Plant Regeneration from Seeds

A Global Warming Perspective

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Chapter 21

Soil seed banks under a warming climate

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Introduction

Global warming is an important driver of recent and projected future changes in the distribution of species (Urban, 2015; Kerr, 2020), and its effects have become evident in various ecosystems and taxonomic groups worldwide (Parmesan and Yohe, 2003; Parmesan, 2006; Baldwin et al., 2014; IPCC, 2014). Along with global warming, increases in the frequency and magnitude of extreme climatic events (IPCC, 2013, 2014) are being proposed as one of the causes of present-day extinction of species (Root et al., 2003; Urban, 2015). A warming climate can have cascading effects on plant populations and community dynamics and ultimately on plant distribution. Among the most evident effects of climate change are alterations in community composition (Parmesan and Yohe, 2003), phenology (Miller-Rushing et al., 2010; Ovaskainen et al., 2013; Orsenigo et al., 2015), selective adaptation (Hoffmann and Sgrò, 2011; Merritt et al., 2014), and species distribution. The distribution of a species is associated with conditions that have become unsuitable, or for some species more suitable, for survival, growth, and/or recruitment. Distributional changes include the loss of populations from previously occupied areas and the poleward and upward/elevational expansion in the distribution of many plants (Grabherr et al., 1994; Lenoir et al., 2008; Doak and Morris, 2010; Urban, 2015; Manish et al., 2016; Kerr, 2020), supporting earlier predictions of a widespread redistribution of species, as well as accelerated extinction rates (Peters and Darling, 1985).

In some cases, shifts in the distribution of individual species associated with a warming climate have resulted in the formation of novel communities (Parmesan and Yohe, 2003; Manish et al., 2016; Giménez-Benavides et al., 2018; Løkken et al., 2019), while in cases where individual species have similar responses, community composition has remained largely intact (Beckage et al., 2008; Lenoir et al., 2008; Shevtsova et al., 2009; Pucko et al., 2011). However, changes in the distribution of individual species will likely become increasingly divergent as they approach warming-related environmental thresholds (Pucko et al., 2011). Moreover, while climate change is expected to have the greatest impact at the margins of a species' distribution (Manish et al., 2016), there is evidence that it also can affect the core of their distribution (Lenoir et al., 2008).

Since many distributional shifts are occurring more rapidly than originally anticipated (Beckage et al., 2008), predicting the magnitude, direction, and speed of response to range modifications and the resilience of plant communities to any changes is a critical conservation issue (Corlett and Westcott, 2013; Van Looy et al., 2016; Løkken et al., 2019). Ultimately, the ability of a species to disperse to new sites and to track the altered climatic conditions will be critical in shaping its future distribution (Peters and Darling, 1985; Bertrand et al., 2011; Baldwin et al., 2014). It is also considered unlikely that most plant species can disperse fast enough to keep pace with the rate of rapid climate change (Bertrand et al., 2011; Corlett and Westcott, 2013). The question then is whether these species can adapt to the new conditions (Skelly et al., 2007) via selection of individuals with increased fitness or whether they possess the phenotypic plasticity required to survive in the changed environment (Parmesan, 2006; Hoffmann and Sgrò, 2011; Manish et al., 2016; Colautti et al., 2017).

For terrestrial plants, limitations in short-distance seed dispersal (Bertrand et al., 2011) and/or abiotic constraints on germination, growth, and establishment (Lloret et al., 2005; Shevtsova et al., 2009) can limit their ability to keep pace with the changing climatic conditions (Baldwin et al., 2014). Alternatively, the ability to persist in a community as

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latent propagules/seeds that allow a species to spread not only in space but also through time (Harper, 1977, Fenner and Thompson, 2005) could play a key role in determining future plant community dynamics (Ooi et al., 2009; Walck et al., 2011). A key distinction for understanding the potential contribution of soil seed banks (hereafter seed banks) to the future responses of individual plants and communities to a warming climate is the difference between persistent and transient seed banks. Persistent seed banks are composed of seeds that retain their viability in the soil for >1 year or to the second germination season, while transient seed banks are those whose seeds lose viability and/or germinate in ≤1 year or do not persist until the second germination season (Thompson et al., 1997; Walck et al., 2005).

Relying on seeds that may persist in the soil over multiple germination seasons has long been regarded as a bet-hedging strategy against the risks of reproductive failure associated with unpredictable environmental conditions (Cohen, 1966; Venable and Brown, 1988; Venable, 2007; Tielbörger et al., 2012; Larson and Funk, 2016). As reserves of genetic variability (Templeton and Levin, 1979; Honnay et al., 2008), persistent seed banks also might play an important role in determining the evolutionary response of seed plants to environmental unpredictability (Venable and Brown, 1988; Baskin et al., 1998; Donohue et al., 2005, 2010), although there is little evidence for this. However, the ability to form a persistent seed bank has been recognized as a major component of ecosystem resilience (Hopfensperger, 2007; González-Alday et al., 2009; Walck et al., 2011; Plue et al., 2013, 2021; Blossey et al., 2017; Ma et al., 2019).

Since temperature is a critical factor influencing the persistence of seeds in the soil (Baskin and Baskin, 2014), a warming climate can have profound effects on the composition and structure of the seed bank and, in turn, on the persistence of individual species and communities (Walck et al., 2011; Hoyle et al., 2013; Long et al., 2015; Bernareggi et al., 2016; Giménez-Benavides et al., 2018). However, assessments of the effects of a warming climate on the seed bank have received less attention than the standing vegetation (Grime et al., 2000, 2008; Ooi et al., 2009; Briceño et al., 2015; Basto et al., 2018). Here, we review recent evidence for climate and climate-related changes in the persistence and structure (richness, size, and composition) of seed banks across different ecosystems and biomes. While excellent studies have described the mechanisms by which a warming climate may affect seed bank persistence and regeneration from seeds (Walck et al., 2011; Ooi, 2012; Jaganathan et al., 2015), we focus on the observed and predicted changes in the seed bank and discuss their role in promoting ecosystem resilience by preventing species extinctions and contributing to the migration of species.

Effects of a warming climate on seed bank persistence and density

A warming climate may have a cascading effect on the persistence and size of the seed bank of individual species. Seed persistence in the soil is a function of a range of seed traits and pre- and postdispersal biotic and abiotic conditions (Thompson et al., 1993, 2003; Bekker et al., 1998; Long et al., 2008, 2015), which define the seed ecological spectrum (Saatkamp et al., 2019). Seed bank size is defined here as the number of seeds in/on the soil per surface area of the soil and represents the balance between seed inputs and seed outputs.

There are concerns that global warming may accelerate losses of species from the seed bank through adverse effects on seed aging, viability, and longevity (Fig. 21.1). Several experimental studies provide evidence for accelerated seed aging under high temperatures (Bekker et al., 1998; Leishman et al., 2000; Murdoch and Ellis, 2000; Parmesan, 2006; Long et al., 2008, 2015; Kochanek et al., 2011; Bernareggi et al., 2015; Panetta et al., 2018; Luna, 2020), although the response to artificial aging conditions may differ from that of seeds aging naturally in the seed bank (Roach et al., 2018). Also, the imposition of short-term increases in temperature in laboratory experiments may not reflect the generally slower longer-term temperature increases expected in the field. Field evidence suggests that cold and wet postdispersal environments can reduce seed deterioration (Cavieres and Arroyo, 2000; Bewley et al., 2013), thereby promoting seed persistence and the accumulation of seeds in the soil (Pakeman et al., 1999; Cummins and Miller, 2002). In contrast, decreased persistence in the soil due to accelerated aging and reduced viability could deplete the seed bank and its regeneration potential (Ooi, 2012; Bewley et al., 2013). However, shorter-term environmental variations can result in marked transgenerational changes in seed longevity (Kochanek et al., 2011). Increases in seed longevity resulting from warming-related population shifts that select phenotypes with increased resistance to warming could play an important role in promoting survival of plants and long-term adaptation to a rapidly changing environment (Nicotra et al., 2010; Mondoni et al., 2014; Bernareggi et al., 2015). Selection of phenotypes resistant to warming might explain why species from warmer and drier regions generally produce longer-lived seeds than species from cooler regions (Probert et al., 2009; Mondoni et al., 2011; Merritt et al., 2014). Clearly, the effects of a warmer parental environment on seed longevity may interact with other environmental conditions, including the generally drier, but possibly wetter, conditions associated with warming (Probert et al., 2009; Kochanek et al., 2011).

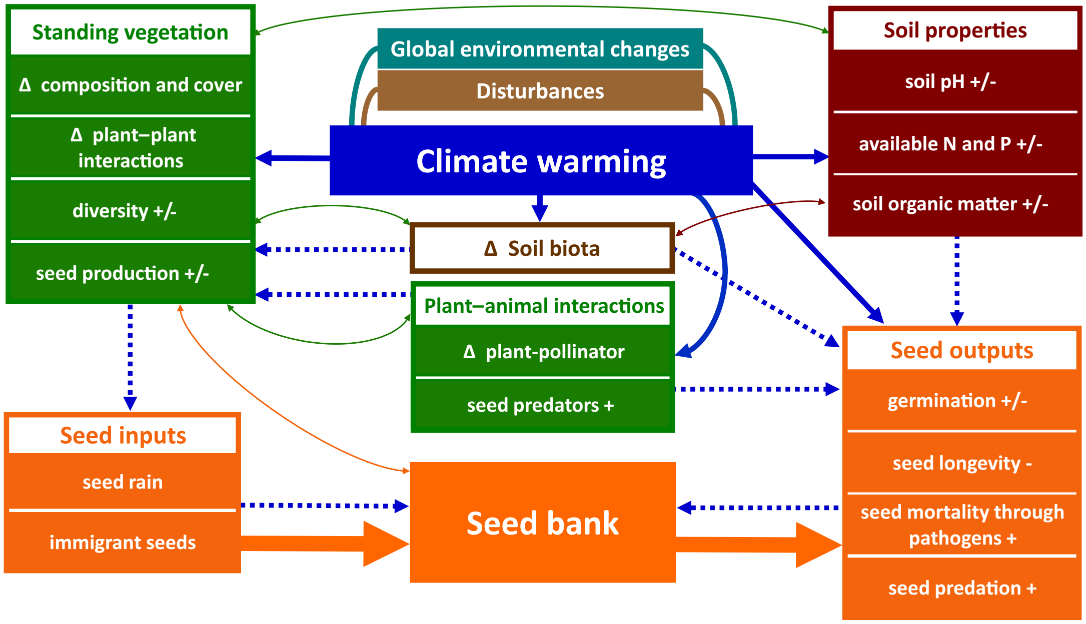

FIGURE 21.1 A summary of the main direct and indirect effects of climate warming on the soil seed bank, including interactions with the standing vegetation, soil physiochemical properties, and soil biota. Solid *blue arrows* indicate the direct effects of climate warming and dashed *blue arrows* indirect effects on seed bank inputs and outputs, with inflows and outflows from the seed bank shown by thick *orange lines*. Interactions between climate warming and other global environmental changes and disturbances are shown by solid lines, and thin arrows represent double-loop feedback processes. The main positive (+) or negative (−) effects and changes (Δ) associated with climate warming identified in the literature are highlighted.

Another important way for loss of seeds from the seed bank is germination (Fig. 21.1). The documented impacts of increased pre- and postdispersal temperatures on germination include dormancy alleviation for increasing proportions of physically dormant seeds and of physiologically dormant seeds of many species (e.g., Auld and O'Connell, 1991; Baskin and Baskin, 2014; Bernareggi et al., 2016; Aragón-Gastélum et al., 2018; Footitt et al., 2018). Also, soil warming may increase or reduce germination and shift the timing of germination (Petrů and Tielbörger, 2008; Milbau et al., 2009; Ooi et al., 2009; Shevtsova et al., 2009; Walck et al., 2011; Jaganathan et al., 2015; Orsenigo et al., 2015; Footitt et al., 2018), although soil type has been shown to buffer some of these effects (Petrů and Tielbörger, 2008). Germination responses to warming may be species-specific, depending on the temperature requirements for dormancy-break and germination, the class of dormancy, and seasonal environmental variability in the extent of dormancy (Walck et al., 2011; Baskin and Baskin, 2014; Blossey et al., 2017; Rubio de Casas et al., 2017; Footitt et al., 2018).

The longer-term effects of accelerated germination on the seed bank depend on the postgermination environmental risks experienced by seedlings and their effects on the persistence of species in a community. In polar and subpolar zones and alpine ecosystems characterized by a short growing season, higher, earlier, or faster germination might improve the probability of seedling survival and thus successful regeneration from the seed bank, allowing for the exploitation of the longer growing season (Milbau et al., 2009). However, in other climate zones increased germination may lead to higher seedling mortality by exposing young plants to environmental constraints unfavorable for growth (Shevtsova et al., 2009; Ooi et al., 2012; Porceddu et al., 2020) as well as increasing predation or reducing the formation of mutualisms (Graee et al., 2008; Connolly and Orrock, 2015; Gómez-Ruiz and Lacher, 2019). The effects of warming will be greater for species with narrow temperature windows for germination, although this may depend on interactions between temperature and moisture availability (Cochrane, 2016). Moreover, parental environmental effects on the germination response of seeds to the environment might mediate the effects of increased soil temperatures (Long et al., 2008; Kochanek et al., 2011; Ooi et al., 2012; Meineri et al., 2013; Mondoni et al., 2014, 2015; Bernareggi et al., 2016).

One of the main direct effects of a warming climate on the seed bank is through changes in the seed rain associated with alterations in the structure and composition of the standing vegetation and/or changes in seed production (Fig. 21.1; Cleland et al., 2007; Springer et al., 2008; Briceño et al., 2015; Ma et al., 2019, 2020; An et al., 2020; Prevéy, 2020). Evidence from wetlands and grasslands suggests that climatic warming might alter both the standing vegetation and the seed bank through negative effects on species coexistence and competitive interactions associated with changes in the timing of germination of individual species. Changes in the standing vegetation include the displacement of subordinate species by dominant species (Brock, 2011; Baldwin et al., 2014; Basto et al., 2018) and shifts from perennial to annual communities (Ma et al., 2010) and from perennial- to woody-dominated communities (Fridley and Wright, 2018). Positive feedbacks between the standing vegetation and seed bank are to be expected (del Cacho et al., 2012; Panetta et al., 2018), with changes in the seed bank likely to be exacerbated by any potential negative effects of warming on the standing vegetation.

Demographic compensation mechanisms, such as increased seed production (Akinola et al., 1998; García-Camacho et al., 2012; Ibáñez et al., 2017), could mitigate any adverse effects of climate warming on the seed bank (Doak and Morris, 2010; Sheth and Angert, 2018). Mitigation would explain why only minor changes in the size, composition, and diversity of the seed bank have been observed under warmer conditions, at least in the short term (Akinola et al., 1998). In alpine systems, increased seed production and seed quality associated with earlier snowmelt and a longer growing season have been reported (Arft et al., 1999; Springer et al., 2008). Shifts in flowering time and an increase in the length of the flowering period can also increase the probability and frequency of seed set, thereby increasing the number of flowers and ultimately the number of seeds produced (Thórhallsdóttir, 1998; Teller et al., 2016). However, increased seed production might not be sufficient to compensate for increased losses from the seed bank if warmer conditions reduce seedling survival and establishment. Potential reduction in the size of the seed bank is more likely to occur in ecosystems characterized by low seed production, such as arctic and alpine ecosystems (Onipchenko et al., 1998) and other communities dominated by perennial species. Seed production may also be decreased if a warmer climate results in asynchronous phenology between the flowering of plants and their pollinators (Gilman et al., 2010; Gómez-Ruiz and Lacher, 2019) or in the disruption of other multitrophic relationships (Miller-Rushing et al., 2010). Thus, the need to include biotic interactions across trophic levels to understand and predict the response of species to climate change has been recommended (Van der Putten et al., 2010).

Experiments examining the effects of projected temperature increases on seed aging, longevity, and germination responses provide indirect information on the potential impact of warming on the seed bank. However, the complexity of the effects of warming on ecosystems makes it difficult to extrapolate many results to the field and to estimate seed viability and longevity in the soil (Cooper et al., 2004; Walck et al., 2011; Blossey et al., 2017). Moreover, warmer temperatures are only one component of a warming climate (Jaganathan and Dalrymple, 2016). Our inability to make large-scale conclusions on the response of individual plant species and communities to climate warming is also confounded by differences in seed collection methods, dormancy-breaking treatments, and germination test conditions used in various studies (Jaganathan and Dalrymple, 2016). Long-term, field studies can however provide important information on the effects of a warming climate on the species composition of seed banks as well as the standing vegetation. For this reason, studies of the potential effects of a warming climate on the seed bank have increased in recent years using a variety of approaches that consider individual species, groups of species, and entire communities.

Changes in the composition and structure of seed banks under a warming climate

Mountain ecosystems and elevation gradients

Studies on the potential effects of climate change on the seed bank have revealed the difficulty of untangling direct and indirect effects (Fig. 21.1). These difficulties include indirect effects related to modifications in soil properties (Ma et al., 2019, 2020; An et al., 2020), plant-soil feedbacks (Pugnaire et al., 2019), and the impact of pathogens (Sharma et al., 2006; Pucko et al., 2011; Ma et al., 2020). A warming climate also has been shown to increase pre- and postdispersal seed predations that have negative effects on the seed bank (McKone et al., 1998; Arroyo et al., 2006; Pucko et al., 2011; Del Cacho et al., 2012; Noroozi et al., 2016; Naoe et al., 2019). Evidence of increased postdispersal seed predation in transient compared to persistent seed banks (Hulme, 1998) suggests that the indirect effects of climate change on seed predation will be stronger for species that form only transient seed banks. In contrast, dispersal by animals can help plants avoid climate warming (Naoe et al., 2016, 2019; González-Varo et al., 2017), albeit temporarily. However, it is still unclear whether this will be sufficient to allow some plants to escape current global warming (Naoe et al., 2019).

Despite these difficulties, an increasing number of studies recognize the critical role of seed banks for plant regeneration in many types of communities. To date, most information is from studies examining seed bank communities along elevational or latitudinal gradients with natural climatic gradients, although differences in climate might not be the main or only driver of seed bank variation. Moreover, the temperature gradient in these studies might not be broad enough to detect significant patterns, since above- and/or belowground effects of temperature might become evident only when a certain temperature threshold is exceeded (An et al., 2020). These studies have reported increases (Funes et al., 2003; Espinosa et al., 2013), decreases (Ortega et al., 1997; Cummins and Miller, 2002; An et al., 2020), hump-shaped (Hegazy et al., 2009), or no (Lippok et al., 2013) changes in seed densities and species richness along elevational gradients. The overall effects of warming in mountain regions depend on habitat-specific characteristics, with evidence from mountain systems that the correlation between seed bank properties and elevation varies with the type of vegetation (Erfanzadeh et al., 2013; Ma et al., 2020), disturbance regime (Cooper et al., 2004; Espinosa et al., 2013; Hoyle et al., 2013), and interactions between climatic variables and elevational gradients (Espinosa et al., 2013).

Mountain ecosystems are among those that have been examined most extensively for the potential effects of climate warming on seed banks, given their recognized vulnerability to even small temperature increases (Grabherr et al., 1994; Hughes et al., 2003; Cramer et al., 2014). Increasing evidence indicates that the formation of persistent seed banks is a key survival strategy in these systems. Seed banks buffer the systems against the effects of environmental variability and climate change, although the importance of vegetative propagation relative to regeneration from seeds tends to increase with elevation (Onipchenko et al., 1998). However, the presence of large, species-rich, long-term persistent seed banks in alpine ecosystems supports experimental evidence that seed bank persistence is a life-history trait that has been selected for in these environments (Arroyo et al., 1999; Cavieres and Arroyo, 2001). The same environmental conditions that constrain biomass and seed production can, in fact, promote the formation of persistent seed banks by reducing seed deterioration (Cavieres and Arroyo, 2000; Murdoch and Ellis, 2000; Walck et al., 2005, 2011; Ma et al., 2010).

An interesting example of how climate warming might affect natural seed banks in alpine regions is from recent studies on the Tibetan Plateau. These seed banks have a large number of species that are absent from the vegetation, and the seeds have high longevity (Ma et al., 2010). Several studies have examined variations in seed bank communities on the Tibetan Plateau along elevational gradients (or levels) and the role of seed banks as drivers of ecosystem resilience in different types of meadows (e.g., Ma et al., 2010, 2013, 2017, 2019, 2020; An et al., 2020). Mean annual temperature and precipitation appear to have an important effect on the seed bank by directly affecting the richness and abundance of the standing vegetation as well as influencing soil properties (mainly pH but also total N and P), which in turn affect the alpine vegetation. Patterns in the seed bank on the Tibetan Plateau tend to be driven by increases in the proportion of perennial versus annual species with increasing elevation (Ma et al., 2010; An et al., 2020). These results support earlier suggestions that clonal propagation is a better survival strategy in cold and unstable systems, where biomass and seed production are constrained by a short growing season (Onipchenko et al., 1998). However, the seed banks of these alpine meadows tend to be dominated by perennial species, indicating that seed bank formation is an important strategy not only for annuals (Venable, 2007) but also for perennial herbs that can rely on other strategies for persistence in a community (Grime, 2001; Honnay and Bossuyt, 2005; Clarke et al., 2013). This finding is further supported by evidence that the formation of a persistent (as opposed to a transient) seed bank is the most frequent strategy at high elevations in these ecosystems (Ma et al., 2010).

That a persistent seed bank is a key survival strategy for many species at high elevations (Funes et al., 2003) and contributes to an increased resilience is supported by field observations globally. Persistent seed banks play an important role in maintaining species diversity in the Australian Alps, including the diversity of obligate alpine species, supporting species range shifts, and moderating dominance along elevational gradients (Venn and Morgan, 2010; Hoyle et al., 2013). Increases in the proportion of species forming persistent seed banks as elevation increases have been documented in tall tussock grasslands in the Córdoba mountains, central Argentina (Funes et al., 2003) and in Mediterranean pasture communities in central Spain (Ortega et al., 1997), with certain species forming persistent seed banks only at high but not at low elevations. Espinosa et al. (2013) found differences in seed bank richness and density along elevational gradients in dry mountain scrub communities, but such differences were not significant when only the persistent component of the seed bank was accounted for, providing further evidence that persistent, but not transient, seed banks can increase ecosystem resilience.

Seed banks confer increased resilience in extreme environments

Evidence for the importance of persistent seed banks as a survival strategy in response to a warming climate also comes from Arctic and Antarctic ecosystems, where large and persistent seed banks have been recorded (e.g., McGraw and Vavrek, 1989; Lévesque and Svoboda, 1995; McGraw and Day, 1997; Arroyo et al., 2004; Cooper et al., 2004; Jónsdóttir, 2011; Williams et al., 2016). Based on the available knowledge of plant survival in the high Arctic since pre-Holocene times and examination of contemporary populations in these regions, Crawford and Abbott (1994) concluded that some Arctic species may form long-term persistent seed banks that might confer increased resilience against climate change. Field evidence of this resilience was provided by Cooper et al. (2004), who examined seedling emergence in six dry-mesic habitats on Svalbard. These authors found that 50 of 72 species were present in the standing vegetation as mature plants emerged from the seed bank. However, thermophilic species failed to germinate under natural conditions. Moreover, some species present at/in several sites/habitats germinated only from the thermophilic heath seed bank, suggesting that current climatic conditions constrain any recruitment from seeds, while warmer conditions could deplete the seed bank by promoting germination.

Concerns that a warming climate might compromise the bet-hedging role of soil seed banks also comes from studies on arid and semiarid ecosystems, where formation of a persistent seed bank is a critical survival strategy for species with short life cycles (Venable and Brown, 1988; Arroyo et al., 2006; Venable, 2007). In these systems, warming is expected to exacerbate the effects of extreme climatic events (Alpert et al., 2008; Kafle and Bruins, 2009; Ooi et al., 2009, 2012; del Cacho and Lloret, 2012; Basto et al., 2018) through reduced seed viability, increased soil temperatures and subsequent increases in seedling mortality due to temperature-related reductions in water availability (Ooi et al., 2012). Increased germination under warmer conditions may also deplete the seed bank, even when projected increases in temperature fall within the thermal germination range of a species (Aragón-Gastélum et al., 2018). Increased lightning strikes in arid regions (Veblen et al., 2011) may increase fire frequency and intensity, further compromising the persistence of plant populations dependent on long-term persistent seed banks (Ooi et al., 2012, 2014). Manipulation studies in these systems have shown reductions in seed bank richness and density with increased temperatures, especially for short-lived species, potentially resulting in positive feedbacks that exacerbate the loss of vegetation cover (del Cacho et al., 2012) and a reduction in species with facultative pyrogenic dormancy (Ooi et al., 2014).

Buffering the effects of climate warming: temporary resilience?

Although there is evidence that persistent seed banks can play a critical role in buffering the effects of climate warming, this might be only temporary (Plue et al., 2021). Calcareous grasslands that support high vascular plant species richness, including many rare and threatened species (Hutchings and Stewart, 2002; Van Looy et al., 2016) are resistant to climatic changes in the short term (Akinola et al., 1998) but not in the longer term (Basto et al., 2018). In a manipulation study in a species-rich calcareous grassland, Basto et al. (2018) found significant changes in the composition of the seed banks after 14 years, with decreases in both seed bank richness and density. Changes in the seed bank were also larger than those in the vegetation and did not reflect only aboveground changes, suggesting that changed climatic conditions altered seed viability and longevity and/or seed production. Since perennial species often dominate calcareous grasslands, a modified climate might reduce the importance of seed production for regeneration relative to vegetative propagation, partly explaining why only minor changes in productivity and/or composition have been observed in these systems (Grime et al., 2008).

The well-known importance of persistent seed banks in promoting species persistence and ecosystem resilience in wetlands (Leck et al., 1989) might also be only temporary. In ephemeral wetlands, persistent seed banks contribute to inter- and intraannual environmental resilience (Deil, 2005) and act as a reservoir for protected and rare annual species that are absent in the standing vegetation (Aponte et al., 2010). These seed banks tend to be dominated by seeds of annual species (Deil, 2005; Leck et al., 1989; Aponte et al., 2010). A warming climate might affect these communities by increasing the duration of dry versus wet phases. For example, Brock (2011) found that five Australian temporary wetlands supported species-rich, long-term persistent seed banks that were not depleted by successive germination events. However, seed bank composition changed with increasing duration of the dry phases and the number of successive germination events, indicating that the resilience role of the seed bank might be only temporary. Brock (2011) suggested that the "most resilient" species pool in these systems consisted of species that survive the longest dry periods and several wetting and drying events with little depletion of the seed bank, while the "least resilient" species are characterized by shorter survival times and their rapid decline in the seed bank.

Seed banks and plant migration potential under a warming climate

Knowledge of changes in the structure of the soil seed bank is a key factor in understanding the long-term implications of a warming climate on plant communities. Formation of a persistent seed bank may facilitate the ability of a species to colonize new areas and is often regarded as a potential indicator of community trajectories (González-Alday et al., 2009; Kottler and Gedan, 2020). The seed bank shows which species can disperse into the area and can persist and subsequently germinate under suitable environmental conditions (Wang et al., 2013). In fact, a warming climate might create spatial or temporal niches that promote the germination and establishment of seeds of species dispersed from distant localities, assisting the migration of species and contributing to a reduced risk of extinction. Large-scale evidence based on the distribution of European plant species indicates that those forming persistent seed banks and those with a high dispersal capacity have the smallest climate-related range limitations (Estrada et al., 2015). Persistent seed banks can assist migration of species under warmer conditions in different ecosystems (Erfanzadeh et al., 2013; Hoyle et al., 2013; Estrada et al., 2015; Kottler and Gedan, 2020). Clearly, migration of species might facilitate survival of individual species, but at the community level it could promote successful establishment of alien species or species generally regarded to have low conservation value, potentially exacerbating the negative effects of climatic warming on native and endemic species (Hoyle et al., 2013).

Challenges and future research directions

Our understanding of the long-term implications of a warming climate on plant regeneration from seeds through its effects on the seed bank is limited by the lack of studies examining the impact of global warming on the various sources and sinks of seeds in the soil and the early recruitment processes, including any demographic changes. More information is needed on the impact of increased temperatures on seed production. Although increasing evidence indicates that warming might deplete soil seed banks, increased seed production could mitigate or counteract any negative effects (Akinola et al., 1998; Doak and Morris, 2010; Ibáñez et al., 2017; Sheth and Angert, 2018).

Our review strongly points to the need for improved protocols in studies estimating both the direct and indirect effects of climate warming on seed banks and the magnitude and direction of feedbacks on the seed bank and standing vegetation. Only a combination of long-term observations and manipulation studies that examine the response and adaptive capacity of seed banks to climate change can improve our ability to predict the future risk of extinction vis-a-vis modifications in the distribution of species and whole communities, especially where they are subjected to temporally stochastic disturbances (Parmesan, 2006; Keith et al., 2008; Walck et al., 2011; Ooi et al., 2012; Jaganathan and Dalrymple, 2016). Temperature has a significant impact on plants at all stages of their life cycle (Trudgill et al., 2005) and is a major factor controlling plant distribution. However, a complete understanding of the future effect of global warming on soil seed banks needs to recognize the interacting effects of warming with other climate-related changes, including alterations in precipitation patterns and water availability (Ooi et al., 2009, 2012; Basto et al., 2015, 2018; An et al., 2020; Ma et al., 2020) and increases in atmospheric CO_2 (Seibert et al., 2019). Changes in land use (Ortega et al., 1997; Espinosa et al., 2013), atmospheric nitrogen deposition (Grime et al., 2000; Basto et al., 2015; Ma et al., 2020), changes in fire frequency and intensity (Ooi et al., 2009; Enright et al., 2014; Camac et al., 2017), and the introduction of alien species (Hoyle et al., 2013; Gioria and Osborne, 2014; Hou et al., 2014) are also expected to have major impacts on soil seed banks. The effects of antagonistic or beneficial biotic interactions among species also need to be considered (Pucko et al., 2011; Ash et al., 2017; Ma et al., 2017, 2020; Gómez-Ruiz and Lacher, 2019; An et al., 2020; Giejsztowt et al., 2020). The magnitude and frequency of extreme climatic events also require further consideration since they may have disproportionate effects on plant communities and ecosystems and thus could undermine predictions based on short-term field experiments.

A better understanding of how seed banks may affect the evolutionary responses of plants to environmental change is much needed. The adaptive ability of species relying on long-term persistent seed banks for survival will depend on several factors, including generation time, time between recruitment events, and the level of change required to adapt to new conditions. Genetic adaptation of seed and seedling traits may be more rapid in annuals due to their shorter life cycles than in perennial herbaceous or woody species (Smith and Beaulieu, 2009). However, whether genetic adaptations can track the speed of climate change remains largely unknown (Walck et al., 2011; Parmesan and Hanley, 2015). Rapid evolutionary changes that optimize the timing of germination or the ability of seeds to survive in the seed bank have been observed for some invasive alien plants (Blossey et al., 2017). In this respect, insights into the rate of adaptation can be obtained from studies examining alien species that have recently expanded their geographical ranges into new areas.

Knowledge of how seed bank properties are distributed globally across latitudes and habitats can help identify the species most likely to persist and contribute to the improved resilience of communities exposed to a warming climate and other environmental changes. Seed bank data based on field collections are becoming increasingly available from most regions and biomes (Jaganathan et al., 2015; Gioria et al., 2020). Analyses of global seed bank data from the native range of 2350 species of flowering plants show that climate and latitude have relatively smaller effects on local seed bank persistence and densities than habitat-related variables (Gioria et al., 2020). These results are consistent with field evidence that disturbances mediate the effects of a warming climate on soil seed banks and regeneration from seeds (del Cacho et al., 2012; Espinosa et al., 2013; Ma et al., 2013, 2018), although this needs to be explored more broadly.

It is possible that microclimatic conditions might mask the effects of broad-scale climatic patterns. For example, facilitative plant−plant interactions are thought to ameliorate the severe microenvironmental conditions in alpine plant communities (Cavieres and Sierra-Almeida, 2012). Although future climate change scenarios will likely include increased temperatures and altered precipitation patterns (IPCC, 2013, 2014), specific microenvironmental conditions could create favorable microhabitats and preserve the bet-hedging role of seed banks, buffering local populations against rapid climatic changes (Denney et al., 2020). However, more evidence for the preservation of the bet-hedging role of seed banks under climate change is needed.

Concluding remarks

Studies of natural seed banks are a key factor for an improved understanding of the long-term implications of a warming climate on plant distribution and diversity. Increasing evidence shows that persistent seed banks provide resilience to a warming climate, especially in the most vulnerable ecosystems. Seed banks reduce the likelihood of ecosystem extinction by supporting a high diversity of native and endemic species, while allowing the survival of species no longer present in the standing vegetation. This resilience has been observed not only for annual species, but also for perennial species.

There is growing concern that climate warming might rapidly and negatively impact the bet-hedging role of persistent seed banks, through both direct and indirect effects on seed persistence in the soil and increased seedling mortality. Furthermore, the role of persistent seed banks in buffering the effects of climatic changes may be only temporary. Little is known about the extent to which compensation via genetic adaptation or phenotypic plasticity might determine the long-term responses of plants to a warming climate. More information is needed on the role of seed dispersers in facilitating plant distributional shifts and in preventing their extinction.

Ultimately, the long-term implications of a warming climate on plant communities via the seed bank will depend on its effect on seed longevity and on the net balance between seed input and losses from the seed bank, as well as on the risks associated with postgermination environmental conditions. Accelerated germination will be important only if it ultimately balances any seed losses. The ability to form long-term persistent seed banks could become more important in the future, and it has been suggested that plant species may respond to a changing environment by relying less on dispersal through space and more through time (Johnson et al., 2019). The ability to form a persistent seed bank is expected to be especially critical for the survival of species with limited dispersal ability, such as alpine species (Morgan and Venn, 2017), species unable to adapt rapidly to a warming climate, and those at the limits of their distributional range (Hughes et al., 1996; Parmesan and Yohe, 2003). In contrast, transient or short-term persistent seed banks are less likely to prevent species extinctions. There is also evidence for lower resilience in communities composed of short- than of long-term persistent seed banks (Van Looy et al., 2016). Expanding on the concept of Brock (2011) on the resilience of plants in ephemeral wetlands, the species less likely to be impacted by climate warming will be those whose seeds can survive in persistent seed banks that are not rapidly depleted by temperature increases or other related environmental changes.

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