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## Restoration of open ecosystems in the face of climate change

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### Abstract

Open ecosystems occur all around the world in various forms including temperate and tropical grasslands, savannas, shrublands, heathlands, among others. They are home to unique biodiversity, provide key ecosystem services and sustain traditional livelihoods of nearly two billion people. In the face of ongoing climate change, practitioners aiming to restore open ecosystems need the support of the scientific community more than ever. The aim of this Special Issue (SI) is to provide an attention-grabbing collection of high-quality publications addressing the growing challenges of open ecosystems restoration. The SI contains 14 papers that fill various, often interdisciplinary knowledge gaps. Three papers deal with the challenges of identifying the right target states, including the genetic composition of constituting plant species, for restoration under changing environmental conditions and competing stakeholder interests. Five papers advance our understanding on the appropriate timing and methodological toolkit to actively ignite re-assembly of the target plant communities, while two papers focus on situations where spontaneous processes can still also be relied on. The interaction of open ecosystems health and recovery with higher trophic levels, particularly grazers, is also discussed in three papers. Finally, a review paper systematically identifies further knowledge gaps, such as the role of soil microbes in grassland recovery and makes clear guidelines how to fill them. Due to the variety of topics and the rigorous content, this SI provides strong support for open ecosystems restoration policy and practice under the UN Decade on Ecosystem Restoration and beyond.

**Keywords:** climate-ready genotype, Global South, grassland restoration, knowledge gap, propagule transfer, spontaneous recovery

## Introduction

Open ecosystems thrive from tropical grasslands and savannas through temperate steppes to alpine regions, both in the most pristine, untouched parts of the Earth and also in cultural landscapes managed by humans for millennia (Suttie et al. 2005, Squires et al. 2018, Scholtz & Twidwell 2022). Due to the widespread occurrences and high diversity of grasslands, the threats they face are also diverse and include anthropogenic transformation, overuse or abandonment, biological invasions, the disruption of nutrient and water regimes, novel fire regimes, and woody encroachment (Török et al. 2018, Bardgett et al. 2021). Climate change can have several direct effects on native grasslands (Barnett & Facey 2016). But it can also affect them indirectly, as our actions to mitigate climate change by removing excess carbon dioxide from the atmosphere threatens ancient grasslands with afforestation, particularly in the Global South (Bond et al. 2019, Parr et al. 2024).

At small scales, grasslands are among the most species-rich ecosystem types (Wilson et al. 2012), comparable to tropical rainforests (Murphy et al. 2016), which alone calls for measures to halt their decline. The need for their conservation is reinforced by our dependence on vital ecosystem services delivered by grasslands to billions of people, such as providing forage for livestock, nesting and foraging ground for pollinators of crop plants, preventing soil erosion, purifying water, and as an emerging ecosystem service by sequestering carbon in the soil (Zhao et al. 2020, Bai & Cotrufo 2022, Lindborg et al. 2023). The conservation of remaining grasslands, however, is no longer enough; we need to actively recover lost grasslands. Grassland restoration has a massive scientific literature, which helps us understand the intricate ecological mechanisms that drive the (re-)assembly of grassland communities, and provides evidence-based methodological background for restoration practitioners. However, there are still many gaps in our knowledge, which is accentuated by climate change by posing never-before environmental settings, where historical ecosystems states are of decreasing relevance (Lyons et al. 2023, #this issue).

This Special Issue is dedicated to filling various knowledge gaps of grassland restoration, with an emphasis on the challenges posed by climate change (Figure 1). We present some strikingly new approaches alongside refinements of traditional methodologies and cover new insights of grassland restoration gained with advanced molecular techniques and also with methods of social sciences. It is our hope that the papers published in this Special Issue will provide support for enhanced grassland restoration policy and practice under the UN Decade on Ecosystem Restoration and beyond.

### What to restore?

Grassland ecosystem services are differentially appreciated by different stakeholders, who thus tend to optimize restoration to meet their requirements, leading to divergent targets. Möhrle et al. (2024, #this issue) identified several different visions of restored grasslands including short, species-poor stands designed by turf-managers, productive swards favoured by farmers, and multifunctional grassland communities preferred by restoration ecologists. However, the

restoration or creation of each of these grasslands poses its own challenges. Criteria for species selection are grassland-specific, leading to very different species composition and therefore different establishment success, management requirements and resilience to stochastic environmental impacts. Thus, identifying relevant stakeholders and their needs are important early steps to properly draw from available knowledge, restoration planning, goal setting, monitoring and adaptive management.

Further challenges may emerge, when different stakeholders aim to pursue their activities on the same restored grassland. There, conflicting requirements need to be reconciled. One approach is combining grassland restoration with productive systems to support farmers. To this end, Dullau et al. (2023, #this issue) tested how different fertilizer levels applied to restored European grasslands to increase yield for farmers correspond with targets for grassland biodiversity restoration. Previous literature establishes that high nutrient loads favour grasses over forbs and allow strong competitors to exclude other species and thereby reduce species richness (e.g., Plantureux et al. 2005), and the impact of fertilization is long-lasting, impacting community composition decades after cessation of the practice (Heinsoo et al. 2020). Dullau et al. (2023, #this issue) also suggest that the best option for conservation purposes is avoiding fertilization, but species richness was barely affected by moderate levels of nitrogen addition, satisfying the needs of both conservation practitioners and farmers simultaneously, and making the restored grasslands truly multifunctional and sustainable. However, both farmers and conservationists need to account for climate change, such as prolonged droughts, which threaten both grassland yield and the survival of sensitive plant species of conservation importance. Dullau et al. (2023, #this issue) found that high species richness, which is achieved by avoiding high fertilization levels, lends considerable resilience to the restored communities both in yield and species composition. This case study serves as a prime example for the synergies of farmers' and conservation practitioners' needs, and visions of the target grassland under climate change.

### **Kicking in community re-assembly**

Once an agreement among stakeholders about the restoration targets is reached, most interventions start with site preparation and the introduction of propagules of the right species in right proportions. However, the appropriate timing of this intervention is increasingly challenging due to climate change. Germination is optimal under moist conditions but precipitation patterns are becoming unpredictable in some regions. Yet, Wang et al. (2022a, #this issue) found some patterns in temperate grasslands in China and developed a monitoring system that can be directly used to fine-tune the timing of propagule introduction. Adapting their system to other regions could make restoration activities more time- and cost-effective in the future.

After determining the right time to introduce the propagules, practitioners need to find the best method. In many cases this is often direct seeding. However, to acquire seeds of native, often rare species in sufficient quantities can be challenging. In Europe and North-America, there is a well-developed market of native seeds, often with region-specific genotypes, but this type of

seed supply is limited in low-income countries (Lyons et al. 2023, #this issue) but see Schmidt et al. (2019) for an exception. Australia has a special position in this respect, as ecological restoration has a long history in the continent but has traditionally focused on woody vegetation, while open grasslands, which cover large areas of the continent, have so far been neglected. This outstanding limitation for Australian temperate grassland restoration is reviewed by Gibson-Roy (2023, this issue), who, despite the many difficulties, also outline some promising success stories regarding native seed production and machinery improvements for effective seeding. The emerging biodiversity credit schemes of Australia may provide further incentive to this developing sector in the country and beyond.

The importance of direct seeding is highlighted by the often unreliable spontaneous establishment of species. Grassland specialist species rarely have persistent seed banks, and native seed rain can be hindered by the lack of source populations in heavily transformed landscapes. To make things worse, Florentine (2023, this issue) showed that the prevalence and density of non-native invasive species can be high in the seed bank in some Australian grasslands subjected to restoration, and their dominance in the seed rain can reduce restoration success. For this reason, some sites are better avoided during restoration planning or require seeding with sufficiently high amounts of native species.

An alternative, occasionally more cost-effective way of propagule transfer is the introduction of freshly mowed, seed-rich hay from donor sites (Kiehl et al. 2010). This method has been shown to be effective in restoring plant communities (Gerrits et al. 2023), but is limited by the availability of donor sites, the difficulties to properly time the harvest and the fact that only a subset of the species can be transferred in a single harvest due to the asynchronous seed ripening of different species. To cope with these difficulties, evidence-based guidelines are available in the scientific literature. However, Sommer et al. (2023) showed that the real-life obstacles practitioners face do not fully overlap with what literature covers. Interviews with practitioners revealed that although success depends on the above technical and ecological considerations, organizational deficiencies, such as the often limited experience of involved personnel, and the lack of trust among stakeholders, can hinder efficient hay transfer more strongly. This is an alarming mismatch, which calls for a rigorous re-evaluation of the efficiency of other grassland restoration methods to reveal so far overlooked obstacles therein. It is also a reminder that restoration outcomes commonly benefit from projects emphasizing the links between biological and social sciences.

### **Sometimes, life finds a way**

Despite the widespread need for active propagule re-introduction, some environmental settings still allow for a spontaneous (re-)colonization of grassland species. Ballesteros et al. (2024, #this issue) showed that mid-successional stages during temperate forest recovery are within the niches of many grassland specialist species. These species can spontaneously take over the ruderal flora of early successional stages but, more interestingly, do not necessarily give way to the eventual forest understory flora and can persist for long periods even after the closure of the tree canopy. In this study, they clearly showed that secondary temperate woodlands provide

more suitable surrogate habitats for grassland species than previously thought, expanding the scope of grassland species conservation.

Krickl & Poschlod (2023, #this issue) showed that the connection between temperate forests and grassland restoration has some further dimensions in that cleared forests represent better starting conditions for calcareous grassland restoration than, for instance, nutrient enriched ex-arable fields where the seed and bud banks are overwhelmed by ruderal species. Using a uniquely long-term and high-resolution monitoring dataset, they showed that the functional composition of such grassland could spontaneously recover, and become barely distinguishable from adjacent old-growth grasslands. However, this is also the result of low dispersal limitation, as an old-growth grassland was in the immediate vicinity of the cleared forest site, and they both were managed with sheep grazing, which is a known mediator of successful grassland community reassembly (Tölgyesi et al. 2022).

However, grazing can also be detrimental for grasslands, if the stocking rate is too high. Overgrazing is responsible for the degradation of vast Asian grasslands, and, according to Bai et al. (2023, #this issue), the best way to restore overgrazed grasslands is to suspend grazing for certain periods of time. They found that 8-14 years of grazing exclusion is optimal to restore the species richness and carbon sequestration capacity of Inner Mongolian *Stipa grandis* steppes. However, even in these low-productivity grasslands, the complete, long-term cessation of grazing is not recommended, supporting the idea that managing, rather than excluding disturbance is vital for grassland stability (Buisson et al. 2022). Dong et al. (2022, #this issue) showed that light grazing does not decrease species richness but reduces soil erosion due to topsoil compaction, which is an interesting addition to the favourable effects of light grazing besides the traditionally scrutinized implications of the intermediate disturbance hypothesis (Gao & Carmel 2020).

### **The good old is not always the right way**

One of the most extensively studied effects of climate change is that species shift their current ranges to track areas where environmental conditions are within their limit of tolerance (Davis & Shaw 2001, MacLean & Beissinger 2017). This should also be considered during restoration planning, as the species composition of historical communities may not be relevant under new climates (Baer et al. 2019). Introducing non-native species from adjacent, formerly climatically different regions seems the right solution but is still a highly controversial topic (Twardek et al. 2023). It is probably less problematic to stick to the former species but introduce genotypes that better tolerate the new conditions. To justify the validity of this approach, Atamian & Funk (2023, #this issue) demonstrated that offspring of drought-adapted *Artemisia californica* populations showed higher resilience to droughts than offspring of populations from milder environments. Thus, identifying and using climate-ready genotypes should be an important aspect to consider in biological sourcing for future grassland restoration to increase restoration outcomes.

Failures can be further minimized, if changes in the habitat features of the restoration site are considered in setting the initial density of introduced plants. If conditions turn more extreme and favour fast-growing, pioneer-type plant species, higher propagule densities may be needed, as this plant strategy often entails higher mortality, as described by the growth-survival trade-off (Chapin et al. 1993). This guideline in setting initial population densities has rarely been used for grassland restoration (Negreiros et al. 2016). However, Fantinato et al. (2023, #this issue) showed that the trade-off is also fully operational in herbaceous species in Mediterranean grasslands. They found that fast-growing species of pioneer habitats in a sand dune system indeed grew fast but exhibit higher mortality. Thus, they confirmed that higher initial population densities should be applied for fast-growing species to secure long-term establishment in early successional habitats, while lower densities are enough for slow-growing species in more settled environments.

Changing habitat conditions affect not only the suitable targets in terms of species and genetic conditions and plant strategy types but also affect higher trophic levels, which can feed back on the vegetation, further complicating the situation. The Tibetan Plateau is one of the largest continuous grassland regions of the globe, and is also facing severe degradation, mostly due to overgrazing by livestock (Wang et al. 2022b). Restoration is gaining momentum there too, but needs to consider interactive effects with climate change and changing grassland use patterns of native grazers. Wei et al. (2023, #this issue) showed that the Tibetan Antelope will undergo significant range shifts during the upcoming decades. This alone does not threaten the species or the grasslands they use. However, human grassland use patterns, including both active grazing and attempts to restore degraded spots by reducing grazing pressure, may result in conflicts with the new native ungulate distribution patterns, which should be considered well in advance to prevent negative consequences.

### **Conclusions and the way forward**

All in all, the restoration of open ecosystems, particularly grasslands, has a long tradition and massive literature that practitioners can draw from. However, climate change creates new challenges, necessitating continuous improvements of old methods and approaches, developing new ones, and utilizing advances of other disciplines, including molecular biology, soil microbiology as well as social sciences. This Special Issue is dedicated to such improvements from all aspects pertaining to grassland restoration. This diversity of grassland restoration research illustrates the increased demand to reinstate these valuable ecosystems globally. Grasslands are functionally and ecologically diverse covering broad gradients of precipitation, climate, soil fertility, and disturbance, so prescribing the right restoration treatment for each of them remains a distant goal (Medeiros et al. 2024).

Although the papers published in this Special Issue cover many of these aspects in temperate grasslands, much remains to be learnt in terms of tropical grassland restoration, particularly in understudied regions such as tropical Africa and Asia (Carbutt & Kirkman 2022, Nerlekar et al. 2022, Medeiros et al. 2024). In South Asia, grasslands, historically perceived as unproductive wastelands by government administrators, have some of the highest rates of

conversion to other land uses such as agriculture, industrial estates and settlements, especially in lowland areas (Vanak et al 2015, Madhusudan & Vanak 2023). The grasslands that remain today are fragmented, overgrazed as their extents have shrunk, eroded, and many are severely encroached by invasive woody plants (Ratnam et al 2016, Madhusudan & Vanak 2023). In Africa, studies are mostly concentrated in South Africa (Carbutt & Kirkman 2022), with large unexplored regions of Sub-Saharan Africa (Medeiros et al. 2024). In the Neotropics, there are more examples of grassland restoration both in temperate (Thomas et al. 2023) and tropical (Pilon et al. 2023) grasslands and savannas, but many knowledge gaps still persist. Across the tropics, these open ecosystems are in urgent need of restoration both to conserve their diversity, and to serve as healthy grazing pastures for livestock. However, efforts at grassland restoration are in their infancy, and methods, including strategies for choosing species to use for restoration, ensuring supply chains of propagules, best techniques for planting in target areas and follow-up actions to ensure restoration success, remain to be systematically determined. Research in these areas, in both lowland and high-altitude grasslands is urgently needed.

Although our fight to mitigate climate change has traditionally been overshadowed by forest restoration, we are learning the significance of open ecosystems in this respect as well (e.g. Bai & Cotrufo 2022), dissolving potential conflicts among our strategies to tackle the crises of climate change and biodiversity collapse. Certainly, the road is still rough ahead, but the encouraging success stories and inspiring new findings of this Special Issue give grounds for high hopes for the upcoming years.

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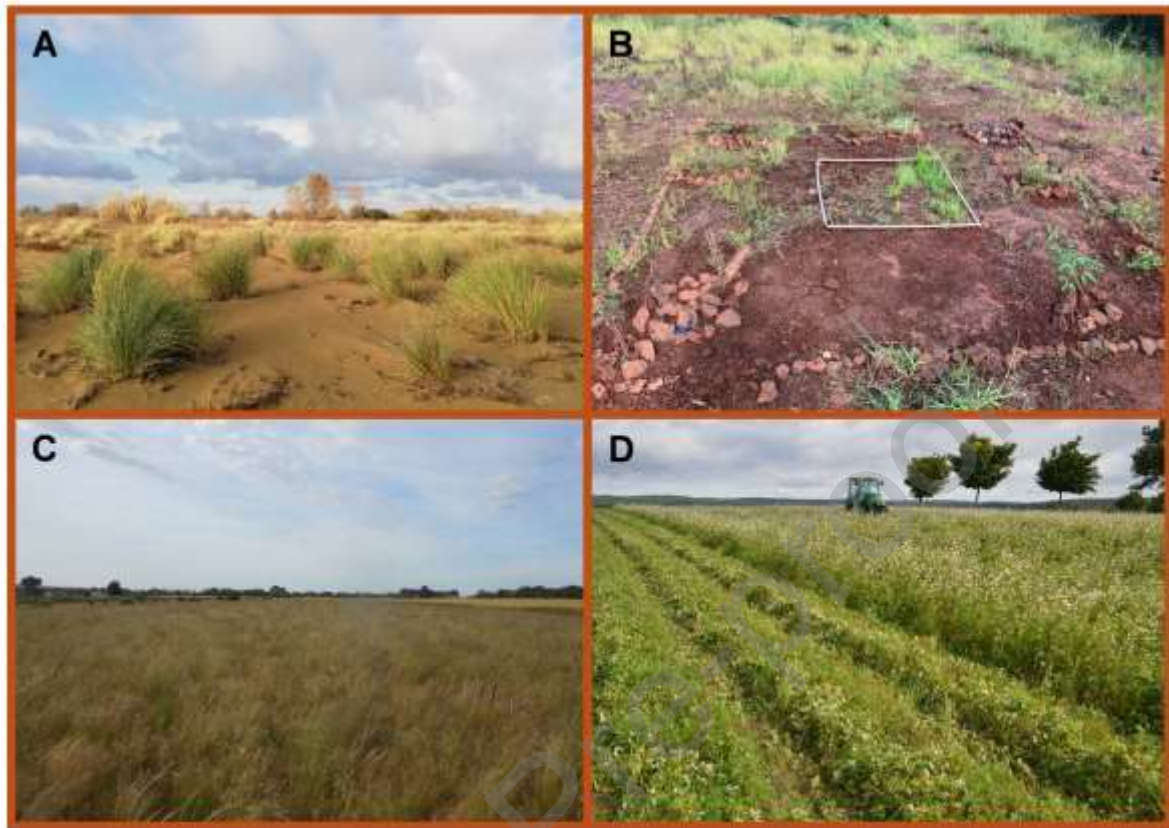
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**Figure 1.** Open ecosystem restorations around the World. A) Shifting dunes along the shoreline with *Calamagrostis arenaria*, restored by LIFE Redune, Italy, Europe; B) Small-scale grassland restoration experiment in Brazil, South America; C) Dry grassland restored on an ex-farming land, Australia; D) Mowing of restored lowland hay meadow in Hayn, Harz Mountains, Germany, Europe.

Photo credits: A – Edy Fantinato; B- Fernando Silveira; C – Paul Gibson-Roy; D – Sandra Dulau.

**Declaration of interests**

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

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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