Role of seed bank in aboveground vegetation regeneration signal ecosystem transition from arid grassland to shrubland with decreasing soil moisture

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Abstract

Aims This study aimed to evaluate the role of seed bank during ecosystem transitions from arid grassland to shrubland.

Methods We explored the aboveground vegetation, seed bank and soil environmental factors at 29 sites along a moisture gradient that served as a space-for-time substitution in the Qaidam Basin on the Tibetan Plateau to test whether changes seed bank composition or changes in the ability of the seed bank to restore aboveground vegetation could lead to ecosystem transition.

Results We found that the composition of the aboveground vegetation presented nonlinear changes with decreased soil moisture and showed an inflection point in the threshold zone on the spatial scale of ecosystem transition from arid grassland to shrubland; however, an inflection point was not observed for the seed bank. Surprisingly, we also found the similarity between the aboveground vegetation and seed bank decreased obviously when soil moisture crosses the critical threshold.

Conclusions Our results suggest that the transition from arid grassland to shrubland ecosystem is not caused by changes of the seed bank composition but by the inhibition of the seed bank’s restorability to aboveground vegetation. Future work on changes in vegetation composition and species diversity with ecosystem transitions should consider the belowground seed bank.

Keywords Arid grassland · Ecosystem transition · Shrubland · Soil seed bank · Soil moisture · Threshold

Abbreviations

AN Available nitrogen
TN Total nitrogen
SOM Soil organic matter
AP Available phosphorus
TP Total phosphorus
SM Soil moisture
NMDS Nonmetric multidimensional scaling

Introduction

Ecological thresholds are often interpreted as ecological processes or responses to anthropogenic activities and rapidly intensifying global climate changes that are nonlinear and are specifically presented as abrupt changes at a point or in a zone (Huggett 2005; Groffman et al. 2006; Sasaki et al. 2008; Li et al. .
Exceeding the threshold causing abrupt transitions in the state of ecosystems (Holling 1973; Ratajczak et al. 2017; Hu et al. 2018), which may reduce ecosystem services via the loss of ecosystem functions and biodiversity (Diaz et al. 2001; Sasaki et al. 2008; Hu et al. 2018), and it is difficult to reverse these transitions.

Previous studies have shown that substantial changes in the ecosystem structure of arid grasslands cause the systems to crash and form new systems, for example, via replacement by woody plants (Bestelmeyer et al. 2013). Such state transitions from arid grassland to shrubland are occurring globally (Huenneke et al. 2002; Ratajczak et al. 2017). The state transition from arid grassland to shrubland can be viewed as a two-step process (Fig. 1), which may be subsequently regulated by positive feedback (Coop et al. 2020). First, environmental driver can cause decrease of dominant species coverage and diversity in the arid grassland, creating the conditions for the colonization of shrubs (D’Odorico et al. 2006; Ratajczak et al. 2012, 2017). Second, the recovery is inhibited due to loss of seed resources or failure of seedling recruitment. Unfortunately, despite its importance to the resilience of ecosystems, the role of the seed bank in this process has hardly been studied (Ma et al. 2021).

Species loss from the aboveground vegetation cause by environmental change; however, seeds of these species may be buried and remain dormant in the seed bank through the storage effect (Basto et al. 2015a). The aboveground vegetation in arid ecosystems is dominated by annual plants, which produce long-lived seeds with multiyear dormancy, leading to the formation of a substantial and potentially persistent seed bank (Ooi et al. 2009), offering the potential to bridge periods of unfavourable conditions (Ooi et al. 2009; Ooi 2012; Baskin and Baskin 2014). This strategy contributes to the maintenance of species diversity (Royo and Ristau 2013) and the reestablishment of species lost from aboveground vegetation (Kalamees et al. 2012). Thus, the observed loss of a species from aboveground vegetation may not signal a loss of the species from the community (LaForgia et al. 2018).

Increasing evidence has revealed that the water availability/soil moisture is a more important driver during the transition from arid grassland to the shrubland ecosystem (Eldridge et al. 2011; Ratajczak et al. 2012, 2014). For example, the state transition is accelerated with decreased water availability/soil moisture because shrubs can take advantage of deeper soil moisture, which is not conducive where the aboveground vegetation undergoes state transition. In case 1, the species composition of seed bank changes abruptly when it is close to the critical threshold, consistent with aboveground vegetation. In this scenario, the lack of seed resources leads to reduced ecosystem resilience, resulting in state transition. In case 2, the composition of the seed bank does not change before and after the critical threshold. In this scenario, the ability of the seed bank to restore aboveground vegetation may be inhibited near the critical threshold, which leads to the transition from arid grassland to shrubland (b).

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Fig. 1 Schematic illustration of the mechanisms of the state transition from arid grassland to the shrubland ecosystem. First step: increasing environmental driver (red solid arrows) initiates the state transition in arid grassland. Second step: the recovery is inhibited (green dotted arrows). The length of the arrow indicates the magnitude of the environmental driver. For example, the longer the red arrow, the stronger the environmental driver, and the longer the green dotted arrow, the more inhibited the recovery process. The grey dotted circle represents subsequent regulation by possible positive feedback (a). Two hypothetical scenarios of changes of species composition in the seed bank, where the aboveground vegetation undergoes state transition. In case 1, the species composition of seed bank changes abruptly when it is close to the critical threshold, consistent with aboveground vegetation. In this scenario, the lack of seed resources leads to reduced ecosystem resilience, resulting in state transition. In case 2, the composition of the seed bank does not change before and after the critical threshold. In this scenario, the ability of the seed bank to restore aboveground vegetation may be inhibited near the critical threshold, which leads to the transition from arid grassland to shrubland (b).
to grass growth (Gheardi et al. 2015). However, the role of the seed bank in regulating state transitions has not been identified (Ma et al. 2021). Specially, previous studies have found that increasing drought can increase the seed germination failure rate and seedling mortality (Ooi 2012; Kranner et al. 2010). These results can limit aboveground vegetation recovery with a decrease in soil moisture and may contribute to state transition. In fact, the seed bank dynamics are regulated by drivers such as soil moisture and other environmental factors (such as pH), which will, in turn, profoundly affect plant regeneration, population dynamics and species persistence (Plue et al. 2013) and ultimately influence the ecosystem state transition. Therefore, we need to consider the responses of both aboveground vegetation and the seed bank to the drivers of the state transition from arid grassland to the shrubland ecosystem.

An important challenge to understanding the mechanism of the state transition is the change in ecosystem resilience resulting from changes in species composition of the seed bank and the resulting effects on the ability of the seed bank to regenerate aboveground vegetation. In this study, we used the species composition similarity between the seed bank and aboveground vegetation to represent capacity for the seed bank to regenerate aboveground vegetation because the similarity between the seed bank and aboveground vegetation can provide insight into whether the seed bank is driving aboveground vegetation (Hopfensperger 2007). This information can reflect the contribution of the seed bank to restoring aboveground vegetation and is widely used as an indicator of ecosystem resilience (Bossuyt and Honnay 2008). Here, we outline a framework to establish a linkage between the seed bank and state transition theory. We predict that with state transition from arid grassland to shrubland, the seed bank may exhibit two patterns (Fig. 1b). First, the composition of the seed bank changes abruptly when it is close to the critical threshold, consistent with aboveground vegetation. In this scenario, the lack of seed resources leads to reduced ecosystem resilience, resulting in state transition. Second, the composition of the seed bank does not change before and after the critical threshold. In this scenario, the restorability of the seed bank to aboveground vegetation may be inhibited near the critical threshold, which leads to the transition from arid grassland to the shrubland.

It is very difficult to identify the change in the composition of the seed bank and its restorability to aboveground vegetation during the state transition because the seed bank cannot be directly observed and lack of long-term experimental data on the seed bank and aboveground vegetation before and after state transition. Because of these limitations, we used a spatial approach rather than a temporal approach to collect data from 29 sites across arid grassland and shrubland ecosystems in Qaidam Basin on the Tibetan Plateau. We collected data on the composition both of the seed bank and aboveground vegetation as well as data on soil environmental factors and calculated the composition similarity between the seed bank and aboveground vegetation. We aimed to identify 1) whether the soil moisture is a driver in determining the dynamics of both the seed bank and aboveground vegetation during the ecosystem transition from arid grassland to shrubland. 2) Then, we assessed whether there is a consistent spatial pattern of species composition in both the seed bank and aboveground vegetation in response to the drivers of this process. 3) In addition, we evaluated the spatial composition similarity between the seed bank and aboveground vegetation to identify whether the similarity can predict a state transition from arid grassland to the shrubland.

Materials and methods

Study site

The study was carried out in the Qaidam Basin on the northeastern Tibetan Plateau (Fig. S1), which is the largest intermontane basin in western China (Liu et al. 1998; Xia et al. 2001). The average altitude of the basin is approximately 3000 m, and the mountains rise to over 5000 m (Wang et al. 1999; Xia et al. 2001; Owen et al. 2006). The annual mean temperature is 2–4 °C, the annual mean precipitation is less than 100 mm (Wang et al. 1999, 2005; Zhao et al. 2007), and the annual mean evaporation is more than 2500 mm. Overall, the basin is a region with extreme drought, cold temperatures and salinization (Wang...
et al. 2005). The plant community structure is simple, with low vegetation cover. The predominant soil type is solonchak (Wang et al. 2018). The vegetation is characterized by xerophytes, dominated by rapidly regenerating grasses, herbs and short semishrubs (Zeng and Yang 2009). Local plant taxa include members of *Leymus*, Chenopodiaceae (*Salsola abrotanoides, Kalidium gracile, Ceratoides latens*, etc.), Compositae and *Nitraria* (Zhao et al. 2007; Wang et al. 2018). Specifically, the shrubland is dominated by shrubs and subshrubs, vegetation with low coverage (5%-30%), large areas of bare land and low diversity (13–7 species per quadrat). The arid grassland is characterized by grasses and annual forbs, and the vegetation has relatively high coverage (20%-50%) and diversity (6–12 species per quadrat) (DAHV and GSAHV 1996).

Soil seed bank sampling and aboveground vegetation investigation

We collected samples of the soil seed bank and investigated aboveground vegetation at 29 sites, including 21 shrubland sites and 8 arid grassland sites, in the Qaidam Basin during the peak growing season in August 2014. We selected typical vegetation at each site, and they all have been experiencing moderate grazing for many years.

For seed bank sampling, five plots (20 m × 20 m) were randomly selected at each site (200 m × 200 m). Five subplots (5 m × 5 m) were randomly distributed in each plot. Within each subplot, 10 soil cores (d = 3.6 cm) were randomly extracted to a depth of 10 cm. The soil cores were divided into 2 layers, namely, the shallow layer (0–5 cm) and the second layer (5–10 cm), and we pooled 10 cores from each depth in each subplot into one soil sample. Overall, there were a total of 50 samples (5 plots × 5 subplots × 2 soil layers) from each site and 1450 samples (50 samples × 29 sites) for the entire study.

In the aboveground vegetation survey, the names and numbers of individuals were determined and recorded in five quadrats, which were randomly distributed at each of the sites where the seed bank and soil were sampled, resulting in a total of 145 quadrats (5 quadrats × 29 sites). The characteristics of plant community type we sampled, as described in the appendix (Table S1).

Seedling emergence experiment

The seed germination experiment was carried out at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University (Hezuo Branch), Gansu Province, China, which is also located on the northeastern Tibetan Plateau (34°55′ N, 102°53′ E, 2900 m). The seedling emergence method was used to determine seed bank composition (Thompson et al. 1997). The collected seed bank samples were sun dried and sieved (to 4 mm) to carefully remove plant fragments and coarse debris (Ma et al. 2013). Some seeds of desert species require exposure to low temperatures to break dormancy (Peters 2002); therefore, the samples were stored in a storeroom for the entire winter (Nov 2014-April 2015) at low temperatures to break seed dormancy (Ma et al. 2017). The germination period lasted from 1 May to 10 October 2015. The samples were spread evenly over 15-cm-deep sterilized sand on top of 10-cm-deep soil (>1.5 m), which improved the water storage capacity, in plastic pots. Thirty control pots containing sterilized sand were placed next to the experimental pots to test for wind-dispersed seeds. All pots were placed outside on the ground at the start of the experiment, watered every day to maintain moisture and monitored several times per week (Ma et al. 2011). The emerging seedlings were identified and removed. We identified and counted emerging seedlings at weekly intervals until the end of the experiment, when no more seedlings emerged for several consecutive weeks.

Analyses of soil environmental properties

Three soil cores were randomly extracted from each plot and mixed into one soil sample, and 5 mixed samples were collected from each site. Hence, there were 145 soil samples (5 samples × 29 sites) overall. The samples were used to analyse soil characteristics. After compositing, one of the subsamples was air dried and sieved (to <0.2 mm) to remove large pebbles and roots and was used to analyse soil pH, soil organic matter (SOM), total nitrogen (TN), and total phosphorus (TP). The other subsamples were stored at 4 °C and used to analyse available nitrogen (AN), available phosphorus (AP) and soil moisture (SM). Soil moisture was determined gravimetrically after ~48 h of oven drying at 105 °C. Soil pH was obtained by using a pH meter to measure a
slurry of fresh soil and deionized water in a 1:2.5 ratio (Cahenzli et al. 2018). TN was measured by the Kjeldahl method (Institute of Soil Science, Academia Sinica 1978). TP was measured using molybdenum blue colorimetry after digestion by HClO4-H2SO4 (Parkinson and Allen 2008). SOM was measured using the K2Cr2O7 method (Miller and Keeney 1982). AN was determined using a flow injection analyser (San+, Skalar, Netherlands). AP was measured by the Bray method (Bray and Kurtz 1945).

Data analyses

All statistical analyses were performed using R version 3.3.3 (R Core Team 2018). Variables of the seed bank, aboveground vegetation and soil environment factors among the 29 sites were assessed, and we used the average values of samples representing each site for the data analyses after all of the data were log transformed.

In our study area, saline-alkali soil is also one of the main characteristics, and many studies have found that soil pH is one of the main drivers of grassland diversity and composition (Basto et al. 2015b; Ma et al. 2017). To improve the robustness of the results, we used soil moisture and pH as the dependent variables. To determine how soil moisture and pH affect the seed bank and aboveground vegetation, we evaluated the relationships between the relationships between aboveground vegetation variables (species richness and abundance of aboveground vegetation in each quadrat were standardized to 1 m²), seed bank and soil moisture, soil pH using ordinary least squares (OLS) regression. To test whether soil moisture and pH have independent effects on species richness and seed density of seed bank in each soil layer (0–5 cm and 5–10 cm) and the total soil (0–10 cm), we built a linear mixed effects model using the lme4 package (Bates et al. 2015). All models were fitted with soil moisture, pH as the fixed effects and plot and subplot as a random effect with the Poisson error distribution.

To identify the change in the composition of both the seed bank and aboveground vegetation, nonmetric multidimensional scaling (NMDS) was carried out using Bray–Curtis dissimilarity. Before we calculated Bray–Curtis dissimilarity matrixes, the species data of the seed bank and vegetation were converted to relative abundance data. Furthermore, we evaluated the influence of soil environmental factors on community composition. To determine whether the soil environment was correlated across the NMDS ordination, soil environmental factors were fitted as vectors to the NMDS ordination using the function ‘envfit’ from the vegan package (Oksanen et al. 2019).

To detect the threshold of composition of the seed bank and aboveground vegetation response to decreasing soil moisture, we carried out generalized linear and piecewise regression analyses. Sound evidence for a threshold response requires that one of the piecewise models provides the best fit to the data (Johnson and Omland 2004). The piecewise regression models were fitted using the ‘segmented’ package in R (Muggeo 2008).

To identify the best-fitting model for composition of the seed bank and aboveground vegetation at all sites along a soil moisture gradient, we used Akaikes information criterion (AIC). We compared the AIC values of the models with linear and piecewise regression models. The models with the smallest AIC value were considered the best-fitting models (Bestelmeyer et al. 2011). The same method was used to identify the best-fitting model for soil environmental factors and composition similarity between the seed bank and aboveground vegetation along a soil moisture gradient.

As linear and piecewise regression models work on single response variables, we retained a 2-dimensional solution of NMDS in our analysis. We split the two NMDS dimensions (Delgado-Baquerizo et al. 2017; Ochoa-Hueso et al. 2017), with dimensions 1 and 2 representing composition as the dependent variable and soil moisture as the independent variable, respectively.

Similarity is the opposite of dissimilarity. Dissimilarity (Bray–Curtis distance) was calculated as

\[ BC = \frac{\sum_j x_{ij} - x_{ik}}{\sum_j x_{ij} + x_{ik}} \]

where \( x_{ij} \) is the relative abundance of species \( i \) in community \( j \), \( x_{ik} \) is the relative abundance of species \( i \) in community \( k \), and \( n \) is the total number of species; a value of 0 represents the most similar communities, and 1 represents the most different (Basto et al. 2018).

Moreover, to exclude the possibility that the state transition from arid grassland to shrubland and the abrupt change in composition of aboveground vegetation are caused by the abrupt change in soil moisture, we further analysed the frequency distribution of the
two ecosystem states (arid grassland and shrubland) and the change in composition of aboveground vegetation on the soil moisture isoline.

**Results**

Spatial pattern of arid grassland and shrubland with decreasing soil moisture

Twenty-nine sample sites covering arid grassland and shrubland in Qaidam Basin on Tibetan Plateau were spatially distributed along a continuous soil moisture gradient between 0.5 and 2 (Fig. 2a). Soil moisture decreased equally from 2 to 0.5 along the state transition from arid grassland to shrubland (Fig. 2b). The arid grassland only appeared where the soil moisture was higher than 1.75, arid grassland and shrubland appeared simultaneously where the soil moisture was between 1.25 and 1.75, and the shrubland only appeared where the soil moisture was less than 1.25 (Fig. 2b).

Effects of soil moisture and pH on aboveground vegetation and seed bank

During the study, 4,984 seedlings geminated from the soil seed bank samples, which belong to 68 species and 16 families. Both the species richness and abundance of aboveground vegetation were positively correlated with soil moisture, but there were no significant correlations with soil pH (Fig. 3). Accordingly, both the seed density and species richness of the seed bank exhibited significant positive correlations with soil moisture in each soil layer (0–5 cm and 5–10 cm) (seed density: GLMM; \(0.7302 \pm 0.1189, t = 6.14, P < 0.001\) and GLMM; \(0.2427 \pm 0.0613, t = 3.96, P < 0.001\); species richness: GLMM; \(0.0715 \pm 0.013, t = 5.49, P < 0.001\) and GLMM; \(0.0421 \pm 0.0086, t = 4.81, P < 0.001\)) and the total soil (0–10 cm) (seed density: GLMM; \(0.9730 \pm 0.1686, t = 5.77, P < 0.001\); species richness: GLMM; \(0.0845 \pm 0.0151, t = 5.58, P < 0.001\), whereas no significant correlations were detected with soil pH (Fig. 4) (GLMM; \(P > 0.1\) in all cases).

Based on the NMDS results, the composition of both aboveground vegetation and the seed bank regularly changed with soil moisture (Fig. S2). Further analysis revealed that the composition of aboveground vegetation was affected by soil moisture, AN, TN, TP and SOM (Table 1; Fig. S3a), and the composition of the seed bank was affected by soil moisture, SOM and TP (Table 1; Fig. S3b); however, soil pH had no effect on the composition of aboveground vegetation or the seed bank (Table 1; Fig. S3a, b).

Changes in composition of seed bank and vegetation and their similarity with decreasing soil moisture

The piecewise model provided a better fit to the composition of aboveground vegetation along a soil moisture gradient (Table 2; Fig. 5a, b) and showed that the species composition (NMDS dimensions 1 and 2) abruptly changed before and after the threshold (Fig. 5a, b). However, this trend was not reflected in the composition of the seed bank, which remained nearly invariable along the soil moisture gradient (Fig. 5a, b). The composition of the seed bank was best explained by a linear model, with the smallest AIC value (Table 2; Fig. 5a, b).

The composition similarity between the seed bank and aboveground vegetation was best fit by a piecewise model, with the smallest AIC value (Table 2; Fig. 5c).
Surprisingly, we found that the similarity between the aboveground vegetation and seed bank decreased obviously when soil moisture crosses the critical threshold.

Changes in soil environmental factors with decreasing soil moisture

For the linear and piecewise model fitting of soil environmental factors, we found that half of the soil environmental factors (TN, AN and SOM) were best fit by a piecewise model, with the smallest AIC value, and other soil environmental factors (TP, AP and pH) were best fit by a linear model (Table 2; Fig. S6).

Discussion

Our results provide strong evidence that the ecosystem state transition from arid grassland to shrubland is correlated with a continuous decrease in soil moisture in Qaidam Basin on the Tibetan Plateau. Moreover, we found that compared to the abrupt change in the composition of aboveground vegetation, the composition of the seed bank hardly changes in this process. Further analysis showed that the contribution (similarity between the seed bank and aboveground vegetation) of the seed bank to the aboveground vegetation gradually approached zero as soil moisture crossed the threshold.

The driver of the seed bank and vegetation changes during the state transition

We found that the dynamics of the seed bank and aboveground vegetation were strongly effected by soil moisture. This result supported those of a previous study, which found that water determines the species distribution in arid environments because seed dormancy, germination, plant growth, and completion of life history are closely related to water (Walck et al. 2011). For example, insufficient soil moisture cannot support the completion of the plant life cycle (Ooi et al. 2009), and decreased soil moisture can lead to the loss of species with low drought tolerance (Wang et al. 2007). Moreover, extreme drought may cause seeds to lose physiological repair mechanisms, in turn decreasing seed viability and increasing seed death (Kranner et al. 2010).

Surprisingly, soil pH had no significant effects on the dynamics of both the seed bank and aboveground vegetation. This effect may be due to the following reasons. First, the dynamics of aboveground vegetation are mainly limited by water. For example, a previous study showed that nitrogen addition (soil acidification) had no effect on aboveground vegetation in extremely dry environments due to a lack of water (Ladwig et al. 2011). Second, pH mainly affects the seed bank by affecting pathogenic fungi (Basto et al. 2013). However, microbial populations are small in arid saline environments (Dalling et al. 2011), especially in the Qaidam Basin (Huang et al. 2018).

Composition of seed bank and aboveground vegetation change during state transition

We found a critical threshold in the species composition (NMDS dimensions 1 and 2) of aboveground vegetation along a soil moisture gradient, which is consistent with the threshold zone of the state transition from arid grassland to shrubland on the spatial scale. Our findings suggest that the change in species composition of aboveground vegetation in arid
ecosystems has a nonlinear correlation with decreasing soil moisture.

In contrast to aboveground vegetation, we found no critical threshold in the species composition (NMDS dimensions 1 and 2) of the seed bank along a soil moisture gradient, and this result is not consistent with our first prediction. Our results strongly suggest that the state transition from arid grasslands to shrubland along a soil moisture gradient is not caused by abrupt changes in the composition of the seed bank. We found that the seed density and species richness of the seed bank decrease with decreased soil moisture (Fig. 4), and the composition of the seed bank was regulated by soil moisture (Fig. S3b). However, the change in the composition of the seed bank was far less than that of the aboveground vegetation (Fig. S2). These results indicated that the seed bank remains more stable than aboveground vegetation when subjected to changing environments in arid ecosystems, even if the composition of aboveground vegetation crosses the threshold (state transition from arid grassland to shrubland).

This result is contrary to the previously generally believed results that the seed resources of the native seed bank are exhausted or that the seed rain of invading shrubs changes the composition

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**Table 1** Results of nonmetric multidimensional scaling (NMDS) ordination of the effects of soil environmental factors on the species composition of both aboveground vegetation and the seed bank

| Variable | Vegetation | | Seed bank | |
|----------|------------|---|----------|---|
| R²       | p          | R² | p        |   |
| AN (mg/g) | 0.31 0.007** | 0.09 0.254 | |
| TN (mg/g) | 0.23 0.025*  | 0.16 0.08  | |
| SOM (mg/g) | 0.67 0.001*** | 0.49 0.001*** | |
| AP (mg/g) | 0.09 0.27  | 0.06 0.911 | |
| TP (mg/g) | 0.44 0.001*** | 0.36 0.004** | |
| SM (mg/g) | 0.47 0.001*** | 0.27 0.014*  | |
| pH       | 0.16 0.072  | 0.07 0.342  | |

Asterisks indicate significant correlation coefficients (ns, *p < 0.05, **p < 0.01, ***p < 0.001)

AN available nitrogen, TN total nitrogen, SOM soil organic matter, AP available phosphorus, TP total phosphorus, SM soil moisture

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**Fig. 4** Relationships of seed density and species richness in the soil seed bank with soil moisture and soil pH. Relationships of seed density at 0–5 cm (a), 5–10 cm (b) and 0–10 cm (c), as well as species richness at 0–5 cm (d), 5–10 cm (e) and 0–10 cm (f), in the seed bank with soil moisture are shown. Relationships of seed density at 0–5 cm (g), 5–10 cm (h) and 0–10 cm (i), as well as species richness at 0–5 cm (j), 5–10 cm (k) and 0–10 cm (l), in the seed bank with soil moisture are shown. The red fitted lines are from OLS regression. Grey areas show the 95% confidence interval of the fit
of the native seed bank during the state transition (Suding and Hobbs 2009). In our study, we found a large proportion of annual plants in both the aboveground vegetation (Fig. S4) and the seed bank (Fig. S5). Generally, annuals have a higher input to the seed bank than perennials (Ortega et al. 1997) and form a persistent seed bank (Thompson et al. 1997). Moreover, shrubs often have lower seed production than herbaceous plants (Leishman et al. 2000). Most of the shrubs reproduce asexually (Ratajczak et al. 2011) and thus make few contributions to the seed bank.

Can the similarity between the seed bank and vegetation be used as an early warning signal to predict state transition?

Surprisingly, our results showed that crossing the critical threshold, the seed bank greatly decrease its contribution to aboveground vegetation. This result is consistent with our second prediction. To better understand why this consistency exists, we first need to understand the ecological mechanism of this state transition underlying the ability of the seed bank to restore aboveground vegetation along a soil moisture gradient. We found that the similarity decreased as soil moisture decreased from 2.0–1.5, which indicated that the role of the seed bank in aboveground vegetation regeneration decreased as soil moisture decreased. Decreased soil moisture can promote the dormancy of seeds in arid ecosystems (Ooi et al. 2009; Walck et al. 2011) and increase the germination failure rate and seedling mortality (Basto et al. 2018), which prevents the seed bank from germinating and replenishing aboveground vegetation. During this process, the species diversity and abundance of aboveground vegetation decreased with decreasing soil moisture, while species composition did not cross the threshold.

When the soil moisture dropped to 1.5, the similarity reached a critical point. This point may also be the threshold for seed germination or seedling survival with decreasing soil moisture. At this point, continuous replenishment of aboveground vegetation with seedlings from the seed bank was lost. As the soil moisture continued to decrease to less than 1.5, the similarity crossed the threshold and gradually approached zero. This trend indicated that the role of the seed bank in aboveground vegetation regeneration approached zero. The reason might be that the seeds in the seed bank underwent almost no germination or that germinated seedlings may not have survived.

In an arid ecosystem dominated by annuals, the aboveground vegetation dynamics are mainly driven by the germination of the seed bank (Ooi et al. 2009). Therefore, we believe that the similarity between the seed bank and aboveground vegetation is a more useful indicator for predicting the state transition from arid grassland to the shrubland ecosystem.

The role of the seed bank during the state transition

System transition theory holds that states change abruptly when they reach a critical threshold of external driver. Previous studies have found that such state

| Ecosystem component | Model | Linear \( r^2 \)/AIC | Piecewise \( r^2 \)/AIC |
|---------------------|-------|----------------------|------------------------|
| Aboveground vegetation (NMDS1) | 0.69/-33.83 | 0.74/-34.46 |
| Aboveground vegetation (NMDS2) | 0.03/-12.20 | 0.34/-20.27 |
| Seed bank (NMDS1) | 0.21/-42.73 | 0.23/-39.63 |
| Seed bank (NMDS2) | 0.08/-10.92 | 0.01/-7.20 |
| Similarity between aboveground vegetation and the seed bank | 0.061/-130.70 | 0.66/-191.45 |
| Soil TP (mg/g) | 0.41/-53.07 | 0.44/-50.99 |
| Soil AP (mg/g) | 0.066/-7.15 | 0.083/-3.68 |
| Soil TN (mg/g) | 0.24/27.29 | 0.35/26.82 |
| Soil AN (mg/g) | 0.19/13.98 | 0.39/18.44 |
| Soil SOM (mg/g) | 0.73/3.58 | 0.80/0.26 |
| Soil pH | 0.1/22.51 | 0.14/25.35 |
transition is usually accompanied by a positive feedback (Briske et al. 2006; Scheffer et al. 2009). In our study, we found that TN and AN first cross the threshold, followed by SOM, during the state transition from arid grassland to shrubland. These results are consistent with previous studies showing that open ecosystems dominated by shrubs undergo a loss of nitrogen and soil organic matter, which in turn is detrimental to grass growth (Huenneke et al. 2002). In addition, the use of soil moisture by shrubs and grasses may cause a redistribution of soil moisture and thus a positive feedback (Kefi et al. 2007). However, the state transition in arid ecosystems is more likely controlled by low resilience (Scheffer et al. 2001; Kefi et al. 2007); for example, in our case, we have verified that the state transition from arid grassland to shrubland was due to a limitation in the ability of the seed bank to regenerate aboveground vegetation.

In summary, our results provide a more complete picture of the transition of ecosystems from arid grassland to shrubland since we have considered the composition of both the seed bank and aboveground vegetation changes in response to the driving factor (Fig. 6). With the decrease in soil moisture, the composition of aboveground vegetation crosses a threshold corresponding to the ecosystem state transition from arid grassland to shrubland. The reason for the state transition is not an abrupt change in the composition of the seed bank; rather, the capacity of the seed bank to regenerate aboveground vegetation is overcome. Therefore, in future studies of ecosystem transition, more consideration should be given to the seed bank, especially in low resilience ecosystems, which would help us better understand state transitions and provide guidance for fragile ecosystem management.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-021-05044-2.

Acknowledgements This study was funded by the National Natural Science Foundation of China (31922062), Science and Technology Support Project of Ecological Grassland Restoration and Management in Gansu Province(2020-72).
References

Baskin CC, Baskin JM (2014) Seeds: ecology, biogeography, and evolution of dormancy and germination. Crop Sci 40:564–565. https://doi.org/10.1038/s41467-020-00642-8

Basto S, Dorca-Fornell C, Thompson K et al (2013) Effect of pH buffer solutions on seed germination of Hypericum pulchrum, Campanula rotundifolia and Scabiosa columbaria. Seed Sci Technol 41:298–302. https://doi.org/10.1525/ssst.2013.41.2.12

Basto S, Thompson K, Phoenix G et al (2015a) Long-term nitrogen deposition depletes grassland seed banks. Nat Commun 6:1–6. https://doi.org/10.1038/ncomms7185

Basto S, Thompson K, Rees M (2015b) The effect of soil pH on persistence of seeds of grassland species in soil. Plant Ecol 216:1163–1175. https://doi.org/10.1007/s11258-015-0499-z

Basto S, Thompson K, Grime JP et al (2018) Severe effects of long-term drought on calcareous grassland seed banks. npj Clim Atmos Sci 1:1–7. https://doi.org/10.1038/s41612-018-0004-3

Bates D, Maechler M, Bolker BM et al (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. http://CRAN.R-project.org/package=lme4

Bestelmeyer BT, Ellison AM, Fraser WR et al (2011) Analysis of abrupt transitions in ecological systems. Ecosphere 2:1–26. https://doi.org/10.1002/ecs2.1050-3

Bestelmeyer BT, Duniphy MC, James DK et al (2013) A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. Ecol Lett 16:339–345. https://doi.org/10.1111/ele.12045

Bossuyt B, Honnay O (2008) Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. J Veg Sci 19:875–884. https://doi.org/10.1111/j.1111.0007-3693.2008.00078.x

Bray RH, Kurtz LT (1945) Determination of total organic, and available forms of phosphorus in soils. Soil Sci 59:39–45. https://doi.org/10.1097/00010694-194501000-00006

Briske DD, Fuhlendorf SD, Smeins FE (2006) A unified framework for assessment and application of ecological thresholds. Rangel Ecol Manag 59:225–236. https://doi.org/10.2458/azu_jrm_v59i3_briske

Cahenzli F, Bonetti C, Erhardt A (2018) Divergent strategies in pre- and postzygotic reproductive isolation between two closely related Dianthus species. Evolution 72:1851–1862. https://doi.org/10.1111/evo.13556

Coop JD, Parks SA, Stevens-Rumann CS et al (2020) Wildfire-driven forest conversion in Western North American Landscapes. Bioscience 70:659–673. https://doi.org/10.1093/biosci/biaa061

Delgado-Baquerizo M, Bissett A, Eldridge DJ et al (2017) Palaeoclimate explains a unique proportion of the global variation in soil bacterial communities. Nat Ecol Evol 1:1339–1347. https://doi.org/10.1038/s41559-017-0259-7

DAHV (Department of Animal Husbandry and Veterinary, Ministry of Agriculture), GS AHV (General Station of Animal Husbandry and Veterinary, Ministry of Agriculture) (1996) Rangeland and resources of China. China Science and Technology Press, Beijing (in Chinese)

Dalling JW, Davis AS, Schutte BJ et al (2011) Seed survival in soil: interacting effects of predation, dormancy and the soil microbial community. J Ecol 99:89–95. https://doi.org/10.1111/j.1365-2745.2010.01739.x

D’Odorico P, Laio F, Ridolfi L et al (2006) A probabilistic analysis of fire- induced tree-grass coexistence in savannas. Am Nat 167:79–87. https://doi.org/10.1086/500617

Diaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbageous plants be predicted from simple vegetative traits? J Appl Ecol 38:497–508. https://doi.org/10.1046/j.1365-2664.2001.00635.x

Eldridge DJ, Bowker MA, Maestre FT et al (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14:709–722. https://doi.org/10.1111/j.1461-0248.2011.01630.x

Gheardi LA, Sala OE, Penuelas J et al (2015) Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. Ecol Lett 18:1293–1300. https://doi.org/10.1111/ele.12523

Groffman PM, Baron JS, Blett T et al (2006) Ecological thresholds: the key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13. https://doi.org/10.1007/s10021-003-0142-z

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Hopfensperger KN (2007) A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116:1438–1448. https://doi.org/10.1111/j.0030-1299.2007.15818.x

Hu ZM, Guo Q, Li SG et al (2018) Transitions in the dynamics of productivity signal ecosystem state transitions at the biome-scale. Ecol Lett 21:1457–1466. https://doi.org/10.1111/ele.13126

Huang T, Wang R, Xiao L et al (2018) Dalangtan Playa (Qaidam Basin, NW China): Its microbial life and physicochemical characteristics and their astrobiological implications. PLoS ONE 13:e0200949. https://doi.org/10.1371/journal.pone.0200949

Huenneke LF, Anderson JP, Remmenga M et al (2002) Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. Glob Chang Biol 8:247–264. https://doi.org/10.1046/j.1365-2486.2002.00473.x

Huggett AJ (2005) The concept and utility of ‘ecological thresholds’ in biodiversity conservation. Biol Conserv 124:301–310. https://doi.org/10.1016/j.biocon.2005.01.037

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:108. https://doi.org/10.1016/j.tree.2003.10.013

Kalamees R, Pussa K, Zobel K et al (2012) Restoration potential of the persistent soil seed bank in successional calcareous (alvar) grasslands in Estonia. AppI Veg Sci 15:208–218. https://doi.org/10.1111/j.1654-109X.2011.01169.x

Kefi S, Rietkerk M, Alados CL et al (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213–215. https://doi.org/10.1038/nature06111
Kraner I, Minibayeva FV, Beckett RP et al (2010) What is stress? Concepts, definitions and applications in seed science. New Phytol 188:655–673. https://doi.org/10.1111/j.1469-8137.2010.03461.x

Ladwig LM, Collins SL, Swann AL et al (2011) Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. Oecologia 169:177–185. https://doi.org/10.1007/s00442-011-2173-z

LaForgia ML, Collins SL, Swann AL et al (2018) Seed banks of native forbs, but not exotic grasses, increase during extreme drought. Ecology 99:896–903. https://doi.org/10.1002/ecy.2160

Leishman MR, Masters GJ, Clarke IP et al (2000) Seed Bank dynamics: The role of fungal pathogens and climate change. Funct Ecol 14:293–299. https://doi.org/10.1046/j.1365-2435.2000.00425.x

Li WH, Xu FW, Zheng SX et al (2016) Patterns and thresholds of grazed-induced changes in community structure and ecosystem functioning: species-level responses and the critical role of species traits. J Appl Ecol 54:963–975. https://doi.org/10.1111/1365-2664.12806

Liu ZC, Wang YJ, Chen Y et al (1998) Magnetostratigraphy and sedimentologically derived geochronology of the Quaternary lacustrine deposits of a 3000 m thick sequence in the central Qaidam basin, western China. Paleogeogr Paleoclimatol Paleoecol 140:459–473. https://doi.org/10.1016/S0031-0182(98)00048-0

Ma M, Zhou XH, Du GZ et al (2011) Soil seed bank dynamics in alpine wetland succession on the Tibetan Plateau. Plant Soil 346:19–28. https://doi.org/10.1007/s11104-011-0790-2

Ma M, Zhou XH, Du GZ et al (2013) Effects of disturbance intensity on seasonal dynamics of alpine meadow soil seed banks on the Tibetan Plateau. Plant Soil 369:283–295. https://doi.org/10.1007/s11104-012-1560-5

Ma M, Baskin CC, Yu KL et al (2017) Wetland drying indirectly influences plant community and seed bank diversity through soil pH. Ecol Indic 80:186–195. https://doi.org/10.1016/j.ecolind.2017.05.027

Ma M, Collins SL, Ratjaczek Z et al (2021) Soil seed banks, alternative stable state theory and ecosystem resilience. Bioscience. https://doi.org/10.1093/biosci/biaa011

Miller RH, Keeney DR (1982) Methods of soil analysis. Part 2. Chemical and microbiological properties. Exchangeable cations. Soil Sci Soc Am J 1982:159–166

Muggeo VMR (2008) Package ‘Segmented’: an R package to fit regression models with broken-line relationships. https://CRAN.R-project.org/package=segmented/

Ochoa-Hueso R, Collins SL, Delgado-Baquerizo M et al (2017) Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. Glob Chang Biol 24:2818–2827. https://doi.org/10.1111/gcb.14113

Oksanen J, Blanchet FG, Friendly M et al (2019) Package ‘Vegan’: community ecology package. http://cran.r-project.org/package=vegan/

Ooi MKJ (2012) Seed bank persistence and climate change. Seed Sci Res 22:53–60. https://doi.org/10.1017/S0960258511000407

Ooi MKJ, Auld TD, Denham AJ (2009) Climate change and bet-hedging: interactions between increased soil temperatures and seed bank persistence. Glob Change Biol 15:2375–2386. https://doi.org/10.1111/j.1365-2486.2009.01887.x

Ortega M, Levassor C, Peco B (1997) Seasonal dynamics of Mediterranean pasture seed banks along environmental gradients. J Biogeogr 24:177–195. https://doi.org/10.1046/j.1365-2699.1997.00080.x

Owen LA, Finkel RC, Zhou MH et al (2006) Late Quaternary landscape evolution in the Kunlun Mountains and Qaidam Basin, Northern Tibet: A framework for examining the links between glaciation, lake level changes and alluvial fan formation. Quat Int 154:73–86. https://doi.org/10.1016/j.quaint.2006.02.008

Parkinson JA, Allen AS (2008) A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun Soil Sci Plant Anal 39:6:1–11. https://doi.org/10.1080/00103627509366539

Peters DPC (2002) Recruitment potential of two perennial grasses with different growth forms at a semiarid-arid transition zone. Am J Bot 89:1616–1623. https://doi.org/10.3732/ajb.89.10.1616

Plue J, De Frenne P, Acharya K et al (2013) Climatic control of forest herb seed banks along a latitudinal gradient. Glob Ecol Biogeogr 22:1106–1117. https://doi.org/10.1111/gcb.12068

Institute of Soil Science, Academia Sinica (1978) Soils of China. Science Press, Beijing (in Chinese)

R Core Team (2018) R: a language and environment for statistical computing. http://www.R-project.org/

Ratajczak ZR, Nippert JB, Hartman JC (2011) Positive feedbacks amplify rates of woody encroaching in mesic tallgrass prairie. Ecosphere 2:art121. https://doi.org/10.1890/ES11-00212.1

Ratajczak Z, Nippert JB, Collins SL (2012) Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93:697–703. https://doi.org/10.1111/j.1190.01199.1

Ratajczak Z, Nippert JB, Ocheltree TW (2014) Abrupt transition of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime transitions. Ecol 95:2633–2645. https://doi.org/10.1890/13-1369.1

Ratajczak Z, D’Odorico P, Nippert JB et al (2017) Changes in spatial variance during a grassland to shrubland state transition. J Ecol 105:750–760. https://doi.org/10.1111/j.1365-2745.2016.12969

Royo AA, Ristau TE (2013) Stochastic and deterministic processes regulate spatio-temporal variation in seed bank diversity. J Veg Sci 24:724–734. https://doi.org/10.1111/jvs.12011

Sasaki T, Okayasu T, Jamsran U (2008) Threshold changes in growth signals for critical transitions. Nature 461:53–59. https://doi.org/10.1038/nature07100

Scheffer M, Carpenter S, Foley JA et al (2001) Catastrophic shifts in ecosystems. Nature 413:591–596. https://doi.org/10.1038/35098000

Scheffer M, Bascompte J, Brock WA et al (2009) Early-warning signals for critical transitions. Nature 461:53–59. https://doi.org/10.1038/nature083510

Suding KN, Hobbs RJ (2009) Thresholds models in restoration and conservation, a developing framework. Trends Ecol Evol 24:271–279. https://doi.org/10.1016/j.tree.2008.11.012
Thompson K, Bakker JP, Bekker RM (1997) The Soil Seed Banks of North West Europe: methodology, density and longevity. Cambridge University Press, Cambridge
Walck JL, Hidayati SN, Dixon KW et al (2011) Climate change and plant regeneration from seed. Glob Chang Biol 17:2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x
Wang J, Wang YJ, Liu ZC et al (1999) Cenozoic environmental evolution of the Qaidam Basin and its implications for the uplift of the Tibetan Plateau and the drying of central Asia. Paleogeogr Paleoclimato Paleocool 152:37–47. https://doi.org/10.1101/S0031-0182(99)00038-3
Wang YD, Mosbrugger V, Zhang H (2005) Early to Middle Jurassic vegetation and climatic events in the Qaidam Basin, northwest China. Paleogeogr Paleoclimato Paleocool 224:200–216. https://doi.org/10.1016/j.palaeo.2005.03.035
Wang Y, Yu S, Wang J (2007) Biomass-dependent susceptibility to drought in experimental grassland communities. Ecol Lett 10:401–410. https://doi.org/10.1111/j.1461-0248.2007.01031.x
Wang XJ, Kong FJ, Kong WG et al (2018) Edaphic characterization and plant zonation in the Qaidam Basin, Tibetan Plateau. Sci Rep 8:1–9. https://doi.org/10.1038/s41598-018-20163-0
Xia WC, Zhang N, Yuan XP et al (2001) Cenozoic Qaidam basin, China: a stronger tectonic inversed, extensional rifted basin. AAPG Bull 85:715–736. https://doi.org/10.1306/8626C98D-173B-11D7-8645000102C1865D
Zeng BA, Yang TB (2009) Natural vegetation responses to warming climates in Qaidam Basin 1982–2003. Int J Remote Sens 30:5685–5701. https://doi.org/10.1080/01431160902729556
Zhao Y, Yu ZC, Chen FH et al (2007) Holocene vegetation and climate history at Hurleg Lake in the Qaidam Basin, northwest China. Rev Palaeobot Palynology 145:275–288. https://doi.org/10.1016/j.revpalbo.2006.12.002

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