

Soil Seed Banks, Alternative Stable State Theory, and Ecosystem Resilience

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In restoration ecology, the transition from desired to degraded state is based solely on the composition of the aboveground plant community, whereas belowground propagules are often neglected. We developed a conceptual framework integrating seed bank dynamics into alternative stable state theory, highlighting the important relationship between aboveground and belowground composition. This integration emphasizes the role of resilience in systems that appear to have shifted to an “undesirable” state. Belowground propagules, especially soil seed and bud banks, provide buffering capacity and may serve as valuable indicators of potential resistance to state transition based on the degree of similarity between belowground and aboveground vegetation composition. Ecosystem states may have multiple components that differ in their rate of change, as well as in their capacity to promote resilience. We recommend that the application of alternative stable state theory from a management perspective should incorporate components of both above- and belowground vegetation.

Keywords: alternative stable states, ecosystem resilience, warning indicator, restoration, soil seed bank

Ecosystems worldwide have experienced extensive pressures from localized human activities (e.g., agriculture, urbanization, industrial development) and global environmental change (e.g., warming, precipitation change, climate extremes). Managing and restoring ecosystems and conserving biodiversity under multiple environmental stressors are an important challenge for stakeholders and policymakers. Moreover, ecosystem dynamics can exhibit nonlinear threshold effects, which are less predictable than linear relationships between drivers and ecosystem state (Levin 1999), further complicating adaptive management.

Some models predict that changing environmental drivers can lead to a proportional change in biotic community composition (Kéfi et al. 2007), resulting in a linear relationship between drivers and system state (Suding et al. 2004). Some of these linear models are built primarily around succession theory, which assumes that if historical disturbance or management regimes or abiotic features are reestablished, the ecosystem will return to its original state naturally along a successional trajectory. In these linear systems, restoration efforts have focused on reestablishing historical disturbance regimes and environmental conditions (Suding and Hobbs 2009). However, despite large and costly management interventions, some degraded ecosystems do not respond to traditional succession-based restoration efforts because key species have been lost or

new feedback mechanisms now favor a degraded state (Gunderson and Pritchard 2002).

A growing number of practitioners are using threshold and alternative stable state theory, which provides a conceptual basis for management and restoration in ecosystems with the potential for thresholds and strong feedback mechanisms (Suding et al. 2004, Walker and Salt 2006, Standish et al. 2014). Threshold and alternative state models predict that changes in environmental conditions lead to very little change in community composition or function until a threshold is crossed, triggering a sudden change in composition or function (Walker and Salt 2006). In such cases, degraded systems do not respond predictably to management efforts, producing inconsistent and sometimes unexpected results (Hobbs and Harris 2001, Zedler 2000). Moreover, in systems with alternative states, returning management conditions below the original threshold can fail to return the ecosystem to its previous state, a behavior referred to as hysteresis. In hysteretic systems, the degraded ecosystem has transitioned to an alternative state that can be resistant to further restoration efforts (Scheffer et al. 2001). Thresholds, with or without hysteresis, often occur because of strong feedbacks between species and their environment (Scheffer et al. 2001, Walker and Salt 2006). These strong self-reinforcing feedbacks can make a degraded ecosystem resistant to succession-based

restoration efforts (Bakker and Berendse 1999, Zedler 2000, Collins et al. 2021).

Alternative stable state theory can provide an important guide for ecosystem restoration. However, components of this theory in restoration and management contexts remain underdeveloped. In particular, it is well known that soil seed banks and other forms of belowground propagules (e.g., bud banks) play a fundamental role in ecosystem restoration (Bossuyt and Honnay 2008, VanderWeide and Hartnett 2015, Ma et al. 2019). However, most assessments of degradation are based on aboveground communities. Although, Westoby and colleagues (1989) mentioned seed bank dynamics in their state and transition model from Australia and South Africa, work on the role of soil seed banks and other persistent underground life stages in alternative stable state theory has yet to be fully incorporated into state and transition models for restoration.

Function of soil seed banks in ecosystem restoration

The soil seed bank includes all viable seeds present in a soil profile and on the soil surface (Simpson et al. 1989). Many seeds may be dormant in the soil but remain viable for years. The soil seed bank has been classified into transient and persistent seed components, depending on whether seeds persist in the soil for less or more than a year. Furthermore, persistent seed banks can be loosely categorized as short (persist for 1–5 years) or long term (persist for more than 5 years; Thompson et al. 1997).

Persistent seed banks reflect a long-term vegetation history, and play an important role in determining future vegetation composition, especially following perturbations (Warr et al. 1993). Furthermore, seed banks are thought to play a crucial role in species coexistence through the storage effect (Angert et al. 2009). Only a proportion of the seed bank germinates as a result of any perturbation, a bet-hedging strategy that reduces the probability or risk of population extinction (Venable 2007). One consequence of the storage effect is that seed banks can promote coexistence among species that differ in their responses to disturbances and fluctuating environments (Nathan and Muller-Landau 2000). Seed banks also represent valuable ecological memory for restoration of local vegetation in the face of environmental degradation (Bossuyt and Honnay 2008, Johnstone et al. 2016). In the present article, we argue that the species richness and density of seed banks, in concert with other belowground propagules, represent a potentially underused resource for resilience of degraded vegetation (Thompson et al. 1997, Grime 2001, Ma et al. 2018).

Similar to seed banks, belowground meristems (bud banks) also provide an important source of propagules that may or may not reflect aboveground composition. Although the longevity of belowground meristems is poorly quantified, experimental and observational studies suggest that many belowground meristems of grasses can survive at least 2 years of drought (VanderWeide

and Hartnett 2015), and many may be able to survive for almost a decade (Weaver 1954). For example, Hiiesalu and colleagues (2021) found that belowground plant diversity (roots, rhizomes, bud and seed banks) served as a buffer against aboveground species loss during short-term land-use change. Although all forms of belowground propagules (buds, rhizomes, seeds) should be considered when assessing resilience, we focus our framework primarily on soil seed banks because they are well studied in many ecosystems.

Role of soil seed banks in alternative stable state theory

Although much research has highlighted the functional importance of soil seed banks (Saatkamp et al. 2014, Moreno-De Las Heras et al. 2016), alternative stable state theory has largely ignored the importance of seed banks for ecosystem resilience or as an ecological early warning system of decreasing resilience (but see Bhattachan et al. 2014, Johnstone et al. 2016). In a restoration context, the basic alternative stable state model proposes that at least two stable states exist: desired and degraded (Suding et al. 2004). Often the transition from desired to degraded state is based solely on the composition of the aboveground plant community. However, if the seed bank and other propagules belowground still reflect the desired state then the system has some inherent resilience and may not have fully crossed a transition threshold. Of course, this assumes conditions where the abiotic environment remains suitable to recolonization by the desired species, which becomes less likely as degradation continues. In the present article, we present a conceptual framework integrating seed bank dynamics into alternative stable state theory highlighting differences between aboveground and belowground composition potentially resulting in a window of time when degraded aboveground but desirable belowground communities co-occur. We illustrate this conceptual framework with examples from two well-defined alternative stable state systems—restoration of grasslands degraded by long-term grazing (Noy-Meir 1975, Suding and Hobbs 2009) and woody plant encroachment of grasslands (D’Odorico et al. 2012, Ratajczak et al. 2017a, 2017b). We then integrate these observations into a fold bifurcation, which is a common explanation for the existence of alternative states.

Soil seed banks are an important part of ecosystem resilience

Ecological resilience is the capacity of an ecosystem to absorb changes in disturbances and other changes in environmental drivers while maintaining the same structure, function, identity, and feedback loops (Folke et al. 2004, Oliver et al. 2015). At its simplest, resilience is a measure of bounce back or recovery following relaxation of some type of perturbation (e.g., Tilman and Downing 1994). When drivers are undergoing directional change, such as a warming climate or increasing grazing pressure, resilience reflects

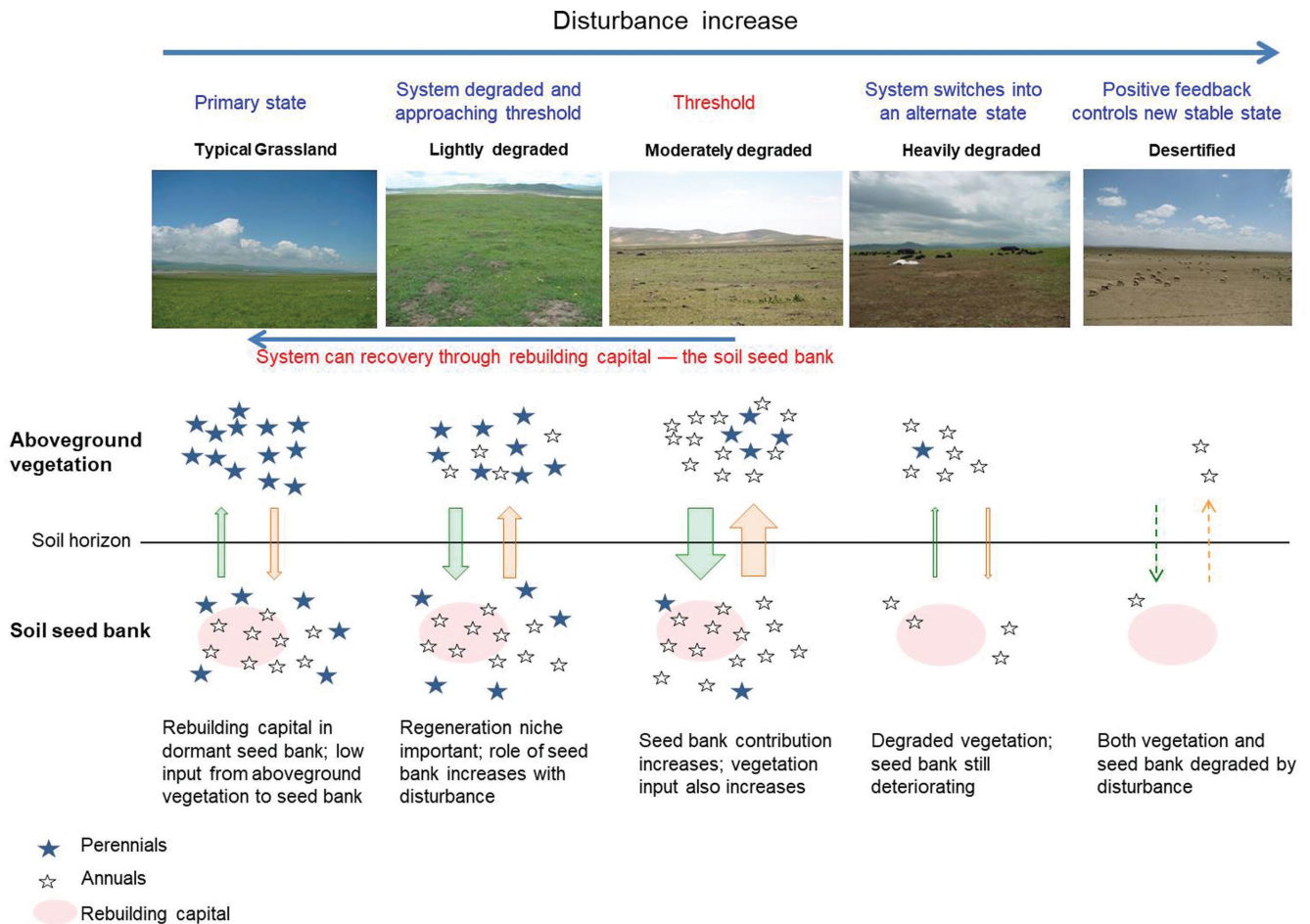


Figure 1. Changes in species composition of aboveground vegetation and soil seed bank as grazing pressure increases. Above- and belowground life-form composition of vegetation and the soil seed bank, respectively. Solid stars represent perennials and open stars represent annuals. The light red shading in the seed bank represents “rebuilding capital” or “ecological memory” of the system—a crucial part of a persistent seed bank that may be used for vegetation regeneration and restoration.

the ability to avoid lasting changes in function and structure (Folke et al. 2004). Because seed banks are an important potential resource for ecological restoration (e.g., Ooi et al. 2009, Basto et al. 2015, An et al. 2020), we developed a conceptual model that integrates aboveground vegetation and soil seed bank change into alternative stable state theory for ecological restoration and management (figure 1). We illustrate this framework in response to grazing pressure and shrub encroachment.

Grazing. Theory predicts that gradual environmental changes, such as an increase in grazing pressure, may reduce the resilience of a stable state in a plant community regulated by interspecific competition, increasing the likelihood that the system will cross a threshold into a new undesirable alternative state dominated by unpalatable species (van Nes and Scheffer 2004, Ratajczak et al. 2017a). As was noted previously (Ma et al. 2013), once the proportion of

perennials is reduced by increased grazing pressure, annual and biennial (often r-strategy) species gradually increase. Contrary to annuals, perennials may make a relatively small contribution to the soil seed bank because their reproductive strategy results in low viable seed production, or short-lived seeds (Ma et al. 2019). If the grazing disturbance is sustained (slightly degraded grassland), some patches would exhibit low vegetation cover dominated by annuals and biennials, and these patches may be bordered by bare soil areas as grazing pressure increases further (degraded grassland; figure 1; Ma et al. 2013). Meanwhile, the lack of vegetation cover in some gaps could lead to further degradation through loss of soil nutrients and water to runoff. However, if grazing pressure is reduced before reaching a threshold, aboveground vegetation can recover to the desired state through a combination of growth from new seeds, tillers from surviving plants, and new recruits from the seed and bud banks (figure 1).

If elevated grazing pressure is sustained, the aboveground vegetation can be pushed across a threshold into a degraded state, where aboveground vegetation is almost completely lost and the soil seed bank resources are nearly lost (figure 1). At this point, vegetation reestablishment is likely limited by multiple factors, including loss of soil resources resulting from the lack of vegetation cover and increased wind and water erosion (Okin et al. 2015). The intensification of soil erosion impedes vegetation recovery (Turnbull et al. 2008), which increases abrasion, burial and uprooting. These factors create a feedback loop further reinforcing loss of vegetation cover (e.g., D'Odorico et al. 2013). Therefore, under consistent and intense grazing pressure, species composition changes, species diversity declines, and the grassland remains in a degraded state with limited capacity for resilience (figure 1).

Generally, annuals and biennials often have higher seed input to the soil seed bank compared with perennials (e.g., Grime 2001). The high relative contribution of ruderal strategists in the seed bank is a function of their rapid growth, high seed production, and seed bank persistence, all of which are adaptations to disturbed conditions (Thompson et al. 1997, Fenner and Thompson 2005). Persistent disturbance can then lead to an increase in ruderals in the seed bank (Wellstein et al. 2007). Therefore, the seed bank composition of desirable species often declines and seed input of ruderals increases as annuals and biennials dominate under sustained grazing pressure (figure 1).

There are limited regeneration niches for seeds in the soil seed bank under low disturbance levels (Grubb 1986). Successful establishment from seed is generally favored through disturbances that create gaps in vegetation (Grime 2001, Fenner and Thompson 2005). Aboveground plant community composition changes as disturbance (e.g., grazing pressure) increases, but changes belowground are often slower, requiring longer periods of time to cross a threshold for changes in the seed bank (Chang et al. 2001, Ma et al. 2020). Therefore, as disturbance intensity increases, the role of belowground propagules generally increases and aboveground vegetation nears the threshold to a degraded state.

Theory predicts a positive relationship exists between the intensity of disturbance and the percentage of species with long-term persistent seed banks (Thompson et al. 1998, Grime 2001). In addition, a trade-off exists between adult life span and seed longevity (Venable and Brown 1988, Rees 1996). As a consequence, short-lived species rely more on persistent seed banks compared with long-lived species (Thompson et al. 1998, Hopfensperger 2007, Ma et al. 2018). Also, much research has demonstrated that early successional stage vegetation has high input to the soil seed bank, and that most species from early successional stages remain in the soil seed bank throughout succession (e.g., Bossuyt and Hermy 2004, Ma et al. 2019). Early successional species represent ecological memory (figure 1) that remains relatively intact as aboveground vegetation approaches a degradation threshold.

Although much research has found that seed density increases in disturbed habitats (e.g., Bakker and Berendse 1999, Fenner and Thompson 2005, Kalamees et al. 2012), grazing pressure can increase the transient seed bank but decrease the persistent seed bank (Ma et al. 2018). There can be a large difference between composition of the aboveground plant community and belowground propagules. This difference means that even if the aboveground portion has crossed a threshold, the belowground portion might allow the system to remain resilient longer.

If overgrazing continues, a threshold point would be crossed when aboveground vegetation permanently loses the ability to regenerate either clonally or via the seed bank once the seed bank reaches a depleted state. At this point, increased disturbance creates harsh conditions for seed germination because of, for example, wind abrasion that can damage small seedlings. Once aboveground vegetation has been degraded, aeolian processes and background decay of seeds reduce the soil seed bank (Li et al. 2007, Bhattachan et al. 2014), trapping vegetation in a degraded state (figure 1). That is, the ecological memory has been depleted and the recovery of aboveground vegetation is therefore impeded after crossing the threshold (figure 1).

Woody plant encroachment. Hundreds of millions of hectares of arid and semiarid grasslands have been lost via woody plant encroachment (D'Odorico et al. 2012, Turnbull et al. 2014, Maestre et al. 2016). Dominance by woody plants alters numerous ecosystem properties and services, such as soil erosion (Eldridge et al. 2011) and biodiversity and community stability (Ratajczak et al. 2012). We suggest that seed banks also contribute resilience to encroachment, in which grasslands and a state dominated by woody plants (shrubs or trees) are considered to be alternative stable states (Staver et al. 2011, D'Odorico et al. 2012, Collins et al. 2021).

In the grassland state, the aboveground plant community is dominated by herbaceous species that provide a constant input into the soil seed bank and in some systems, a robust bud bank (figure 2; Dalglish and Hartnett 2006). Woody plant encroachment occurs in response to a variety of environmental drivers including climate change, elevated atmospheric carbon dioxide concentration, and management decisions (fire suppression, grazing intensity; Archer et al. 2017). During the early stages of woody plant encroachment, the vegetation remains dominated by grasses, but includes scattered woody plants (Ratajczak et al. 2017a). At this point, changes in management might reverse the transition to dominance by shrubs or trees (Ratajczak et al. 2017a). However, continued changes in environmental drivers, such as increasing aridity (Rudgers et al. 2018), may alter the competitive balance between grasses and woody plants, creating a positive feedback loop that enhances the rate of woody plant encroachment (D'Odorico et al. 2010). At this point, woody species contribute the most to the soil seed bank, further enhancing persistence of woody species

Shrub encroachment

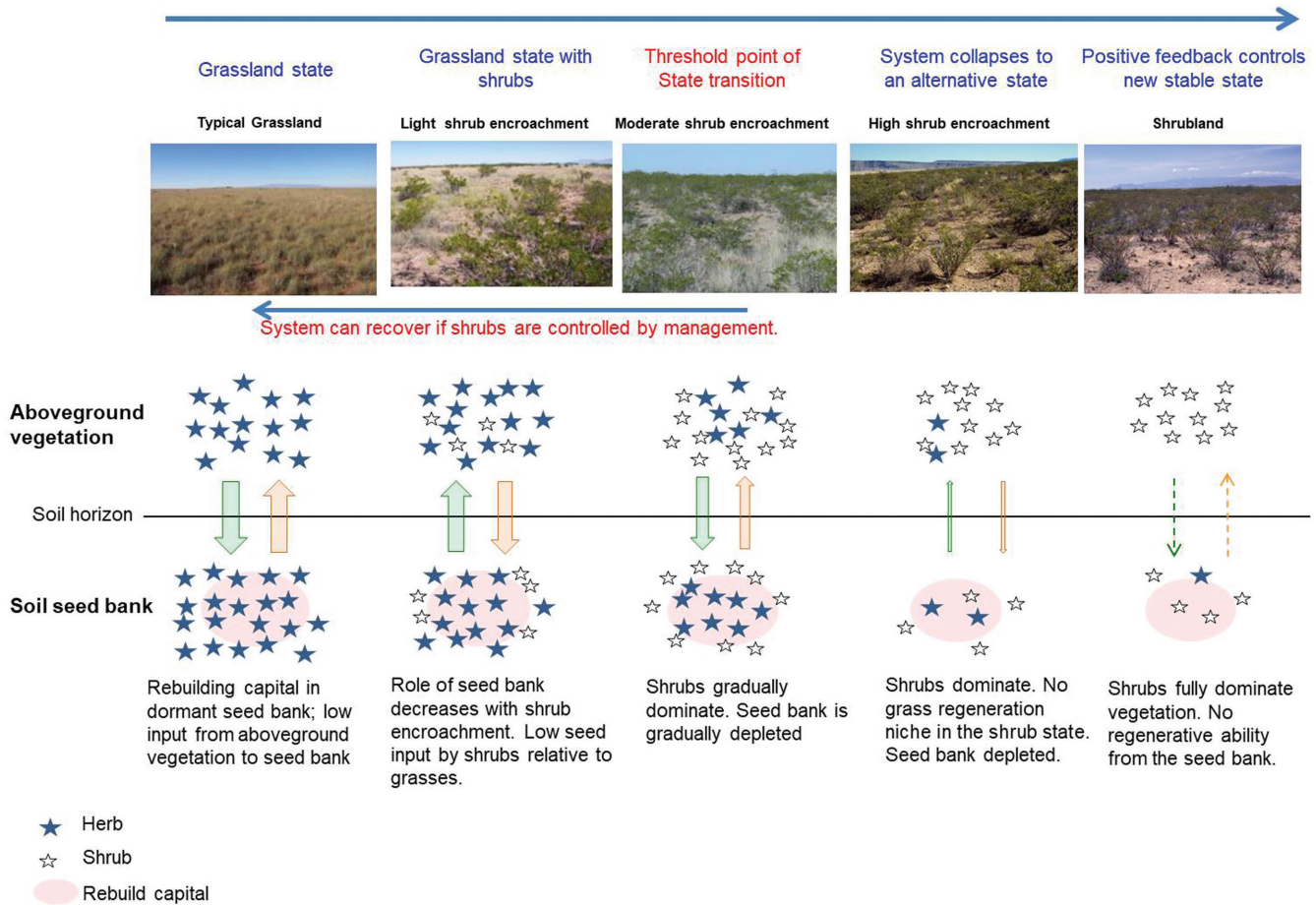


Figure 2. Changes in species composition of aboveground vegetation and soil seed bank as shrub encroachment occurs. Above- and belowground life-form composition of vegetation and the soil seed bank, respectively. Solid stars represent herbaceous species and open stars represent shrubs. The light red shading in the seed bank represents “rebuilding capital” or “ecological memory”—a crucial part of the persistent seed bank that may be managed for vegetation regeneration and restoration.

at the expense of herbaceous vegetation (e.g., Houghton et al. 2013).

Characterizing the seed bank of woody plant encroached and native grassland species is important to understand seed bank dynamics (Gioria and Pyšek 2016). Knowledge of the characteristics of seed bank dynamics during shrub encroachment is crucial to assess the potential for successful recruitment from the seed bank, estimating the implications of shrub encroachment and recovery potential of grassland species after shrub encroachment has occurred (Vosse et al. 2008, Gioria and Osborne 2010). Seed banks often support more species than the aboveground plant community in encroached grasslands (Robertson and Hickman 2012, Gooden and French 2014). At some point during woody plant encroachment, however, the soil seed bank—and, in some cases, the bud bank—will begin to reflect aboveground dominance by woody species, especially with encroachment by clonal shrubs.

In the grassland state (figure 2), the soil seed and bud bank primarily consist of propagules from herbaceous species, which contribute to the maintenance of the grassland state. Once again, the soil seed bank represents the ecological memory available for restoration. In the earliest stages of degradation, the bud bank may also represent the primary mechanism of resilience.

In the second stage, woody plants still have a relatively limited impact on seed bank composition (figure 2). Over time, however, seed input from aboveground vegetation gradually decreases with woody plant encroachment (Houghton et al. 2013) by species with relatively lower seed production compared with herbaceous plants (Leishman et al. 2000). In general, trees and shrubs negatively affect species richness and seed density of resident seed banks (Gaertner et al. 2011, Marchante et al. 2011), especially for native species (e.g., Gioria and Osborne 2009). When environmental conditions are suitable for seed germination,

species lost from aboveground vegetation because of shrub encroachment may be recruited from the soil seed bank. But now those seedlings must compete with adult woody plants. Therefore, the role of the soil seed bank is relatively reduced compared with the previous stage of vegetation regeneration. Moreover, the similarity in species composition between aboveground vegetation and the soil seed bank is lower at shrub encroached sites compared with that at unencroached sites (Gioria and Pyšek 2016).

The third stage constitutes the potential threshold for a state transition of the seed bank (figure 2), where shrub seeds start to outnumber herbaceous species. At this stage, shrubs increase in abundance in the absence of disturbance and may even benefit from disturbances that free resources and primary space (Vosse et al. 2008, Gioria and Osborne 2010). For example, Moreno-De Las Heras and colleagues (2016) found that mean density of viable seeds was generally lower in a grass–shrub ecotone than in grassland. In addition, abundance of herbaceous species declines in aboveground vegetation because of a range of mechanisms under woody plant encroachment, such as resource competition (Gioria et al. 2014). However, seeds of formerly dominant herbaceous species still exist in the soil seed bank for at least several years, once again reflecting the past buildup of ecological memory (figure 2). In this situation, active and effective management (e.g., Ravi et al. 2010) could still potentially restore a site to the grassland state.

In the fourth and last stage, aboveground vegetation is dominated by woody species, diminishing opportunities for grassland species recruitment from the soil seed bank (figure 2). Indeed, in the northern Chihuahuan Desert, Moreno-De Las Heras and colleagues (2016) found that shrub encroachment by *Larrea tridentata* resulted in significantly lower seed densities of herbaceous species in shrub-dominated areas. In this system, shrub dominance accelerates change in biotic and abiotic conditions, which, in semiarid areas, includes increased wind and water erosion (Turnbull et al. 2010, Okin et al. 2018), increased soil moisture heterogeneity (Schlessinger et al. 1990), and lower density of seeds in the soil seed bank, all of which may constrain the reestablishment of herbaceous species (Peters and Yao 2012). Therefore, quantifying the proportion or densities of woody species in the soil propagule bank as woody plant encroachment is occurring is crucial for estimating the restoration potential to the desired grassland state.

Seed banks and resilience to disturbance

One common alternative state model is a fold bifurcation (e.g., Scheffer et al. 2001). In a system defined by a fold bifurcation, the system state is attracted to one of two stable states (see solid lines in figure 3a), depending on the value of a driver variable and the system's current state. For values of a driver variable where both stable states are possible, the two states are separated by a critical threshold (the dashed line in figure 3a). Above this critical threshold, the system is attracted to the upper stable state; below this threshold, the

system is attracted to the lower stable state (see the arrows in figure 3a). For certain values of the driver variable, only one of the two states is favored. As a result, if a driver variable is pushed across a threshold or bifurcation point (see the star in figure 3a), a critical transition to the other alternative state commences (Scheffer et al. 2001), taking less than a year in faster systems (e.g., lakes) but over a decade in slower systems, such as grasslands (Ratajczak et al. 2017b, Collins et al. 2021).

We argue that long-lived soil seed banks can modify the shape of critical thresholds, providing a larger window of opportunity to maintain the resilience of aboveground vegetation (figure 3b, 3c). In a system with a short-lived or depleted seed bank, this is depicted as a bending of the critical threshold to higher values of the system state (figure 3b). In this hypothetical example, a driver variable is pushed beyond a bifurcation point (time steps 0 to 1 in figure 3b), and as a result, the system starts to transition to an alternative state (shown as the dashed arrows in figure 3b). Even if the change in driver is reversed part way through the transition, the system is already below its critical threshold, and the system transitions to the alternative state (see time steps 4 to 6 in figure 3b). In a hypothetical system with a more long-lived and abundant seed bank of desirable species, the critical threshold is bent downward, meaning that it takes larger changes in state before hysteresis occurs. In this system, we can, again, push the driver variable beyond the bifurcation point (time steps 0 to 1 in figure 3c), initiating a transition to an alternative state (time steps 0 to 4 in figure 3c). The difference between this and the short-lived or depleted seed bank is that when we reverse the change in the driver, the system state is now above the critical threshold, and as a result, the system is still attracted to its original state (time steps 5 to 6 in figure 3c).

Fast and slow transition

Some natural or anthropogenic disturbances can push driver variables across thresholds leading to the onset of state transitions (e.g., Hastings and Wysham 2010). However, different system components (e.g., aboveground vegetation, soil seed bank) change at different rates over time and differ in their resilience. The soil seed bank represents valuable ecological memory that may rescue a system from state transition once aboveground vegetation has crossed an apparent threshold. Aboveground vegetation generally changes faster than the composition of the soil seed bank given that the seed bank is an accumulation of historical vegetation, whereas aboveground vegetation reflects more immediate impacts of environmental drivers. The yellow area shows the total deficit of species diversity or biomass if only aboveground vegetation is considered for recovery to the desirable state (figure 4). The bud bank is an important component of resilience of short to intermediate duration for perennial plants (Weaver 1954, Vanderweide and Hartnett 2015). These differences in the rates of response by components of vegetation, from fast (aboveground vegetation) to slow

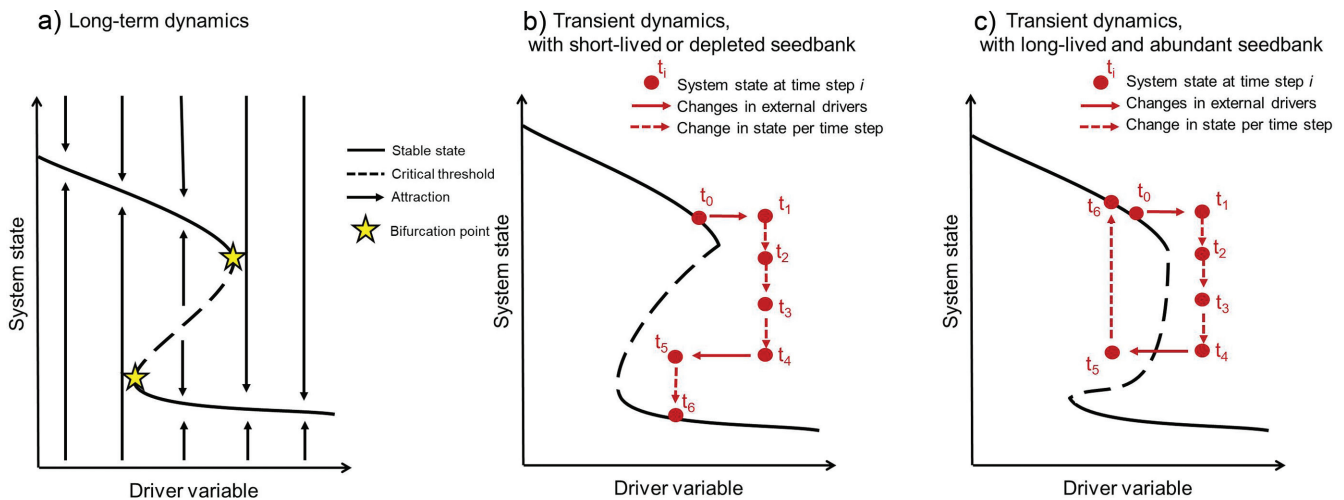


Figure 3. (a) Shows a fold bifurcation, which describes the long-term dynamics of some systems with alternative states (e.g., grassland and shrubland). The solid lines are stable states to which the system is attracted for the corresponding value of a driver variable (e.g., fire frequency). Arrows show the direction that the system state will move for combinations of system state and driver variable values. The dashed line is a critical threshold that separates basins of attraction for the two alternative states. Stars show bifurcation points (see text). (b) depicts the transient dynamics of hypothetical system with a short-lived or depleted seed bank. The circles indicate the system state at different time steps. The red arrows with solid lines show changes in driver variables, whereas the red arrows with dashed lines show transient dynamics of the system over single time steps. All other notation follows panel (a). Panel (c) depicts a hypothetical system with an abundant seed bank of long lived seeds. All notations in panel (c) follow panel (b). Note that the primary difference between panels (b) and (c) is the shape of the critical threshold.

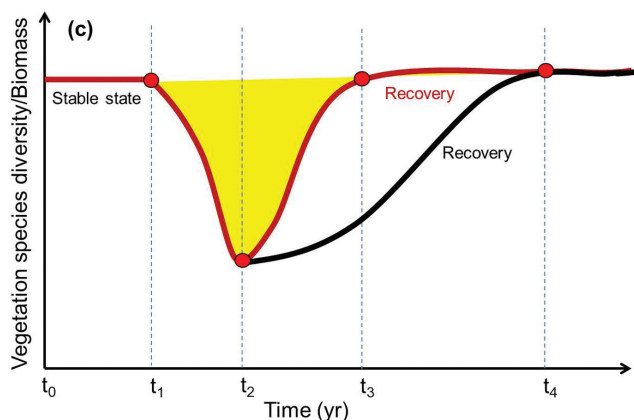


Figure 4. Species diversity or biomass of system change under constant high disturbance (t_1-t_2) and when disturbance is relaxed (t_2-t_4) with time. Starting from t_2 , the system only considers aboveground vegetation (the red line, t_2-t_3) or seed bank (the black line, t_2-t_4) for system recovery, and the systems follow different recover trajectories following disturbance. The red dot at t_1 marks the starting point of disturbance, at t_2 vegetation diversity or biomass is at a minimum under disturbance, and t_3 to t_4 shows the system's recovery to the primary state based on aboveground vegetation and soil propagule bank, respectively. The yellow area shows the total deficit of species diversity or biomass if only aboveground vegetation is considered for recovery to the desirable state.

(seed and bud banks), result in differences in resilience, a property that extends opportunities for management under environmental change.

The role of seed bank as an early warning system

It is important to develop tools and policies to prevent undesired state transitions because of their potential societal costs and loss of key ecosystem services (Reynolds et al. 2007, Stafford-Smith et al. 2007, Bestelmeyer et al. 2013). Advanced warning and monitoring of ecosystem degradation processes, and particularly the development of early warning indicators of imminent state transitions is important in ecosystem restoration and management (Briske et al. 2006). Several potential warning signs in vegetation patterns and increasing spatial variance of vegetation have been proposed (Rietkerk et al. 2004, Kéfi et al. 2007, Dakos et al. 2011). All rely on aboveground vegetation. For example, monitoring of plant cover has long served this role in drylands (Herrick et al. 2005). However, the potential for belowground dynamics to serve as early warning signs is unexplored.

We propose an alternative early warning system by calculating the similarity between species composition in the soil seed bank and aboveground vegetation (figure 5). In a stable ecosystem, vegetation will remain in its current state when disturbance regimes remain within a historical range. In this case, there is a relatively stable ratio between the abundance of species in aboveground vegetation and the seed bank.

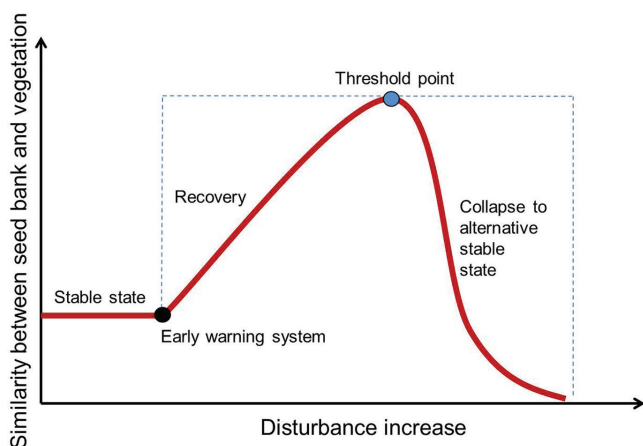


Figure 5. Role of soil seed bank as an ecosystem warning system. Similarity between soil seed bank and aboveground vegetation changes as disturbance increases. The black dot indicates the point at which compositional similarity between the seed bank and aboveground vegetation starts to increase. As similarity increases, this serves as an early warning signal that the system is approaching a threshold. The blue dot occurs when the system has the highest similarity between seed bank and aboveground vegetation, which indicates the critical threshold point of state transition.

Assuming a system that starts with less disturbance, we would expect some dissimilarity between the aboveground vegetation and seed bank, because dominant perennials are less prominent in seed banks than annuals and other ruderals (figure 5; e.g., Edwards and Crawley 1999, Ma et al. 2019).

This dissimilarity establishes a baseline with which change in both aboveground and seed bank species composition can be compared. As disturbance continues, the aboveground system begins to deviate from the desired state, but the soil seed bank may still reflect the composition of the desired state. That is, the soil seed bank can confer resilience while serving as an early warning system based on changes in similarity between above- and belowground composition (figure 5). If the similarity between the soil seed bank and aboveground vegetation increases under anthropogenic pressure, this indicates that the aboveground vegetation is increasingly characterized by species from the soil seed bank. The degree of similarity can serve as a warning signal to reduce anthropogenic pressure and allow the belowground system to maintain resilience. If disturbance continues, the similarity between the soil seed bank and aboveground vegetation will again increase as the composition of the seed bank increasingly reflects that of the degraded state of aboveground vegetation. The maximum similarity between the soil seed bank and aboveground vegetation will mark the threshold point leading to a stable degraded state (figure 5). At this point the system has lost resilience and requires intervention to facilitate restoration.

When this early warning first appears the system potentially retains some intrinsic resilience, as a consequence of a viable persistent seed bank that still reflects components of the desired state. In contrast, if we relied only on aboveground indicators we might conclude early on that the resilience of the system is higher than it actually is (as the seed bank is changing) and, later on, lower than predicted (when the seed bank still reflects some of the antecedent vegetation). As the similarity between the seed bank and aboveground vegetation increases, it serves as an early warning sign that the system is approaching a threshold for permanent change to a degraded state. To monitor and repair degraded ecosystems, we might be able to combine resilience of the soil seed bank with timely management interventions to prevent collapse into a degraded, undesirable state. Changes in the compositional similarity between the soil seed bank and aboveground vegetation serve as an early warning signal to predict when interventions are both necessary and likely to be effective.

Conclusions

We developed a conceptual framework integrating seed bank dynamics into alternative stable state theory highlighting differences between aboveground and belowground composition resulting in a transient period of degraded aboveground but desirable belowground communities. Often, the transition from desired to degraded state is based solely on composition of the aboveground plant community. However, if the belowground propagule bank still reflects the desired state to some degree then the system might still retain inherent resilience. This is because aboveground vegetation often changes faster than the composition of the soil seed bank given that the seed bank is an accumulation of historical vegetation, whereas aboveground vegetation reflects more immediate impacts of environmental drivers, such as disturbance. Therefore, we argue that a single system can have both fast (aboveground vegetation) and slow (seed bank) components simultaneously and that this property extends opportunities for resilience under environmental change. Therefore, conclusions about alternative stable states should more carefully consider all aspects of the plant community both above and below ground. Differences between aboveground vegetation and soil seed banks can also serve as a component of an early warning system. We conclude that a fuller integration of aboveground vegetation and seed banks has the potential to advance our understanding of ecosystem warning systems, resilience and recovery, with clear practical applications to management and restoration of degraded ecosystems.

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References cited

- An H, Zhao Y, Ma M. 2020. Precipitation controls seed bank size and its role in alpine meadow community regeneration with increasing altitude. *Global Change Biology* 26: 5767–5777.
- Angert AL, Huxman TE, Chesson P, Venable DL. 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences* 106: 11641–11645.
- Archer SR, Andersen EM, Predick KI, Schwinning S, Steidl RJ, Woods SR. 2017. Woody plant encroachment: Causes and consequences. Pages 25–83 in Briske DD, ed. *Rangeland Systems: Processes, Management and Challenges*. Springer.
- Bakker JP, Berendse F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution*. 14: 63–6.
- Basto S, Thompson K, Phoenix G, Sloan V, Leake J, Rees M. 2015. Long-term nitrogen deposition depletes grassland seed banks. *Nature Communications* 6: 6185.
- Bestelmeyer BT, Duniway MC, James DK, Burkett LM, Haversustad KM. 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystems, more resilience than we thought. *Ecology Letters* 16: 339–345.
- Bhattachan A, D'Odorico P, Dintwe K, Okin GS, Collins SL. 2014. Resilience and recovery potential of duneland vegetation in the southern Kalahari. *Ecosphere* 5: 2.
- Bossuyt B, Hermy M. 2004. Seed bank assembly follows vegetation succession in dune slacks. *Journal Vegetation Science* 15: 449–456.
- Bossuyt B, Honnay O. 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science* 19: 875–884.
- Briske DD, Fuhlendorf SD, Smeins FE. 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology and Management* 59: 225–236.
- Chang ER, Jefferies RL, Carleton TJ. 2001. Relationship between vegetation and soil seed banks in an arctic coastal marsh. *Journal of Ecology* 89: 367–384.
- Collins SL, Nipper J, Blair JM, Briggs JM, Blackmore P, Ratajczak Z. 2021. Fire frequency, state change and hysteresis in tallgrass prairie. *Ecology Letters* 24: e1.13676. <https://onlinelibrary.wiley.com/doi/10.1111/ele.13676>
- Dakos V, Kéfi S, Rietkerk M, van Nes EH, Scheffer M. 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. *American Naturalist* 177: 154–166.
- Dalgleish HJ, Hartnett DC. 2006. Below-ground bud banks increase along a precipitation gradient of the north American great plains: A test of the meristem limitation hypothesis. *New Phytologist* 171: 81–89.
- D'Odorico P, Fuentes JD, Pockman WT, Collins SL, He Y, Medeiros JS, De Wekker S, Litvak ME. 2010. Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. *Ecosphere* 1: art17.
- D'Odorico P, Okin GS, Bestelmeyer BT. 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecology* 93: 520–530.
- D'Odorico P, Bhattachan A, Davis KF, Ravi S, Runyan CW. 2013. Global desertification: Drivers and feedbacks. *Advances in Water Resources* 51: 326–344.
- Edwards GR, Crawley MJ. 1999. Herbivores, seed banks and seedling recruitment in mesic grassland. *Journal of Ecology* 87: 423–435.
- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. *Ecology Letters* 14: 709–722.
- Fenner M, Thompson K. 2005. *The Ecology of Seeds*. Cambridge University Press.
- Folke C, Carpenter S, Walker B, Sheffer M, Elmqvist T, Gunderson L, Holling CS. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35: 557–581.
- Gaertner M, Richardson DM, Privett SDJ. 2011. Effects of alien plants on ecosystem structure and functioning and implications for restoration: Insights from three degraded sites in South African fynbos. *Environmental Management* 48: 57–69.
- Gioria M, Osborne BA. 2009. Assessing the impact of plant invasions on soil seed bank communities: Use of univariate and multivariate statistical approaches. *Journal of Vegetation Science* 20: 547–556.
- Gioria M, Osborne BA. 2010. Similarities in the impact of three large invasive plant species on soil seed bank communities. *Biological Invasions* 12: 1671–1683.
- Gioria M, Pyšek P. 2016. The legacy of plant invasions: Changes in the soil seed bank of invaded plant communities. *BioScience* 66: 40–53.
- Gioria M, Jarošík V, Pyšek P. 2014. Impact of invasive alien plants on the soil seed bank: Emerging patterns. *Perspectives in Plant Ecology, Evolution, and Systematics* 16: 132–142.
- Gooden B, French K. 2014. Impacts of alien grass invasion in coastal seed banks vary among native growth forms and dispersal strategies. *Biological Conservation* 171: 14–26.
- Grime JP. 2001. *Plant Strategies, Vegetation Processes and Ecosystem Properties* 2nd ed. Wiley.
- Grubb PJ. 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. Pages 207–225 in Diamond J, Case TJ, eds. *Community Ecology*. Harper and Row.
- Gunderson LH, Pritchard L, eds. 2002. *Resilience and the Behavior of Large-Scale Ecosystems*. Island Press.
- Hasting A, Wysham DB. 2010. Regimes shifts in ecological systems can occur with no warning. *Ecology Letters* 13: 464–472.
- Herrick JE, Van Zee JW, Haversustad KM, Burkett LM, Whitford WG. 2005. *Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems*. USDAARS Jornada Experimental Range.
- Hiiesalu I, Klimešová, Doležal J, Mudrák O, Götzenberger L, Horník J, de Bello F. 2021. Hidden below-ground plant diversity buffers against species loss during land-use change in species-rich grasslands. *Journal of Vegetation Science*. <https://onlinelibrary.wiley.com/doi/abs/10.1111/jvs.12971>. doi:10.1111/jvs.12971
- Hobbs RJ, Harris JA. 2001. Restoration ecology: Repairing the Earth's ecosystems in the new millennium. *Restoration Ecology* 9: 209–219.
- Hopfensperger KN. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* 116: 1438–1448.
- Houghton J, Thompson K, Rees M. 2013. Does seed mass drive the differences in relative growth rate between growth forms? *Proceedings of the Royal Society B* 280: 1–6.
- Johnstone JF, et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14: 369–378.
- Kalamees R, Püssa K, Zobel K, Zobel M. 2012. Restoration potential of the persistent soil seed bank in successional calcareous (alvar) grasslands in Estonia. *Applied Vegetation Science* 15: 208–218.
- Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, de Ruiter PC. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449: 213–218.
- Leishman MR, Wright IJ, Moles AT, Westoby M. 2000. The evolutionary ecology of seed size. Pages 31–57 in M Fenner M, ed. *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International.
- Levin SA. 1999. *Fragile Dominion: Complexity and the Commons*. Perseus Books.
- Li J, Okin GS, Alvarez L, Epstein H. 2007. Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico, USA. *Biogeochemistry* 85: 317–332.
- Ma M, Zhou X, Du G. 2013. Effects of disturbance intensity on seasonal dynamics of alpine meadow soil seed banks on the Tibetan Plateau. *Plant and Soil* 369: 283–295.

- Ma M, Walck JL, Ma Z, Wang L, Du G. 2018. Grazing disturbance increase transient but decrease persistent soil seed bank. *Ecological Applications* 28: 1020–1031.
- Ma M, Baskin CC, Li W, Zhao YP, Zhao Y, Zhao L, Chen N, Du D. 2019. Seed banks trigger ecological resilience in subalpine meadows abandoned after arable farming on the Tibetan Plateau. *Ecological Applications* 29: e01959.
- Ma M, Collins SL, Du G. 2020. Direct and indirect effects of temperature and precipitation on alpine seed banks in the Tibetan Plateau. *Ecological Applications* 30: e02096
- Maestre FT, et al. 2016. Structure and functioning of dryland ecosystems in a changing world. *Annual Review of Ecology, Evolution, and Systematics* 47: 215–237.
- Marchante H, Freitas H, Hoffmann JH. 2011. The potential role of seed banks in the recovery of dune ecosystems after removal of invasive plant species. *Applied Vegetation Science* 14: 107–119.
- Moreno-De Las Heras M, Turnbull L, Wainwright J. 2016. Seed bank structure and plant-recruitment conditions regulate the dynamics of a grassland–shrubland Chihuahuan ecotone. *Ecology* 97: 2303–2318.
- Nathan R, Muller-Landau HC. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285.
- Noy-Meir I. 1975. Stability of grazing systems: An application of predator–prey graphs. *Journal of Ecology* 63: 459–481.
- Okin GS, las Heras MM, Saco PM, Throop HL, Vivoni ER, Parsons AJ, Wainwright J, Peters DPC. 2015. Connectivity in dryland landscapes: Shifting concepts of spatial interactions. *Frontiers in Ecology and the Environment* 13: 20–27.
- Okin GS, Sala OE, Vivoni E, Zhang J, Bhattachan A. 2018. The interactive role of wind and water in functioning of drylands: What does the future hold? *BioScience* 68: 670–677.
- Oliver TH, et al. 2015. Biodiversity and Resilience of Ecosystem Functions. *Trends in Ecology and Evolution* 30: 673–684.
- Ooi MKJ, Auld TD, Denham AJ. 2009. Climate change and bet-hedging: Interactions between increased soil temperatures and seed bank persistence. *Global Change Biology* 15: 2375–2386.
- Peters DPC, Yao J. 2012. Long-term experimental loss of foundation species: Consequences for dynamics at ecotones across heterogeneous landscapes. *Ecosphere* 3: 27.
- Ratajczak Z, Nippert JB, Collins SL. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93: 697–703.
- Ratajczak Z, D’Odorico P, Nippert JB, Collins SL, Bestelmeyer BT, Isbell FI, Nippert JB. 2017a. The interactive effects of press/pulse intensity and duration on regime shifts at multiple scale. *Ecological Monographs* 87: 198–218.
- Ratajczak Z, D’Odorico P, Nippert JB, Collins SL, Brunsell NA., Ravi S. 2017b. Changes in spatial variance during a grassland to shrubland state transition. *Journal of Ecology* 105: 750–760.
- Ravi S, D’Odorico P, Huxman TE, Collins SL. 2010. Interactions between soil erosion processes and fires: Implications for the dynamics of fertility islands. *Rangeland Ecology and Management* 63: 267–274.
- Rees M. 1996. Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions: Biological Sciences* 351: 1299–1308.
- Reynolds JF, et al. 2007. Global desertification: Building a science for dry-land development. *Science* 316: 847–851.
- Rietkerk M, Dekker SC, de Ruiter P, van de Koppel J. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305: 1926–1929.
- Rudgers JA, Chung YA, Maurer GE, Moore DI, Muldavin EH, Litvak ME, Collins SL. 2018. Climate sensitivity functions and net primary production: A framework for incorporating climate mean and variability. *Ecology* 3: 576–582.
- Robertson SG, Hickman KR. 2012. Aboveground plant community and seed bank composition along an invasion gradient. *Plant Ecology* 213: 1461–1475.
- Saatkamp A, Poschlod P, Venable DL. 2014. The functional role of soil seed banks in natural communities. Pages 263–295 in Gallagher RS, ed. *The Ecology of Regeneration in Plant Communities*. CAB International.
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. *Science* 247: 1043–1048.
- Simpson RL, Leck MA, Parker VT. 1989. Seed banks, general concepts and methodological issues. Pages 3–8 in Leck MA, Parker VT, Simpson RL, eds. *Ecology of soil seed banks*. Academic Press.
- Stafford Smith DM, et al. 2007. Learning from episodes of degradation and recovery in variable Australian rangelands. *Proceedings of the National Academy of Sciences* 104: 20690–20695.
- Standish RJ, et al. 2014. Resilience in ecology: Abstraction, distraction, or where the action is? *Biological Conservation* 177: 43–51.
- Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334: 230–232.
- Suding KN, Hobbs RJ. 2009. Thresholds models in restoration and conservation, a developing framework. *Trends in Ecology and Evolution* 24: 271–279.
- Suding KN, Gross KL, Houseman GR. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19: 46–53.
- Thompson K, Bakker JP, Bekker RM. 1997. *The Soil Seed Banks of North West Europe, Methodology, Density and Longevity*. Cambridge University Press.
- Thompson K, Bakker JP, Bekker RM, Hodgson JG. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology* 86: 163–169.
- Tilman D, Downing J. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365.
- Turnbull L, Wainwright J, Brazier R. 2008. A conceptual framework for understanding semi-arid land degradation: Ecohydrological interactions across multiple-space and time scales. *Ecohydrology* 1: 23–34.
- Turnbull L, Wainwright J, Brazier R, Bol R. 2010. Biotic and abiotic changes in ecosystem structure over a shrub-encroachment gradient in the southwestern USA. *Ecosystems* 13: 1239–1255.
- Turnbull L, Wainwright J, Ravi S. 2014. Vegetation change in the southwestern USA: Patterns and processes. Pages 289–313 in Mueller EN, Wainwright J, Parsons AJ, Turnbull L, eds. *Patterns of Land Degradation in Drylands, Understanding Self-Organised Ecogeomorphic Systems*. Springer.
- van Nes EH, Scheffer M. 2004. Large species shifts triggered by small forces. *American Naturalist* 164: 255–266.
- VanderWeide BL, Hartnett DC. 2015. Belowground bud bank response to grazing under severe, short-term drought. *Oecologia* 178: 795–806.
- Venable DL. 2007. Bet hedging in a guild of desert annuals. *Ecology* 88: 1086–1090.
- Venable DL, Brown JS. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131: 360–384.
- Vosse S, Esler KJ, Richardson DM, Holmes PM. 2008. Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa. *South African Journal of Botany* 74: 432–444.
- Walker B, Salt D. 2006. *Resilience Thinking: Sustaining Ecosystems and People in a Changing World*. Island Press.
- Warr SJ, Thompson K, Kent M. 1993. Seed banks as a neglected area of biogeographic research, a review of literature and sampling techniques. *Progress in Physical Geography* 17: 329–347.
- Weaver JE. 1954. *North American Prairie*. Johnson.

- Wellstein C, Otte A, Waldhardt R. 2007. Seed bank diversity in mesic grasslands in relation to vegetation type, management and site conditions. *Journal of Vegetation Science* 18: 153–162.
- Westoby M, Walker B, Noy-Meir I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42: 266–274.
- Zedler JB. 2000. Progress in wetland restoration ecology. *Trends in Ecology and Evolution* 15: 402–407.

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