

Divergent driving mechanisms of community temporal stability in drylands of China

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May 10, 2023

Abstract

Climate change and human activities are changing the structure and function of dryland ecosystems at unprecedented rate, thus threatening the stability of ecosystems. The stability of dryland ecosystems is vital for ecological security and local livelihoods. However, the mechanisms that underlie ecosystem stability in drylands remain uncertain due to limited field data from regional studies. Combined with transect survey in the drylands of China along the aridity gradient and remote sensing data, we characterized community temporal stability and identified its driving mechanisms along the aridity gradient. The results showed the community temporal stability in drylands of China revealed a U-shaped curve with increasing aridity and its major driving mechanisms shifted at an aridity level of ~ 0.88 . In regions where aridity is below 0.88, increasing precipitation and species richness resulted in higher community productivity and community stability. In regions where aridity is above 0.88, however, higher soil organic carbon content and species richness may lead to higher variability of community productivity and lower ecosystem stability. Overall, our findings revealed that there existed an aridity threshold leading to abrupt changes on community stability in drylands of China. Our study also suggested divergent driving mechanisms of community stability above and below the threshold, which should be considered in policy making regarding the ecosystem management of drylands.

1 Introduction

Drylands, defined as regions with an aridity index (AI, i.e., the ratio of average annual precipitation to average annual potential evapotranspiration) below 0.65, occupy 41% of the Earth's land area and support more than 38% of the world human population (Maestre, Quero, et al., 2012). Most drylands are characterized by low and highly variable precipitation, relatively poor soils, sparse vegetation, and fragile ecosystems (Reynolds et al., 2007). It is predicted that climate change will increase the rate of global dryland expansion during this century, and that drylands may cover half of the global land surface by the end of the century (Huang et al., 2016). Several studies suggest that future dryland ecosystems will experience more extreme climate events and more intense aridity (Cook, Ault, & Smerdon, 2015). The intensification of aridity and the reduction in rainfall in dryland ecosystems have changed the life form of dominant plant species (e.g., from herbs to shrubs) (Soliveres et al., 2014), reduced vegetation coverage (Delgado-Baquerizo et al., 2013) and soil microbial diversity (Maestre et al., 2015), and decoupled the soil nutrient cycle (Delgado-Baquerizo et al., 2013), which may lead to a decline in ecosystem function.

The adverse effects of aridity intensification on dryland ecosystems depend on the ability of the ecosystem to adapt to environmental changes. Ecosystem stability refers to the ability of an ecosystem to maintain or be restored to its original state after being disturbed and is one of the basic attributes of an ecosystem (Pimm, 1984). Ecosystem attributes will significantly respond to environmental changes, especially for the droughts. A study has shown that increasing aridity may even lead to systematic and abrupt changes in

plant productivity, soil fertility, and plant cover and richness when aridity level (1-AI, i.e., higher values indicated drier conditions) more than 0.54, 0.7, and 0.8, respectively (Berdugo et al., 2020). Considering the ecosystem attributes may undergo nonlinear and abrupt changes along the aridity gradient, it is of great significance to examine the response of dryland ecosystems stability to increasing drought.

The community temporal stability depends on biodiversity, climate and soil conditions (Chen et al., 2021; Gilbert et al., 2020). Biodiversity mainly enhances community temporal stability through three main mechanisms: portfolio effects, overyielding effects and species asynchrony (de Mazancourt et al., 2013; Loreau & de Mazancourt, 2013; Thibaut & Connolly, 2013). Portfolio effects suggest that community temporal stability increases with the number of species (Thibaut & Connolly, 2013), because communities with more diverse population dynamics are less likely to be affected by fluctuations in individual populations. Overyielding effects suggest that higher diversity leads to higher productivity and reduces the effects of statistical stochasticity on the whole community, thus stabilizing the community (de Mazancourt et al., 2013). The species asynchrony theory suggests that, species within a community have different attributes and are thus unlikely to respond identically to environmental disturbances (Loreau & de Mazancourt, 2008). Their lagging or over-response to environmental disturbances produces temporal niche partition, which reduces the overall fluctuation of the community (Loreau & de Mazancourt, 2013).

Similarly, abiotic factors such as climate and soil conditions also have a significant impact on community stability. Climate change can alter ecosystem functions, cause biodiversity loss and species composition changes, increase ecosystem vulnerability, and threaten ecosystem production (Zhang et al., 2018). In fact, recent studies have found that climate warming and the decrease in the annual precipitation may lead to a decrease in temporal stability of plant community biomass production by altering species dynamics of plant community (Hallett et al., 2014; Ma et al., 2017). Moreover, extreme climate events, such as daily temperature and precipitation extremes, have changed in terms of intensity and frequency over recent decades (Ummenhofer & Meehl, 2017). The increase in climate variability, for example increase in precipitation variability, also may tend to reduce community stability (Zhang et al., 2018). In addition, local soil conditions also impose impacts on community stability through affecting ecological factors. Previous studies suggest that local soil conditions, especially soil organic matter, can affect community stability directly by increasing mean net primary productivity more quickly than its temporal variability and the direct impact of climate on stability is lower than that of local soil conditions (Gilbert et al., 2020). Furthermore, interactions of climate change, soil conditions and biodiversity make the maintenance mechanism of community stability more complex (Chen et al., 2021; Gilbert et al., 2020).

Ecosystem attributes are highly correlated, and changes in a given attribute caused by climate change may trigger changes in other attributes that rely on this attribute but operate at different spatiotemporal scales (Reynolds et al., 2007). The response of ecosystem attributes to climate change may exist thresholds, and the climate threshold that causes a sudden change in a certain attribute may trigger changes in a range of related ecological attributes (Berdugo et al., 2020; Sun et al., 2023). Specifically, the response of community stability to climate change may undergo sudden changes beyond a certain threshold, which may also cause changes in plant and soil attributes that affect community stability. Therefore, identifying this threshold helps us understand these chain changes and clarify the driving mechanisms of community stability more clearly. Recent studies on mechanisms driving ecosystem stability have mainly come from local-scale experiments, where the included species have been randomly selected and stability has been assessed under limited environmental conditions (García-Palacios et al., 2018). Especially in the fragile dryland ecosystems, research on the interactive mechanisms that underlie ecosystem stability is limited.

China has approximately 6.6 million km² of drylands, with significant differences in environmental conditions and vegetation types (Yang, Wu, et al., 2011; Li, Fu, et al., 2021). These drylands are vulnerable and sensitive to environmental change (Xu & Zhang, 2020); thus, a number of land protection and ecological restoration projects has been implemented to mitigate land degradation in China's dryland since the 1970s (Bryan et al., 2018). However, these large-scale projects increased the pressure on water supplies, thus exacerbated the tradeoff between carbon and water (Su & Shangguan, 2019; Li, Bai, You, Hou, & Li, 2021). Due to

increased aridity, there is also a risk of drylands expansion. The stability of the ecosystem is a determining factor in whether degradation of dryland ecosystems will occur and whether vegetation restoration efforts will be sustainable.

Ecosystem stability is a multifaceted and multidimensional concept with diverse metrics in practical studies (Donohue et al., 2016), while it is usually measured in terms of the temporal stability of ecosystem functions. Most studies have focused on the temporal stability of community productivity, defined by the ratio of time-mean biomass to its standard deviation (Tilman, Reich, & Knops, 2006). Thus, we characterized community as a MODIS NDVI time series product and defined community stability as the ratio of the mean annual peak NDVI to its standard deviation (Chen et al., 2021). The main objective is to analyze the variation of community stability along an aridity gradient in the drylands of China and explore whether there was an aridity threshold leading to nonlinear variation on community stability. By combining the transect survey data with satellite data, we further analyzed the underlying driving mechanisms of species richness, climate and soil properties on community stability.

2 Materials and methods

2.1 Study area

The study area is located in the dryland ecosystems of northern China (Fig. 1), with a latitudinal range from 31deg42' N to 53deg23' N and a longitudinal range from 73deg40' E to 126deg04' E. The whole region is located inside the Eurasian continent, with a dry climate, large annual temperature ranges and windy weather. The annual precipitation ranges from 21 mm to 453 mm, and the average annual temperature ranges from -4 to 13 . The vegetation types from east to west are meadow grassland, typical grassland, scrub, desert grassland and desert (Hu, Ran, et al., 2021). The survey sites in study area encompass the 14 soil types, i.e., Aeolian soil, Alluvial soils, Brown desert soil, Brown pedocals, Castanozems, Cultivated loessial soils, Desert solonchaks, Fluvo-aquic soils, Gray desert soils, Gray-brown desert soils, Litho soils, Meadow soils, Sierozems, Skeletal soils(<https://www.resdc.cn/>).

2.2 Field community survey

Along the aridity gradient, we set one 45x45 m sample plot at each survey site, either grassland or shrubland depending on the dominant ecosystem in each survey site, and the latitude and longitude of the plot were recorded. We set 45 sample points along the aridity gradient. These plots were selected as far away as possible from the impact of human activities and other disturbances on plants and soil. Four sample lines with 10-m intervals were laid in each sample plot, and five 1mx1m survey quadrats were randomly set on each sample line. All species occurring in the quadrats were surveyed and recorded, and plant species richness was quantified as the sum of species in all quadrats (Maestre, Quero, et al., 2012). The specific leaf area (SLA) is the ratio of leaf area to leaf dry weight. We measured the SLA of dominant species at each sample plot, and the leaf area of each dominant species was measured with a leaf area meter (Yaxin-1241). Soil cores with a diameter of 6 cm were collected at a depth of 0-30 cm on the upper, middle and lower slopes of each sample plot and brought to the laboratory for the measurement of soil properties.

To expand the sample size, the species richness and soil properties from four related studies were collected using ISI Web of Science and China National Knowledge Infrastructure (Supporting Information Data S1; a list of the data sources is given in Supporting Information Appendix S1). The ecosystems involved in these four studies are all natural grassland or shrubland ecosystems, and the quadrat size is the same as our study. We obtained the table-form data directly and extracted graphical data using Get Data Graph Digitizer 2.20 (Zhang, Sun, Huettmann, & Liu, 2022). The total number of sampling plots was 109, including 48 sample points in the semiarid region, 53 sample points in the arid region and 8 sample points in the hyper-arid region.

2.3 Climatic and soil variables

Meteorological data were obtained from the China Meteorological Data Network (<http://data.cma.cn/>), and multiyear temperature and multiyear precipitation were obtained by spatial interpolation of relevant

meteorological data from 2000-2016 at meteorological stations near the sampling sites using Anusplin software (Hutchinson and Xu, 2004). Potential evapotranspiration was calculated for each site by the Penman-Monteith formula (Allen, Pereira, Raes, & Smith, 1998). Based on the above variables, we calculated the aridity index ($AI = \text{precipitation} / \text{potential evapotranspiration}$), which is widely used to measure the degree of aridity worldwide (Garcia-Palacios et al., 2018). To facilitate the interpretation of the results, we used $1-AI$ to represent the level of aridity in our analysis, i.e., higher values indicated drier conditions. To assess climate change, the following four indicators were used: (i) mean annual precipitation, (ii) interannual precipitation variability (standard deviation of annual precipitation), (iii) mean annual temperature, and (iv) interannual temperature variability (standard deviation of annual temperature), which were the main climate drivers used to assess terrestrial net primary productivity (Gherardi & Sala, 2020). We used soil organic carbon and soil clay to assess the soil properties at each site, as these soil properties play a key role in water availability and plant growth and are important drivers of plant diversity and ecosystem function in dryland ecosystems (Brahim, Blavet, Gallali, & Bernoux, 2011); additionally, they tended to be relatively constant over the time scales considered in the paper (Ehrenfeld, Ravit, & Elgersma, 2005). The soil organic carbon was determined using the potassium dichromate volumetric method (Maestre, Quero, et al., 2012), and the soil clay was extracted from the SoilGrids system (<https://soilgrids.org/>).

2.4 Community productivity stability

Since it is difficult to obtain continuous community productivity data for long time series, remote sensing provides a feasible way to solve this problem (Chen et al., 2021). We used the NDVI to represent the aboveground net primary productivity of the community. The NDVI characterizes vegetation cover, is linearly correlated with photosynthetically active radiation, and is considered a good proxy for aboveground biomass (Li, Deng, Liang, & Huang, 2010). The NDVI data for each site were acquired using the MOD13Q1 product from the Moderate Resolution Imaging Spectroradiometer (<https://daac.ornl.gov/>), which provides data 23 times per year (every 16 days) at a pixel size of 250 m x 250 m. Garcia-Palacios et al. (2018) indicated that in global dryland ecosystems, the spatial scale mismatch between field survey sample plots and remote sensing data is very small, so the NDVI can represent the community productivity of our sample plots. The peak NDVI within each year from 2000-2016 was used as a proxy for community productivity in that year, and the temporal stability of community productivity was calculated as follows:

$$\text{Stability} = \mu / \delta \quad (1)$$

where μ and δ are the annual mean peak NDVI and the standard deviation (SD) of the annual peak NDVI, respectively.

2.5 Statistical analyses

We selected species richness, annual mean and interannual variability of temperature and precipitation, soil organic carbon and soil clay content to characterize the biodiversity, climate and soil properties, respectively, and further explored the effects of these environmental and ecological factors on community stability. First, we used the locally weighted regression to fit the nonlinear changes of community stability and ecological factors along the aridity gradient, and used the segmented linear regression model to identify tipping points by the “segmented” package (Muggeo, 2008). When there are multiple responses states of the corresponding variable with the change of the independent variable, they are difficult to be explained by one regression model. Segmented regression can find the appropriate breakpoint location according to the response state, thus dividing the independent variable into a limited number of intervals, and describing the relationship between them separately in different intervals (Muggeo, 2008). Then we identified the aridity threshold for abrupt changes of the community stability in drylands of China. We first established a linear mixed-effects model to test the relationships between the species richness or soil organic carbon and the community stability using “lme4” and “lmerTest” packages (Douglas et al., 2015; Kuznetsova et al., 2017):

$$\begin{aligned} \text{Community stability} \sim & \text{Aridity} + \text{Species richness} + \text{Soil organic carbon} + \text{Soil Clay content} + \\ & \text{Aridity} \times \text{Species richness} + \text{Aridity} \times \text{Soil organic carbon} + \text{Aridity} \times \text{Species richness} \times \text{Soil organic} \end{aligned}$$

carbon + (1|Soil.type) + (1|Vegetation.type), where $\times$ indicates an interaction term.

We extracted the effect value of species richness or soil organic carbon on community stability under a certain aridity value through the moving-window analysis with a window of 65. In order to improve the robustness of the results, we added the bootstrap method (the number of permutations was 500) to the moving-window analysis. Based on the above extracted effect values, we constructed the relationship between the effect value and aridity and used segmented linear regression to identify the aridity threshold. Finally, to identify the direct and indirect effects of these ecological factors on community stability above and below the threshold, we used the piecewise structural equation modelling based on the directional separation method. The structural equation modelling (SEM) was a probability model, which integrated multiple prediction factors and response variables in a causal network. Compared with the standard SEM, the piecewise structural equation modelling allowed us to relax some of the limitations, including nonnormal data, nonlinear relationships between variables and small sample sizes (Lefcheck, 2016). The piecewise structural equation models were constructed using the "PiecewiseSEM" package (Lefcheck, 2016). Before performing SEM operations, the variables were log transformed or square root transformed to meet homogeneity and normality requirements. All the above analyses were performed using R 4.1.1 (R Core Team, 2021).

3 Results

3.1 The responses of community stability and environmental and ecological factors to aridity

The changes in community stability along the aridity gradient showed a U-shaped curve, decreasing and then increasing with increasing aridity; shifts occurred at aridity=0.86 (Fig. 2a). The annual mean peak NDVI and the SD of the peak NDVI, which are components of community stability, turned at aridity=0.90 and aridity=0.81, respectively, where the mean peak NDVI decreased with increasing aridity above aridity=0.90 and did not change with aridity below aridity=0.90 (Fig. 2b). The SD of the peak NDVI did not vary with aridity until aridity=0.81 and decreased with increasing aridity below aridity=0.81 (Fig. 2c). Species richness and soil organic carbon content turned at aridity=0.89 and aridity=0.83, respectively, and their reduction rates were faster below the turning point than above (Fig. 2d and e). Soil clay content showed a U-shaped curve, turning at aridity=0.79 (Fig. 2f). Moreover, Both the mean annual precipitation and the SD of the annual precipitation decreased significantly with increasing aridity (Fig. S1a and b). The mean annual temperature also showed a U-shaped curve on the aridity gradient, turning at aridity=0.72 (Fig. S1c), while the SD of annual temperature did not change with aridity (Fig. S1d).

3.2 The aridity threshold causing sudden change in community stability

The effects of species richness, soil organic carbon, interaction between species richness and aridity, and interaction between soil organic carbon and aridity on community stability all showed abrupt changes when the aridity value was 0.88 (Fig. 3a-d). Thus, no surprise that the aridity threshold for sudden change in driving mechanisms of community stability was 0.88. Specifically, the effect value of species richness on community stability increased when aridity less than 0.88 and then decreased with aridity. In contrast, the effect value of interaction between species richness and aridity decreased on community stability when aridity less than 0.88 and then increased with aridity. Moreover, the effect value of soil organic carbon on community stability increased with aridity, yet the slope of the relationship between soil organic carbon and community stability was larger when aridity more than 0.88. However, the effect value of interaction between soil organic carbon and aridity on community along aridity gradient was opposite to that of soil organic carbon.

3.3 Direct and indirect effects of climate, species richness and soil properties on community stability

In regions with aridity < 0.88, SEM explained 72%, 87%, and 28% of the variation in community stability (Fig. 4a) and the variation in its components of the mean peak NDVI (Fig. 4b) and the SD of the peak NDVI (Fig. 4c), respectively, and the effects of climate, species richness, and soil properties on ecosystem stability mainly acted on the mean peak NDVI. Plant richness had a positive effect on community stability mainly by reducing the SD of the peak NDVI rather than by increasing the mean peak NDVI (Fig. 4b and c,

$p > 0.1$). Plant communities with high precipitation and high soil clay content were more stable. Meanwhile, plant communities with high precipitation had higher community species richness, which indirectly improved community stability (Fig. 4a). Since the effect of soil organic carbon on both the mean peak NDVI and the SD of the peak NDVI was weak ($p > 0.1$), it did not significantly affect community stability (Fig. 4b and c, $p > 0.1$).

In regions with aridity > 0.88 , SEM explained 53%, 39%, and 53% of the variation in the community stability (Fig. 4d) and the variation in its components of the mean peak NDVI (Fig. 4e) and the SD of the peak NDVI (Fig. 4f), respectively, and the effects of climate, species richness, and soil properties on ecosystem stability mainly acted on the SD of the peak NDVI. The SD of precipitation had a direct and significant positive effect on the SD of the peak NDVI, so the communities with a small SD of precipitation were more stable (Fig. 4f). Species richness had a negative effect on the SD of the peak NDVI, but it did not significantly affect community stability (Fig. 4d, $p > 0.1$) due to the similar effect of species richness on the mean peak NDVI and the SD of the peak NDVI (Fig. 4e and f, standard path coefficient: 0.45 vs. 0.37). Plant communities with a high mean annual precipitation and a low SD of temperature had high soil organic carbon, and the increase in soil organic carbon reduced community stability by increasing the SD of the peak NDVI (Fig. 4f). Soil clay did not directly affect community stability but indirectly affected community stability through soil organic carbon (Fig. 4d).

4 Discussion

4.1 Impacts of climate change, biodiversity and soil properties on community stability

Some studies have explored the impact of ecological factors such as climate change and biodiversity on community stability (Ma et al., 2017; Zhang et al., 2018), and have also discovered different driving mechanisms of community stability under climate thresholds (García-Palacios et al., 2018). For example, a study on the global dryland ecosystems stability shows that under low aridity level (aridity < 0.6), the diversity of leaf traits is more likely to drive stability, while under high aridity level (aridity > 0.6), species richness plays a greater role in stability (García-Palacios et al., 2018). However, the division of aridity level in this study is quite subjective, and no statistical method is used to identify the aridity threshold. By combining segmented linear regression with moving-window analysis, our study showed that community stability responds nonlinearly to increasing aridity, and changes suddenly at aridity = 0.88. Our results are similar with those of Berdugo et al. (2020), who found that ecosystems may experience an "ecosystem breakdown" phase with an extreme reduction in plant cover when aridity > 0.83 . Of particular concern is the transition from grassland ecosystems to desert shrub ecosystems at this critical threshold in China's dryland. In regions with aridity > 0.88 , community stability increased with increasing aridity, possibly due to the extreme sparseness of plants in this region. During the transect investigation, we found that the abundance and richness of species were relatively low, which may lead to small fluctuations of community in responses to disturbances. The driving mechanisms above and below the threshold change depends on the climate, vegetation differences, and soil properties (Fig. 5). In regions with aridity < 0.88 , climate played a leading role in the community stability (Fig. S4a-c). In contrast, species richness and soil properties had a greater effect on community stability than climate in regions with aridity > 0.88 (Fig. S4d-f).

Through SEM (Fig. 4a-c), we found that the increase in mean annual precipitation improved community stability by increasing the mean productivity in regions with aridity < 0.88 , which are consistent with previous studies (Su et al., 2022; Zhang et al., 2018). The mean precipitation and precipitation variability are important factors driving the spatial and temporal dynamics of ecosystem communities (Hallett et al., 2014; Zhang et al., 2018). A global meta-analysis indicated that an increase in precipitation enhances the community temporal stability mainly by increasing the average productivity (Su et al., 2022). In addition, the increase in interannual precipitation variability diminished community stability by increasing variability of productivity in regions with aridity > 0.88 (Fig. 4d-f). In these regions, plants are mostly drought-tolerant shrubs, with deep roots, enabling them to access deep soil water resources (Groom, 2004), and buffer the effect of mean annual precipitation on the mean productivity. However, increasing variability in interannual precipitation may increase community fluctuations and increase variability of community productivity (Zhang, Li, Zhang,

Zhang, & Chen, 2016), which further affects community stability.

In contrast, the effects of temperature and temperature variability on community stability were general weak in both regions due to water limitation. The increase in variability of annual temperature rather than the mean annual temperature improved community stability in regions with aridity < 0.88 of China's drylands (Fig. 4a). This result may be because the majority of the sample sites had mean annual temperatures in limited range of 7-9°C, and the temperature variability amplified the effect of temperature on biomass, which led to an increase in community stability (Fig. 4b). In regions with aridity > 0.88 , neither the mean annual temperature nor the variability in annual temperature had a significant effect on community stability (Fig. 4d), which were different from previous studies. Although some studies indicated that climate warming may reduce community stability (Gao et al., 2022; Liu et al., 2021), Liu et al. (2021) found that the decrease in community stability is caused by the decrease in productivity due to increased water limitation by increase temperature. Therefore, the impact of temperature change on community stability likely depends on water constraints. Due to the larger water limitation in regions with aridity above 0.88, temperature change may not have a significant impact of on community stability.

In regions with aridity < 0.88 , the increase in species richness improved community stability by reducing the variability in productivity (Fig. 4c), while it had non-significant positive effect on the mean productivity in this region (Fig. 4b). In contrast, the increase in species richness weakened community stability by increasing the variability in productivity (Fig. 4f), and it had significant positive effect on the mean productivity in this region (Fig. 4e). The productivity and stability of plant community are ecosystem properties emerging from species interaction and population dynamics (Wang et al., 2021). Biodiversity enhances productivity mainly through complementary effects and selection effects (Loreau & Hector, 2001), thereby affects stability of community productivity through portfolio effects or overyielding effects (Wang et al., 2021). If the utilization of resources is different among species, an increase in species diversity will improve the utilization efficiency of the overall resources, and complementary effects will occur (Tilman, Lehman, & Thomson, 1997). If the interaction between species leads to the dominance of species with higher productivity in the community, selection effects will occur (Thibaut & Connolly, 2013). As ecological niche complementation promotes species coexistence, it will produce stronger portfolio effects, overyielding effects and community stability (Isbell et al., 2009; Thibaut & Connolly, 2013). In contrast, selection effects tend to increase the dominance of high-yielding species, thereby reducing species evenness, leading to a decrease of portfolio effects and community stability (Isbell et al., 2009; Thibaut & Connolly, 2013). Through the community model, Wang et al. (2021) also indicated that complementary effects enhance stability by increasing portfolio effects, while selection effects diminish stability through selecting species with high productivity but low tolerance. In regions with aridity < 0.88 , communities with higher species richness had smaller fluctuations in productivity and higher community stability. In response to aridity stress, resource utilization is higher in communities with higher species richness due to ecological niche differentiation promoting species coexistence, which facilitates community stability (Godoy, Gómez-Aparicio, Matías, Pérez-Ramos, & Allan, 2020). The results may indicate that complementary effects mainly affect productivity, thereby improve community stability. In contrast, species richness increased the variability in productivity and diminished community stability in regions with aridity > 0.88 . These regions are desert ecosystems dominated by drought-tolerant communities, mostly mono-dominant shrubs. In response to aridity stress, the productivity of non-dominant populations in communities with high species richness fluctuated more than that in communities with low species richness (Lepš, 2004), thus leading to a greater variability in the overall productivity of the community. In addition, we found that in this region, the SLA of the dominant species increased with species richness (Fig. S2). Generally, plants with higher SLA have higher photosynthetic capacity, productivity and lower tolerance (Gross et al., 2013; Hao et al., 2020). Thus, compared to communities with low species richness, the dominant population has higher productivity but relatively lower tolerance in communities with high species richness, which also promoted the variability of community productivity (Gross et al., 2013). Moreover, the increase in the dominance of high-yielding species led to a decrease in community evenness, which weakened the portfolio effect and ultimately increased the variability in productivity (de Mazancourt et al., 2013; Wang et al., 2021). These results are similar to those of the community model by Wang et

al. (2021), therefore, these results may indicate that selection effects mainly affect productivity, thereby diminish community stability.

Soil properties are important abiotic factors affecting plant growth and vegetation distribution, which can further influence community stability. In regions with aridity < 0.88 , a higher soil clay and organic carbon content resulted in greater community stability (Fig. 4a-c). In this region, the water and temperature conditions were relatively suitable for plant growth, which resulted in high plant productivity and carbon input into the soil. Meanwhile, the high clay content facilitated the accumulation of soil organic carbon (Zhong et al., 2018). Higher soil organic carbon positively feeds back to plants, leading an increase in species richness and community stability. However, the dominant climatic conditions in this region might mask the effect of soil organic carbon on community stability leading this effect to be non-significant (Fig. 4a). In regions with aridity > 0.88 , however, communities with higher soil organic carbon contents had greater variability in productivity and lower community stability. This is possibly because biomass accumulated in wet years declined more rapidly in dry years for communities with higher soil organic carbon contents (Fig. S3). In addition, occasional precipitation may increase microbial activity due to the priming effect (Jones et al., 2018; Xu et al., 2017), which allows microorganisms to use more organic carbon. Thus, the communities with high soil clay contents have lower soil organic carbon contents, which instead improves the stability of these communities in regions with aridity > 0.88 (Fig. 4d-f).

In a word, our results showed that the increase in mean annual precipitation, plant species richness and soil clay content promoted mean productivity, thereby improving community stability in regions with aridity below 0.88. Specifically, plant species richness might promote mean productivity by complementary effects, thereby improving community stability (Fig. 5). In contrast, the increase in variability of annual precipitation, plant species richness, and soil organic carbon content promoted variability of productivity, thereby weakening community stability in regions with aridity above 0.88. In addition, plant species richness might promote variability of productivity by selection effects, thereby weakening community stability in this region (Fig. 5).

4.2 Guidance for ecosystem management

Our study indicated precipitation was the main climatic factor influencing community stability in the drylands of China. Climate models predict that the frequency of extreme precipitation in China's drylands is likely to increase in the future, and moderate to heavy rainfall and rainstorm events will occur more frequently, especially in the northwest (Hui et al., 2018; Li, Bai, You, Hou, & Li, 2021). Moreover, the frequency of drought events also may increase in the future (Hui et al., 2018). In the face of deteriorating climatic conditions in the future, the community stability of drylands in China might be drastically reduced according to our results, especially in the regions with aridity level below 0.88. This reduction may have irreversible adverse effects on the structure, function, biodiversity and soil properties of dryland ecosystems (Huang et al., 2017), leading to land degradation and desertification. Our results indicate that ecosystems with aridity level around 0.88 are extremely unstable and need to be protected and managed as a priority. Therefore, the adverse impact of future climate change on ecosystem stability should be considered in the ecosystem management of China's drylands.

Facing the intensification of drought and extreme climate events in the future, one of the main purposes of dryland ecological restoration is to establish a relatively stable plant community in terms of community structure and function under deteriorating environmental conditions (Seabloom, 2007). A stable plant community has low variability, deviates only slightly from its average state in the case of environmental change, and can return to its equilibrium state quickly after disturbances (Lu, Zhao, Wu, Dai, & Gao, 2019). Our result suggests that plant diversity is an important biological factor for establishing a stable plant community under climate change, highlighting the need to enhance the protection and restoration of plant communities in drylands of China. Although the implementation of the afforestation projects in China has generally greened vast regions of China's dryland, plant diversity has not been considered as a key factor in the implementation of these projects.

Hence, the ecological restoration project of drylands should be adjusted to improve community stability. Considering the divergent effects of species richness on community stability along the arid gradient, we suggest that in relatively humid regions (i.e., aridity<0.88), the richness and evenness of plant communities should be considered, whereas monocultures should be avoided in the process of ecological restoration in drylands of China. By contrast, in regions with aridity>0.88, single species with a high tolerance should be planted first in the early stage of plant community construction or restoration, and more species should be gradually and evenly allocated after the local environment is improved. More importantly, the driving mechanisms of community stability under different levels of aridity should be considered for protection and restoration of drylands in a changing climate.

4.3 Limitations and uncertainties

Vegetation is sparse in drylands, which may increase the uncertainty of satellite observations of vegetation indexes (e.g., the NDVI) (Hu, Jiang, et al., 2021). Some studies have shown that the uncertainties of using NDVI to detect the trend of vegetation growth and change under frequent drought conditions in Northwest China (Li, Deng, Liang, & Huang, 2010). Although it has become common to explore the impact of ecological factors on ecosystem functions by combining observational data with remote sensing data (Chen et al., 2021; García-Palacios et al., 2018; van Rooijen et al., 2015), the analysis of vegetation change using the NDVI needs to be carried out with caution for regions with sparse vegetation due to the interference of the soil background (Huete, 1988). Regarding the spatial scale mismatch between field survey sample plots and remote sensing data, García-Palacios et al. (2018) showed that it was very small in global dryland ecosystems, and high-resolution remote sensing data and long-term monitoring data might help address this issue. Furthermore, a recent study showed that above- and belowground biodiversity both drive ecosystem stability in natural alpine grasslands on the Tibetan Plateau (Chen et al., 2021). Thus, ignoring the impact of belowground organisms in our study may underestimate the role of biodiversity on ecosystem stability.

5 Conclusions

An aridity threshold value leading to abrupt changes on community stability in drylands of China was detected at aridity=0.88. The influence degree and mechanism of ecological and environmental factors on community stability above and below the threshold were different. In particular, species richness played an opposite role. In regions with aridity level below 0.88, each driver affected community stability mainly by influencing the mean productivity, with climate playing a dominant role and species richness promoting mean productivity by complementary effects, thereby improving community stability. In contrast, each driver affected community stability mainly by influencing the variability of productivity in regions with aridity level above 0.88, with soil properties playing a dominant role and species richness promoting variability of productivity, thereby reducing community stability. Detecting the threshold and identifying the contrasting driving mechanisms in the community stability of dryland ecosystems can help develop adaptive measures to cope with aridification stress and provide guidance for sustainable ecosystem management. The roles of soil organisms in maintaining ecosystem stability through plant–soil feedbacks should be incorporated in future research.

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Data archiving statement

Data are available from the National Ecosystem Research Network Data Center (<http://www.nesdc.org.cn/>).

Conflict of interest statement

We declared that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

Ethics statement

We confirm that this article does not present research with ethical considerations.

Funding statement

This study was jointly funded by the National Natural Science Foundation of China (grant numbers 41991233 and 41807153) and the Ma Shijun Young Talent Sponsorship Program by State Key Laboratory of Urban and Regional Ecology.

Figures

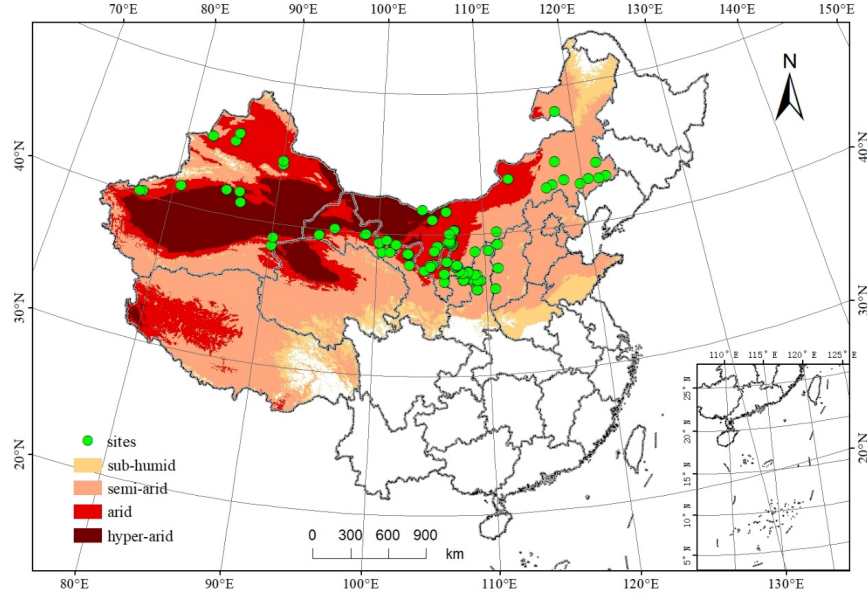


Fig. 1 Distribution of sampling sites in drylands of China

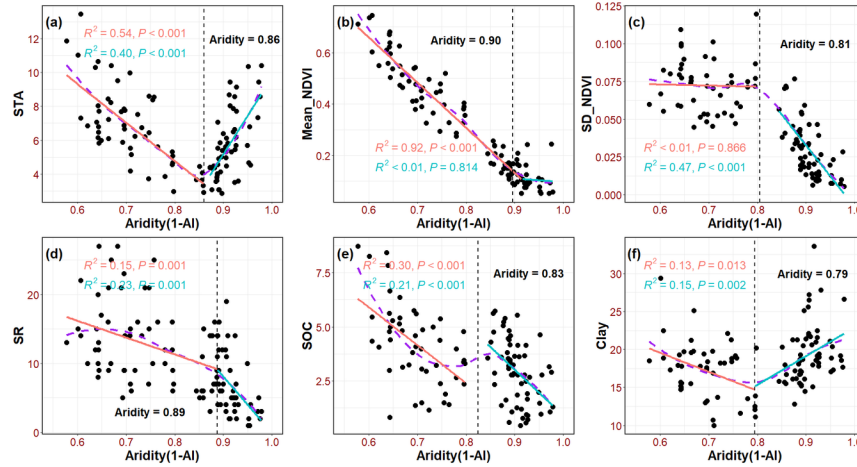


Fig. 2 The response of community stability and its components, species richness, and soil properties with increasing aridity. Nonlinear variation in (a) STA (community temporal stability), (b) Mean_NDVI (the mean peak NDVI), (c) SD_NDVI (the SD of the peak NDVI), (d) SR (species richness), (e) SOC (soil organic carbon), and (f) clay (soil clay) with increasing aridity and their aridity thresholds. The red and green solid lines indicate the linear regression fitting curves above and below the threshold, respectively, and the purple dashed line indicates the overall locally weighted regression curves.

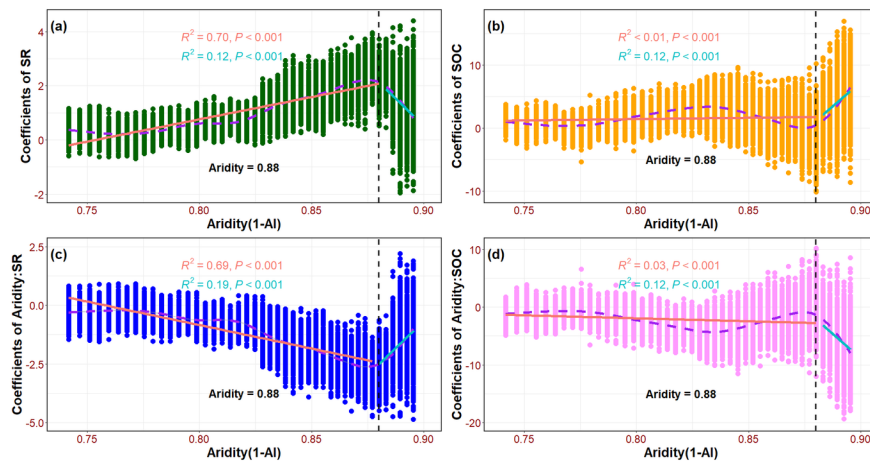


Fig. 3 The effects of species richness, soil organic carbon, interaction between species richness and aridity, and interaction between soil organic carbon and aridity on community stability. SOC = soil organic carbon, SR = species richness, “:” = interaction. The red and green solid lines indicate the linear regression fitting curves above and below the threshold, respectively, and the purple dashed line indicates the overall locally weighted regression curves.

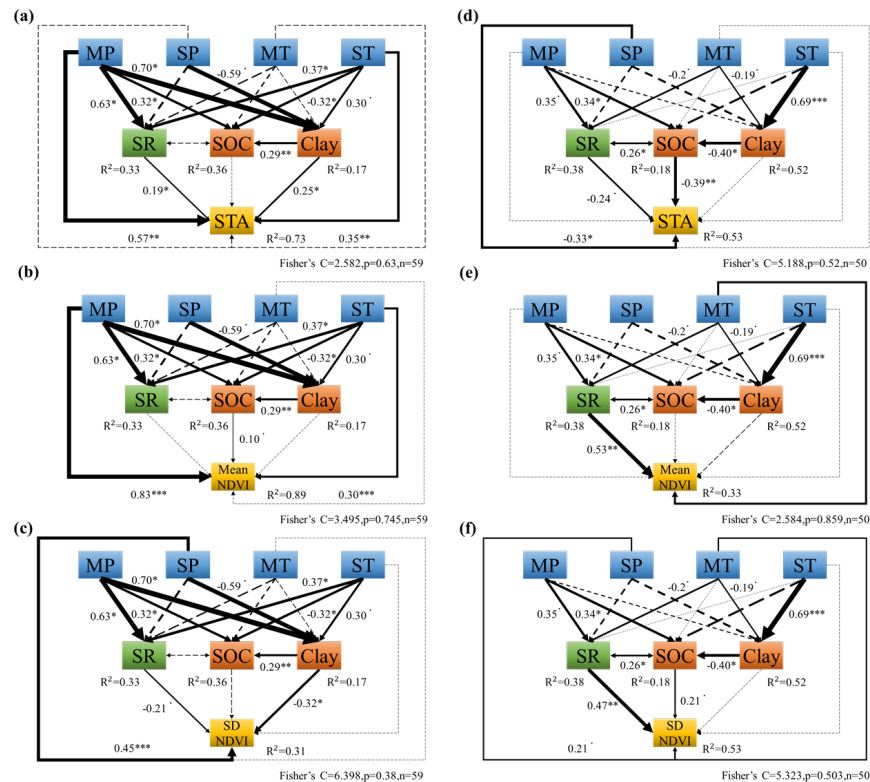


Fig. 4 Relationships between climate, species richness, soil properties and community stability and its components. Aridity<0.88, direct and indirect effects of climate, species richness, and soil properties on (a) community stability (STA), (b) the mean peak NDVI (Mean_NDVI), and (c) the SD of the peak NDVI

(SD_NDVI). Aridity>0.88, direct and indirect effects of climate, species richness, and soil properties on (d) community stability (STA), (e) the mean peak NDVI (Mean_NDVI), and (f) the SD of the peak NDVI (SD_NDVI). The black continuous arrows and black dashed arrows indicate statistically significant and insignificant path coefficients between variables, respectively, and the width of the arrows indicates the strength of the relationship between variables, as measured by the standardized path coefficients. (**p<0.001, **p<0.05, *p<0.01, .p<0.1.)

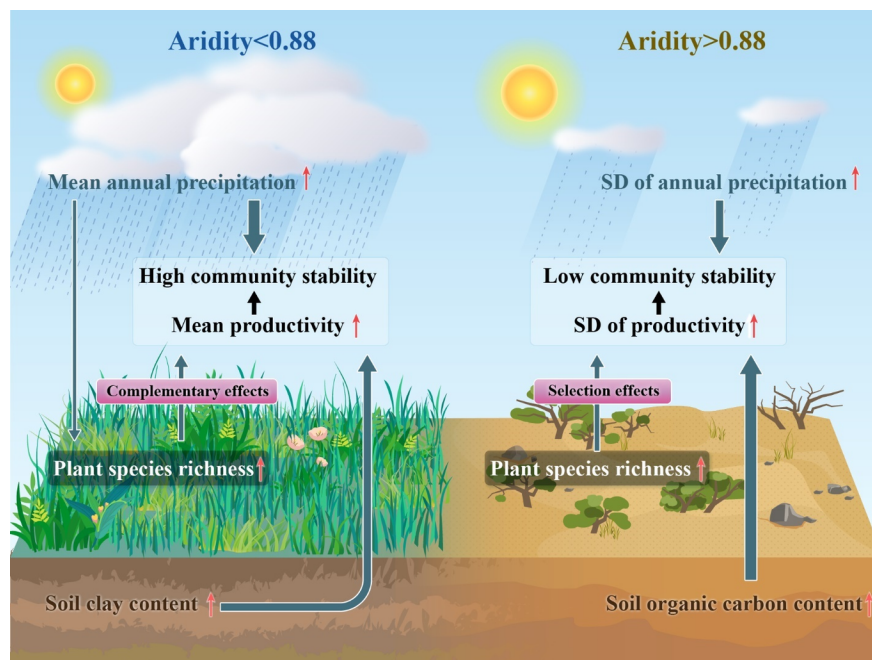


Fig. 5 Conceptual diagram of the impact of driving factors on community stability above and below the threshold