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

Yunpeng Zhao
Lanzhou University
Guozhen Du
Lanzhou University
Wei Qi
Lanzhou University
Hang An
Lanzhou University
Lipei Wang
Lanzhou University
Shuaiwei Luo
Lanzhou University
Beibei Ma
Lanzhou University
Miaojun Ma (✉ mamiaojun@gmail.com)
Lanzhou University https://orcid.org/0000-0001-7046-9574

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Abstract

Purpose 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, an inflection point of the similarity between the aboveground vegetation and seed bank also emerged at this threshold zone (ecosystem transition from arid grassland and shrubland).

Conclusions Our results suggest that the transition from arid grassland to shrub 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.

Introduction

Ecological thresholds are often interpreted as ecological processes or responses to disturbances 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. 2016). Anthropogenic activities and rapidly intensifying global climate changes push drivers across ecological thresholds, causing abrupt transitions in the state of ecosystems (Holling 1973; Ratajczak et al. 2017; Hu et al. 2018). Such state transitions 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 state 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), with considerable consequences for livestock forage and the landscape. The state transition from arid grassland to shrubland can be viewed as a two-step process (Fig. 1), which may be subsequently regulated by disturbance–vegetation feedback (Coop et al. 2020). First, excessive disturbance (intensity + duration) can cause decrease of biomass, 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; Ratajczak et al. 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).

Disturbance causes species loss from the aboveground vegetation; 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). The seed bank can spread germination over time, aiding in the prevention of large population declines and 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; Ratajczak et al. 2014). For example, the state transition from grassland to the shrubland ecosystem is accelerated with decreased water availability/soil moisture because shrubs can take advantage of deeper soil moisture, which is not conducive 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). Under extremely dry soil conditions, seed loss of physiological repair mechanisms leads to a decrease in seed viability (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 from arid grassland to shrubland is the change in ecosystem resilience resulting from changes in species composition in 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 ecosystem.

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 because of the 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 driving factor 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 ecosystem.

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; Wang et al. 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 coverage. 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 (3-7 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.

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 size of the quadrats varied with plant community type, 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 $HClO_4$-H_2SO_4 (Parkinson and Allen 2008). SOM was measured using the $K_2Cr_2O_7$ method (Miller and Keeny 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 seed bank variables and soil moisture and soil pH, and the relationships between aboveground vegetation variables and soil moisture and soil pH using ordinary least squares (OLS) regression.

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 Akaike’s 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

$$BC = \sum_i^n \left| x_{ij} - x_{ik} \right| / \sum_i^n x_{ij} + x_{ik} \qquad (1)$$

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 changing 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 ecosystem 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 environmental factors on aboveground vegetation and seed bank dynamics

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) and the total soil (0–10 cm), whereas no significant correlations were detected with soil pH (Fig. 4).

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 determined by soil moisture, AN, TN, TP and SOM (Table 1; Fig. S3a), and the composition of the seed bank was determined 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).

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. 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.

Variable	Vegetation		Seed bank	
	R^2	p	R^2	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

Changes in species composition of the seed bank and aboveground vegetation and their similarity along a soil moisture gradient

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).

Table 2
Akaike’s information criterion (AIC) values for the models used to identify threshold changes in the varying ecosystem components along a soil moisture gradient at 29 sites. Values in bold indicate the smallest AIC (i.e., the best fit). AN: available nitrogen; TN: total nitrogen; SOM: soil organic matter; AP: available phosphorus; TP: total phosphorus; SM: soil moisture.

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	0.8/**0.26**
Soil pH	0.1/**22.51**	0.14/25.35

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 an inflection point (soil moisture = 1.5) in composition similarity between the seed bank and aboveground vegetation, which was consistent with the inflection of the composition of aboveground vegetation (Fig. 5a, b), and this inflection point was also consistent with the observed state transition from arid grassland to shrubland (Fig. 2; Fig. 5). Before the threshold, the similarity decreased significantly as soil moisture decreased, whereas beyond the threshold, the similarity gradually approached zero.

Changes in soil environmental factors along a soil moisture gradient

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 has a threshold along a soil moisture gradient, which perfectly coincides with the threshold zone of observed state transition from arid grassland to shrubland.

The driver of the seed bank and aboveground vegetation dynamics during the state transition of arid grassland to shrubland

We found that the dynamics of the seed bank and aboveground vegetation were strongly determined 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).

Species composition of seed bank and aboveground vegetation change during state transition from arid grassland to the shrubland ecosystem

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 disturbance or 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 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 composition similarity between the seed bank and aboveground vegetation be used as an early warning signal to predict the ecosystem state transition?

Surprisingly, our results showed that the critical threshold of similarity between seed bank and aboveground vegetation highly coincide with the ecosystem state transition from arid grassland to shrubland along a soil moisture gradient on the spatial scale. 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 from arid grassland to shrubland

System transition theory holds that states change abruptly when they reach a critical threshold of external disturbance. Previous studies have found that such state transition is usually accompanied by a positive feedback of disturbance–vegetation (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.

Declarations

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Figures

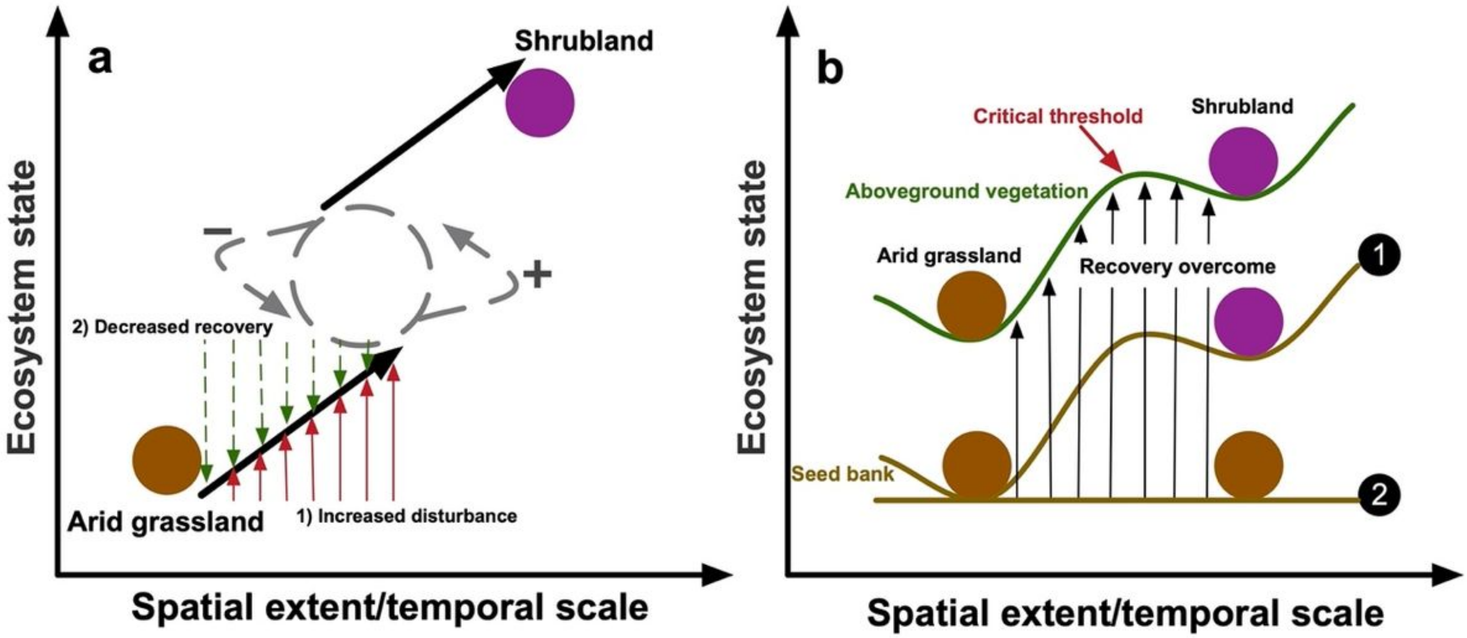

Figure 1

Schematic illustration of the mechanisms of the state transition from arid grassland to the shrubland ecosystem. First step: increasing disturbance (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 disturbance. For example, the longer the red arrow, the stronger the disturbance, and the longer the green dotted arrow, the more inhibited the recovery process. The grey dotted circle represents subsequent regulation by possible feedback of disturbance–vegetation (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).

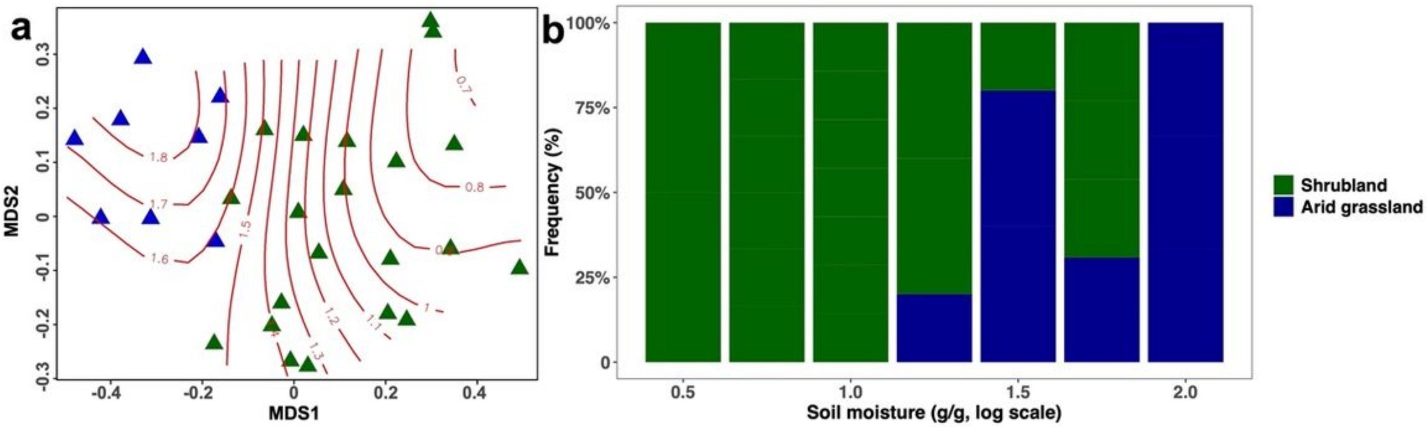

Figure 2

Nonmetric multidimensional scaling (NMDS) ordination of the species composition of aboveground vegetation of all the sampling sites from arid grassland to shrubland ecosystems. Green and blue triangles represent shrubland and arid grassland ecosystems, respectively, and the red lines are soil moisture isolines (a). Frequency distribution of aboveground vegetation across arid grassland and shrubland along a gradually changing soil moisture gradient (b).

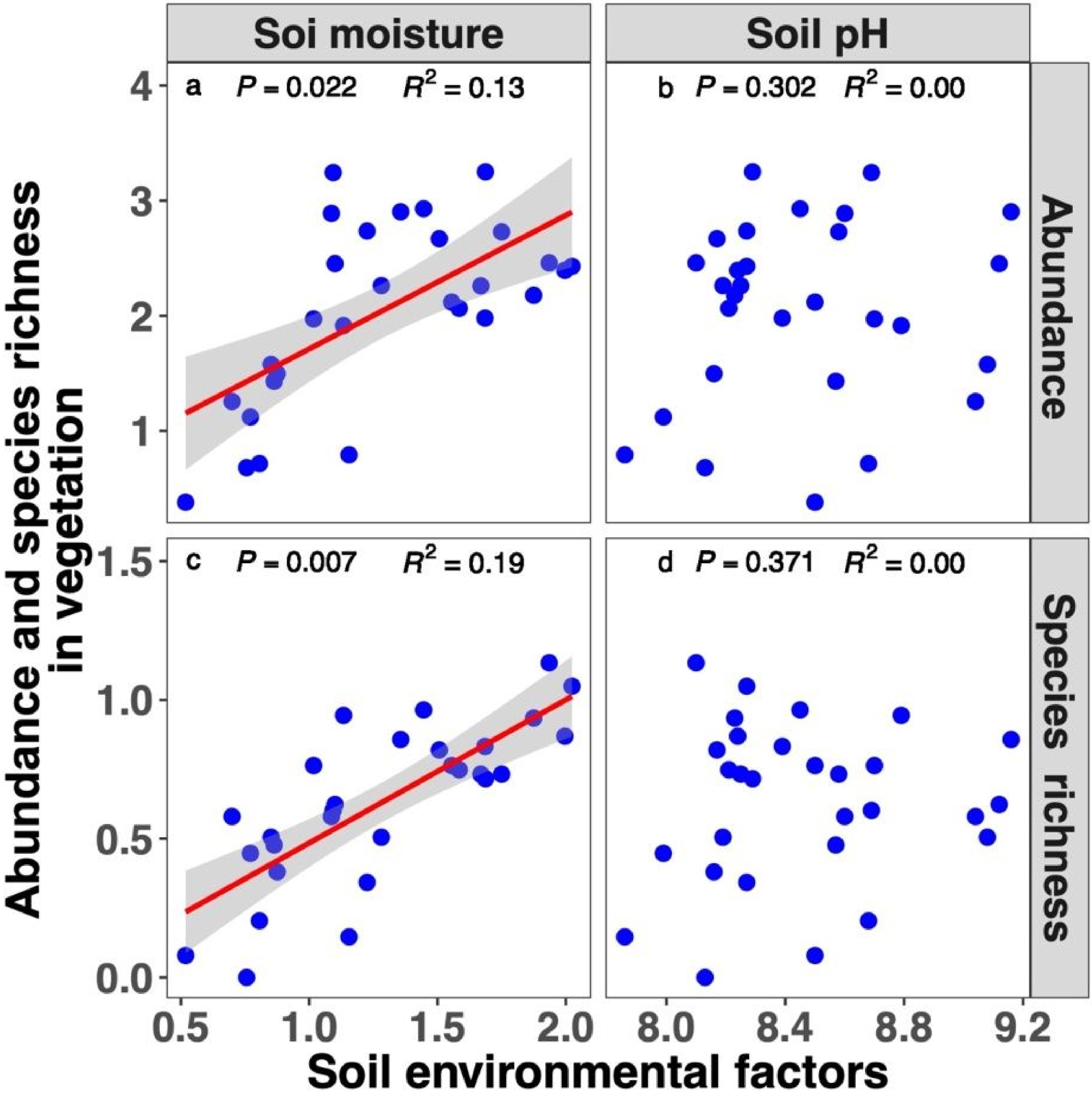

Figure 3

Relationships of abundance in aboveground vegetation with soil moisture (a) and pH (b). Relationships of species richness in aboveground vegetation with soil moisture (c) and pH (d). The red fitted lines are from OLS regression. Grey areas show the 95% confidence interval of the fit.

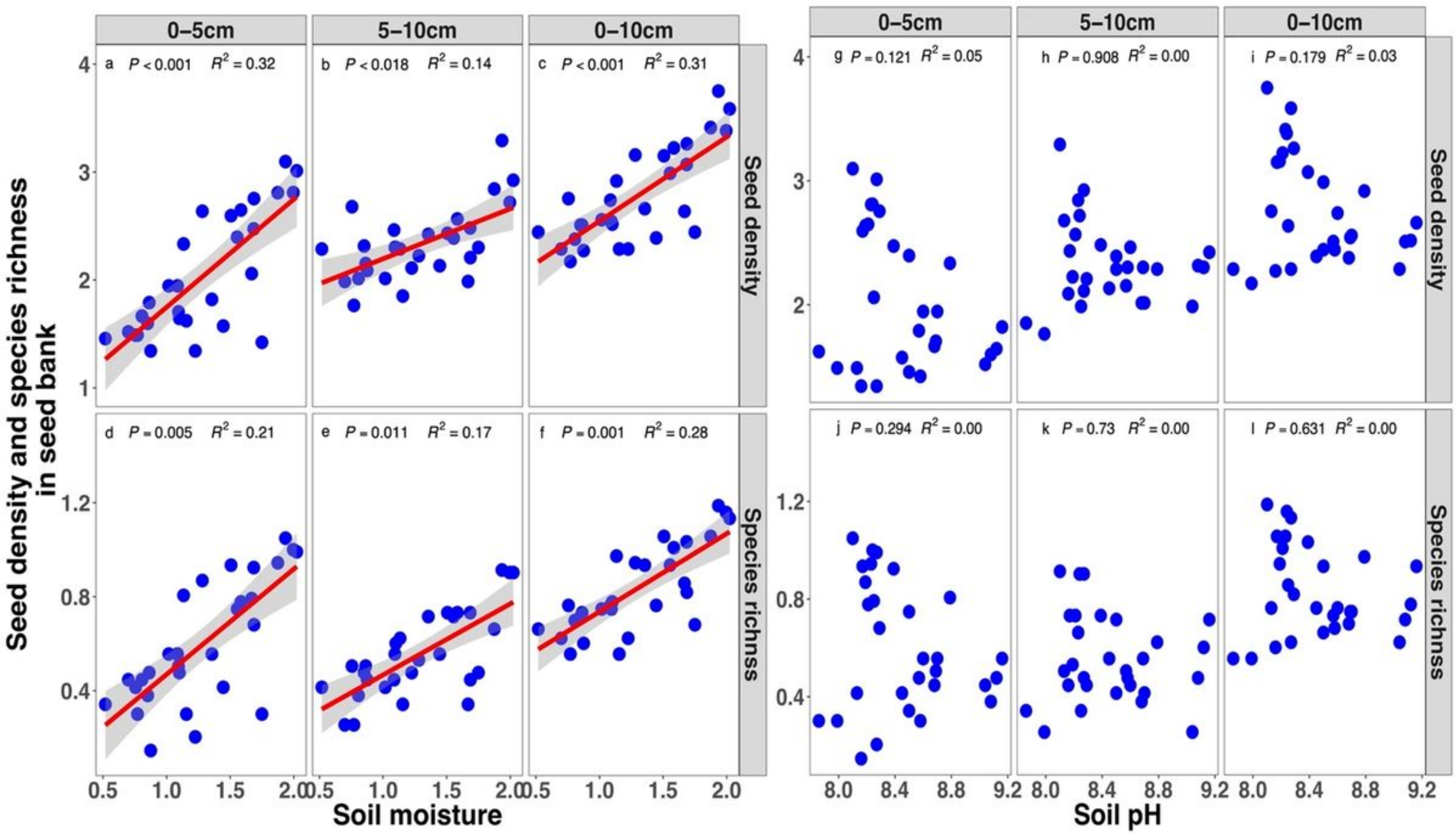

Figure 4

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.

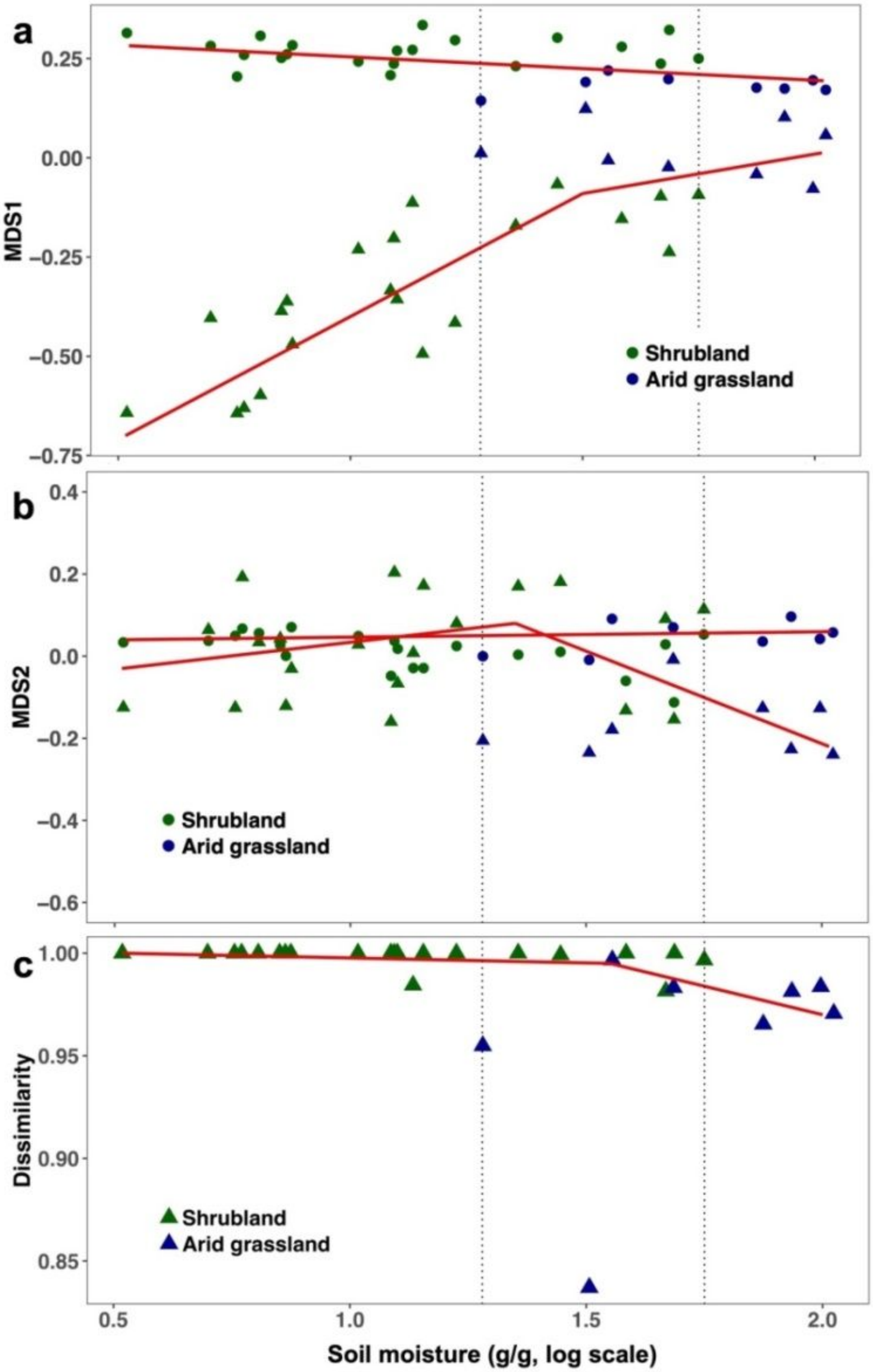

Figure 5

Best-fitting models for NMDS dimension 1 (a) and dimension 2 (b) of species composition of both aboveground vegetation and the seed bank as well as composition similarity between aboveground vegetation and the seed bank along a soil moisture gradient. The vertical dashed lines indicate the threshold zones of the state transition from arid grassland to shrubland. The dots and triangles represent the seed bank and the aboveground vegetation, respectively. Green and blue represent shrubland and arid grassland, respectively.

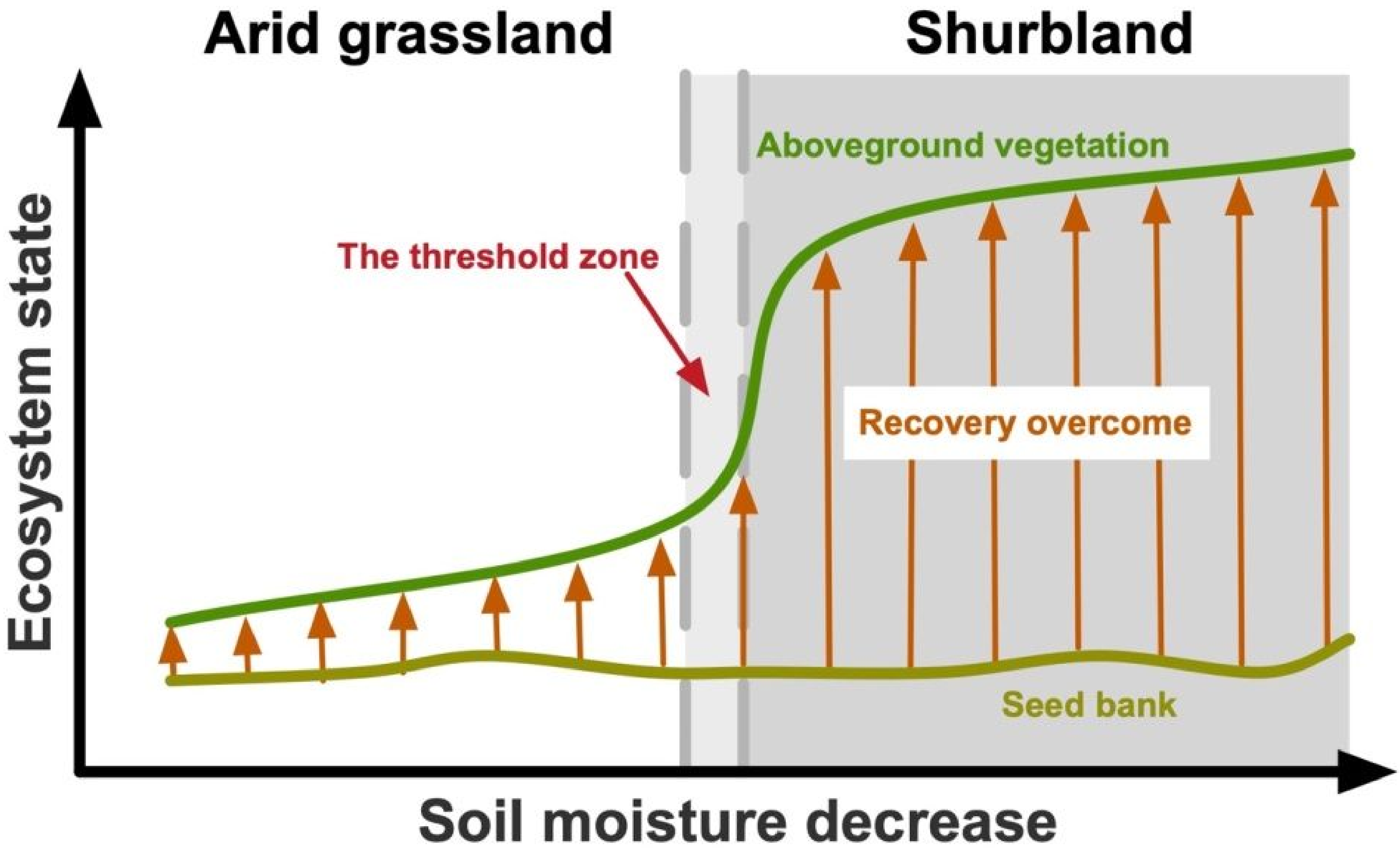

Figure 6

Schematic illustration of the mechanisms causing state transition from arid grassland to shrubland with decreased soil moisture. The state transition from arid grassland to shrubland is not due to an abrupt change in the composition of the seed bank but because the recovery process is overcome near the threshold zone as the soil moisture decreases.

Supplementary Files

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