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Review

The Importance of Soil Seed Bank Function in Studies of Grassland Degradation

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Abstract: The world's grasslands are under increasing threat of degradation. Given the potential for multiple drivers of decline, precise diagnosis of degradation is best achieved by comparison with a local, sustainable grassland community. Comparisons of this kind are becoming increasingly common for regional grassland plant communities, but these studies largely overlook interactions between soil responses to system degradation and the effective functioning of the soil seed bank. Surveys of grassland degradation studies have revealed that only around 5% include information on soil seed bank composition and no one aspect of community structure features across all studies. Furthermore, the majority of studies provide information only on ground coverage, sward biomass or species diversity in the plant subcommunity, with very few including information on the health of the soil seed bank or how changes in the soil environment could drive further deterioration in the plant community size, structure or effective functioning of the soil seed bank. We consider that soil responses to sward degradation are likely to exacerbate rather than mitigate impacts on soil seed bank function, leading to a spiral of system degradation in the absence of timely and targeted intervention. We propose improvements for future studies seeking to diagnose and quantify grassland degradation.

Keywords: plant life cycle; soil permeability; dormancy; Poaceae; soil organic matter

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1. Introduction

Grasslands comprise around 40% of the terrestrial landscape, almost 70% of agricultural land [1–3] and extend geographically from the tropics to the margins of the Arctic Circle [4]. Collectively, grasslands are home to a rich diversity of the world's flora and fauna, and help to support an array of essential ecosystem services, including carbon source–sink balance, pollinator viability, landscape hydrology, pasture and erosion control [5,6]. Stable grasslands also contribute to the economies of many countries by providing a free source of grazing for livestock-based food production. Given their value, there are growing concerns that this vital resource is eroding. For example, it is now estimated that losses of original grasslands continue at a rate of 2% per year in the Brazilian Cerrado [7] and North American Plains, where half of these grasslands have been lost already [8]. Changes in land use has historically accounted for most of these losses, following the conversion of natural grasslands to intensive arable systems or to commercial forestry [9,10] or even to reforestation initiatives [11]. However, the unintended loss of grasslands through degradation has

become a recent focus of intense concern, with almost half of the world's grasslands deemed to be at least partially degraded [12,13]. Indeed, Bardgett et al. [14] point out that grassland degradation now presents a global challenge of such magnitude that it may compromise the world's ability to achieve many of the agreed targets of biodiversity agendas, including those outlined in the Aichi Biodiversity Targets of the Convention on Biological Diversity (CBD) and the United Nations Sustainable Development Goals (SDGs). While there are multiple legislative options available to address the issue of land use change, regulating to limit grassland attrition through degradation poses a far greater challenge.

This review considers three key functional components that collectively contribute to the stability of sustainable grasslands, viz.: plant sward dynamics, soil seed bank dynamics and soil properties. We seek to explore the much-overlooked importance of collecting data that relate to all three elements when seeking to diagnose and grade grassland degradation. We question whether it is appropriate to use the term 'degradation' in the absence of data relating to all three functional elements and finally consider how best to classify grassland degradation in a way that fully reflects the status of each functional element.

2. Definition of Terms

Clear diagnosis of the nature and state of grassland degradation is a prerequisite for its protection, as well as for timely and effective remedial action. However, definitions of the term grassland degradation are often vague, highly variable and at least partly dependent on the subdiscipline of study [15]. Indeed, interpretation of the term frequently emphasizes only one valued aspect of the studied grassland and may focus primarily on species diversity [16,17], increased presence of invasive species [18], a mixture of soil features and species diversity [19], ground coverage [20], reduced agronomic productivity [21,22] or the diminution of ecosystem services [23]. At the same time, however, identification of the drivers of degradation is important if restoration is to be effective and sustainable. It is in this respect that we feel there is a need for broader consideration of the processes that have led to a loss of ecological stability in a grassland deemed to be in a degraded state. Specifically, we contend that the term grassland degradation can be usefully defined as "the loss of stability in the relationship between the plant sward, the soil seed bank and the properties of the soil". We define the plant sward as "all living seedlings and plants within the grassland" and sward dynamics as "temporal fluctuation in the size and species composition of the living plant subcommunity". We define the soil seed bank as "all viable seeds within the soil environment" and its dynamics as "temporal fluctuation in the size and species composition of the viable seed subcommunity in the soil". We define the soil properties of the grassland as "the physical, biotic and chemical attributes of the soil".

3. Sward Dynamics and the Need for Early Detection of Grassland Degradation

Identifying probable causes of degradation is now recognized as being far more challenging than originally presumed and highly context-dependent [4,24]. Diagnosis therefore best starts with a clear vision of the differences between degraded and pristine grasslands within a locality [25]. Degradation is a progressive process and systems have often been crudely divided into three or four broad categories; for example, mild, moderate and severe [26]. While there is broad consensus that more degraded systems may have previously transitioned through lesser degrees of degradation [4,24], there is a marked absence of works specifying the period of time over which grasslands pass between these categories or have remained in such states. For reasons outlined below, the timescale of degradation holds particular resonance when degradation involves disruption of the dynamics of soil seed banks in decline.

The primary ambition for the long-term maintenance of natural grasslands is to identify the degradation process at a sufficiently early stage that remedial action is likely to be tractable, timely and inexpensive. However, this goal is not without problems if grassland classification is based only on the visible, above-ground plant community. Moreover, we argue that reliance on sward dynamics alone to diagnose degradation carries considerable risks. Specifically, there is a danger that the essential role played by the soil seed bank in maintaining community structure and resilience may be overlooked. This gives rise to the possibility of falsely classifying degraded grasslands as sustainable (type 1 error) based on an apparently stable plant sward composition while missing the inability of depleted soil seed banks to maintain sward integrity in the long term, especially following severe growing seasons or sustained mismanagement. Conversely, grasslands that suffer substantial plant losses in unfavorable years may be falsely deemed to be degraded (type II error) even though a fully functional soil seed bank would support recovery of the community from a stress without the need for substantial intervention. It is therefore important to collect data that allows comparison of the relative status of both plant and seed subcommunities from pristine and degraded grasslands within similar localities.

Despite this need, studies characterizing grassland degradation often lack data relating to the functioning, composition or size of the soil seed bank. For example, Lu et al. [27] surveyed studies of grasslands in the Qinghai–Tibet Plateau of China and found that just 8% (5/61) included information on seed density in the soil; 5% (3/61) provided information on species composition of seed samples. We similarly surveyed publications on Chinese grasslands, written in Chinese and English, using the search terms degradation, grassland, soil seed bank and soil on Web of Science. We found 3203 and 20400 publications, respectively, on the topic of grassland degradation, of which only 102 and 232 (3.2 and 1.1%) included information on soil seed banks (Supplementary Materials Tables S1 and S2). However, even when information is available on the composition and size of the soil seed banks of component species in the community, this alone does not provide a clear indication of its capacity to fill sward gaps via seedling recruitment. Moreover, not all seeds present in the soil will be alive and some will be dormant, and these proportions will vary between species and years. Thus, the proportion of seeds that are able to germinate in any one study year is not directly related to the number of seeds present.

Species vary widely in their seed longevity (e.g., [28–31]), germination cues [32–34], dormancy characteristics [35–37], timing and extent of seed predation [38–40], seed penetration of the soil [39,41,42] and in the timing of seed production [43,44]. For these reasons, the proportion of germinating seedlings in a year is not a simple function of the number of seeds present. Many researchers have sought to use demographic modelling approaches to infer soil seed bank viability, although the robustness of these approaches varies according to the type of modelling used, the volume, type and quality of data used for parameterization and the assumptions made [45–48]. Several studies have chosen to directly assess seedling recruitment, either by exploiting naturally formed sward gaps [49] or by artificially creating gaps in sward cover [50] or by comparing both approaches (e.g., [51]). There are consequently several approaches that can be deployed to estimate the functional capability of the soil seed bank to fill annual gaps in the sward of sustainable grasslands created by plant mortality. Functional failure of all or a component part of the soil seed bank to fulfil this purpose will inevitably lead to medium/long-term changes in the plant community structure and/or sward integrity, with the potential for system degradation. Here, we concentrate on this under-studied category of drivers that can lead to grassland degradation, with a particular focus on those relating to changes in the belowground environment.

4. Importance of the Underground Environment as a Cause of Grassland Degradation

There is an extensive body of literature proposing causes of grassland degradation (e.g., [14]), with the vast majority focusing on drivers that directly impact the growing plant component of the community, including overgrazing of Patagonian and Inner Mongolian grasslands [52,53], changes in water availability globally and in northern China [54,55], global temperature shifts [56], salinity [57], the presence of alien invasives [58] and agricultural abandonment, such as that occurring in Estonia [59]. By comparison, there has been relatively little attention paid to how changes in the underground environment can lead indirectly to community degradation. The soil seed bank and the soil environment represent two essential parts of a sustainable and stable grassland, and the disruption of either component has the potential to cause cryptic, delayed or accentuated degradation. Diagnosis of these sources of degradation first requires consideration of their functions in stable, sustainable grassland communities.

4.1. Soil Seed Bank Function in Sustainable Grasslands

The plant and soil seed bank subcommunities of grasslands are in a state of equilibrium over time, with seed return from the plant subcommunity broadly matching losses to the soil seed bank caused by seed death and germination (Figure 1). However, changes in the soil environment associated with degradation have the capacity to alter seed refreshment, longevity or germinability, and so have the potential to disrupt this equilibrium. Soil seed bank refreshment is primarily dominated by factors that affect the growing plants in the community and include climatic conditions during each growing season (for example, in Switzerland [60]), the species of interest [61], grazing pressure (for example, in Patagonia) [52] and the trait profile of plants in the population [62]. At the ground surface, permeability of untilled soils [63] and invertebrate activity (e.g., [64,65]) affect seed burial and its depth profile, the latter study focusing on beetles in Ugandan ecosystems. In contrast, losses from the extant soil seed bank are determined by features of the subterranean environment that affect seed longevity or the proportion of seeds that germinate. There are numerous factors that affect seed losses through mortality, most notably seed predation, as found in the Hungarian Great Plain [66], fungal attack [67,68] (the former study relating to Californian grasslands), unfavorable water relations and anoxia [41,67], seed traits [69], adverse soil chemistry [70] and fire regimes (for example, in Australia) [71]. These features all vary with soil depth and, given the large variance in seed size among community members, are likely to vary on an annual basis between species. Likewise, species respond to very different trigger variables (temperature, water, daylength, frost, fire) and thresholds that initiate germination [72,73]. Seed depth penetration will vary with seed size, with larger seeds being concentrated near the surface unless buried by invertebrate action [74,75] (Thompson et al., 1993; Bekker et al., 1998). Thus, the variables that control losses from the soil seed bank are uncoupled from those that cause its replenishment and vary between member species. This in turn means that equilibrium for most grasslands will be cyclical rather than fixed [76,77]. This feature has the potential to confound early diagnosis of degradation, particularly if the soil environment is overlooked (Figure 2b).

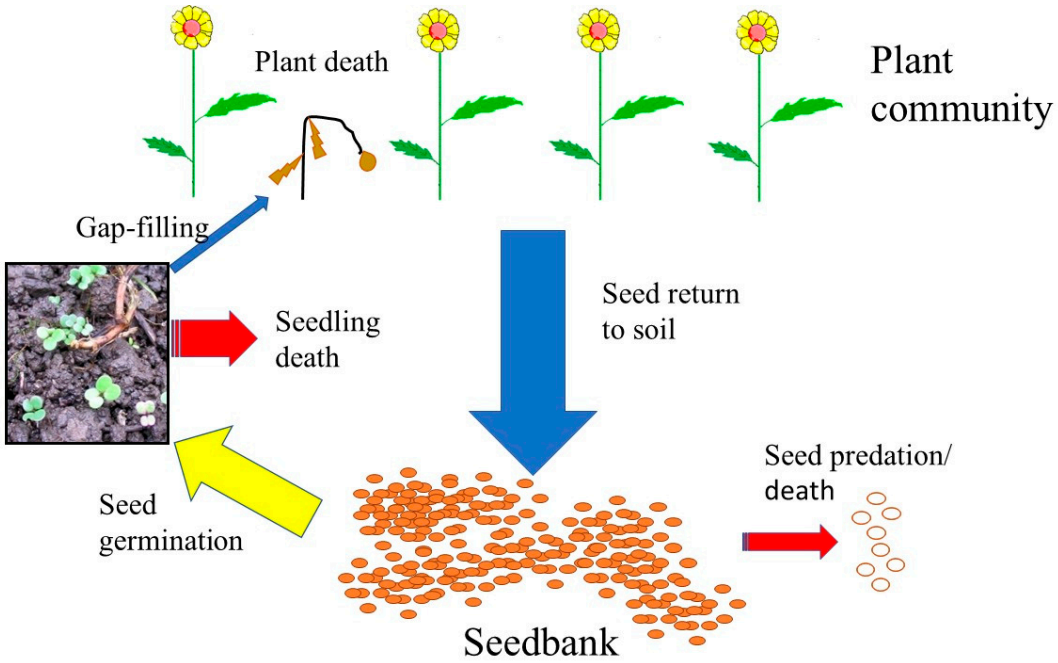

Figure 1. Schematic illustrating soil seed bank function in a sustainable, stable grassland system. The downward arrow indicates large numbers of seeds from sward plants entering the soil seed bank. A proportion of seeds in the soil seed bank are lost to mortality (red arrow) each season and a proportion are lost to germination (yellow arrow). Many of these germinated seedlings die prior to maturity (red arrow) but survive long enough to fill the gaps left by sward plants that died to ensure equilibrium over time between seed return to the soil and seed losses from the soil seed bank.

(**a**)

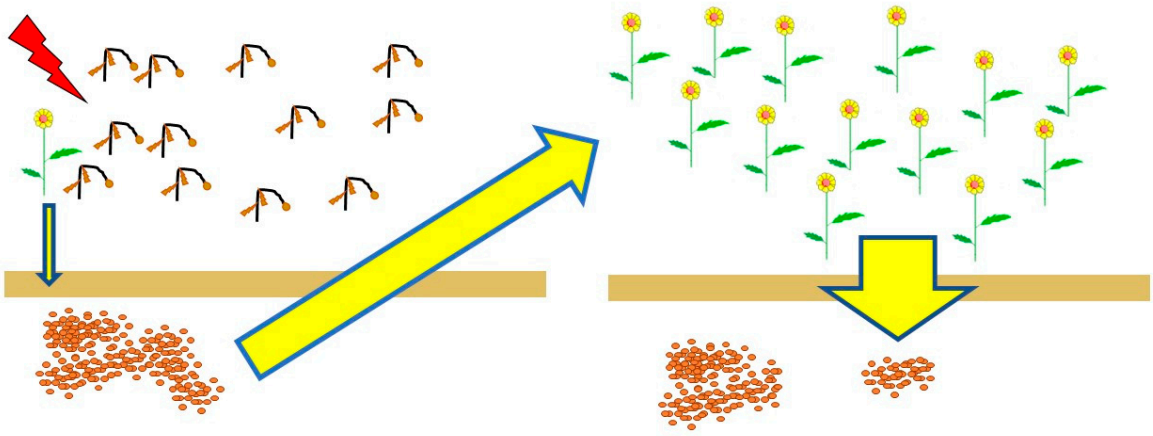

Figure 2. *Cont.*

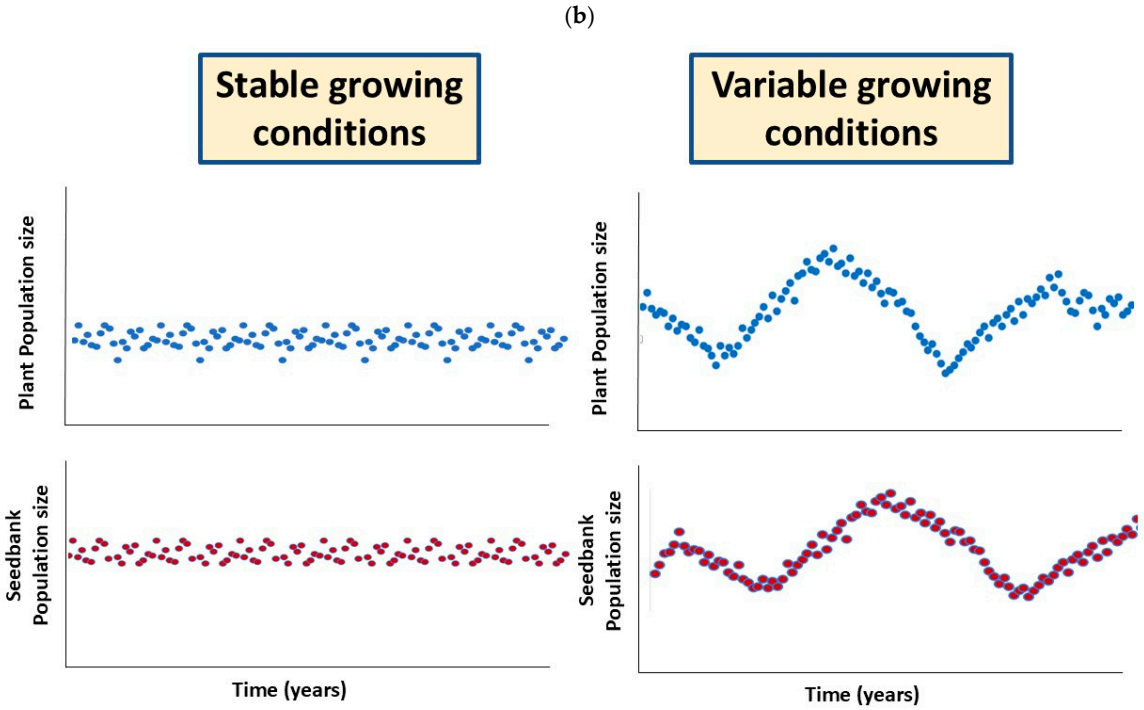

Figure 2. Sustainable soil seed bank function in a variable environment. (**a**) Schematic depicting the soil seed bank-mediated (yellow arrows from left to right indicate reduced seed inputs, germination and reinstated seed inputs) recovery of a plant community following a severe event (red arrow) that killed most plants in the community. (**b**) Graphic illustrating year-to-year variability in plant and soil seed bank population sizes in stable (left-hand graphic) and variable (right-hand graphic) living environment.

4.2. The Soil Environment in Sustainable Grasslands

The soils of functional natural grasslands vary widely according to location and yet typically share a relatively high soil organic matter content and stable aggregation, which promotes surface water infiltration and water holding capacity [78]. Efficient recycling of nutrients by plants is critical in extensively managed grasslands if swards are to persist [79]. These physiochemical conditions are associated with unrestricted root growth supporting a more consistent biomass production [80], and also sustain abundant, diverse faunal and microbial communities [81], as found in German and UK studies, respectively. Natural and semi-natural grasslands are also typically low-input systems that favor fungal over bacterial decomposition pathways. A more heterogeneous habitat and resource leads to domination by fungi, as found in a Dutch field trial [82] and in UK studies of fungal-feeding fauna [81]. Extensive fungal networks often form mutualistic connections between plants, enabling inter-plant transfers of nutrients [83].

The relationships between soil biota and plants are complex and interdependent. For example, arbuscular mycorrhizal fungi have been found to benefit late rather than early succession of Prairie and Moroccan grassland species [84,85]. The importance of the soil microbial community structure to the stability of the soil environment has only recently started to emerge. For instance, Zandt et al. [86] assembled soil microbiome network data over 13 years and showed that grassland community stability is associated with a decoupling of prokaryote and fungal networks, and is facilitated by plant–soil interactions. Several other studies have shown that sustainable, species-diverse grasslands tend to support lower proportions of plant pathogens, as found in a perennial grassland experiment in Minnesota, USA (e.g., [87]). Soil faunal populations are at least partly regulated by the quality and quantity of resources available in the soil, with plants being

the primary resource origin in tall grass prairies [88]. At the same time, macro- and microfauna play an important but varied role in influencing the distribution of nutrients across the soil profile [89]. The diversity, size and vertical distribution of soil fauna varies between stable grasslands, and their impact on system function appears to vary with climate. For example, a temperate European study showed that earthworms, as a guild, become rarer as the climate becomes drier and species diverge in their capacity to redistribute nutrients along vertical and horizontal planes [90]. The soils of stable grasslands are therefore highly complex systems in which equilibrium is maintained by intricate interactions between the plants, animals, fungi and other microorganisms that inhabit them. Any significant distortion to the chemistry, structure or biodiversity of this stable state has the potential to disrupt the key processes of soil seed bank function needed to maintain plant community structure, production and sward integrity.

5. Degradation via Soil Seed Bank Depletion

In simplistic terms, soil seed bank equilibrium is predicated on the balance between replenishment from the plant community (seed return) and losses arising from seed death and germination (Figure 1). Changes in the soil environment have the capacity to alter both processes but this factor has been largely overlooked in relation to grassland degradation. Both are explored in more detail below.

6. Soil Seed Bank Refreshment and Degradation

The return of fresh seeds to the soil of a stable grassland is vital for the maintenance of soil seed bank stability (Figure 1). Plants must divide resources between defense (from herbivory and pathogens), growth, vegetative reserves (ensuring survival to the next flowering season) and seed return (soil seed bank refreshment). It follows that the proportion of resources available for seed production is dependent on multiple abiotic and biotic factors that vary profoundly between years. Several studies have reported wide variance between years in global seed return estimates within grassland communities (e.g., [44,52,91]). Therefore, reliable estimates of seed refreshment are best assembled over several years (e.g., [92–94]).

Several factors have been shown to have a marked effect on the decline in seed production associated with grassland degradation. For example, Gonzalez and Ghermandi [52] showed that overgrazing profoundly reduced soil seed bank replenishment in degraded Patagonian grasslands when compared with sustainable counterparts. In a later study, Shi et al. [95] performed a global meta-analysis to show that grazing reduced soil seed bank size but did not alter species richness or the compositional similarity between the soil seed bank and the aboveground vegetation. Importantly, the authors noted that, globally, the observed effects of grazing on the soil seed bank diverged from expectations set by studies based solely on aboveground vegetation.

Recent research by Li et al. [96] demonstrated that the seasonal timing of soil seed bank assessments has a strong effect on the estimated size and species composition of the soil seed bank. Consistent with prevailing assumptions, the authors found that the soil seed bank size declined in increasingly degraded sites. However, the authors also showed that soil seed bank size was smallest in August (i.e., after seedling germination) and largest in December (after seed return); they also noted that the transient soil seed bank component (freshly returned seeds) was more numerous than the persistent soil seed bank. The seemingly innocuous point of sample collection timing is therefore vitally important when estimating the effective size and diversity of the soil seed bank. It is also noteworthy that the authors reported that only 15 of the 35 species found were present both in the plant and soil seed bank subcommunities.

Application of N fertilizers to natural grasslands is known to increase biomass productivity [97], though at the cost of reduced species diversity [98]. A meta-analysis by Shi et al. [99] recently showed that this trade-off only applies to the application of inorganic N. An initial application of inorganic N is nevertheless sometimes adopted as a remediation measure for severely degraded grasslands [100], especially where nutrients are limiting plant establishment. However, even in systems where exogenous N is not applied, excreta of grazing animals can provide high concentrations in localized and transient patches of nitrogen nutrients [101].

It is well-established that the application of N fertilizer evokes a rapid and direct increase in forage production for dominant grassland species [102–104]. However, species vary profoundly in the scale and nature of their growth response to N fertilizer application [105–108]. This variability changes the competitive dynamics within a community and ultimately leads to a long-term change in sward composition [109,110], usually resulting in a loss of species diversity, particularly when N is combined with other nutrients such as P and K [111]. Given that numerous works have shown that the soil seed banks of many grasslands are relatively short-lived [112–115], it is unsurprising that long-term changes in sward composition lead to significant diminution of soil seed bank diversity (Basto et al., 2015), such that reseeding is often proposed as an essential component of restoration efforts [116–118].

There is also evidence that the application of N can directly impact soil seed bank size and composition. Various fertilizer input experiments have revealed that higher concentrations of soil N are associated with increased losses from the soil seed bank, either via raised germination rates, as described above, or by indirect effects. For example, Basto et al. [70] considered that the net reduction in soil seed bank size associated with N inputs in UK grasslands may in part be attributed to attacks by pathogenic microorganisms. This factor has been identified as a major source of seed mortality in soil, and it may be that one effect of N deposition is to promote microbial seed pathogenesis [32]. Indeed, Phoenix et al. [119] showed that the application of inorganic N to a range of UK habitats increased the susceptibility of plants to pathogen attack. These authors also noted that the application of inorganic nitrogen fertilizers can reduce overall seed production. Finally, in a UK restoration trial, the consistent application of N-based fertilizers led to an increase in the litter layer, which may act as a barrier to the entry of seeds to the soil seed bank [120]. Natural grasslands rarely receive fertilizer N applications, but the patchiness of soil nitrogen in the soil arising from the urine and feces of herbivores may create spatial diversity in the soil seed bank and thus contribute to the species diversity of the grassland.

As stated previously, most nutrients show a decline in total and available pools as grassland system degradation develops. As a result of nutrient resource limitations, seed production and seed germination in northeastern Chinese grasslands both declined progressively [121], leading to soil seed bank and sward erosion in the absence of mitigative action. The propensity of N to stimulate germination and circumvent secondary dormancy [70,122] also means that seed persistence may increase over the same time period as N levels decline. The speed and extent of these trends will naturally vary between species, leading to a gradual change in sward composition as degradative processes progress.

7. Soil Seed Bank Losses

Losses from the soil seed bank arise from seed death or from seed germination (Figure 1). Both processes are affected by conditions in the subterranean environment [123] and so are potentially sensitive to any disruption in the soil characteristics found in stable grassland communities. The importance of each is outlined below.

7.1. Seed Death

Stöcklin and Fischer [30] demonstrated the importance of seed longevity when they reported that grassland species with long-lived seeds had a significantly lower chance of local extinction across a range of Swiss grasslands. In addition to species differences, there is now a growing body of evidence to indicate that a range of soil edaphic factors are important in determining the life span of seeds. For instance, there is a complex relationship between soil depth and seed longevity. Seed size and shape is acknowledged to be important in determining the proportion of seeds found beyond the surface of the soil. Species with larger seeds are presumed to be less likely to penetrate passively or to be moved to deeper layers through the action of earthworms or other animals, as found in the UK and northern European grasslands [124,125]. However, there is a complex interaction between seed size, shape, soil penetration and seed longevity across species. Bekker et al. [41] interrogated a large data set (n = 153) using soil from nine sites and found a loose linear relationship ($R^2 < 0.22$) between seed shape and soil depth across all species and sites. The authors also found that despite wide variance between species, seed longevity in deeper soil layers was significantly higher than those restricted to the surface layer. Similarly, Mašková and Poschlod [126] performed seed burial experiments in Germany across 28 grassland species and found that, although again there was considerable variation between species, seed survival was positively correlated with burial depth. Several other studies have shown that seed predation also reduces significantly with soil depth [39,65,127], adding to the lifetime-extending impact of deep seed burial. For these reasons, it is preferable that estimates of soil seed bank condition should discriminate between species present and should also differentiate between soil depth layers.

In Californian and Canadian grasslands, soil moisture is a key variable that can influence seed longevity. It can favor both seed germination [128] or fungal decay in grasslands [67,129]. There is evidence for both direct and indirect influences of soil moisture content on seed longevity. Several seed burial studies have found that soil water content has significant but contrasting effects on the seed longevity of different species [41,42]. Others have shown that changes in soil moisture alter the seed losses of several grassland species to soil fungi [67,129]. Thus, when changed soil water regimes are identified as a candidate causal agent of altered soil seed bank longevity, fluxes in the soil fungal community should also be considered.

Soil invertebrates' role in soil seed bank dynamics extends beyond that of seed burial. For example, fungal grazers such as Collembola reduce seed mortality attributable to fungal decay and can thereby directly impact soil seed bank dynamics [130]. Other soil invertebrates, such as earthworms [64] and beetles [65], have been implicated in soil seed bank dynamics with outcomes for seedling recruitment. These effects appear to be both invertebrate- and plant-species-specific.

Changes in the soil organic content and its quality in degrading systems may indirectly affect seed longevity, given its core influence on soil biology and physiochemical properties. Several reports across different grassland biomes have found that soil organic matter contents are lower and C–N ratios are higher in degraded grasslands compared with non-degraded Tibetan and South African systems (e.g., [131,132]), and these trends were consistent across different grassland types on the Qinghai–Tibet Plateau [133]. However, the timescales over which such transitions occur remain largely uncharacterized, with pitifully few studies specifying the duration of divergent soil states. Thus, the rate of organic matter depletion and degradation of associated soil properties, along with the potential impacts on soil seed bank dynamics, remains unclear.

Several studies have shown that reductions in stabilizing organic compounds in soil tends to accelerate the dispersal of surface soil aggregates (e.g., [132–135]). This effect is

thought to be facilitated by raindrop impacts and exacerbates surface capping of the soil, with associated implications for the perturbation of passive seed burial processes. Studies on degrading grasslands have shown that soil invertebrate populations also tend to decline with reductions in organic matter content, as seen in the Qinghai–Tibet Plateau grasslands (e.g., [136]). This effect meant that soil macroinvertebrate communities of moderately and severely degraded alpine meadow systems exhibited adversely affected structures, diversity and size as the levels of organic matter and nutrients declined [137]. Shifts in the abundance and composition of invertebrate communities also have the potential to impact seed persistence (e.g., [130]). For example, Pakeman et al. [29] found that seed survival was extended when the soil possessed a low C–N ratio. Likewise, Rotundo and Aguiar [138] reported that seed longevity in Patagonian steppe grassland was extended when present in the litter layer of soil, a feature likely to accumulate where earthworms and other detrivores have been lost from a system.

Soil moisture and broader hydrology features are often limiting for plants in natural grasslands, as indicated by the outcomes of a global meta-analysis [139], and vary with season and location. Differences in the physical condition of soil, for example pore size distribution as affected by texture and aggregation, may either mitigate or exacerbate climatic stresses, such as changes in key rainfall patterns (e.g., [140]). Nevertheless, in a review of research on grassland degradation due to grazing in the Qinghai–Tibet Plateau, Lu et al. [27] found none of the listed studies had investigated soil physical indicators in the affected locations or investigated their impacts. For this reason, there is an urgent need to refocus on differences in soil moisture characteristics between sustainable and degrading grasslands. In rare exceptions, Nui et al. [141] reported that degrading systems globally have soils with reduced surface water infiltration and lower water conservation, while Yuan et al. [142] noted that degradation in the Qinghai–Tibet grasslands was associated with increased soil bulk density. In similar systems soil changes of this kind led to more of the rainfed water resource being lost as runoff, a greater susceptibility to evaporation and limited retention of water within the soil profile [143]. Increased overland flow alone means that surface seeds may be redistributed laterally or following extreme rainfall events, lost entirely along with surface soil to sheet erosion [144].

In line with trends in organic matter content, several works have reported that stocks of total N and P (but not K) decrease as semi-tropical South African and Qinghai alpine systems degrade (e.g., [132,145]). Differences between sustainable and degraded soils in plant available nutrients are less consistent but, in most cases, these also decline with degradation. As noted above, fertilizer applications have been shown to affect both the production and persistence of seeds [146], due to increasing soil concentrations of nutrients. As noted previously, nutrient concentrations across bulk soils in natural grassland soils are likely to be markedly lower except when associated with patches of excreta as found in grazed UK grasslands [147], leading to marked spatial heterogeneity of the soil that would naturally attenuate as stocking rates decline or in the event of agricultural abandonment. Thus, in addition to the need for basic information on the longitudinal variation of litter, N, P and K when comparing soils from pristine and degraded site, it is also important to include sufficient sample replication to provide information on the degree of spatial heterogeneity between study sites. These data sets can then be associated with changes in soil seed bank function and help enable the design of robust restoration strategies.

7.2. Losses from Germination to Replacement

The primary function of the soil seed bank is to replace gaps in the sward following the death of individuals (Figure 2a). By definition, this replacement process causes depletion of the soil seed bank. In a stable grassland, this process will occur without significant

change to the sward in terms of coverage or species composition. Sward gaps appearing within a stable grassland through plant death will be matched by their replacement from the emergent seedling subpopulation. In balance, the proportion of seedlings surviving to maturity should broadly equate to the species profile in the extant mature plant community. However, factors that distort competition between species to fill the gaps available can lead to changes in the sward community. In extreme cases, when insufficient seedlings survive to maturity, then sward coverage will decline at the expense of expanding bare ground. This provides the most obvious symptom of grassland degradation that is widely used in the literature (e.g., [15,136]). In the earlier stages of degradation, however, more subtle changes in seedling competition can lead to a change in plant community composition. There are several drivers that can perturb the existing seedling survivorship profiles of a grassland community.

Losses that occur between germination and sward gap replacement therefore represent inefficiencies in soil seed bank function that vary with context and species. The germination of non-dormant, viable seed varies between species and contexts but, as noted above, is generally dependent on abiotic variables such as soil moisture content, light and temperature and fire [34,71]. The first three of these factors are likely affected by the degradation itself and therefore impact germination rates from the soil seed bank as found in Spanish semi-arid grasslands [148]. Perturbation of any of these variables outside the appropriate range for the species can lead to either secondary dormancy (e.g., [35,149,150]) or poorly timed germination that increases seedling death rates and so potentially reduces soil seed bank function efficiency. Several works have linked changes in the environmental triggers associated with the variable increase in secondary dormancy between species [36,37]. These plastic responses, generally instigated by light or temperature, act to buffer the soil seed bank against excessive losses via germination at inappropriate times. However, even for seedlings that germinate at an appropriate time, there are numerous factors often identified as drivers of degradation that affect the proportion of germinated seedlings that survive to reach maturity.

Increased soil salinity is a particular feature reported in some degrading grasslands [151,152] in the Qinghai–Tibet Plateau and northeastern Chinese grasslands, generally associated with shallow saline groundwater. This problem may be exacerbated by changes in rainfall patterns and consequential reduced leaching of salts [153]. In addition, adverse physical conditions in the soils of degrading systems may restrict water (and salt) movement to depth (e.g., in some Qinghai–Tibetan regions [154]). Many studies have shown that increased salinity directly reduces germination rates (secondary dormancy) (e.g., [57,133,155,156]) but also slows plant growth rate [33,157]. Both processes extend the time needed for sward gap closure. In research on prairie systems, such effects are highly variable between species [156], meaning that increased soil salinity is likely to change the species composition of sward replacement as well as reducing global biomass production.

Altered soil disturbance regimes also have the potential to affect survivorship among competing seedlings. Jakobsson and Eriksson [51] compared the survival rates of seedlings from 50 species sown into either disturbed or naïve temperate grassland soils. Recruitment rates varied widely between species, and disturbance improved these rates among only 16 of the 45 species for which sward recruitment was found to be seed-limited.

The ingress of an invasive species into a grassland community also has the potential to distort seedling survival profiles for at least some of the native member species. The absence of natural herbivore pressure can provide seedlings of unpalatable invasive species with a competitive advantage over native seedlings. Brian et al. [158] elegantly illustrated the pressure imposed on native seedlings by arthropod herbivory in a Minnesota, USA field trial. By contrasting the survival of untreated seedlings with that of those that were hand-

painted with pesticides, they found a 56% improvement in survival on average. Repression of arthropod herbivory in ungrazed plots through the application of insecticides had the greatest effects on sward recruitment during the autumn months. The importance of herbivore pressure extends beyond any advantage that may be conferred to invasive species. For example, Watt and Gibson [159] constructed herbivore exclusion experiments at various seasonal time points on calcareous European grasslands and found that, in plots heavily grazed by sheep, forb seedlings had higher establishment rates than grasses, but annual seedlings belonging to the grass genus *Bromus* were better able to fill small sward gaps than forbs. Overall, heavy sheep grazing reduced sward coverage and the proportion of the area covered by grasses.

Changes in soil structure or chemistry may also evoke changes in the survivorship expectations of the seedling subcommunity. The exogenous application of nitrogen-based fertilizer is associated with a decline in Inner Mongolian grassland species diversity (e.g., [160,161]) but has a positive association with plant growth and overall biomass productivity in Australian grasslands [162]. The beneficial effects of exogenous N and P are highly species-dependent [160,163] and have the potential to severely skew seedling survivorship rates in favor of the few species that benefit most. This, in turn, drives a loss of species richness in the grassland. For example, Basto et al. [70] found that UK soils receiving more than 140 kg N/ha per year experienced a reduction in soil seed bank size, species richness and in the abundance of forbs, sedges and grasses. The authors identified a large array of factors that contribute to the observed decline, including the well-known property of nitrate, nitrite and ammonium to stimulate seed germination [164,165] and so diminish soil seed bank size. The increased flush of germinated seedlings associated with this effect would occur with no concurrent increase in the sward gaps available and so lead to a reduction in soil seed bank size without any visible change in the plant community. Thus, over time, the soil seed bank diminishes in size to such a point that it becomes insufficient to maintain sward integrity, initially for the less abundant seed species but ultimately for the entire community [166]. Again, the net effect is an increase in seedling competition without associated changes to sward gap availability. Elsewhere, Gao et al. [167] provided empirical support for the impact on seedling competition when they found that exogenous application of nitrogen fertilizer directly increased overall *Leymus chinensis* seedling biomass in Songnen (NE China) grasslands, where this species had emerged to dominate ground cover.

Invasive species of grasslands are notable for their tendency to rapidly increase their proportion of cover soon after first appearing. Here again, there are several studies illustrating the importance of high relative seedling competitiveness of invasive grassland species when compared to native grasses, including *Bromus* in the prairies [168], *Pennisetum setaceum* in Mediterranean grasslands [169] and *Spartina alterniflora* in coastal grasslands in China [170]. In a few cases, the competitiveness of invasive seedlings was found to be enhanced via allelopathy (e.g., [171,172]). There is also evidence of seed-to-seed allelopathic effects. For example, *Ligularia virgaurea* seeds in Qinghai–Tibetan soils have potential allelopathic effects on seed germination, mean time to germination and root growth rates of native grass species [173]. At the same time, there is evidence that some invasive species alter their rhizosphere biota and that these alterations interact differently with the seedlings of other species. For example, soil inoculation with *Stellera chamaejasme* biota favored the early growth of forbs but inhibited that of grasses [174], with differing AMF and a relative abundance of plant pathogens within their fungal populations offering one possible explanation for these findings.

Thus, changes in the abundance and/or relative competitiveness of seedlings in a stable grassland can lead to the distortion of community composition and/or to the loss

of cover. The ability to detect any changes in recruitment efficacy therefore has value in discriminating between stable and unstable grassland communities.

8. The Scope for Improved Diagnosis of Grassland Degradation

Ultimately, we argue firstly that sustainable grassland communities are predicated on a dynamic stability. The relative importance of the plant and soil seed bank subcommunities in ensuring their equilibrium over time is both complex and uneven. The state of the plant community is primarily important for regulating seed return and therefore controls the process of soil seed bank replenishment. The number of gaps appearing in the sward is determined by the strength and number of stressors experienced by mature plants in the community, with most of these stresses applying to the above-ground environment (e.g., adverse grazing management, pathogen attack, climatic conditions, etc.). However, the structure and composition of the plant community is in turn heavily dependent on the effective functioning of the soil seed bank. Sward gap replacement relies on fresh germination from the soil seed bank. The capacity to generate sufficient seedlings to fill sward gaps is dependent on the size and composition of the active (non-dormant) portion of the soil seed bank and is therefore most sensitive to changes in the soil environment as a consequence of system degradation, as described above. We conclude that the net effect of these changes in the soils of degraded systems on the soil seed bank is likely to negatively impact seed refreshment, persistence and germination. While there is a paucity of chronological data, we can only speculate that nutrient depletion and soil physical deterioration in soil are most likely to occur after changes in the sward or soil seed bank, but once established, they will probably accelerate the degradation process. However, the number of germinating seeds required to replace the lost plants from the community varies between species, with some more able than others to survive and successfully grow to fill available gaps. Such interspecific differences in seedling survivorship are partly determined by innate features of the species concerned but are also reliant on the climatic growing conditions during the establishment period. Importantly, this variability in the competitiveness of different seedling species means that soil seed bank profiles alone typically provide poor indicators of sward composition. We therefore contend that more information is needed on the relative competitiveness and survival of seedlings during this phase of the life cycle if we are to be better able to assess the functional stability of the study grassland. At its simplest, this could be achieved through direct comparisons of the sward composition in the community with those generated in plots following plant removal (e.g., [51,159]).

A second issue originates from the simplicity and inconsistency in the use of the term ‘degraded’. In this review, we have focused on the loss of stability as the starting point for degradation rather than the loss of any of a grassland’s favored attributes. This choice does not disregard the importance of the desired attributes to various stakeholders, but we contend that the first priority should be to ensure grassland is stable and self-sustaining, regardless of whatever positive social, economic, biodiversity or agricultural features it may possess. We also argue that the term ‘degradation’ is too simplistic and too frequently is used indiscriminately to describe changes to one or more attributes of the community [15–17,20–22] or the diminution of ecosystem services [23]. This inconsistency severely complicates comparisons between studies. Instead, we propose that future studies should explicitly state which life stages or components of the system are being judged to be degraded, and which aspects have not been addressed. Ideally, comprehensive studies would provide information on degradation that relates to plants, the soil seed bank, the soil, soil fauna and ideally even the microbiota, where degradation is defined as a change from the reference sustainable grassland comparator. To date, there has been an imbalance, for

example, between soil microbial and invertebrate investigations and between soil chemical and physical properties. It cannot be assumed that all of these component aspects of a grassland will change in synchrony; therefore, the provision of information on each aspect of the community helps identify which aspect changed first and ultimately helps provide more robust models of the study system. By definition, this approach means that the majority of historical studies have only provided information on the degradation of the plant community, with a minority of works also addressing other aspects. Specifying in this way which aspect of the grassland has been assessed also allows for more meaningful comparisons between works.

A third area of grassland degradation studies that we feel requires future attention is the time frame over which studies are conducted. As outlined above, natural fluctuations between growing seasons can lead to asynchrony between replenishment of the soil seed bank and gap-filling of the sward. Thus, the soil seed bank and plants of a grassland community can be in a buffered cyclical equilibrium, in a manner broadly analogous to predator–prey population oscillations (e.g., [175]; Figure 2b). This means it is important that sufficient years are included in a study to distinguish between the normal variability expected for a system in equilibrium and one that has lost stability and is becoming truly degraded. Furthermore, comparative studies have been based on the endpoints of degradation (e.g., severe) rather than the pressures and timescales leading to these outcomes. As a result, it is not possible to determine the rate of any changes that have occurred. We would also like to encourage more studies to follow the lead of earlier investigations [96,176] by accounting for the seasonal influence on the transient component of grassland soil seed banks via the careful timing of sampling dates.

9. Implications for the Future of Grassland Restoration

The presence of a fully functional soil seed bank provides important system resilience for sustainable grasslands. The loss of capacity to buffer against the impact of distortions to the composition of the growing plant subcommunity vary according to the scale, nature and timing of the stressor(s) concerned. Restoration of lost resilience would be highly dependent on possessing a clear understanding of the extent and nature of soil seed bank function loss. In some scenarios, passive recovery may be possible, especially where the plant community has suffered from exposure to moderate stress events over a short time period and soil impacts are limited. However, in instances where the stress exposure has been particularly severe or recurrent, both soil seed bank function and soil properties may be affected. In these circumstances, artificial reseeding efforts may be needed to augment the denuded soil seed bank to its former state and further measures may be needed to reinstate the underpinning soil properties. Achieving this aim naturally requires data on the size, composition and depth profile of soil seed banks from pristine and degraded sites so that seed replenishment or sward augmentation accurately targets areas of deficiency. However, in some situations there is also a danger that associated changes in the soil environment could disrupt the longevity and/or germinability of even a restored soil seed bank. Here, there is a risk of feedback leading to a degradation spiral involving the deterioration of soil nutrient and water availability, microbiota and complex shifts in the soil biotic community and soil physical conditions, such that the plant–soil seed bank relationship is irreversibly changed (Figure 3). These scenarios may lead to permanent changes in sward and soil seed bank composition and thus cause permanent community change. Where these changes increase bare ground coverage, there is also an increased soil erosion risk. The effectiveness of restoration is therefore at least partly dependent on early diagnosis of the extent and type of degradation. Where both aboveground and belowground components of the grassland systems have degraded, recovery to a fully functioning system may be unlikely or at best

require informed action over decades; alternative system states may be a more realistic restoration target.

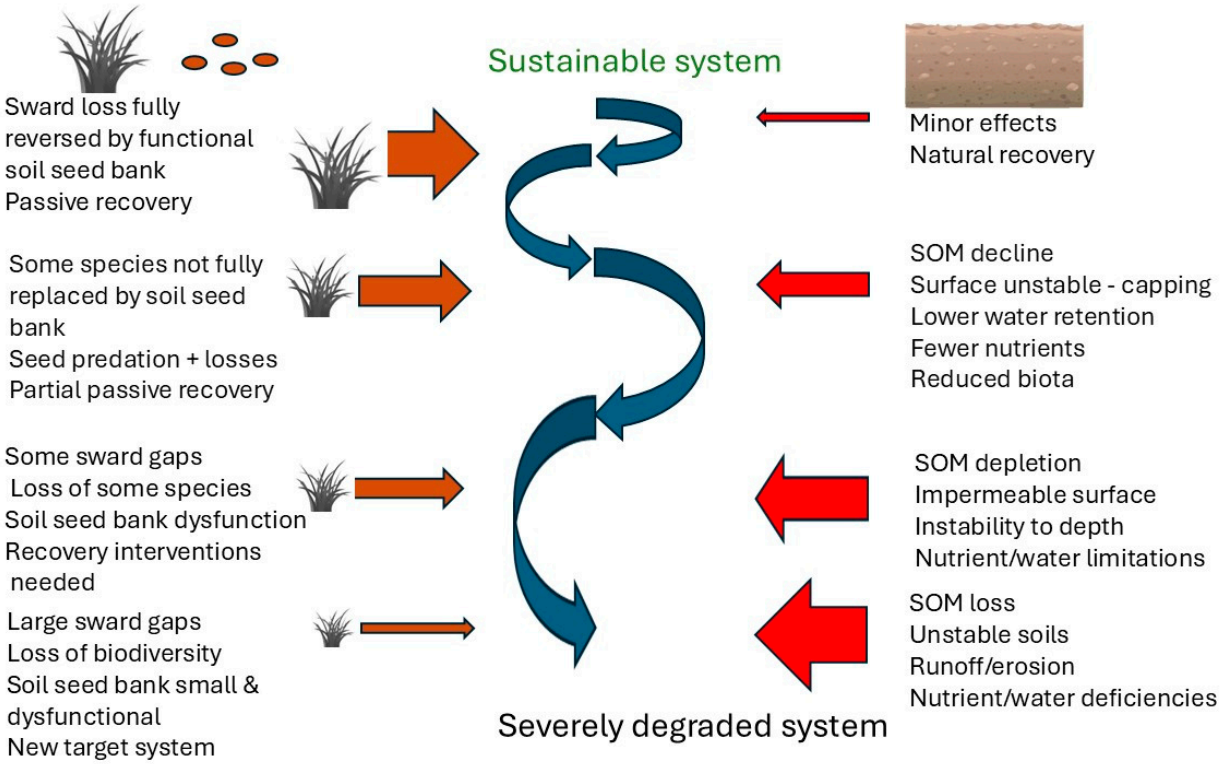

Figure 3. Plant–soil and soil–plant feedback during system degradation. Diminishing returns of organic matter (brown arrows) and reduced surface cover as plant growth declines lead to a deterioration of soil conditions. Deteriorating soil conditions exacerbate (red arrows) the decline in productivity and enhance surface seed predation to set up a degradation spiral. Barriers to full recovery become more difficult to overcome with each degradation cycle.

10. Conclusions

We would like to encourage far greater attention to changes in the underground environment that have the capacity to distort the size, composition or functioning of the soil seed bank. We would particularly like to advocate for even more effort to be placed on interactions between growing plants and their associated megafauna, microfauna, bacteria and fungi as a source of disturbance of the normal functioning of grassland soil seed banks. Looking ahead, pronouncements of degradation would be far more useful if they specified which aspects of the plant–seed–soil system have changed relative to pristine systems. Ideally, this should include comparisons of plant communities, the long-term (non-transient) soil seed bank, and seedling-derived and extant sward compositions (seedling survival). The net impact on the grassland system of changes in soil properties during degradation processes is likely to have exacerbated plant driven responses; key soil properties thus need to be recorded. Ideally, timescales of degradation should be transparent in any system comparison studies. These sources of information will allow for more targeted, timely and effective restorative management.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17010042/s1. Table S1: Published literature on China studies reported in Chinese. Table S2: Published literature on China studies reported in English.

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