ecosystem is stable, self-perpetuating, and irreversible. An example is the degraded stable state known as 'Intermountain West annual grasslands' in the Great Basin of the western USA (Davies et al., 2021b). This state has resulted from crossing a threshold from the native perennial sagebrush-bunchgrass ecosystem. Smith et al. (2022) documented an eight-fold increase in annual grass-dominated areas in the Great Basin over a 30-year period (1990–2020), corresponding to a 0.6% annual increase in area. This includes invasion into higher elevations and north-facing aspects. Climate change is expected to favor annuals due to warmer winters, altered precipitation patterns, and an earlier and more-active fire season (Davies et al., 2021b).

4 Approaches to grassland and rangeland rewilding: passive restoration

Rewilding has been described as assisting the natural regeneration of natural habitats through the passive management of ecological succession to restore natural ecosystem processes and reduce human control of formerly agricultural landscapes (Navarro and Pereira, 2015; Gillson et al., 2011). According to this plant-based definition, former crop- or grazing lands are allowed to assemble vegetation without seeding (Navarro and Pereira, 2015), thus success depends on the quality of the native seed bank (Rey Benayas et al., 2012) and seed dispersal from adjacent wildland tracts if present. Active intervention is minimal, though it may be required in the early stages of rewilding (Navarro and Pereira, 2015). Succession often leads to scrubland and possibly later to forest (Conti and Fagarazzi, 2005). While rewilding has been disregarded by restoration practitioners until recently in Europe, it does provide a low-cost opportunity to increase biodiversity (Navarro and Pereira, 2015).

In central and eastern Europe, large areas of marginal cropland located on poor soils are being abandoned, but researchers posed the question as to whether these grassland dunes of calcareous sand could experience spontaneous recovery (i.e. respond to passive restoration) (Török et al., 2018). On reference sites in central Hungary, the composition of seed banks correlated poorly with extant vegetation, and seeds of characteristic species were mostly lacking in seed banks of both reference and restoration sites. However, over time, both vegetation and seed banks progressed toward the target, while weedy seeds decreased. This pattern suggests that succession was driven by seeds that dispersed across space by vectors rather than via the seed bank.

Invasion by exotic trees and shrubs is the greatest threat to the last remaining natural grasslands of South America (Cuevas and Zalba, 2010). The Pampas grasslands of central Argentina were originally free of trees, but by the early twentieth century, they were populated by woody exotics. Cuevas and Zalba (2010) sought to restore low-altitude (550 m) and high-altitude (700 m) montane grasslands suffering from a dense invasion of Aleppo pine (*Pinus halepensis*) that was reducing light penetration and lowering soil pH. Felling of the trees launched a slow recovery of native grasses that displaced exotic herbs (Cuevas and Zalba, 2010). Monitored over 4 years, recovery of the low-altitude clearing was fueled by its native seed bank alone, as it was surrounded by pines. The high-altitude site, on the other hand, benefitted from both its native seed bank and dispersal from adjacent natural grassland upslope. Due to early intervention (i.e. trees were less than 12 years old when felled), native recruitment was not seed limited, enabling spontaneous recovery. Despite a substantial pine seed bank, seedling recruitment was low. The authors suggested low pine-seedling recruitment might be a consequence of winter

felling followed by regeneration of native vegetation in spring, which possibly interfered with pine seedling recruitment in fall.

It may be uncertain whether a native seed bank is able to regenerate a plant community, for example, when restoring a formerly cultivated field. Growing out a soil sample can determine the frequency and identity of native species present on the site. If the native-plant community was removed some time ago, seeds of species with seed dormancy are more likely to be present than those of readily germinating species. Alternatively, seed dispersal from nearby intact sites may facilitate recolonization. Both recruitment from the seed bank and dispersal from nearby sites qualify as passive restoration. It simply requires a source of propagules and dispersal vectors plus moderate soil fertility (Török et al., 2018). While passive restoration may be successful under certain circumstances, many grassland species lack good seed-dispersal mechanisms (Redhead et al., 2014). Moreover, this problem is greatly exacerbated by a high degree of grassland fragmentation (Hedberg and Kotowski, 2010). When a site is seed limited, active restoration (i.e. seeding) will be required to increase biodiversity, but this may not be feasible if appropriate seed is unavailable.

5 Approaches to grassland and rangeland rewilding: active restoration

Compared to passive restoration, active restoration has a longer history and is much more widely practiced in Europe (Navarro and Pereira, 2015). Low levels of agricultural practice are maintained, which tend to counter successional processes. Wet meadow is a species-diverse grassland ecosystem that occurs throughout northern Europe and is maintained by haying and sometimes grazing (Wedin, 1992). In the Netherlands, wet meadows have become highly productive by applying high levels of N fertilizer. This has supported dairying on a small land base but has also led to declines in species diversity. For policy reasons, intensive agriculture has been largely halted in these areas, providing an opportunity for restoration research.

Reintroducing cattle grazing and eliminating fertilization initially failed to restore the native-plant communities. However, after mowing was applied in place of grazing animals and clippings were removed over 45 years, historical species composition returned to near-historical levels as soil nutrients dwindled. Nevertheless, N levels became elevated due to the atmospheric deposition of N from agricultural and industrial nutrient pollution. Under this scenario, it became possible to reintroduce cattle. However, modern breeds selected for utilizing high-quality forage were unable to subsist on the low-quality rushes, orchids, and forbs of the wet meadows. Nonetheless, imported Scottish Highland cattle have been able to thrive on this low-quality diet.

Persistent seed banks that better support passive restoration occur frequently in wetlands and at sites where historical disturbances are frequent and unpredictable, as they are better able to buffer disturbance (Kiss et al., 2018). However, active restoration is likely to be required where seed banks are transient and associated with the lack of historical disturbance. These systems are most likely to suffer severe changes in species composition upon disturbance or climate change. A changing climate is also expected to drive species with good spatial dispersal ability to higher altitudes or toward either pole (Walther et al., 2002).

The Cerrado, in the highlands of central Brazil, is the world's most biodiverse savanna region, equaling the richness of the Brazilian Amazon, with almost 37% of Cerrado species being endemic (Lewis et al., 2022). Species distribution models were used to identify restoration hotspots, areas expected to provide the greatest economic return on restoration investment (Lewis et al., 2022). Four hotspots were identified, the central Cerrado and three transitional areas between biomes. Each hotspot displayed high species diversity and high potential C sequestration with a relatively low degree of fragmentation.

Exotic annual grasses, especially downy brome and medusahead wildrye (*Taeniatherum caput-medusae*), are occupying increasing portions of the Great Basin, USA, a vast semi-arid to arid region stretching from Nevada to western Utah, southern Idaho, and southeastern Oregon (Davies et al., 2021b). Downy brome alone occupies 21 million ha, almost a third of the region (Bradley et al., 2018), and perennial plant communities are converting to exotic annual grasslands at a rate of nearly 200 000 ha annually (Smith et al., 2022). These annual grasslands are now recognized as a stable state that is very difficult to reclaim with perennial species (Davies et al., 2021b; Clements et al., 2017). Furthermore, the litter from these annual species fuels recurring wildfires that favor the annuals, exacerbating the problem (Davies et al., 2021b).

Downy brome is a prolific seed producer that builds persistent seed banks at or near the soil surface. In northern Nevada, USA, Clements et al. (2017) implemented a seed-bank strategy to control the highly flammable invasive annual grass, downy brome. When wildfire burns a big sagebrush community, the high fire intensity consumes most of the downy brome seed. But once sagebrush has been removed by a previous wildfire, the fire intensity is often too low to deplete the downy brome seed bank, triggering recurring wildfire. Spring disking removed downy brome plants before the seed set and buried the seed bank, reducing seed density by 82%. In another tactic, the use of pre-emergent herbicides achieved over 95% reduction in seed density.

Once this competitive weed was controlled, the objective of establishing perennial grasses for long-term suppression was attainable (Clements et al., 2017). Seeding native perennial grasses was subject to a high failure rate due to the challenging environment. An alternative may be a reclamation seeding

of crested wheatgrass (*Agropyron* spp.). This exotic is easier to establish than the native grasses due to its high seedling vigor. A crested wheatgrass seeding achieved 92% control of downy brome and stabilized the site.

5.1 Green hay as a seed source

A common source of seed used in Europe for grassland restoration is green hay (Wagner et al., 2021; Kiehl et al., 2010), a practice that dates from the Roman era (Kiehl et al., 2010). A hay cut is timed to maximize its seed content and is then spread on a prepared seedbed within 24 h to avoid seed-shattering losses (Wagner et al., 2021; Kiehl et al., 2010). Baasch et al. (2016) reported similar results for green hay and threshing material for seeding a lowland hay meadow in Saxony-Anhalt, Germany.

When a regional commercial seed mix was added to either green hay or threshing material, Baasch et al. (2016) achieved greater success in terms of the number of target species that were established. Over the next few years, species spread into adjacent undisturbed grassland. Depending on its source, green hay may be a viable option to deliver local native seeds to the restoration site, particularly if those are unavailable commercially (Kiehl et al., 2010). It may also provide propagules of non-vascular plants, such as mosses and lichens (i.e. biocrust species).

5.2 Biological soil crusts

Biological soil crusts, or biocrusts, are communities of mosses, lichens, cyanobacteria, eukaryotic algae, liverworts, and other organisms that form a thin horizontal layer on the soil surface of many rangeland ecosystems (Bowker, 2007; Bowker et al., 2018). Biocrusts are found across a diversity of biomes and on all continents (Reed et al., 2019). They require high light, hence an open canopy, thus they predominate in arid and polar ecosystems (Reed et al., 2019). Biocrust species are regarded as both ecosystem engineers (Muñoz-Rojas et al., 2021) and indicators of rangeland health (Bowker, 2007).

Cyanobacteria are fast-growing pioneer biocrust organisms (Rubio and Lázaro, 2023) that can survive under extreme temperatures, saline conditions, long-term drought, and high UV irradiance (Muñoz-Ramos et al., 2021). Biocrust succession begins with cyanobacteria, which tolerate high irradiance, and proceeds as shade increases. In southern Spain, succession may continue with cosmopolitan generalist moss species, sometimes referred to as 'fire mosses' (Muñoz-Ramos et al., 2021). Succession then proceeds with fast-growing lichen species, and finally, slow-growing lichens and mosses that prefer shade. Rubio and Lázaro (2023) described the microbial crust as an all-encompassing matrix, with a lichen crust developing upon or replacing that matrix.

Biocrusts provide numerous ecosystem services, including soil aggregation and stabilization, N-fixation, nutrient cycling, dust-trapping, hydrological functioning, and thermal-energy balance (Bowker et al., 2018). They are also believed to facilitate secondary succession (Bowker, 2007). Interestingly, seeds of certain native species 'bio-primed' with cyanobacterial strains from the Pilbara region of Western Australia demonstrated superior radicle or shoot growth, though other species did not (Chua et al., 2020). In Gansu, northwestern China, biocrusts play an ecological filtering role by promoting one vascular-plant species but limiting two others, a process called sieving (Song et al., 2022). Furthermore, biocrusts may preclude seed penetration, which may explain observations that biocrusts are associated with reduced exotic-plant cover (Antoninka et al., 2020). This may be a mechanism by which biocrusts limit the crossing of ecological thresholds to less desirable states (Bowker, 2007).

In some cases, biocrusts may be restored passively, which requires varying lengths of time (Condon et al., 2020; Hilty et al., 2004). They may or may not be sensitive to livestock grazing, depending on the biocrust organism (Condon et al., 2020). Installation of a physical structure, such as jute netting, offers wind protection, creates some shade, and captures wind-blown propagules (Rosentreter, 2020).

Active restoration of biocrusts may be initiated by inoculation with salvaged dry material from the restoration site or with a slurry that has been reared ex situ (Young et al., 2016). Inoculants salvaged from the restoration site may be presumed to be adapted to that site, and they avoid the problem that some species are difficult to culture (Chiquoine et al., 2016). However, salvage efforts may be challenging and expensive, particularly if large quantities of inoculum are required for extensive projects.

Culturing biocrust species ex situ requires facilities, equipment, and time (Chiquoine et al., 2016). Cyanobacterial inoculants have been cultured for large-scale application in Almeria, southern Spain (Roncero-Ramos et al., 2019). Chiquoine et al. (2016) suggested using the salvage technique for species difficult to culture, such as lichens, and the slurry technique for producing cyanobacteria inoculum. Incorporation of topsoil from the restoration site proved to be less effective for biocrust restoration than either salvaging or culturing (Chiquoine et al., 2016).

5.3 Seeding native forbs

Perennial grass species are widely seeded for grassland restoration, but perennial forbs are used to a much lesser extent due to high cost and low availability of seed, as well as the difficulty of field collection (Jones, 2019). Many forb species can be present in the tallgrass prairie ecosystem of North America, so they often make a large contribution to species richness (Grman et al., 2021).

However, forb seedings often establish poorly or succumb to competition from grasses. Thus, species richness and diversity can be compromised in restoration seedings, especially because grasses tend to be more competitive than forbs.

A tallgrass prairie restoration experiment tested the impact of four C_4 grass species, big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and Indiangrass (*Sorghastrum nutans*), on forbs in 78 ex-arable field seedings in Illinois, Indiana, and Michigan, USA (Grman et al., 2021). These native grasses are widely used in tallgrass prairie seedings because they dominate reference sites, generate economical seed crops, produce sufficient biomass to fuel burns, and compete against weeds. Big bluestem and, to a lesser extent, little bluestem had a direct negative impact on forbs. To rectify this problem, Grman et al. (2021) recommended decreasing seeding rates of warm-season (C_4) grasses, increasing seeding rates of forbs, and burning more frequently to limit grass competition.

5.4 Strip seeding and restoration islands

Strip seeding is a technique designed to reduce costs yet enhance the probability of seeding success on a limited scale (Rayburn and Laca, 2013). Strip seeding concentrates resources, such as seed and weed control, on a linear strip of land without seeding adjacent sections, where weeds may be easily controlled. Segregation of seeded species within the strip allows less competitive species to avoid competition from more vigorous species. While only a minority of the land is seeded, colonization of the adjacent vacant areas can begin once the seeded plants mature.

Restoration islands can be used to concentrate high-value plant material on relatively small sites that can then expand or 'nucleate' to the vicinity (Hulvey et al., 2017). The small island area allows expensive resources to be concentrated to ultimately maximize impact on the surrounding area. Such resources include creation of favorable microsites, high seeding rates, supplemental water, and weed control. Islands may be strategically located for microclimate, topography, soil quality and moisture, minimal weed competition, and fire avoidance. Islands should be designed to minimize edge-to-area ratio to limit perimeter encroachment, and seeded species may be chosen for good seed-dispersal ability. Islands provide an opportunity to sow high-value seeds that could not be seeded across the entire restoration site due to prohibitive cost.

To evaluate a seeding of 35 target species and to examine their dispersal into adjacent areas, Kiss et al. (2021) tilled three sizes (1, 4, and 16 m^2) of 'establishment gaps' into a species-poor 8-year-old grass seeding in the Great Hungarian Plain, Hungary. They then seeded the high-diversity seed mix into the gaps. Within 5 years, colonization of the species-poor surrounding area had begun despite a 1-year drought. The intermediate-sized gaps displayed

the best dispersal. Their smaller edge-to-area ratio offered more protection from recolonization by the matrix species than the small-sized gaps. Yet the intermediate-sized gaps were more inconspicuous to grazing cattle than the large-sized gaps.

6 Approaches to grassland and rangeland rewilding: prescribed burning

Prescribed burning is widely employed in the USA, especially in the tallgrass prairie ecosystem of the Midwest (Rowe, 2010). Practitioners aim to burn a tallgrass prairie seeding as soon as it produces sufficient fuel to carry a fire, averaging 2 years and ranging from one to six (Rowe, 2010). The management goals of burning tallgrass prairie are to increase forb diversity (Rowe, 2010), maintain dominant C_4 grasses, remove litter to warm the soil, and stimulate early spring green-up (Wagle and Gowda, 2018). To favor a particular functional group, the site is burned when that functional group is dormant, but when a group needs to be controlled, the burn is implemented in its peak growth season. For example, forbs may be increased by early spring or fall burning, while cool-season (C_3) and C_4 grasses may be controlled by frequent spring and summer burning, respectively (Wagle and Gowda, 2018). Early-September burns remove the growth of dominant C_4 grasses without damaging them, thus favoring subdominant grasses and forbs and increasing species richness (Copeland et al., 2002). Frequent burning favors C_4 grasses but decreases C_3 grasses, while forbs are favored by infrequent burning or grazing (Wagle and Gowda, 2018).

Prescribed burning can be an effective tool to manage restored tracts of land when fire is a component of the ecosystem being restored. A selling point of prescribed burning is its low expense. However, a minimum fuel load is required to carry a fire, and specific weather conditions are necessary to safely complete the plan (Toledo et al., 2012). While prescribed burning has the potential to be a useful tool for many ecosystems, perceived safety and legal concerns have hindered its adoption (Toledo et al., 2012). In parts of Texas, USA, the landowner can join a regional prescribed burn association, a cooperative organization that promotes safe and effective burning on a landscape scale through training, pooled equipment and labor, and insurance policies. Members join because, while they favor prescribed burning due to its low cost, ease of implementation, and high efficacy, they lack the personal financial resources to implement a burn on their own. A common realization is that it is better to consume fuels through a prescribed burn than to experience a catastrophic event with unforeseeable consequences.

In the high-altitude Himalayan meadows of Bhutan, invasion by rhododendrons has reduced yak carrying capacity (Wangchuk et al., 2013).

Prescribed burning controlled rhododendron, stimulating the growth of grasses, sedges, and broadleaf herbaceous plants, thereby restoring grassland. While the traditional practice had been to burn annually, a 6-year burn interval informed by this research is now recommended to generate a fuel load of 1 ton of dry-matter yield per hectare per year.

Burning was once a traditional management tool in Europe to improve forage quality, counter woody encroachment, and reduce litter accumulation (Valkó et al., 2014). However, its use disappeared with the adoption of intensive agricultural practices. Furthermore, burning is prohibited in many European countries due to the potential for damage to life and property, as well as air pollution. In an additional complication, warmer and drier climates are expected in the Mediterranean Region, where abandoned lands accumulate fuels that propel wildfires. Europe has historically lacked extensive fire-adapted C_4 grasslands as were once present in the midwestern USA. Consequently, for prescribed burning to be implemented in Europe, a fire-return interval of at least 3 years may be required because of the fire susceptibility of European vegetation.

While fire is no longer a frequently used restoration tool in Europe, interest in its use has been stimulated by the declines in the extent and species richness of European grasslands (Valkó et al., 2014). These declines have been attributed to reductions in livestock in rural areas and the accompanying disappearance of traditional grazing regimes. The question is whether fire can substitute for grazing and mowing of hay to reverse these richness declines.

7 Species establishment and persistence

7.1 Fire-related germination

Thirty years ago, Brown (1993) reported that smoke could stimulate the germination of fynbos species in the Cape Region, South Africa. About 10 years later, the active ingredient karrikinolide (KAR_1) was identified (Flematti et al., 2004). Effective at levels as low as parts per trillion, KAR_1 links with proteins to generate hydrolytic enzymes that trigger germination once hydrothermal conditions are favorable (Lamont, 2023). KAR_1 operates in the post-dormancy phase, so it stimulates germination rather than breaks dormancy (Dixon et al., 2009; Ramos et al., 2019).

Physiological seed dormancy is common in grasses and is the most common dormancy mechanism in ecosystems with seasonal rainfall, including many fire-prone systems (Ramos et al., 2019), particularly in Mediterranean climates (Lamont, 2023). Species that display physiological dormancy and water-permeable seed coats are more likely to respond to either smoke alone or smoke plus heat than species that do not (Hodges et al., 2021; Cuello et al., 2020). Some species respond to smoke water or fire but not to KAR_1, which

suggests other factors may be operating (Ramos et al., 2019). Germination response to fire is much less consistent in temperate grasslands than in Mediterranean climates (Hodges et al., 2021). However, in the temperate grasslands of southeastern Australia, grass species were the most responsive to smoke (Hodges et al., 2021). In Uruguay's Rio de la Plata temperate sub-humid grassland, however, a field burn favored monocots and dicots similarly (Cuello et al., 2020).

7.2 Seed treatments for establishment

While several pre-emergent herbicides are available for use in restoration seedings, they can negatively impact germinating seedlings following application, delaying seeding a year or more. During this delay, weeds may rebound, defeating the purpose of the herbicide. Holfus et al. (2021) described a 'vortexing' method to coat seeds with activated charcoal that adsorbs the pre-emergent herbicide, rendering the herbicide inactive in the vicinity of the seed. When a pre-emergent herbicide was applied just prior to a greenhouse seeding, no damage was sustained by seedlings germinating from coated bluebunch wheatgrass seeds.

Seed enhancement technologies are being developed for rangeland seeds that increase soil-water availability, enhance seedling emergence from soil crusts, delay germination until conditions become more favorable, improve planting ability and emergence of small-seeded species, and enhance seed distribution of aerial seedings without impacting existing native vegetation (Madsen et al., 2016). While application of these technologies may significantly increase costs, they may offer great savings on cost per established seedling in harsh rangeland environments.

7.3 Stand establishment and persistence

To be useful, restored populations of long-lived perennial species should be able to persist through a variety of environmental stresses, both biotic and abiotic. After 2 years of spraying herbicide and discing, Cox and Anderson (2004) established a thriving native grass and forb community in western Utah, USA, on land previously occupied by crested wheatgrass, an exotic widely seeded in the cold-desert valleys of the Intermountain West. While early results were impressive, native species had been mostly extirpated 20 years later. By this time, crested wheatgrass was in decline, and the site had become colonized by downy brome (Anderson and Johnson, 2020). Contrasting results were seen with a native-plant seeding in a dry montane meadow in central Utah where another perennial exotic, smooth bromegrass (*Bromus inermis*) had been seeded for forage (Anderson and Johnson, 2020). After 2 years, the restoration seeding was regarded as a failure, being covered by weedy annuals. After 10

years, annual species continued to dominate with only a few seeded native species present. Nevertheless, after 20 years, many seeded grasses, forbs, and shrubs had formed a diverse plant community, along with smooth bromegrass as a subdominant. Most surprising was that 15% of the ground was bare despite the presence of the highly rhizomatous smooth bromegrass. But what will the future hold?

High-diversity seed mixes can be recommended as a general practice to enhance the probability of persistence of at least some species in the mix (Wilsey, 2021). Genetic diversity within populations can be increased by mixing populations of a species from across a targeted area (Broadhurst et al., 2008; Larson et al., 2000). Functional diversity, controlled by specific traits, should also prove useful for seed mixes. Such traits can be identified and selected for in restoration populations, including direct selection for persistence (Jones et al., 2022; Chivers et al., 2016).

Testing for persistence requires long-term trials, ideally in many different environments. With patience, field experiments designed to collect establishment data can also be extremely useful sources of persistence data. Alternatively, persistence data at the species level may be collected from long-term monitoring of restoration seedings though priority effects may come in to play if species are introduced sequentially (Wilsey, 2021).

Robins et al. (2013) reported testing results for 18 cool-season grass plant materials in 34 trials conducted in eight western states, USA. Sites receiving less than 310 mm of average annual precipitation displayed relatively poor establishment at 1-year post-seeding and relatively poor persistence at 3 years post-seeding. Rhizomes were able to increase the stand percentage of the native, western wheatgrass (*Pascopyrum smithii*), from 1 to 3 years but not for another rhizomatous native, thickspike wheatgrass (*Elymus lanceolatus*), though this species displayed the greatest establishment at low-precipitation sites. Rigby et al. (2018) tested 32 plant materials of seven native and two introduced C_3 grass species in the western USA states of Idaho, Utah, and Wyoming. The native grasses bottlebrush squirreltail (*E. elymoides*), bluebunch wheatgrass (*Pseudoroegneria spicata*), slender wheatgrass (*E. trachycaulus*), and Snake River wheatgrass (*E. wawawaiensis*) displayed establishment percentages as good as the successful exotic, 'Vavilov II' Siberian wheatgrass (*Agropyron fragile*). However, by 5 years post-seeding, western wheatgrass, thickspike wheatgrass, and Snake River wheatgrass were the only native grasses equaling Vavilov II.

In central Utah, USA, Clifford (2023) evaluated 52 plant materials of 10 native and three exotic grass species for establishment and persistence traits. Based on a multivariate analysis of data, 25 plant materials qualified for Group 2, which scored higher for both establishment and persistence than three other groups. These included all plant materials of the three exotic species, all plant

materials of natives basin wildrye (*Leymus cinereus*) and Snake River wheatgrass, and some plant materials of the natives, bluebunch wheatgrass, salina wildrye (*Leymus salina*), and thickspike wheatgrass. These kinds of evaluation data are invaluable for informing seed-mix design.

8 The native seed industry

8.1 United States of America

Due to high demand for native seed and the ability of the native seed industry in the Intermountain West to supply that demand, the magnitude of this industry is greater than anywhere else in the world (Jones, 2019). Demand is driven by state and federal government response to wildfire, government nonemergency needs, private landowners participating in government programs, and corporate procurement to fulfill government mandates. Unfortunately, increasing disturbance, particularly increasing wildfire combined with exotic annual grass invasions, is driving increasing demand.

Aridity in the Intermountain West is a challenge to restoration with native species, but success has been increasing. Native seeds are supplied by an industry of private companies. Some specialize in wildland-seed collection, mostly of shrub seed, particularly Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) (Stevenson, 2016). Other companies specialize in the field production of herbaceous species, primarily a diverse array of native cool-season grasses, along with several native forbs (Jones, 2019), while many companies offer both. In the more arid areas, success has been much greater with species introduced from central Asia (Rigby et al., 2018; Clements et al., 2017; Robins et al., 2013). Thus, most companies produce or offer seeds of exotic cool-season grasses and forbs as well as natives (Jones, 2019).

The wildland seed collection industry originally developed in central Utah and now dominates supply for the western USA. Two hundred species may be collected in a typical year (Stevenson, 2016). While shrub species are the primary objective of wildland collection, forb and grass species are collected as well. Most shrubs do not lend themselves to field production, as they may take several years to reach reproductive maturity, which makes them less profitable in a cultivated setting than herbaceous species (Jones, 2019). Wildland-collected seed constitutes about a third of the seed sold to the Bureau of Land Management, the primary federal agency responsible for rangeland management and the largest seed-buying customer in the Intermountain West (Stevenson, 2016). Roughly similar quantities of this seed are harvested from state and federal lands versus privately owned lands. Annual harvests of big sagebrush seed may net over 450 000 kg, with totals of all species collected ranging from 567 000–800 000 kg annually.

While land ownership in the Intermountain West is predominantly public (Jones 2019), land ownership in the Midwest, USA it is mostly private, with the predominant use being cropland. Thus, the biggest driver of restoration acreage in the Midwest has been the Conservation Reserve Program. This federal cost-share program encourages agricultural producers to establish habitat-friendly seedings for wildlife that sequester more soil C on existing farmland than annual crops (Zinnen and Matthews, 2022).

Like the Intermountain West, the Midwest also has a well-developed native-plant seed industry. Zinnen and Matthews (2022) examined how this industry is serving the needs of restoration in the region with native-seed mixes. Their database included 1031 seed mixes from 32 vendors, encompassing 486 native species. The seed mixes were divided into six categories: pollinator habitat, tallgrass prairie, wetland, wet prairie, dry prairie, and woodland/savanna. Species richness was greatest for pollinator habitat and least for tallgrass prairie, while the percentage of graminoids in the mix displayed a reverse pattern. Zinnen and Matthews (2022) concluded that seed-mix diversity is lacking. For example, the most diverse relict areas display over 100 native species, but most mixes had fewer than 30 species with a mean species richness of 22.5, leading to simplified plantings. An important component, Cyperaceae species (sedges), was either absent or underrepresented. Mixes had few, if any, early blooming forbs, which may be due to their slow growth and/or poor seed-production potential. Zinnen and Matthews (2022) identified 'popular species,' based on the percentage of mixes that included the species and its percentage contribution by weight. The most popular species, in this case warm- and cool-season grasses and early seral showy forbs, are known in the seed industry as 'workhorse species.' They establish easily, display broad adaptation, produce prolific quantities of seed, dominate the seed trade, and sell for a reasonable price. While low seed cost is advantageous to practitioners' budgets, it may lead to overuse of these species, thus reducing diversity within and among seedings.

The USA has a well-developed system for native-seed certification termed 'pre-variety germplasm' (PVG; Jones and Young, 2005). PVGs may be released under two tracks (natural or manipulated) and four classes (source identified, selected, tested, or variety/cultivar). Manipulated track indicates hybridization and/or artificial selection, the intentional selection for specific traits, while natural track indicates their absence. The four PVG classes refer to the amount of research-testing data provided at the time of release, i.e. comparisons of the given pre-variety germplasm with other plant materials of the same species. This ranges from no testing (source identified) to a single year of testing (selected) to testing across generations to establish heritability (tested) to cultivar (multiple years). Along with track and class, the generation number (downstream from the original source) is included on the seed tag.

8.2 Europe

Compared to the USA, the scale of restoration in Europe is small. Wildland-harvested seed is limited by both availability and demand (Tischew et al., 2011). The European native-seed industry primarily consists of small- to medium-sized companies, which favor the development of seed-transfer zones, geographical regions within which seed from a particular point-of-origin can be used (De Vitis et al., 2017). In 2017, 100 native-seed production organizations were identified in Europe, 93% of which were private companies and nearly half of which were concentrated in Germany, Spain, Switzerland, and the UK. This industry focuses on herbaceous species for grassland restoration but is limited by a lack of experience with many individual native species and high production costs.

Prior to 2010, trade in wild seeds of commercial forage species was prohibited in Germany, but since 2020, legislation has allowed only native seeds to be used in the wild (Mainz and Wieden, 2019). Native seed companies have been hampered, on one hand, by seed legislation that limits wild seed production of forage species to protect the forage seed industry, and on the other, by the lack of EU Nature Conservation standards requiring proof of provenance, zones of seed origin, and seed propagation within these zones. For example, seed companies must compete with inexpensive foreign wildflower-seed mixes, which are currently legal if they don't include any of the 44 regulated forage species. Some European countries have regulations like Germany (e.g. Austria, France, Italy, Switzerland, UK, and Spain), while others have no regulations. Specific recommendations for native seed policy were made by Abbandonato et al. (2018).

8.3 Australia

In Australia, over 90% of restoration seed is wildland collected (Broadhurst et al., 2016). Wildland-collected seed is generally much more expensive than field-produced seed, but the quality tends to be poorer due to sub-optimal environments, such as drought conditions (Broadhurst et al., 2016). Contamination with invasive-species seed is also a problem. Small, fragmented native-species remnants used for wildland collection may be genetically depauperate (Broadhurst et al., 2008). Researchers have supported broader seed-transfer zones to expand genetic diversity and to accommodate changing climates (Prober et al., 2015; Breed et al., 2013).

Australia's acute need for much greater volumes of restoration seed has long been recognized (Broadhurst et al., 2015, 2016; Mortlock et al., 2000). Seed of many species needed for restoration are unavailable in the marketplace (Broadhurst et al., 2016). Meeting restoration targets, especially given climate change, will be challenging. Much more infrastructure, specifically strategically

located seed production areas with warehousing space for seed storage, is critically needed (Broadhurst et al., 2015).

9 Weed management in restoration projects

Examples presented next describe successes and failures of efforts to control annual and perennial weedy species in restoration projects. Some weeds are pernicious despite multiple control techniques, including mowing herbaceous plants, cutting down trees, mowing shrubs, seeding competitive mixtures, and applying herbicides. Monitoring weed populations on the ground and sometimes in the seed bank is critical for guiding weed-control efforts.

9.1 Chemical control of rangeland weeds

Wilson and Pärtel (2003) applied glyphosate to initiate replacement of a 50-year-old rangeland stand of the exotic forage, crested wheatgrass, with a C_3/C_4 grassland in Grasslands National Park in southwestern Saskatchewan, Canada. An early May herbicide application was timed to control crested wheatgrass when it was actively growing but before blue grama (*Bouteloua gracilis*), the desired native C_4 grass, began to grow. Blue grama was broadcast-seeded on slightly tilled soil shortly after the herbicide was applied. By fall, crested wheatgrass control was only about 50% (Wilson and Pärtel, 2003). Therefore, glyphosate was applied with a tractor-mounted wick applicator multiple times in each of the four following years to control the taller crested wheatgrass amongst the shorter native grasses. This was followed by herbicide application with a hand-held wick for two more years. For additional control, a 1-cm clipping treatment was applied four times annually for 3 years. However, no combination of seeding, glyphosate, and mowing controlled crested wheatgrass, suggesting it will be very difficult to remove over the long term. Anderson and Johnson (2020) came to a similar conclusion for this species in Utah, USA.

Spotted knapweed (*Centaurea stoebe*) and downy brome were targeted for control in western Montana, USA, using treatments of broadleaf, grass, and glyphosate herbicides in combination with seedings of five perennial cool-season grass species, four being native (Mangold et al., 2015). Good weed control was achieved with herbicides, while a successful seeding helped to suppress knapweed but had little impact on downy brome. One of the native species, bluebunch wheatgrass, and the exotic, tall wheatgrass (*Thinopyrum ponticum*) were successful 4 years post-seeding, though initially they appeared to have only negligible establishment. This result affirms the conventional wisdom that one should avoid premature judgments regarding seeding success.

A fall application of pre-emergent herbicide successfully controlled two invasive annual grasses, downy brome and medusahead wildrye, on

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) rangeland in northeastern California, USA (Kyser et al., 2013). Control of the invasive grasses increased cover of native forbs.

9.2 Mechanical control of rangeland shrubs

Degraded Wyoming big sagebrush plant communities, featuring high shrub cover and a depleted herbaceous perennial understory, are widespread in western North America (Davies et al., 2021a). Mowing big sagebrush, followed by drill-seeding large native bunchgrasses, has been recommended to rejuvenate the understory, thus limiting invasion by exotic annual grasses. However, slow-to-recover biocrusts may sustain damage from the mechanical disturbances of mowing and seeding, and exposed microsites offer an opportunity for invasive annuals to gain a foothold, particularly with sagebrush dominance curtailed. Furthermore, big sagebrush cover rebounded over an 11-year recovery period. Similar results were previously reported by Wilder et al. (2019), who suggested that this shrub-reduction approach offers limited long-term success, particularly on sites with low resilience to disturbance.

9.3 Mechanical control of grassland weeds

In eastern Hungary, Török et al. (2012) addressed weed-control issues for grassland restoration of former cropland by seeding low-diversity, native cool-season grass seed mixtures. Basic grass diversity was recovered within 3 years using the seed mixtures, combined with annual mowing. These treatments successfully controlled annual weeds. However, control of perennial weeds, such as *Elymus repens*, *Thinopyrum intermedium*, and *Cirsium arvense*, proved to be much more difficult. No herbicides were used in this restoration experiment.

In the Great Hungarian Plain in eastern Hungary, Valkó et al. (2021) compared post-seeding weed response to 8 years of mowing vs. mowing for only 3 years, followed by abandonment. This study, in one of the largest (760 ha) grassland restoration projects in Europe, compared treatment responses in lower-elevation alkaline grasslands on nutrient-poor soils with species-poor vegetation to higher-elevation loess grasslands on highly fertile 'black-earth' soils. Abandonment after 3 years led to a decline of sown grasses, an increase of weeds, and a large weed-dominated seed bank, especially in the alkaline grasslands. The loess grasslands, on the other hand, were able to maintain dominance of native perennial grasses due to the ability of the rhizomatous perennial, smooth bromegrass, to control annual weeds. These results suggest that long-term monitoring, seed-bank analysis, along with long-term mowing, may be required to assure eventual restoration success.

In the Pannonian sand grassland of central Hungary, a plantation of black locust (*Robinia pseudo-acacia*) was cut down, and stumps were treated with herbicide to prevent resprouting (Reis et al., 2021). This leguminous tree is considered the most problematic invasive tree in Europe. Its ability to fix atmospheric N enriches the surrounding soil, impacting the vegetation. Mowing plus hay removal was conducted twice annually for 7 years to control weed and shrub establishment and to reduce N inputs into the soil. Herbicide plus mowing successfully eliminated black locust. However, mowing also encouraged secondary invasions of alien species in areas with low amounts of grassland in the vicinity. Without mowing, however, dense cover of native shrubs returned.

10 Dealing with the legacy of degraded soils

Restoration of plant communities may require restored soils as a prerequisite, particularly when unnaturally high N and/or phosphorus (P) levels are present. Enriched soils drive growth of ruderal and exotic plant species, thus interfering with reestablishment of native-species plant communities. In Flanders, northern Belgium, species-rich semi-natural grasslands are some of the most diverse in the world. This plant community assembled due to a long history of low soil nutrients, resulting from grazing and haying without application of chemical fertilizers (Goossens et al., 2022). After widespread adoption of fertilizers post WWII, however, high levels of soil P and sometimes N were sustained, and most native species were lost.

Soil P can be depleted by mowing and clipping removal, or if that is insufficient, through a slow and labor-intensive process called P mining. This involves N and potassium fertilization to stimulate high P regrowth followed by mowing and clipping removal (Goossens et al., 2022). If the problem persists, removal of the P-enriched topsoil may be required. Once the abiotic soil component is addressed, seeding is needed to enrich the depauperate native-species seed bank, while depleting the ruderal seed bank through weed-control measures.

In Victoria, Australia, most successful restorations have been accomplished on land where N and P levels fall below pre-determined thresholds (Gibson-Roy and McDonald, 2014). Low P favors a greater diversity and quantity of native forbs, while high P favors broad-leaved weeds. Low N favors native grasses, while high N favors exotic grasses. Soil is first tested for N and P levels, as well as seed of ruderal species. If problems are detected, the site is scalped by removing the top 10 cm of soil, as a first step to restoring a grassy ecosystem.

Psammophilous (sand-loving) grasslands of central Europe are nutrient-poor habitats that are threatened by aerial deposition of industrial N and consequent domination by competitive grasses, such as *Calamagrostis epigejos*

(Řehounková et al., 2021). In the southeastern Czech Republic, 10–30 cm of contaminated soil was removed to expose soil low in nutrients and organic matter. This expensive process allowed psammophilous vegetation, collected in the vicinity from intact parcels, to quickly recolonize the impacted area. After 6 years, vegetation of the targeted area approached that of reference sites.

Downy brome is a pernicious, exotic annual weed of Eurasian origin that fuels ecosystem-altering wildfires in the Intermountain West, USA. In this region, downy brome converts soils from a tightly connected nutrient-cycling system, with rapid nutrient uptake by plants and microbes, to a leaky system featuring high nutrient availability courtesy of soil mineralization (Norton et al., 2007). A recurring question is, why is this species invasive in this alien New-World environment yet non-invasive in its home Old-World environment? In the Intermountain West, downy brome can increasingly favor itself over native perennials by increasing soil-nutrient availability via soil mineralization. This response is akin to that of cultivation and wildfire, both of which also release nutrients to the soil (Norton et al., 2007). Thus, not only is downy brome invasive because of its growth traits, but also because of its ability to perpetuate its favored environment. On the other hand, in downy brome's native Old-World environments, nutrient depletion long ago deprived this grassy annual of its ability to spread as an invasive weed.

11 Atmospheric nitrogen deposition

Atmospheric N deposition can dramatically impact low-nutrient grasslands. Rather than being a legacy of the past, however, N deposition from agricultural, industrial, and exhaust emissions is typically an ongoing problem (Fenn et al., 2003). Moreover, it exerts its influence at the landscape level rather being restricted to a locality (Fenn et al., 2003). Nutrient additions can reduce species richness of grasslands by extirpating less-competitive species and by limiting colonization by novel ones (Muehleisen et al., 2023).

Thirteen years of N application reduced the size and richness of the seed bank (forbs, sedges, and C_3 grasses) of an acidic (pH = 3.5–4.0) *Festuca-Agrostis* grassland in the Peak District National Park, UK (Basto et al., 2015). This site, proximal to the historically industrial cities of Manchester, Sheffield, and Leeds in northern England, had received one of the UK's highest rates of twentieth-century N deposition. The impact on the seed bank was greater than on the aboveground vegetation, thereby degrading the seed bank's functions as a buffer against local extinctions and a reservoir of genetic diversity.

In northern California, USA, serpentine grasslands host 10% of the state's endemic plant species, ten times the number expected based on the state's land area occupied by this ecosystem (Hernández et al., 2021). Serpentine soils are stony, shallow, low in macronutrients, and high in heavy metals. Native-species

diversity is high, but under N-enriched conditions, this ecosystem is susceptible to exotic, annual grass invasion, particularly annual ryegrass (*Lolium multiflorum*) (Vallano et al., 2012). A combination of prescribed fire and grazing can counter this threat, but it must be applied on an ongoing basis (Hernández et al., 2021).

12 Soil-carbon sequestration

While prolonged cultivation decomposes soil organic matter, stimulating soil-C emissions to the atmosphere, abandoned agricultural lands can sequester C as succession proceeds (Yang et al., 2019). However, this can be a slow process with limited C sequestration, particularly in the early years of succession. In a tallgrass prairie ecosystem in Minnesota, USA, Yang et al. (2019) reported results from the initial establishment of a high diversity of late-seral species, including grasses and legumes. In this experiment, high levels of C sequestration, comparable to that seen in years 13–22 of a natural succession, were achieved early in the restoration process.

Grassland plants allocate about 60% of their net primary productivity below ground as roots and store about 90% of their total C below ground as root biomass and soil organic C, accounting for about 34% of the global terrestrial stock of C (Bai and Cotrufo, 2022). Though soil is the largest terrestrial reservoir of C globally, soil C is being lost through erosion, respiration, and leaching, both in agricultural and natural ecosystems (De Deyn et al., 2011). In a 16-year experiment in northern England, cessation of NPK fertilizer and seeding of the N_2-fixing native, red clover (*Trifolium pratense*), increased C relative to N storage, reduced ecosystem respiration, increased soil organic matter, and improved soil structure. Soil aggregation likely plays a role in the physical protection of soil organic matter, thus facilitating sequestration of C and N.

Restoration activities that ameliorate degradation will also increase soil-C storage (Bai and Cotrufo, 2022). Because about half of global grasslands are degraded, soil-C sequestration can be favored by improved plant and livestock management. Cessation of tillage upon conversion of cropland to grassland improves C sequestration, while improved vegetation management, particularly seedings of N_2-fixing legumes, is also helpful. In addition, light or rotational grazing favoring plant and soil health can also stimulate soil-C stocks, particularly on grazing-susceptible grasslands dominated by cool-season species.

13 Case study: Utah's Watershed Restoration Initiative and the restoration of sagebrush-steppe rangelands

13.1 Background

In the western USA, piñon–juniper (P–J) woodlands, dominated by piñon pine (*Pinus edulis*) and juniper (*Juniperus monophylla*, *J. osteosperma*),

have expanded from less than 3 million ha prior to European settlement to 50 million ha today (Miller et al., 2019; Fig. 1). Over the last 160 years, these woodlands have encroached into big sagebrush (*Artemisia tridentata*) shrub-steppe communities (Fig. 2). This has resulted from natural range expansion, fire (Fig. 3) suppression, livestock grazing that reduced fuels, and favorable wetter climates in past centuries. In turn, this has led to serious reductions in herbaceous vegetation and species diversity; increases in flammable, exotic annual grasses; and instability, erosion, and impaired hydrology of impacted soils.

Figure 1 Dense piñon–juniper woodland. Source: Photo courtesy of Watershed Restoration Initiative.

Figure 2 Mule deer in big sagebrush. Source: Photo courtesy of Watershed Restoration Initiative.

Figure 3 Wildfire burning on a piñon–juniper site. Source: Photo courtesy of Watershed Restoration Initiative.

Since the 1940s, woody plants, both trees and shrubs, have been removed from the sagebrush steppe to release soil moisture and nutrients for the herbaceous understory, often in combination with seedings of perennial herbaceous species, particularly grasses (Munson et al., 2020; Miller et al., 2019). However, today shrub reduction is practiced much less frequently than in the past (Riginos et al., 2023). This is due to a 2015 moratorium on sagebrush reduction instated by the U.S. Department of the Interior to protect Greater sage-grouse (*Centrocercus urophasianus*) habitat on federal lands. While the moratorium has greatly reduced the loss of sagebrush habitat, losses to wildfire, largely driven by downy brome (Fig. 4), have continued (Riginos et al., 2023).

Utah's Watershed Restoration Initiative (WRI; https://watershed.utah.gov and wri.utah.gov/wri/) is a public–private partnership-driven effort dedicated to improving high-priority watersheds in Utah. WRI focuses on (1) watershed health and biological diversity, (2) water quality and yield, and (3) opportunities for sustainable uses of natural resources. Each of five regions in the state has a team that elects its own leaders, evaluates project proposals, and assists its members in project implementation. Hence, the WRI is designed to be a bottom-up hierarchy. Centralized efforts are administered by the Utah Department of Natural Resources (UDNR) in Salt Lake City but are limited to the project database, administration (contracting, accounting support), fundraising, marketing, and training. In short, the UDNR administration supports local decisions for projects and their implementation.

The WRI assists its local partners in applying restoration treatments, while monitoring data are collected by the Big Game Range Trend Studies program, directed by the Great Basin Research Center in Ephraim, Utah, a unit of the

Figure 4 Downy brome, also known as cheatgrass, occupying a stand of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) in Idaho's Snake River Plain. Source: Photo courtesy of Tom Monaco, USDA-ARS.

UDNR's Division of Wildlife Resources (UDWR). This is where seed is bought in bulk (6.53 million kg through 2022), stored in a seed warehouse (Fig. 5), and mixed before application. Since its inception in 2006, the WRI has completed 2672 projects encompassing 1 million ha (Fig. 6) with US$370 million of state funding plus US$43 million of in-kind funding. Currently, 274 projects are in progress covering 255 000 ha, with more proposed for the future. Proactive restoration accounts for nearly two-thirds of the projects, with the remainder being fire rehabilitation. Most range trend (monitoring) studies are conducted on winter range for mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus canadensis*).

13.2 Restoration treatments

The UDWR applies treatments to modify the vegetation of woodlands and shrublands to improve habitat for wildlife. These treatments are described here. For *herbicide/drill seeding*, a pre-emergent herbicide is sprayed from an aircraft to reduce downy brome (Fig. 7). Then a tractor-drawn rangeland drill is used to plant seed at the specific desired depth (Fig. 8). Woody-reduction treatments include harrowing, chaining, and mastication (i.e. grinding, crushing, or chewing) (Munson et al., 2020). The overall management objective

Figure 5 Interior of the seed warehouse at the Great Basin Research Center, Ephraim, Utah. Source: Photo courtesy of Watershed Restoration Initiative.

of these mechanical treatments is to release perennial grasses and forbs from woody competition, while minimizing increase of flammable annual grasses (Riginos et al., 2019b). Harrowing involves pulling an Ely (toothed) chain or pipe harrow. *Harrowing/broadcast seeding* involves a broadcast seeder pulled behind the harrow (Fig. 9), which may be pulled either *one-way* or *two-way* (in opposite directions), depending on the management goal. *Chaining/aerial seeding* consists of dragging a heavy anchor chain (Fig. 10) in a U-formation between two bulldozers moving in parallel (Fig. 11). Seed is applied aerially (Fig. 12) following the first pass of the chain, which is then covered by a second pass moving in the opposite direction. Like harrowing, chaining may be either one- or two-way. *Mastication/aerial seeding* involves aerial seeding followed by shredding with a mulcher rotor (toothed rotating drum) attached to an excavator or tractor.

Treatments with high disturbance intensity, such as harrowing and chaining, are applied to sites with more advanced woodland invasion (Pyke et al., 2015). These manipulations reduce woody vegetation, but they can also have the undesirable effect of increasing infestations of downy brome due to soil disturbance. While harrowing is either one- or two-way, the latter is more disruptive, effective, and expensive. Seeding often accompanies woody reduction, but the decision whether to seed depends on the extent of herbaceous perennial cover present (Monaco and Gunnell, 2020). For example, sites selected for chaining have a degraded understory and nearly always need to be seeded.

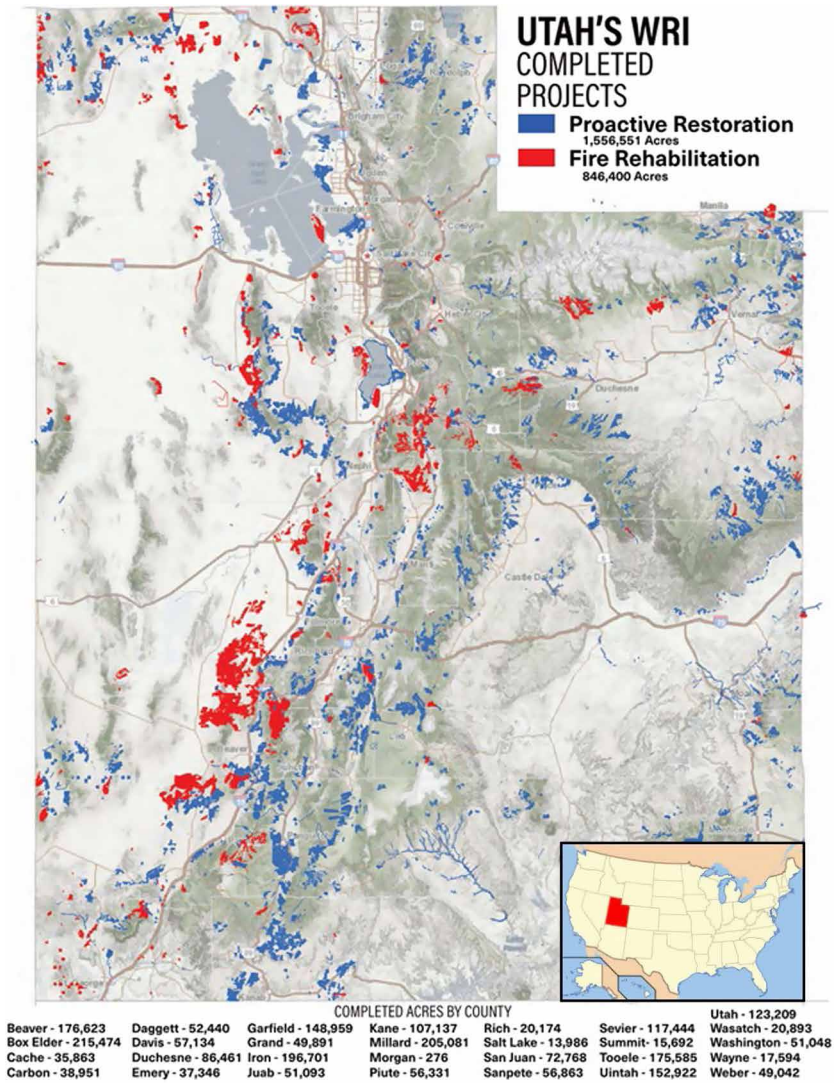

Figure 6 A map of restoration and rehabilitation projects completed by Utah's Watershed Restoration Initiative. In the lower right-hand corner, see an inset USA map with Utah shaded. Source: Photo courtesy of Watershed Restoration Initiative.

Mastication works well for removing trees in an advanced invasion without impacting desirable shrub cover. The mulched residue provides erosion control, but it may also favor establishment of downy brome or reduce emergence of seeded species. The use of mastication is growing due to its selectivity (i.e. greater control over the species and size classes of trees being removed), lower soil disturbance and erosion, and reduced fuel loads on the soil surface)

Figure 7 Spraying pre-emergent herbicide from a helicopter. Source: Photo courtesy of Watershed Restoration Initiative.

(Munson et al., 2020). Consequently, indiscriminate methods of woody-plant removal, such as harrowing and chaining, are being used less frequently than before.

13.3 Response to restoration treatments

Based on the data collected in the Big Game Range Trend Studies program, even 10 years of monitoring data may give false impressions concerning the post-treatment trajectory (Copeland et al., 2019b). For example, recovery of perennials, particularly native perennials, can be underestimated in this time frame. Thus, their efficacy in suppressing downy brome can also be underestimated. The findings presented here have been made possible by long-term collection of monitoring data over an extensive geographic region. Nevertheless, the impact of restoration treatments cannot be determined until a steady state is reached or a trajectory is clear. Thus, it is advisable to continue monitoring until data are analyzed, at which point an informed decision can be made whether to continue or terminate monitoring. Extended monitoring efforts obviously require dedicated funds and personnel.

Riginos et al. (2019b) reported responses of Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*; drier lower elevations) and mountain big sagebrush

Figure 8 Drill-seeding with a ten-row seeder. Furrows are opened with discs, planted with seed from two planter boxes, and followed by chains that cover up the furrows. Source: Photo courtesy of Watershed Restoration Initiative.

(*A. tridentata* ssp. *vaseyana*; moister higher elevations) communities to fire and mechanical shrub-reduction treatments (with or without seeding) across 94 sites in Utah. All four mechanical treatments plus fire reduced sagebrush cover over the short term (1–4 years), but fire was more effective than all but the two-way harrow in the short term. However, this difference was less pronounced over the long term. All treatments increased perennial grass cover in Wyoming big sagebrush communities, probably resulting from the release of a degraded herbaceous understory from sagebrush competition. However, in mountain big sagebrush communities, perennial grass cover only increased following fire, to which big sagebrush is highly susceptible. Forb cover increased with seeding but only in the short term. Over the long term, the fire/seeding treatment resulted in the greatest increase in perennial grass cover, suggesting shrub reduction combined with seeding is necessary to achieve desired outcomes.

Monaco and Gunnell (2020) monitored woodland encroachment over 15 years at 129 sagebrush sites following P–J reduction. P–J reduction increased shrubs and herbaceous vegetation, including downy brome, to varying extents depending on the treatment and sagebrush plant community. However, the longevity of reduction may not exceed a decade, depending on tree density and the native vegetation, two variables that are often inversely related.

Figure 9 A Dixie harrow, used to remove shrubby vegetation and scarify the soil for seeding. Photo courtesy of Watershed Restoration Initiative.

Chaining and mastication are used when tree invasion is advanced. Both treatments resulted in greater herbaceous perennial recovery but greater downy brome issues due to soil disturbance. This may lead to achievement of short-term goals for ecosystem services (e.g. reduced competition for water, stimulation of herbaceous perennials, or predisposition to ecological risks), but also a long-term exacerbation of downy brome. In contrast to these high disturbance-intensity treatments, tree-cutting can be employed in more recent invasions. Cutting, also referred to as 'lop and scatter' (Fig. 13), is more appropriate when tree density is low and seeding is unnecessary (Monaco and Gunnell, 2020; Mller et al., 2019). This method maintains shrub and herbaceous cover with little ground disturbance, but only minimal enhancement of the perennial herbaceous understory is expected, as it was already in good condition.

Recovery of herbaceous perennials was greater on seeded sites, suggesting that these species are often seed limited and seeding is beneficial (Monaco and Gunnell, 2020). However, sagebrush seeding did not enhance sagebrush recovery. Sagebrush establishment may be limited by the infrequency of germination episodes, dry spring weather, grazing by big game, and competition from seeded herbaceous perennials. In summary, seeding strongly improves recovery of the perennial herbaceous understory and is essential for reversal of

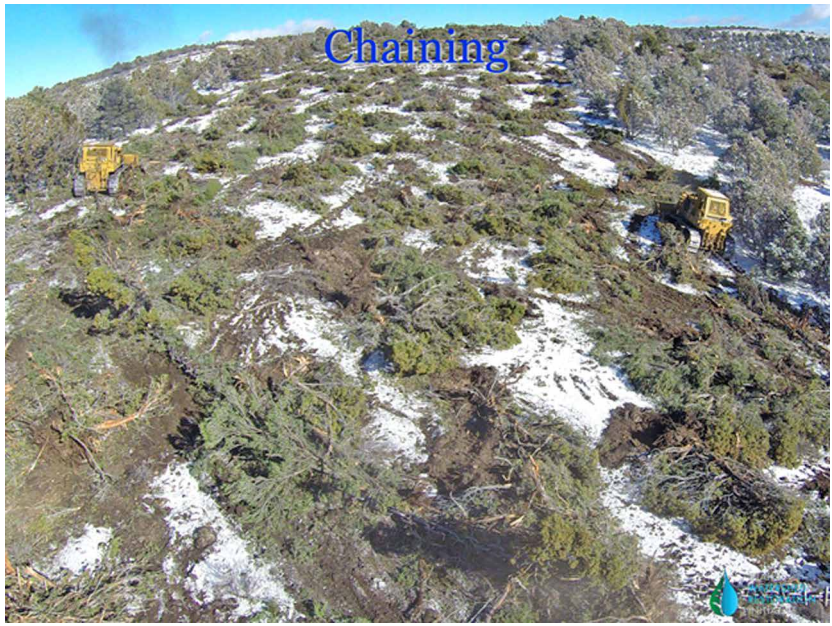

Figure 10 A large chain, pulled by two bulldozers moving in parallel, being used to remove piñon and juniper trees. Photo courtesy of Watershed Restoration Initiative.

Figure 11 A tractor pulling both ends of a chain for treating small areas. Photo courtesy of Watershed Restoration Initiative.

Figure 12 Aerial seeding by helicopter. Photo courtesy of Watershed Restoration Initiative.

P–J encroachment. Though mountain big sagebrush communities have been regarded as more resilient than Wyoming big sagebrush communities due to the former's higher elevation and more favorable environment, their treatment responses were similar.

Due to a dearth of cost-tracking and monitoring data, accountability for restoration and rehabilitation projects has been limited (Munson et al., 2020). However, cost-effectiveness is expected to become increasingly important as project sizes, inflation-adjusted costs, and complexities increase, yet resources fail to keep pace (Munson et al., 2020; Copeland et al., 2018). Munson et al. (2020) examined monitoring results of 74 sites from range trend studies. In this meta-analysis, woody plants regrew similarly regardless of reduction method, either harrowing, chaining, or mastication. All three treatments increased downy brome cover due to soil disturbance caused by heavy equipment. Chaining was more effective at increasing perennial grass cover than harrowing, and a second pass of harrowing led to increased cover over the first pass. Seeding of perennial grasses increased perennial cover relative to downy brome up to 12 years post-treatment. However, while seeding of forbs increased species richness in the short term, forbs began to decline after two to three years as woody plants recovered and perennial grasses established. At 9% of the sites, seeding reduced perennial cover due to the inability to

Figure 13 Lop and scatter (tree-cutting) in a piñon–juniper community. Photo courtesy of Watershed Restoration Initiative.

compensate for reductions caused by the disturbance of the woody-removal operation.

13.4 Climate and weather impacts on restoration efficacy

Recovery of both woody and herbaceous species depends on climate and extreme-weather events, with recovery being limited by low precipitation and high temperatures (Copeland et al., 2019b). Consequently, recovery is expected to be lower in the future, as climate change is expected to result in drier and warmer conditions (Copeland et al., 2019a). As weather may alter competition during establishment, weather anomalies during this time can greatly alter long-term community composition. While positive effects of high precipitation from April to September did not persist after 5 years, extreme annual post-treatment temperatures had long-lasting negative effects. Balazs et al. (2020) also concluded that temperature is a stronger driver of community assembly than precipitation.

13.5 Natives and exotics

Seeding exotic perennial grasses, such as crested wheatgrass, after woody-plant removal can accelerate perennial cover and reduce downy brome but

also inhibit native perennial cover (Copeland et al., 2019b). Nevertheless, exotics continue to be included in seed mixes though at lesser rates. Their inclusion is due to their high establishment, their high productivity, and their ability to stabilize soils and suppress downy brome. Every 10% decrease in downy brome cover resulted in a 1.5% increase in native cover.

13.6 Functional traits of plant materials

Balazs et al. (2020) compared restoration species with varying levels of seed mass, plant height, and specific leaf area (SLA) for their seeding establishment on 150 sites in the Colorado Plateau ecoregion of southeastern Utah, USA. These functional traits were chosen for their relevance to important ecological strategies or trade-offs. For example, seed mass reflects plant strategy for reproduction and colonization. Whereas small seeds are more persistent in seed banks, large seeds promote persistence under limited resources. Plant height represents a trade-off between light competition (tall plants) and stress tolerance (short plants). SLA, leaf mass per unit area, reflects a trade-off between resource capture (high SLA) and resource-use efficiency (low SLA). Balazs et al. (2020) reasoned that choice of the best trait for the best site corresponds to the nature of the trait × environment interaction. They attempted to predict a species' restoration outcome at a site (dependent variable) by fitting the species' trait values, six climatic variables, and species × climate interactions (all independent variables) into a model. Height and seed mass interacted with a particular climate variable, temperature seasonality, which quantifies the divergence between summer and winter temperatures of a site. Thus, Balazs et al. (2020) concluded that both tall species and large-seeded species are favored by high temperature seasonality. In the Colorado Plateau, the sites that display the greatest temperature seasonality (hot summers and cold winters) are valley bottoms. Interestingly, this is where many UDWR rangeland restoration sites are located. Unlike height and seed mass, SLA did not display such an interaction, so no such pattern could be suggested for this trait. These patterns held for both native and exotic species.

13.7 Economic decision-making

In an economic analysis, Munson et al. (2020) evaluated the cost-effectiveness of woody-plant destruction, seeding treatments, and control of annual invasive grasses. Costs of increased perennial grass cover were driven more by woody-plant destruction costs than seeding costs. Increased spending on woody destruction effectively reduced woody-plant cover and favored perennial grass cover due to competitive release. Costs of woody-plant removal per unit removed are similar regardless of treatment. However, due to selective removal, the cost of mastication/aerial seeding is two to three times greater

than other treatments, though this treatment yielded only small improvements in perennial grass cover.

Seeding costs were driven up by the greater expense of native seeds, particularly forbs, relative to crested wheatgrass and other exotic grasses. Seed mixes with more forbs, when applied aerially after mastication or chaining resulted in only a 2–3-year gain in perennial forb cover and species richness, with no measurable benefit thereafter. However, seed-mix costs were unrelated to the composition of perennial grass cover. While more-expensive native seeds increased seed-mix costs, this spending did not lead to greater native cover. Instead, due to its high growth rate and stress tolerance, the use of inexpensive crested wheatgrass seed led to increased exotic grass cover relative to native grass cover.

Herbicide/drill seeding was the only treatment that effectively reduced downy brome. To increase cost-effectiveness, Munson et al. (2020) recommended spending more on a pre-emergent herbicide to suppress downy brome and more on drill-seeding to increase perennial grass cover. Using an herbicide is relatively inexpensive, thus its use is cost effective. However, the herbicide negatively impacted perennial forb cover and species richness.

13.8 Tools

Monitoring on the ground is highly labor intensive and cannot always be achieved across vast rangeland areas. Copeland et al. (2019a) investigated the value of Landsat satellite imagery to alleviate these issues using SATVI (Soil-Adjusted Total Vegetation Index) to estimate vegetation cover, where 'total' refers to green plus senescent cover. They reported a high correlation between SATVI and ground-based data, suggesting this tool has potential for this application. An advantage of SATVI is a continuous data stream instead of infrequent records, as for traditional ground-based monitoring. As SATVI also collects data across geographical space, it avoids the high labor requirements that would limit the number of restoration sites that could be monitored.

Resistance and resilience (R&R) is a concept based on two measures of ecosystem integrity: (1) resistance, the ability to preclude invasion, in this case by downy brome, and (2) resilience, the ability to recover from disturbance (Riginos et al., 2023). High R&R sites display low soil temperature and high soil moisture, and in Utah, these variables are closely related to elevation. Researchers used data from 51 Utah sites to relate R&R classes (high, medium, and low) to changes in plant cover following disturbance. Seeding resulted in increased perennial grass cover following fire or mechanical treatment for all three R&R classes (Riginos et al., 2023). While over the short term (0–4 years), seeding increased perennial grass cover most at the low R&R sites, over the long term (5–12 years), cover increased only at the high R&R sites. Like grass

cover, perennial forb cover increased in all R&R classes in the short term, but over the long term, an increase was only seen at high R&R sites, with an actual decline at low R&R sites. In response to fire or mechanical treatment, over the short term, big sagebrush decreased most at the high R&R sites and least at the low R&R sites. However, recovery appeared to be greater at medium and high R&R sites but lesser at low sites. Over the long term, annual grass cover increased slightly at high and medium R&R sites but declined at low sites. The researchers concluded that the R&R framework is useful for making broad relative predictions of restoration outcomes, but they cautioned that it should be used in concert with other decision-making tools rather than alone.

13.9 Restoration for Greater sage-grouse management

At least 10% cover of big sagebrush is considered necessary for suitability for Greater sage-grouse (Riginos et al., 2019a; Fig. 14), This shrub is in decline over vast areas of the Intermountain West due to its high mortality from wildfire, which is increasing in scope and frequency (Beck et al., 2009). Lower-elevation sagebrush communities are more prone to annual-grass invasion and wildfire than at high elevations (Chambers et al., 2014). The fire-recovery interval of big sagebrush can range from 30 to 120 years, exceeding the time frame of conservation planning (Lesica et al., 2007; Baker, 2006). Thus, the conventional wisdom of wildlife managers is that both wildfire and prescribed burns are detrimental to management of sage-grouse and other sagebrush obligates, as fire rotations in big sagebrush range from 70 to 240 years (Baker, 2006). Thus, the perception is that any fire essentially results in

Figure 14 Greater sage-grouse. Source: Photo courtesy of Watershed Restoration Initiative.

a semi-permanent loss of sage-grouse habitat (Riginos et al., 2019a; Baker, 2006).

Riginos et al. (2019a) found that when pre-fire sagebrush cover fell below 10%, recovery after fire was insufficient to meet habitat standards. However, when pre-burn sagebrush cover exceeded 10%, a recovery trajectory materialized by 6–10 years post fire, suggesting habitat standards could be met. This favorable trajectory was indicated by increasing perennial-grass and forb cover, increasing sagebrush cover, and declining downy brome.

14 Conclusion

Rewilding of grasslands and rangelands is challenged by changing climates, ecosystems, and landscapes that are associated with losses in biodiversity. At the same time, however, opportunities have arisen due to land-use change. Marginal lands being diverted from production agriculture offer a land base for rewilding in many locations around the world. This trend is also favored by increasing populations in urban areas that may provide political and economic support for rewilding. Three components are necessary to systematically move forward in this effort. First, strong ecological monitoring efforts are imperative. Second, newly developed plant materials that are more effective in modified environments must be developed. Third, a reliable demand must exist to support and incentivize a seed-production industry to supply that demand.

15 Future research needs

Our world is subject to increasing ecological modification, which is likely to be exacerbated in the foreseeable future by an increasing human population. Until population growth stabilizes and then begins to decline, research to identify soil and water conservation strategies will be necessary to maintain these resources and prevent large-scale social catastrophes. Prophylactic approaches to wildfire management and wildfire mitigation via restoration are also critical for sustaining ecosystems in a warming world. Control of invasive species must also be a research imperative, given an increasing array of novel ecosystems. Restoration of biocrusts, a burgeoning research area, may play an outsized role in limiting the niche space available to invasive species. A shortage of restoration seeds is commonly cited as a limiting factor for restoration, but research leading to improved seed-production practices is necessary to support a thriving seed industry that can respond to this need. Finally, the greatest challenge may be to apply scientific information in a real-world context that recognizes economic and political realities and limitations.

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