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REVIEW ARTICLE

Grassland seed bank and community resilience in a changing climate

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Plant dispersal and persistence strategies play an increasingly important role in the face of changing climate. Evaluating the restoration potential of soil seed banks as an important component of community resilience is crucial for developing effective grassland conservation and restoration strategies under climate change. Soil seed banks can act as a source for vegetation recovery by preserving species and supporting their establishment by assisting persistence and recolonization. In a systematic review of field and experimental seed bank studies, we evaluated the potential of seed banks in buffering climatic extremities and fluctuations. We found 42 papers testing the first-order (temperature and precipitation changes) and second-order effects of climate change (flooding and fire) on the seed bank in grasslands. We showed that persistent seed banks can support passive restoration especially in wetlands and habitats where unpredictable and frequent disturbance was typical in the historical timescale. We found that active restoration by seed addition will be most important in less disturbance-adapted habitats characterized by species with transient seed banks. In such cases, the introduction of native matrix species that can tolerate the predicted climatic change should be prioritized at degraded sites.

Key words: climate change scenarios, drought, fire, flood, grassland restoration, resistance, review, seed persistence

Implications for Practice

- Persistent seed banks can support passive restoration especially in wetlands and habitats where unpredictable and frequent disturbance has been typical in the historical timescale.
- We suggest considering forecasted climatic changes even in today's restoration projects. Active restoration by seed addition will be most important in less disturbance-adapted habitats characterized by species with transient seed banks. For the restoration of long-term resilient communities, the introduction of native species from the regional species pool that can tolerate the predicted climatic change should be prioritized at degraded sites.
- Species with transient seed banks are especially threatened by climatic changes in many habitats. For their protection, species introduction projects in multiple years will be necessary.

Introduction

Global climate change has fundamental effects on precipitation and temperature patterns worldwide. Several models have been used to forecast future climatic changes (Arnell 1999; Trenberth 2011). The surface temperature is forecasted to increase globally, associated with an increase in winter temperature, the number of warm days and nights, and the length of warm periods (Stocker et al. 2013). Regarding precipitation, most studies expect the "wet-get-wetter" and "dry-get-dryer" effects to occur in most regions (Stocker et al. 2013). In the future, extreme heat and precipitation events are expected to occur more often (Beniston et al. 2007; Luber & McGeehin 2008).

Plant dispersal and phenotypic plasticity have a decisive role in shaping plant species composition of terrestrial habitats under changing climate. Species with good spatial dispersal ability are predicted to migrate poleward or towards higher altitudes due to the forecasted increase in temperature (Walther et al. 2002). Proper microhabitats acting as climatic refuges as well as phenotypic plasticity of plants may also help species to buffer changing environmental conditions to some extent (Valladares et al. 2007). Climate-induced changes in plant phenology may result in shifts in germination, flowering, and seed maturization periods (Cleland et al. 2007). Species that cannot cope with the effects of climate change will face the risk of local, regional, or global extinction. The predicted extinction rates vary between models, species, variables, and buffering mechanism considered. According to Thomas et al. (2004), the extinction rate is higher for species with low dispersal ability (>50%) than

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that for species with high dispersal ability (maximum 27%) in minimum- and medium-level climate change scenarios.

Many studies in different parts of the world aimed at understanding the responses of plant communities to changing climate, the majority of them focusing on the changes of the aboveground vegetation. Despite the importance of the topic, the response of soil seed banks to climate change has rarely been studied and is poorly understood. Ooi (2012) summarized the studies on the potential effect of changing climatic factors on seed longevity and seedling recruitment. Seed dormancy and germination changes driven by changing temperature and water supply regimes were studied by Walck et al. (2011). However, the evaluation of the role of seed bank of native species in community's resistance and composition in the face of climate change is still lacking.

Aims of the Study

The aim of our study was to link the studies on climate change and soil seed bank with those assessing second-order effects of climate change (flooding, inundation, drought, and fires) to evaluate the potential of the seed bank to buffer climatic extremes and uncertainties. We selected grasslands as model ecosystems. We formulated the following questions: (1) How do the forecasted changes in temperature and precipitation influence the density and species composition of soil seed bank in grasslands in tropical and temperate ecozones? (2) Is the seed bank of native species able to buffer the second-order effects of climate change (flooding, drought, and fires)? (3) How can soil seed bank support the resilience of existing grassland communities and act as a basis for restoration actions in the future? We aimed at identifying knowledge gaps and call attention to the necessity of incorporating seed bank research in the conservation and restoration projects in our changing climate.

Methods

Literature Search

We used ISI Thompsons Web of Knowledge to find online articles about the soil seed bank of grasslands all around the world. The keywords used were "seed bank" and "grassland" or "wetland" or "meadow" or "steppe" or "prairie" or "field" or "sward" or "savannah." This literature search resulted in a list of 2,431 articles. We screened the titles and abstracts and considered only those that focused on the soil seed bank of grassland ecosystems and omitted irrelevant studies, for example single-species studies or studies on ex situ conservation. Finally, we selected 308 articles for detailed assessment. From these, we considered those which studied the first-order or second-order effects of climate change on grassland seed bank, in total 42 articles. We used the following inclusion criteria.

Habitat Types. We considered studies performed in any kind of open landscape, including grasslands, wooded grasslands, and wetlands. For model habitats, we selected grasslands, because they occur under various site conditions all over the world and often act as biodiversity hotspots (Dengler et al. 2014; Valkó et al. 2016). We categorized grasslands into four major categories based on their geographical position and moisture regimes as follows: (1) tropical and subtropical wetlands, (2) tropical and subtropical grasslands, (3) temperate wetlands, and (4) temperate grasslands.

Effects of Climate Change. We considered both experimental and field studies on the seed bank that analyzed the first-order or second-order effects of climate change. (1) Our primary goal was to include studies about the first-order effects of climate change, that is changes in temperature and precipitation. For this purpose, the effects of experimental climate manipulation treatments on the seed bank are the most proper sources, but we also included observational studies about the seed bank of grasslands along altitudinal gradients. (2) To further explore the effects of climate change on the soil seed bank, we also included studies about the second-order effects of climate change. These studies included papers on the effects of drought, flooding, and fire, which all are important second-order effects of climate change (Lesk et al. 2016).

Seed Bank Data. We considered those studies that presented qualitative or quantitative data regarding the density and richness of species or functional groups in the seed bank of grasslands.

Climatic Changes

For illustrating climate changes, we used the predicted changes of air temperature and precipitation for the 2016–2035 time interval, based on Coupled Model Intercomparison Project Phase 5 (CMIP5; Taylor et al. 2012). For predictions of the CIMP5, the reference period was 1986–2005 and the projections were made under the Representative Concentration Pathway (RCP4.5) scenario, using the 50th percentiles. According to this scenario, we categorized the predicted climate change in localities of the 42 available seed bank studies into two scenarios: (1) increased precipitation in the growing season and (2) decreased precipitation in the growing season (Tables 1 & 2; Fig. 1). We were unable to consider the potential effects of sea level rise on the particular study sites.

Results and Discussion

Tropical and Subtropical Wetlands

We found four studies from tropical and subtropical moist grasslands. According to the predictions, the temperature will increase by 0.5–1°C and the precipitation will increase on average by 10%. Increased precipitation in the growing season has been predicted for northern South America, South, and Southeast Asia (Table 1; Fig. 1). All four papers focused on the effect of the flooding regime on the grassland seed bank. Based on the forecasted climate change, flooding is expected to

Table 1. Seed bank studies evaluating the first- and second-order effects of climate change in tropical wetlands and grasslands. Numbers in the first column refer to numbers in Figure 1. Arrows represent the direction of significant changes in seed density and seed bank species richness. Notations: ~, not tested/no change; NA, no data.

No.	*Habitat Type*	*Effects of Climate Change*	*Seed Density*	*Species Richness*	*Country*	*References*
Tropical and subtropical wetlands						
Prediction: increased precipitation						
1	Inland wetland	Flooding	↑	~	Brazil	Bao et al. (2014)
2	Inland wetland	Flooding	↑	↑	Brazil	Oliveira et al. (2015)
3	Inland wetland	Flooding, vertical position	~	~	China	Lu et al. (2010)
4	Wet grassland	Flooding	~	↑	Bangladesh	Harun-or-Rashid et al. (2009)
Tropical and subtropical grasslands						
Prediction: increased precipitation						
5	Dry shrubland	Vertical position	↑	↑	Ecuador	Espinosa et al. (2013)
6	Savanna grassland	Fire, heat, smoke	↑	↑	Australia	Scott et al. (2010)
7	Woody savanna	Heat, smoke, precipitation	↑	NA	Tanzania	Anderson et al. (2012)
8	Woody savanna	Fire	↓	↓	Brazil	Mamede and de Araújo (2008)
Prediction: decreased precipitation						
9	Dry grassland	Fire	↓	↓	United States	McLaughlin and Bowers (2007)
10	Dry grassland	Fire, heat, smoke	↑	↑	Australia	Wright and Clarke (2009)
11	Savanna grassland	Fire, heat, smoke	↑	↓	Australia	Williams et al. (2005)
12	Woody savanna	Fire	~	~	Ethiopia	Gashaw et al. (2002)
13	Woody savanna	Fire	~	~	Brazil	de Andrade and Miranda (2014)

increase in these regions because of the forecasted increase in precipitation.

In these flood-dependent ecosystems, the highest density of seed bank was generally found in the lowest and wettest elevations (Bao et al. 2014; Oliveira et al. 2015) or seed density was not affected by flooding frequency and duration (Harun-or-Rashid et al. 2009; Lu et al. 2010). This suggests that these ecosystems will be able to maintain their current species composition if flooding frequency or duration will increase, because flood-adapted plant species will be able to recolonize the sites from the seed bank. Increased flooding activity may even increase grassland area at the expense of mangrove in Bangladesh (Harun-or-Rashid et al. 2009). In this region, the seed banks of grassland, swamp forest, and sand dunes are mostly composed by typical grassland species (grasses, sedges, and herbaceous species). Increased cyclonic events and flooding activity, lead to gap formation, which favors their establishment from the persistent seed bank at the expense of mangrove forests whose dominant species are scarce in seed bank. In the Pantanal wetlands, increased flooding activity will probably also maintain or even increase the area of native grasslands. Here flood acts as an environmental filter, which suppresses the nonflood-adapted invasive *Urochloa humidicola* in the seed bank (Bao et al. 2014).

Tropical and Subtropical Grasslands

We found nine studies from tropical and subtropical grasslands. The rate of temperature increase varies between 0.5 and 1.5°C at all sites. For four sites, situated near to the coastal part of the continents, climate models forecast precipitation increase by 10%. For five sites, generally situated in the central parts of the continents, 10% decrease in precipitation is predicted (Table 1; Fig. 1).

Out of the nine studies, one directly compared seed banks of grasslands in different climates (Espinosa et al. 2013). In tropical dry scrub in the Ecuador, Espinosa et al. (2013) recorded higher species richness and seed density upward along the altitudinal gradient. They argue that climate acted as an environmental filter for seed bank formation; the increased seed density and species richness is likely to be caused by the increased amount of precipitation. Under the more favorable conditions of higher altitudes, more species are able to survive and reproduce, which leads to an increased seed production, seed density, and seed bank species richness. Thus, the forecasted increase in precipitation will be favorable for the seed bank formation in these dry tropical scrub ecosystems.

The other eight studies focused on the effects of fire regimes and fire components on the grassland seed bank (see Table 1). The predicted climatic change will probably modify fire regimes in the tropical and subtropical regions by altering the ignition and fuel parameters (Flannigan et al. 2009). Higher temperature will increase the probability of fire ignition and predicted changes in precipitation can affect the amount of fuel. Increased amount of precipitation will probably lead to a more intense accumulation of combustible biomass, which provides fuel for wildfires; decreased amount of precipitation will likely have the reverse effect. Of course, these general trends can be regionally modulated by several other factors, such as human population density, land use, and fire policy.

In those dry ecosystems, such as Australian savannas and Arizonian dry grasslands, where seasonal precipitation dynamics are well predictable, long-lived seeds form only a minor part of the soil seed bank (McLaughlin & Bowers 2007; Scott et al. 2010). Even though transient seed banks have been a successful strategy under the recent climate regime, such species might not be able to cope with the expected future climate variability and the larger temporal gaps of conditions unsuitable for growth.

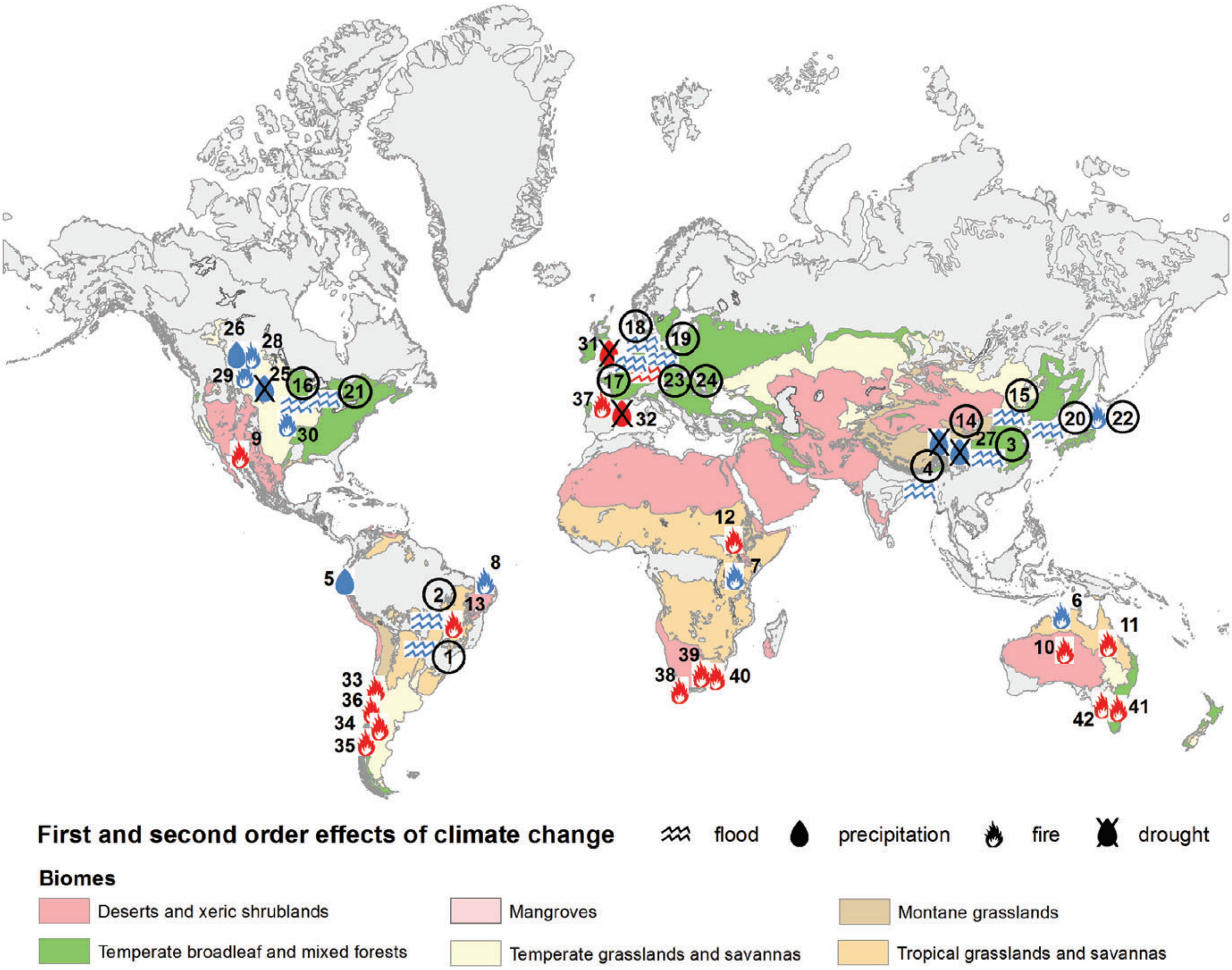

Figure 1. Location of the soil seed bank studies included in the systematic review. Numbers correspond to the study numbering in Tables 1 and 2, wetlands are designated with a circle. Notations for colors of climate change prediction symbols: (blue symbols) increased precipitation is forecasted in the study site; (red symbols) decreased precipitation is forecasted in the study site. Biomes not covered by our study are marked with gray.

Scott et al. (2010) found that high-intensity fires are important drivers of seed germination, but low-intensity fires do not have such effect. Both heat and smoke support seed germination in these fire-prone ecosystems, especially in the dry season, where most of the seeds are in the dormant phase (Scott et al. 2010). The seed bank of native Arizonian dry grasslands is composed of higher-density seed bank, dominated by native species, while the seed bank of burned exotic grassland contains mainly exotic species and fewer seeds (McLaughlin & Bowers 2007). In Arizonian dry grasslands, most native species have a transient seed bank, which means that eradication of exotic grasses must be followed by reseeding of native grasses and herbs in several consecutive years.

Persistent seeds allow species to bridge temporally unsuitable conditions in tropical dry ecosystems, where the water availability or disturbance by fire is unpredictable (Wright & Clarke 2009; Anderson et al. 2012; Williams et al. 2005). In tropical and subtropical grasslands, fire is an important germination signal, especially its smoke component increases germination from the seed bank (Anderson et al. 2012; Williams et al. 2015). Anderson et al. (2012) found that in the savannas of Serengeti National Park, there is a significant interaction between fire and rainfall: low rainfall sites with frequent fire had greater seed germination than low rainfall sites with low fire frequency. In Australian savannas, native perennial grasses lack a persistent seed bank and are strongly seed-limited; thus, grass-woody ratios can be driven by the juxtaposition of seed rain and fire events (Wright & Clarke 2009). Thus, predicted climate-driven changes in fire regimes fundamentally affect ratios of grasses and woody species.

Based on the reviewed studies, the expected increases in rainfall (see Table 1) and fire activity will likely lead to the increased expression of soil seed bank in tropical savannas close to the coastal areas of the continents (Scott et al. 2010; Anderson

Table 2. Seed bank studies evaluating the first- and second-order effects of climate change in temperate wetlands and grasslands. For notations, please see Table 1.

No.	*Habitat Type*	*Effects of Climate Change*	*Seed Density*	*Species Richness*	*Country*	*References*
Temperate wetlands						
Prediction: increased precipitation						
14	Inland wetland	Drought, salinization	~	~	China	Ma et al. (2012)
15	Inland wetland	Flooding	~	NA	China	Hong et al. (2012)
16	Inland wetland	Reflooding	↓	↓	United States	Galatowitsch and van der Valk (1996)
17	Wet grassland	Reflooding	NA	~	The Netherlands	van Dijk et al. (2007)
18	Wet grassland	Reflooding	↓	↓	The Netherlands	van Duren et al. (1998)
19	Wet grassland	Groundwater level	~	~	The Netherlands	Bekker et al. (1998)
20	Inland wetland	Flooding	↓	↓	South Korea	Lee et al. (2014)
21	Coastal wetland	Flooding	↓	↓	United States	Herrick et al. (2007)
22	Inland wetland	Fire, drought	↑	↑	Japan	Kimura and Tsuyuzaki (2011)
Prediction: decreased precipitation						
23	Wet grassland	Flooding	↑	~	Germany	Hölzel and Otte (2001)
24	Wet grassland	Flooding	↑	~	Germany	Hölzel and Otte (2004)
Temperate grasslands						
Prediction: increased precipitation						
25	Prairie	Drought	↓	NA	United States	Hild et al. (2001)
26	Dry grassland	Warming, precipitation	~	~	Canada	White et al. (2012)
27	Dry shrubland	Drought	↓	↓	China	Li et al. (2011)
28	Dry grassland	Fire	↑	↑	Canada	Romo and Gross (2011)
29	Dry grassland	Ash, smoke	↑	↑	Canada	Ren and Bai (2016)
30	Prairie	Fire	↓	~	United States	Abrams (1988)
Prediction: decreased precipitation						
31	Dry grassland	Warming, drought	~	NA	United Kingdom	Akinola et al. (1998)
32	Dry shrubland	Warming, drought	↓	NA	Spain	del Cacho et al. (2012)
33	Dry shrubland	Fire	↑	~	Chile	Figueroa et al. (2004)
34	Dry grassland	Fire	↑	↑	Argentina	Gonzalez and Ghermandi (2008)
35	Dry grassland	Fire, drought	↓	NA	Argentina	Ghermandi and Gonzalez (2009)
36	Steppe	Fire	↓	↓	Argentina	Ghermandi et al. (2013)
37	Dry shrubland	Fire	↑	~	Spain	Fernández et al. (2012)
38	Renosterveld	Smoke	↑	~	South Africa	Heelemann et al. (2013)
39	Dry grassland	Fire	↑	NA	South Africa	Snyman (2013)
40	Mesic grassland	Fire, heat, smoke	~	~	South Africa	Ghebrehiwot et al. (2011)
41	Heathland	Fire, heat	↑	↑	Australia	Wills and Read (2007)
42	Dry grassland	Fire	↓	~	Australia	Morgan (1998)

et al. 2012). This might also lead to a decreased abundance of grasses and increased abundance of forbs that have a higher seed density in the persistent seed bank. In the less fire-prone Caatinga vegetation in Brazil, high-intensity fire decreases total seed density and species richness (Mamede & de Araújo 2008). Thus, in Caatinga ecosystems, the predicted increase in fire severity will probably decrease persistent seed banks, especially those of grasses.

The forecasted decrease in precipitation and expected decrease in fire activity will also affect seed bank dynamics. In Ethiopian wooded savannas, the predicted decreased precipitation level in rainy season and increased rainfall in dry season lead to changes in plant phenology and may favor species with earlier germination and higher seedling mortality (Gashaw et al. 2002). In these woodland savanna ecosystems, the current fire regime of high-frequency and relatively low-intensity fires seems to maintain the dominance of graminoids both in the seed bank and vegetation. Decreased fire frequency might lead to the decrease of open vegetation, as closed woodland is less flammable than grassland, and grassland seed bank is supported by fire. de Andrade and Miranda (2014) found that in the Brazilian cerrado, 1 year after the fire, the monocot seed density did not reach the prefire value, whereas the density of dicot seeds increased 3-fold. After the fire, the viable seed density and species richness decreased with the onset of the rainy season coinciding with germination in the field. The difference in the contributions of dicot and monocot species to the recovery of the density and richness of the soil seed bank suggests that fire frequency and season must be considered in fire management plans of conservation areas to achieve the maximum seed richness in the soil bank.

Temperate Wetlands

We found 11 studies from temperate wetlands. The rate of the predicted temperature increase varied between 0.5 and 1.5°C at all sites. For nine sites, situated in Southeast Asia, Western Europe, and eastern North America, climate models forecast increased precipitation. For two sites, situated in Central Europe, decreased precipitation is predicted (Table 2; Fig. 1).

In total, nine studies focused on the effects of restorative flooding regimes on the seed bank (Table 2). Restoring the formerly typical hydrological regime by rewetting is a widely applied practice in wetland restoration (Verhoeven 2014). Wetlands generally harbor high-density persistent seed banks, especially at sites with unpredictable flooding and drying cycles (Brock et al. 2003; Bossuyt & Honnay 2008). Several studies found that wetland seed banks are proper sources for restoring the targeted species composition at degraded or dried sites if hydrological regimes are restored (Hong et al. 2012; Ma et al. 2012). These studies suggest that wetlands are resilient ecosystems against future drying out caused by increased temperature and evapotranspiration. Given their high-density seed bank no active seed addition is necessary for their restoration. Hong et al. (2012) suggested that translocating the seed bank from natural wetlands to degraded sites is a feasible way for ecological restoration. Other studies highlighted that the complete recovery of wetlands is impossible from seed banks. Galatowitsch and van der Valk (1996) found that in restored (formerly drained and reflooded) North American prairie wetlands the seed bank has lower species richness compared to natural wetlands and the seed bank of submersed aquatic, sedge meadow, and prairie species is lacking. This suggests that due to lack of certain characteristic species the structure of the wetland cannot be completely restored from the seed bank. van Dijk et al. (2007) and van Duren et al. (1998) had similar conclusions regarding the restoration potential of the seed bank in formerly drained peat meadows. They found that without active introduction of target species, the wetland vegetation cannot recover solely from the seed bank.

In many regions where increased precipitation is predicted, floods will become more frequent or may last longer. Bekker et al. (1998) found that the water level is an important driver of seed bank species composition in Dutch wetlands. They demonstrated that the anoxic conditions of the high water-level treatment were beneficial for the survival of seeds of wet grassland species. Species of dry grasslands survived better under aerobic conditions of the low water-level treatment. Severe flooding events may result in the homogenization of seed bank species composition (Lee et al. 2014). Extreme floods decrease seed bank species richness and seed density, can remove the seed bank of wetland plant species, and therefore allow common and ruderal species to establish. Similar patterns have been found in coastal wetlands, where sites exposed to flooding (undiked sites) had lower seed density and species richness than diked wetlands (Herrick et al. 2007).

Decreased precipitation would probably decrease the duration of flooding events in Central Europe. In riverine ecosystems, decreased flood duration may lead to the decrease of seed bank density in higher-elevated flood-meadows in the Rhine valley (Hölzel & Otte 2001). The appearance of disturbance-tolerant species in turf gaps was also found in the case of longer flood duration. The study of Hölzel and Otte (2004) suggests that persistent soil seed banks are of crucial importance for bridging the highly variable hydrological conditions that are typical for flood-meadows in the Rhine valley, thus they might buffer the forecasted changes in climate and flooding regimes.

Due to increased precipitation, the increased water level may result in lower fire severity in a fire-prone reed swamp in Japan (Kimura & Tsuyuzaki 2011). These authors found a positive effect of fire on species richness, seed density, and seed germination. In several regions, the forecasted increase in precipitation will not be able to compensate the more intense evapotranspiration due to increased temperature, which can lead to the salinization and drought of wetlands. Ma et al. (2012) found a species enrichment in the seed bank due to drying and salinization in wetlands of the Tibetan Plateau. They concluded that after the restoration of hydrological conditions, the soil seed bank can be a proper source for restoration of degraded wetlands.

Temperate Grasslands

We found 16 studies from temperate dry grasslands. The temperature has been forecasted to increase by 0.5–1.5°C at all sites. For six sites, situated in Southeast Asia and central North America, climate models forecast a precipitation increase of 10%. At 10 sites, situated in South Africa, West Europe, South Europe, southern South America, and South Australia precipitation will probably decrease by 10% (Table 2; Fig. 1).

Four studies evaluated the first-order effects of climate change, that is by experimental warming and/or water manipulation on soil seed bank of temperate grasslands. In the study of Akinola et al. (1998), soil warming and water deficit over 6 years had only minor effects on the seed bank of British upland calcareous grasslands, affecting only three species. Two climate manipulation experiments suggest that the predicted increase in precipitation may have a positive effect on seed bank density in North American grasslands. Hild et al. (2001) found that in a North American mixed-grass rangeland experimentally induced drought reduced the total seed bank density, especially that of cool-season annual grasses. Increased precipitation may also lead to a shift in species composition according to the climate manipulation experiment of White et al. (2012). In Canadian dry grasslands, seed bank density was unaffected by the warming treatments. They found increased similarity between seed bank and vegetation due to reduced precipitation, so the opposite may occur in the case of precipitation increase. Decreasing precipitation in the Mediterranean region may reduce seed density in scrublands as was shown in a 9-year-long climate manipulation experiment (del Cacho et al. 2012). They found that open microsites are most affected by the climatic changes caused by drought and warming, while closed microsites under shrub canopies provide favorable conditions and might act as refuge sites for the seed bank. These results suggest a decrease of total seed bank density, especially that of short-lived species under drought conditions in Mediterranean scrublands.

Climatic models predict different trends in precipitation for the study sites; however, the majority of the papers evaluated the effects of fire (13 papers) and/or drought (5 papers) on the soil seed bank. The forecasted increase in precipitation will likely increase the density and species richness of the seed bank in dry

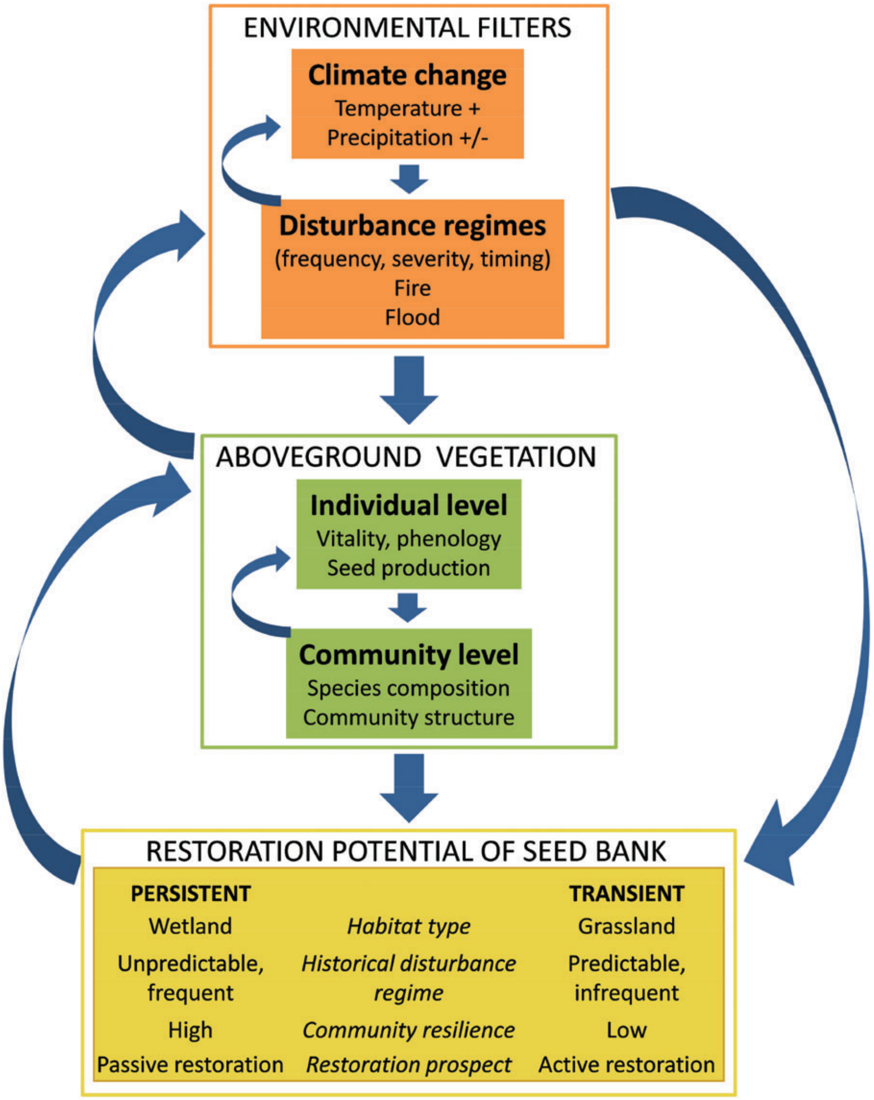

Figure 2. Flow chart showing the relationship between climatic changes, disturbance regimes, aboveground vegetation, and the restoration potential of seed bank.

valleys of China (Li et al. 2011) and probably increase biomass production in North American prairies (Flannigan et al. 2009). Frequency of wildfires and intensity of human-induced fires are expected to increase with increased amount of combustible material (Valkó et al. 2014). Fire has positive effects on seed bank density, species diversity, and evenness of native species 1 year after fire, but later on these effects diminish (Romo & Gross 2011). A study in the same region (Ren & Bai 2016) proved that fire components, such as ash and smoke, supported native forb species, so their soil seed bank density and species richness may increase due to increased fire frequency. Despite this result, Abrams (1988) states that seed density of native species might decrease if too frequent, annual fires would still be present in the Kansas prairie.

In regions for which a decrease in precipitation has been forecasted, drought will likely limit the restoration potential of the seed bank in grasslands. In the Chilean matorral dry shrublands, Figueroa et al. (2004) found that most species have only a transient seed bank. The intensity and frequency of fires may decline due to the decrease of combustible biomass. If fire frequency will decrease due to the decreased fuel availability, seed bank of annual grasses will decrease the most (Figueroa et al. 2004). Fire increases seed bank density and species richness in dry grasslands in Argentina (Gonzalez & Ghermandi 2008), especially that of annual species, while perennials are typical for unburned sites. These authors found that annual species can regenerate faster from seed bank after disturbance compared to perennials. Low-severity fires support the seed bank of fire-adapted short-lived species that have numerous long-term persistent seeds in the soil of Patagonian dry grasslands (Ghermandi & Gonzalez 2009). In these ecosystems, fire is an important driver of community diversity by allowing the coexistence of gap-strategist species germinating from the seed bank. However, high-severity fire is detrimental for the seed bank of fire-adapted short-lived native species and supports exotic species (Ghermandi et al. 2013). This means that climate-driven changes in fire regimes will fundamentally affect the restoration potential of the seed bank in these grasslands.

Fire-prone habitats will be negatively affected by decreased fire activity. In Spanish gorse shrublands, where wildfires are typical, Fernández et al. (2012) found that fires increased seed density and induced seedling emergence, but species richness of the seed bank was not affected. In the Mediterranean region of South Africa, similar patterns were observed (Heelemann et al. 2013). Fire leads to increased seed density in the first years after fire, but has a long-term negative effect on disturbance-sensitive species and a positive effect on species of degraded habitats in semiarid South African rangelands (Snyman 2013). In addition, seed density and seed bank diversity will decrease mainly due to the decrease of species, which do not tolerate disturbance, while the seed bank of disturbance-tolerant species will probably be stable. Ghebrehiwot et al. (2011) found that smoke is an important signal for the germination of grass and forb seeds in mesic grasslands of South Africa, and suggested that smoke treatment may be included as a practice for restoration of degraded land. In southern Australia, the heat component of fire has a positive effect on seed density (Wills & Read 2007). Decreased fire frequency in southern Australia may increase the seed density of dominant exotic species and native perennials preferring unburned sites (Morgan 1998).

Restoration Potential of Seed Banks in the Face of Climate Change

We found that the first- and second-order effects of climate change will likely act as environmental filters, affecting not only aboveground vegetation but also the seed bank of grasslands (Espinosa et al. 2013; Bao et al. 2014). In extremely harsh environment, climate-induced environmental filtering will benefit those native species, which are evolutionarily adapted to unpredictable dynamics of resource availability and disturbance. Many of these species possess a persistent seed bank. We suggest that native grassland resilience by seed bank will largely be determined by the natural disturbance regimes of certain habitats. In habitats characterized by severe, frequent, and unpredictable disturbances, several species rely on regeneration by persistent seed bank. Thus, the vegetation of disturbance-affected ecosystems such as regularly flooded wetlands (Bao et al. 2014; Oliveira et al. 2015) or fire-prone grasslands (Wright & Clarke 2009; Anderson et al. 2012; Williams et al. 2015) can probably buffer climate-driven changes in disturbance regimes by recovery from persistent seed banks. Contrary, in relatively stable habitats, characterized by predictable and less severe disturbance, most native species do not have persistent seed banks (McLaughlin & Bowers 2007; Scott et al. 2010). In such ecosystems climate-induced changes in disturbance regimes cannot be buffered by the soil seed bank, which is especially true for nonfire-prone temperate grasslands. It is important that either increased or decreased disturbance frequency or severity can lead to directional and irreversible changes in species composition and density of the soil seed bank. Thus, the most severe changes in the species composition of both vegetation and seed bank can be expected in currently stable ecosystems.

We found reports from all continents related to seed bank changes triggered by the first- or second-order effects of climate change, but from many regions such studies are still lacking (polar regions, Central America and Caribbean, West and Central Asia, East Asia, and Pacific Islands region). Besides, all regions were represented by only a few studies. Generally, studies in wetlands assessed the potential effects of flooding, while in grasslands, the effects of fire were most frequently tested. We found that besides the scarcity of focused studies on seed banks and climate change, another problem is the lack of regional scenario-based approaches. We found only four experimental studies testing the first-order effects of climate change on the seed bank by manipulating temperature or precipitation regimes. These studies would be essential for being able to plan long-term and sustainable grassland conservation and restoration projects, also considering the possibly changing target vegetation.

Our study has important implications for ecological restoration (Fig. 2). The reviewed studies showed that active restoration by seed addition will be most important in habitats less affected by natural disturbance and characterized by species with transient seed bank. In such cases, the introduction of native species preferably from the regional species pool that can tolerate the predicted climatic change should be prioritized at degraded sites. Persistent seed banks support passive restoration especially in wetlands and habitats where unpredictable and frequent disturbance events have been typical in the historical timescale.

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