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## Research article

### Aridity and soil fertility, not species richness, interact to affect temporal stability of primary productivity along a natural gradient in northern China

Mengjiao Huang<sup>1</sup>, Job de Vries<sup>2</sup> , Shurong Zhou<sup>1</sup>   and Yann Hautier<sup>3</sup> 

<sup>1</sup>Key Laboratory of Genetics and Germplasm Innovation of Tropical Special Forest Trees and Ornamental Plants, Ministry of Education, College of Forestry, Hainan University, Haikou, PR China

<sup>2</sup>Department of Physical Geography, Utrecht University, Utrecht, the Netherlands

<sup>3</sup>Department of Biology, Ecology and Biodiversity Group, Utrecht University, Utrecht, the Netherlands

Correspondence: Shurong Zhou (zhshrong@hainanu.edu.cn)

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There is mounting evidence from experimental studies that drought and nutrient enrichment can interact to impact the biodiversity and productivity of terrestrial ecosystems. Whether such interactive effect influences plant diversity and the temporal stability of community productivity of natural ecosystems is unknown. To fill this knowledge gap, we combined a field survey of plant diversity and soil conditions with remote sensing temporal estimates of primary productivity in grasslands along a natural gradient in northern China. We found that aridity and soil ammonium ( $\text{NH}_4^+\text{-N}$ ) interacted to influence temporal stability of NDVI. That is, the relationship between ammonium and temporal stability of NDVI shifted from positive to negative due to increased standard deviation of NDVI with increasing aridity. Species richness was not related to temporal stability because it influenced the mean and standard deviation of NDVI proportionally. As a result, soil fertility outweighed the contribution of species richness to temporal stability. Our study demonstrates the synergistic effect of aridity and soil fertility, but not species richness, on temporal stability along a large natural gradient. Predicting how environmental drivers affect diversity and the stable provisioning of ecosystem services in real-world ecosystems therefore requires a better understanding of the complex interactions among environmental drivers.

Keywords: aridity, global changes, interactive effects, NDVI, soil fertility, species richness, temporal stability

## Introduction

Global environmental changes induced by human activities are reducing the diversity and stability of grassland ecosystems (Cardinale et al. 2012, Hautier et al. 2015). Previous studies focusing on the temporal stability of primary productivity have established that global changes can impact grassland stability directly but also indirectly by changing plant diversity or by changing the diversity–stability relationship (Hautier



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and Van der Plas 2022). Importantly, global environmental changes may interact to affect the diversity and functioning of ecosystems (Ren et al. 2017, Yahdjian et al. 2011). However, our current knowledge about the impact of interactive global changes on grassland diversity and stability is mostly derived from experimental studies (Bai et al. 2008, Adair et al. 2009, Ren et al. 2017, Ma et al. 2020). Whether aridity and soil nutrients interact to influence plant diversity and the temporal stability of community productivity of natural ecosystems is not well established (Hu et al. 2018).

Aridity, defined as the ratio of precipitation and potential evapotranspiration, is a major abiotic driver of ecosystem structure and functioning in global drylands (Maestre et al. 2016). Increased aridity predicted by the end of this century will increase the total area of drylands covering half of the land surface globally. These changes will lead to reduced carbon sequestration and enhanced regional warming, which will exacerbate land degradation and desertification (Huang et al. 2016). Aridity can decrease plant productivity as plants change their traits to adapt to water shortage at the expense of raw photosynthesis (Berdugo et al. 2020). Extreme aridity can decrease plant cover and richness arising from either changes in community composition (e.g. fast-growing, resource acquisitive species being replaced by stress-tolerant, slow-growing species), an increase in fungal diseases (Berdugo et al. 2020), or a reduction in the cover of the dominant species (Evans et al. 2011).

Changes in plant productivity, cover and richness in response to aridity may impact the temporal stability of community productivity. Temporal stability of productivity is defined here as the inverse of the coefficient of variation (i.e. the temporal mean of productivity divided by its temporal standard deviation), which is a commonly used metric to measure stability (Tilman 1999, Lehman and Tilman 2000). Therefore, temporal stability can be increased by increasing the mean more than the standard deviation, or by decreasing the standard deviation more than the mean. For example, increased precipitation (i.e. decreased aridity) can increase the temporal stability of productivity without changing species richness, by increasing species richness (Hallett et al. 2014), or by increasing the temporal mean of productivity regulated by species richness (Chi et al. 2019). Additionally, changes in species richness and productivity induced by changes in precipitation may not impact the temporal stability of productivity (Ma et al. 2017).

Nutrient enrichment is another major driver of biodiversity and community temporal stability. Human activities produce approximately as much reactive nitrogen as natural processes and the global human contributions to reactive nitrogen flows is predicted to increase by 64% between 1999 and 2050 (Duraiappah et al. 2005). Nitrogen addition usually reduces the temporal stability of primary productivity (Hautier et al. 2014, Zhang et al. 2019, Hautier et al. 2020). This can be through a reduction of the positive effect of plant diversity on stability (Hautier et al. 2014), or independent of changes in plant diversity (Liu et al. 2019, Huang et al. 2020).

Different type of nitrogen, including ammonium ( $\text{NH}_4^+\text{-N}$ ) and nitrate ( $\text{NO}_3^-\text{-N}$ ), can have different impacts on diversity and ecosystem functioning (Boudsocq et al. 2012, Midolo et al. 2019, Ren et al. 2021). For example, ammonium may result in greater loss of plant diversity compared to nitrate because ammonium tends to cause soil acidification and disadvantage the acid sensitive species (van den Berg et al. 2008, Midolo et al. 2019). This could lead to reduced positive diversity contribution to stability. Nitrate is more mobile than ammonium and subject to leaching and denitrification. Soils with high amount of ammonium relative to nitrate may exhibit higher primary productivity and stability (Boudsocq et al. 2009).

Soil organic carbon may also influence biodiversity and ecosystem functioning. Soil organic carbon may positively relate to community productivity and temporal stability by increasing the mean productivity more than the standard deviation. For example, the addition of organic carbon can increase community temporal stability by increasing the biomass of sedges (Zhang et al. 2020a). Gilbert et al. (2020) showed that soil conditions especially with high soil organic matter increased stability by increasing the mean aboveground community biomass.

Aridity can also impact ecosystem functioning via co-limitation with nutrient enrichment. Experimental studies have shown that precipitation and nitrogen can co-limit productivity (Ren et al. 2017). Nitrogen addition can improve the positive relationship between precipitation and productivity (Ma et al. 2017, Yu et al. 2021), or increase rain-use efficiency (the ratio of aboveground net primary production to precipitation) (Bai et al. 2008). A meta-analysis across arid to subhumid ecosystems showed that both water and nitrogen availability limit primary production with frequency of nitrogen limitation increasing and frequency of water limitation decreasing as annual precipitation increases (Yahdjian et al. 2011). Based on water or/and nutrient manipulation experiments, nitrogen addition was found to generally decrease the stability of community productivity in both wet and arid grasslands (Wang et al. 2017). However, in semi-arid grasslands, this negative effect may be offset by the increase in precipitation (Xu et al. 2015). Therefore, the negative effect of nitrogen on temporal stability may be inferred to be stronger in arid conditions. Current evidence about how aridity, nutrient enrichment and their interaction impact diversity and community temporal stability has mostly emerged from manipulated experiments (Xu et al. 2015, Wang et al. 2017). Whether and how natural aridity gradient and soil fertility impact plant diversity and temporal stability of community productivity remain unclear (Hu et al. 2018).

Moreover, studies related to the effects of aridity or/and soil fertility on community stability have focused on relatively small spatial scales with limited environmental heterogeneity (Xu et al. 2015, Ma et al. 2017, Huang et al. 2020). Due to the capacity of remote sensing observations to capture global land surface changes with daily to monthly interval at a spatial resolution between decimeters and 500 m, they can provide suitable spatial and temporal monitoring data.

Recently, remote sensing observations, complemented with field measurements, have become more widely used to assess the influence of biodiversity on ecosystem functioning across climate gradients (van Rooijen et al. 2015, Oehri et al. 2017, García-Palacios et al. 2018, Chen et al. 2021). For example, García-Palacios et al. (2018) reported a strong climate dependency of the biodiversity–ecosystem stability relationship across the global aridity gradient, with diversity of leaf traits driving ecosystem stability at low aridity levels and species richness playing a greater stabilizing role at high aridity levels. Based on time-series of remotely sensed ecosystem productivity, van Rooijen et al. (2015) showed that the negative effect of drought on productivity was stronger with a higher species richness, indicating a stabilizing role of plant species diversity on biomass production through time. However, whether aridity and soil fertility (e.g. nitrogen, carbon and phosphorus) influence temporal stability by influencing species richness, and whether the interactive effects of aridity and soil fertility influence temporal stability was not considered in these studies. More research is needed to explore the role of aridity gradient and soil fertility in influencing temporal stability of plant community productivity at larger scales.

In this study, we constructed a field survey of plant diversity and soil conditions combined with remote sensing estimates of primary productivity in grasslands along an aridity/soil fertility gradient in northern China. We explore the influence of aridity, soil fertility and their interactive effects

on plant diversity and temporal stability of plant productivity in the real-world ranges of environmental conditions. Specifically, we hypothesize that along the aridity/soil fertility gradient: 1) plant diversity and temporal stability of productivity decrease with increased aridity and soil fertility because of water limitation and nutrient enrichment; 2) aridity and soil fertility influences temporal stability directly and indirectly by influencing species richness, mean or standard deviation of productivity; 3) the reduction in temporal stability of productivity with soil fertility is stronger at high aridity (interaction).

## Material and methods

### Study sites and sampling

We surveyed 30 grassland sites during the peak growing season (July–August) in 2020 in northern China, at elevations ranging from 134 to 2894 m a.s.l., mean annual temperatures between 0.8 to 9.2°C, and precipitation ranging from 30 to 453 mm from 1970 to 2000 (Fick and Hijmans 2017) (Fig. 1). The 30 sites represent a strong gradient in aridity and soil fertility (Supporting information). Vegetation at our sites represents three main types of grassland ecosystems, i.e. mesic meadow steppe, semi-arid typical steppe and xeric desert steppe (DAHV and GSAHV 1996). Specifically, desert

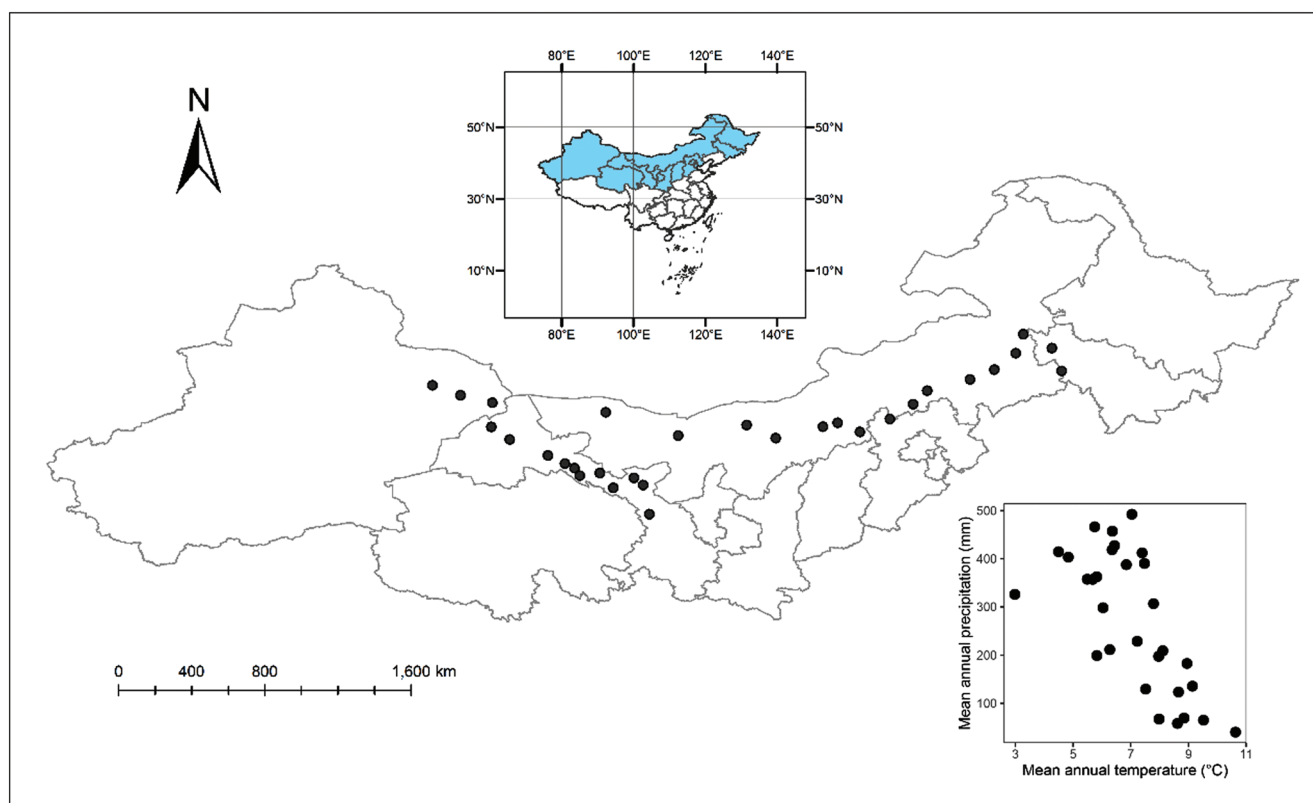


Figure 1. Locations of the 30 sampling sites in grasslands of northern China. The inset at the bottom right shows the spread of mean annual temperature (x-axis) and mean annual precipitation (y-axis) spanned by these sites.

steppe is characterized with short xerophytic species (mainly short shrubs and semi-shrubs), sparse cover and poor species richness. Vegetation in typical steppe (mainly xerophytic tufted perennial grasses) have a higher height, cover and diversity than that in the desert steppe. Plants in meadow steppe (mainly rhizomatous and tufted perennial grasses) are much taller with highest coverage and biodiversity (DAHV and GSAHV 1996, Hu et al. 2018).

At each site, a  $20 \times 20$  m plot was established and three subplots of  $5 \times 5$  m were randomly selected from the four corners of the plot. Then four quadrats of  $1 \times 1$  m each in size were selected at the four corners of each of the three subplots, for a total of twelve  $1 \times 1$  m quadrats for the  $20 \times 20$  m plot at each site. We recorded the latitude and longitude information at about the center of each plot. We recorded species richness in each quadrat and used the total number of the species found in these twelve quadrats as the species richness for this site. We also calculated Shannon diversity and Simpson diversity for each site using Hill numbers with the *hill\_taxa* function in the 'hillR' package (Chao et al. 2014). The sum of the biomass for each species across quadrats at each site was collected as a proxy of species abundance for Shannon and Simpson diversity calculation. Shannon diversity and Simpson diversity are highly correlated to species richness (Supporting information), and the relationships between Shannon diversity or Simpson diversity and temporal stability, mean of NDVI or standard deviation of NDVI are similar to that of species richness (Fig. 2d–f, Supporting information). Therefore, we used species richness as the single proxy for species diversity in our models in the main text. In each subplot, five soil cores (5 cm in diameter and 10 cm in depth) were collected, resulting in a total of 15 soil samples at each site. All soil cores of the same site were combined and analyzed at the laboratory for their pH, soil moisture ( $H_2O$ ), soil organic carbon (SOC), nitrate nitrogen ( $NO_3^-$ -N;  $mg\ kg^{-1}$ ), ammonium nitrogen ( $NH_4^+$ -N;  $mg\ kg^{-1}$ ) and available phosphorus (AP;  $mg\ kg^{-1}$ ). pH was measured using a pH analyzer (PHS-3C pH meter, China) at the supernatant of a 1:5 dry soil-to-water mixture.  $NH_4^+$ -N and  $NO_3^-$ -N were measured using flow injection analysis with an AA3 Continuous Flow Analyzer (Seal Analytical, Germany). AP was measured with an ultraviolet-visible spectrophotometer (UV-754 N, APL, Shanghai, China). SOC was measured by potassium dichromate heating method with an automatic titrator (Brand Titrette, Germany).

### Satellite-based temporal stability

We used the Normalized difference vegetation index (NDVI) derived from the red: near-infrared reflectance ratio (reflected by the vegetation and captured by the sensor of the satellite) as an approximation of plant aboveground biomass production (Pettorelli et al. 2005). We used data from the USGS Landsat satellite mission, which provides global observations continuously since the 1970s with a spatial resolution of 30 m (Cohen and Goward 2004). We used NDVI from the  $30 \times 30$  m pixel to represent the productivity of the  $20 \times 20$

m field survey plot. In order to reduce the spatial mismatch of the inconsistent area, we tried to select the field plots in a homogeneous grassland and extracted the NDVI data at each site according to its latitude and longitude information (Chen et al. 2021). NDVI data between 2013 and 2020 for each site were extracted from two Landsat missions (7 and 8) and Landsat Tier 1 surface reflectance (SR) products to evaluate time-series dynamics of plant productivity over the 8-year period. We obtained NDVI values from Google Earth Engine (Gorelick et al. 2017) as follows: 1) pixels flagged as cloud, snow or shadow in the per pixel quality assessment (QA) layer were masked in the individual images; 2) NDVI was computed for each image in the Landsat 7 and Landsat 8 collection; 3) a harmonic curve was fitted for pixels in the NDVI across years to filter outliers and fill the missing data resulting for example from cloud cover (Shumway and Stoffer 2000) (Supporting information). The harmonic model is as follows:

$$p_t = \beta_0 + \beta_1 t + A \cos(2\pi\omega t - \phi) + e_t$$

where  $p_t$  is a scalar pixel at time  $t$ ,  $e_t$  is a random error,  $A$  is amplitude,  $\omega$  is frequency, and  $\phi$  is phase.

We used  $NDVI_{ratio}$  method to determine the start (SOS), end (EOS), and length of the growing season from remote sensing data of each year as follows (White et al. 1997):

$$NDVI_{ratio} = \frac{NDVI - NDVI_{min}}{NDVI_{max} - NDVI_{min}}$$

SOS and EOS were defined as the first day of the year at which NDVI first exceeded and fell below the mean of its annual minimum ( $NDVI_{min}$ ) and maximum value ( $NDVI_{max}$ ), respectively (Oehri et al. 2017). The average NDVI in SOS and EOS time span was estimated and used as the proxy of primary productivity of the year. We calculated temporal stability as the inverse of coefficient of variation, i.e. the ratio of the annual mean NDVI from 2013 to 2020 (mean NDVI) to the standard deviation of the annual NDVI (SD NDVI) over this period (Lehman and Tilman 2000).

### Topography and climate

For each site, we recorded altitude, longitude and latitude. We also collected monthly air temperature and precipitation data from 2013 to 2020 (except 2018 and 2019) from meteorological stations (China Meteorological Data Service Center; <http://data.cma.cn/>). Potential evapotranspiration was estimated based on the Thornthwaite evapotranspiration equation (Thornthwaite 1948) using the *thornthwaite* function in the 'SPEI' package in R ([www.r-project.org](http://www.r-project.org), Beguería et al. 2017). We calculated the aridity index (AI) of a year as annual precipitation/potential evapotranspiration and calculated the average value of aridity across years. For the ease of interpretation, we used 1-AI to represent the aridity level with higher values for drier conditions (Delgado-Baquerizo et al. 2013b).



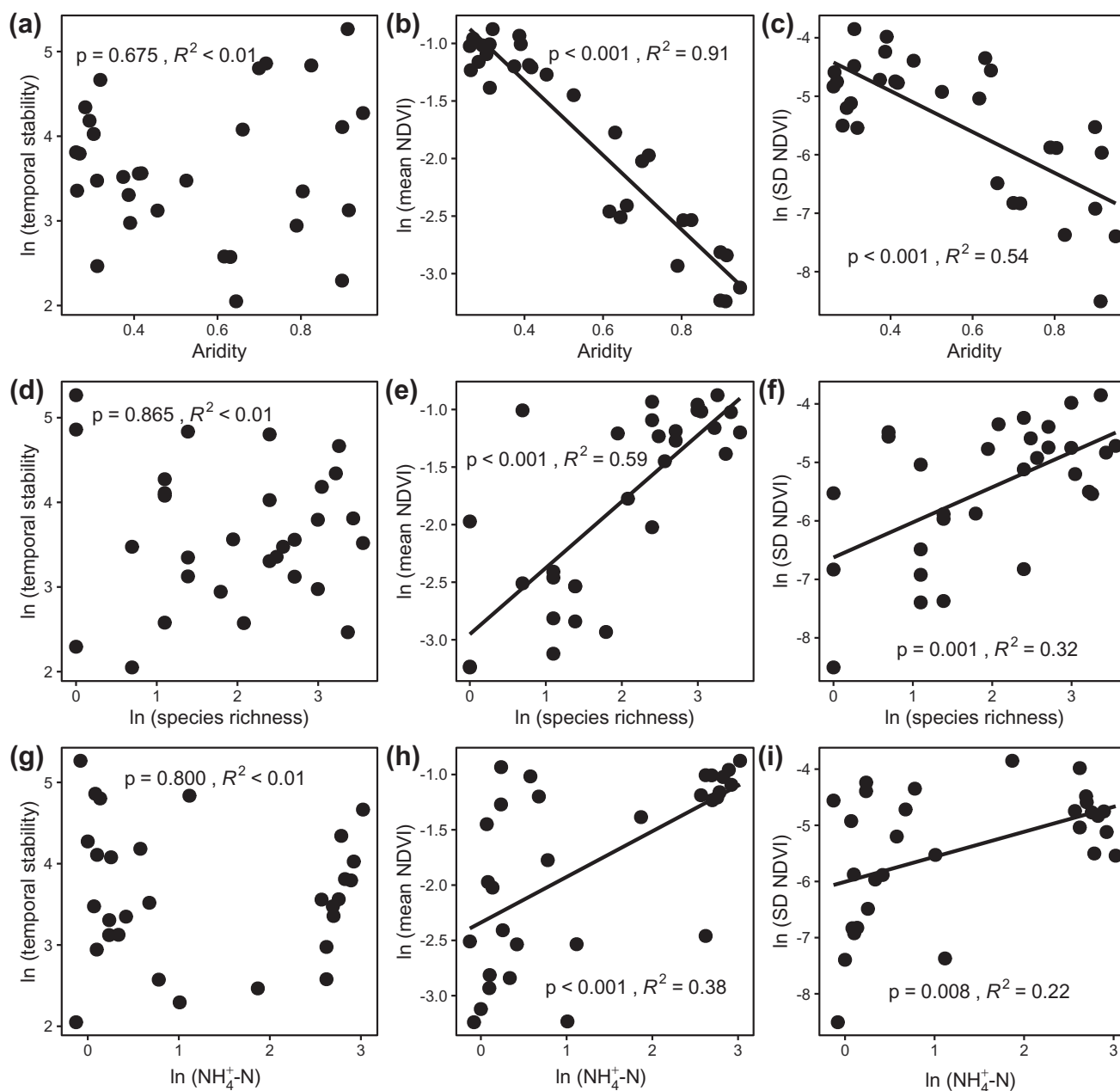


Figure 2. The influence of (a–c) aridity, (d–f) species richness and (g–i) ammonium ( $\text{NH}_4^+\text{-N}$ ) on temporal stability, mean of NDVI and SD of NDVI respectively in all sites ( $n = 30$ ). Temporal stability, mean and SD of NDVI, species richness and  $\text{NH}_4^+\text{-N}$  were logarithm transformed.

### Statistical analyses

We used Pearson correlation coefficient and principal component analysis (PCA) to test the collinearity among abiotic variables (Supporting information). We removed mean annual temperature (MAT) and mean annual precipitation (MAP) in the following analyses as they were highly correlated with aridity ( $r = 0.80$  and  $-0.98$  respectively; Supporting information). We fitted linear model regressions to assess the effect of aridity on temporal stability, mean and SD of NDVI, species richness and soil factors. We fitted linear model regressions

to assess the effect of species richness and soil factors on temporal stability, mean or SD of NDVI, respectively. We also considered the effect of interaction between aridity and soil fertility (i.e. soil organic carbon, nitrate nitrogen, ammonium nitrogen and available phosphorus) on species richness, temporal stability, mean or SD of NDVI, respectively.

To avoid spurious interactions on temporal stability due to correlated explanatory variables and unmodelled nonlinear relationships in our observational study, we included nonlinear relationships by fitting generalized additive models that allow for smooth nonlinear relationships following

Duncan and Kefford (2021). Specifically, we fitted two generalized additive models (GAM) for the interactive effects between aridity ( $x_1$ ) and soil fertility ( $x_2$ ) on temporal stability. One model is in the form of  $y = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$  specifying gaussian errors. The other one is in the form of  $y = s(x_1) + s(x_2) + \beta_3 x_1 x_2$ , where  $s(x_1)$  and  $s(x_2)$  specified smooth terms for the relationships between the two predictors and the outcome variable, and  $\beta_3 x_1 x_2$  was a linear interaction term (Duncan and Kefford 2021). Note that we did not fit the third model proposed by Duncan and Kefford (2021) with a smooth nonlinear interaction in the GAM due to the limited number of observations. Given the strong correlation between aridity and species richness ( $r = -0.75$ ; Supporting information), and aridity and ammonia ( $r = 0.70$ ), we used variation partitioning analysis (Borcard et al. 1992) to identify the confounding and separate variance in temporal stability explained by aridity, ammonia and their interactions and explained by aridity, ammonia, the interaction between aridity and ammonia, and species richness. We used the adjusted  $R^2$  to estimate the percentage of variation attributed to independent and joint fractions, which does not depend on the differences between the numbers of parameters used in the models (Peres-Neto et al. 2006). In addition, we used sensitivity analysis to reassess the effect estimates of ammonium, nitrate, species richness and aridity in all the different models with different predictor combinations and quantify if estimated effects are similar across models or if they depend on inclusion of other variables in the model.

Then we constructed a full model with temporal stability, mean or SD of NDVI as response variables, and aridity, species richness and soil factors as predictors. We included altitude, longitude and latitude in the models to account for the spatial autocorrelation. Before the model selection, we used step-wise selection of geographical and soil factors using variance inflation factors (VIF) and removed collinear variables ( $VIF > 5.0$ ; removing  $H_2O$ , altitude and longitude). We considered the interactive effects between aridity and soil fertility (i.e.  $NO_3^-$ -N,  $NH_4^+$ -N, SOC and AP) which might colimit ecosystem functioning according to previous studies (Ren et al. 2017, García-Palacios et al. 2018). Finally, we performed a model selection procedure based on  $AIC_c$  selection on the full model to select the best predictors (Buckland et al. 1997) using the *glmulti* function in the 'glmulti' package in R (www.r-project.org, Calcagno and de Mazancourt 2010). All possible models were ranked by their  $AIC_c$  values and the importance value for each predictor in the average models was calculated. Before model selection, all independent and response variables were standardized using the Z-score to interpret model coefficients on a comparable scale. To improve normality, temporal stability, mean and SD of NDVI, species richness and soil factors were logarithm transformed before Z-score transformation.

Structural equation modelling (SEM) (Shipley 2016) was used to assess how aridity, soil fertility and their interactive effects influence temporal stability and its two components through species richness. We first constructed a priori model

(Supporting information), then improved the model fit by eliminating non-significant predictors and obtained the final model. The goodness-of-fit test of the model was assessed by Fisher's  $C$  and  $p$ -value. All analyses were conducted in R (www.r-project.org), using *interact\_plot* function in 'interactions' package for plotting two-way interactions with continuous variables (Cohen et al. 2014, Long 2021), *psem* function in 'piecewiseSEM' package for SEM (Lefcheck 2016), and *varpart* function in 'vegan' package for variation partitioning analysis (Oksanen et al. 2007).

## Results

Linear model regressions using a single explanatory variable showed that, aridity was negatively related to the mean (Fig. 2b, Supporting information) and SD (Fig. 2c) of NDVI, but was not related to temporal stability (Fig. 2a). Species richness,  $NH_4^+$ -N,  $H_2O$  and SOC were positively related to mean (Fig. 2e, h, Supporting information) and SD (Fig. 2f, i, Supporting information) of NDVI, but were not related to temporal stability (Fig. 2d, g, Supporting information). pH and AP showed marginally positive relationship with the mean, but were not related to SD of NDVI or temporal stability (Supporting information).  $NO_3^-$ -N was negatively related to the mean and SD of NDVI, but was not related to temporal stability (Supporting information).

The relationship of  $NH_4^+$ -N with the SD of NDVI and temporal stability depended on aridity (Fig. 3a, c, Supporting information). SD of NDVI was negatively related to  $NH_4^+$ -N at low aridity, but positively related to  $NH_4^+$ -N at neutral or high aridity (Fig. 3c). There was no interactive effect between aridity and  $NH_4^+$ -N on mean of NDVI (Fig. 3b). Therefore, temporal stability was positively related to  $NH_4^+$ -N at low aridity, but negatively related to  $NH_4^+$ -N at neutral or high aridity level (Fig. 3a). There was no interactive effect between aridity and  $NO_3^-$ -N (Supporting information), or between aridity and AP (Supporting information) on temporal stability, mean or SD of NDVI. The relationship of SOC with the SD of NDVI depended on aridity (Supporting information). SD of NDVI was negatively related to SOC at low aridity, but was marginally positively related to SOC at high aridity. But there was no interactive effect between aridity and SOC on mean of NDVI or temporal stability (Supporting information).

The results of generalized additive models showed that the models including smooth nonlinear relationships of aridity and soil fertility were very similar to the linear models. This indicates that the relationship of temporal stability with aridity and soil fertility are both essentially linear and thus likely to capture the interactive effect between aridity and soil fertility on temporal stability after excluding the nonlinear effects of aridity or soil fertility (Supporting information). The results of variation partitioning analyses showed that aridity,  $NH_4^+$ -N and their interaction explained 5.8, 11.1 and 13.9% variance of temporal stability alone respectively (Fig. 4a), among which the interaction explained the

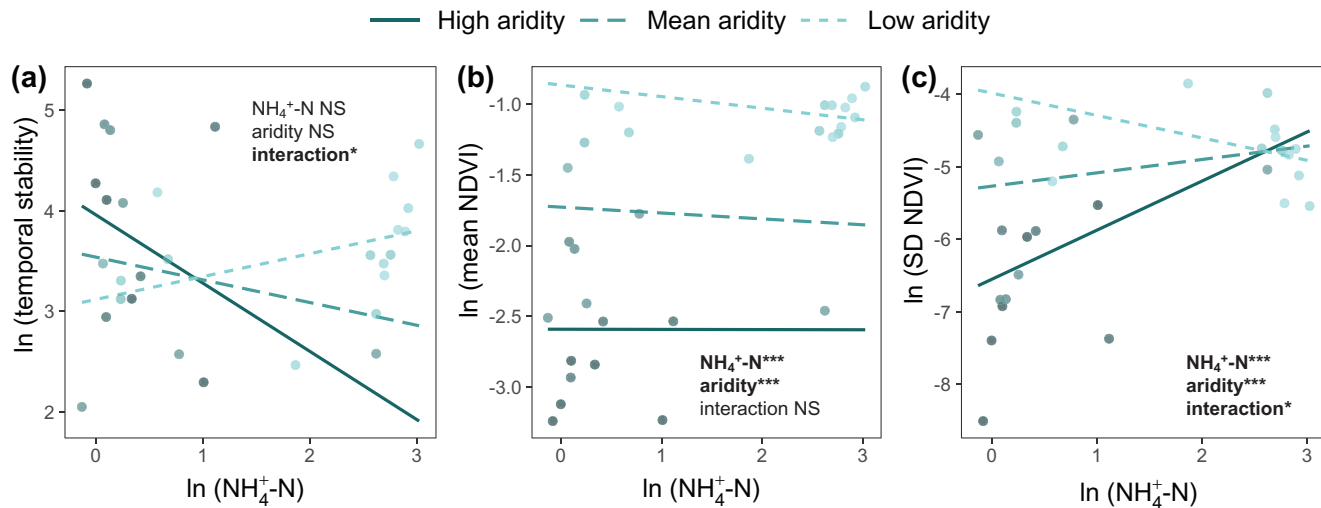


Figure 3. Interaction plots depicting how the relationships between (a) ammonium ( $\text{NH}_4^+\text{-N}$ ) and temporal stability, (b) ammonium ( $\text{NH}_4^+\text{-N}$ ) and mean of NDVI, (c) ammonium ( $\text{NH}_4^+\text{-N}$ ) and SD of NDVI are altered with aridity in all sites ( $n=30$ ). High aridity is defined as being greater than the average value + standard deviation whereas the low aridity is lower than the average value - standard deviation.

largest variance of temporal stability. This was mainly attributed to the explained variance of the interaction of aridity and  $\text{NH}_4^+\text{-N}$  on SD of NDVI (8.9%; Fig. 4b), rather than mean of NDVI ( $< 0.1\%$ ; Fig. 4c). The results of sensitivity analysis showed that the effect estimates of  $\text{NH}_4^+\text{-N}$  changed in different models with different combinations with aridity (model 1c and model 2b, model 1c and model 3a, model 1c and model 3c, model 1c and model 4; Supporting information), suggesting that the effect of  $\text{NH}_4^+\text{-N}$  on temporal stability depended on aridity in the model.

Model selection showed that the interactive effect between aridity and  $\text{NH}_4^+\text{-N}$  was the best predictor explaining temporal stability (Fig. 5a). Aridity was the best predictor explaining both the mean NDVI (Fig. 5b) and the SD of NDVI (Fig. 5c).

SEM showed that high  $\text{NH}_4^+\text{-N}$  led to high temporal stability. Aridity influenced temporal stability by shifting

the relationship between  $\text{NH}_4^+\text{-N}$  and temporal stability (Supporting information) from positive to negative. Higher aridity was related to lower species richness. Higher SOC was related to higher species richness. Species richness was outweighed by the other factors, so it did not explain variance in mean or SD of NDVI thus temporal stability that could not be explained by the others. When considering the two components of temporal stability (i.e. mean and SD of NDVI) in SEM, aridity and soil fertility influenced temporal stability through multiple ways (Fig. 6). First, higher aridity led to lower temporal stability by directly decreasing mean of NDVI, but led to higher temporal stability by directly decreasing SD of NDVI. The approximately proportional changes in mean and SD of NDVI resulted in no effect of aridity on temporal stability (Fig. 2a). Second, higher  $\text{NO}_3^-\text{-N}$  led to higher temporal stability by decreasing SD of NDVI. Third, higher  $\text{NH}_4^+\text{-N}$  led to higher

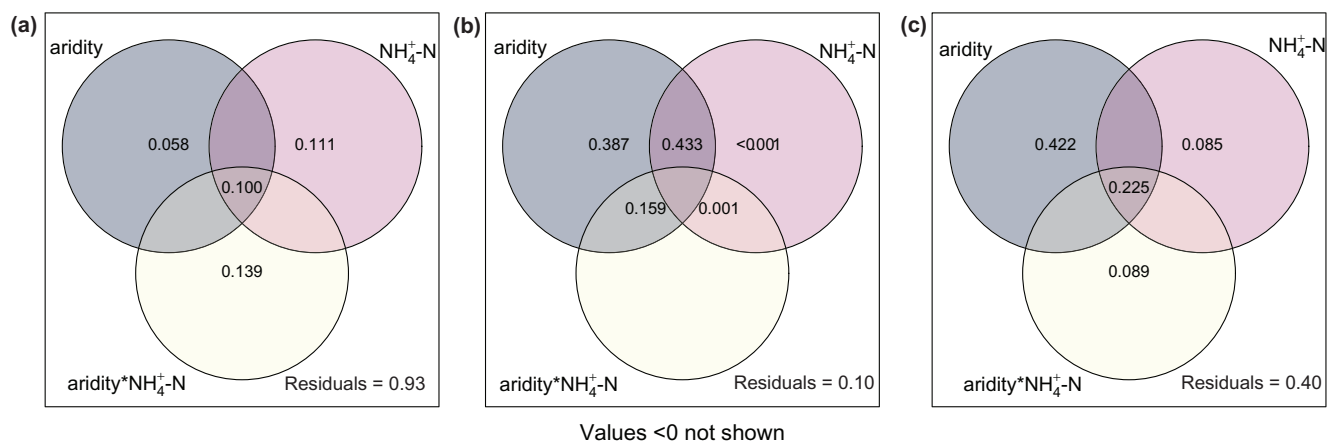


Figure 4. Variation partitioning analyses (adjusted  $R^2$ ) for multiple linear regressions represented by Venn diagrams. Shown are the percentage of variance in (a) temporal stability, (b) mean of NDVI and (c) SD of NDVI explained by aridity, ammonium ( $\text{NH}_4^+\text{-N}$ ) and their interaction ( $\text{aridity}^*\text{NH}_4^+\text{-N}$ ) independently and jointly.

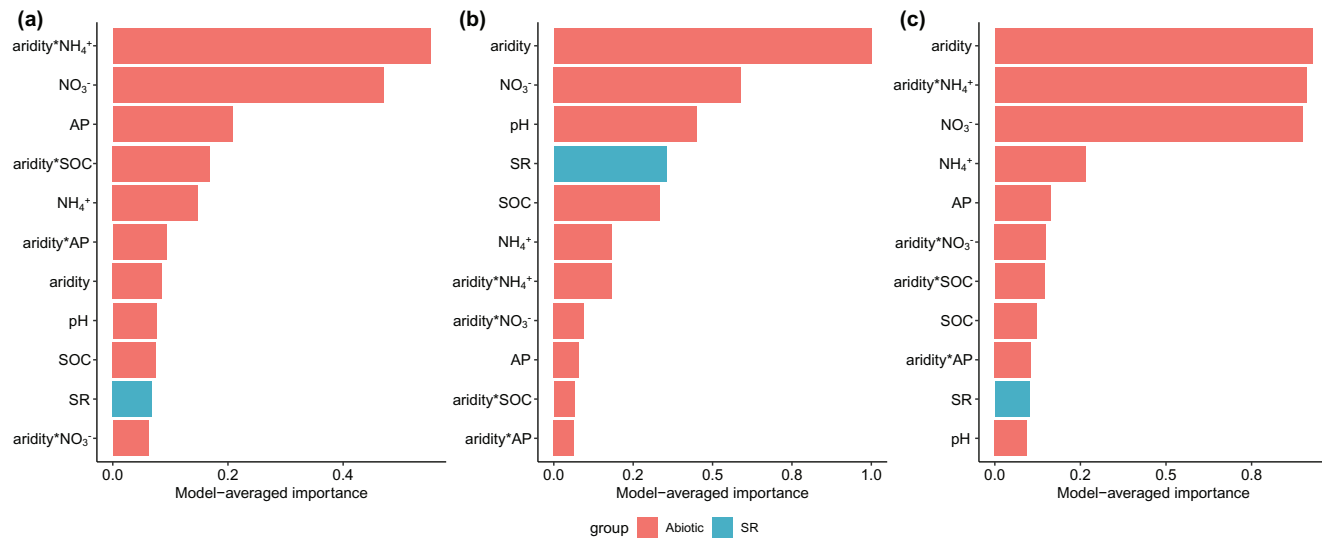


Figure 5. Importance values of species richness (SR), aridity, soil fertility, and interactive effects between aridity and soil fertility across the average models for (a) temporal stability, (b) mean and (c) SD of NDVI in all sites (n = 30). \*\*\*p < 0.001; \*\*p < 0.01; \*p < 0.05; .p < 0.1. NO<sub>3</sub><sup>-</sup>-N = nitrate nitrogen; NH<sub>4</sub><sup>+</sup>-N = ammonia nitrogen; SOC = soil organic carbon; SR = species richness, available phosphorus (AP).

temporal stability by decreasing SD of NDVI. The interaction between aridity and NH<sub>4</sub><sup>+</sup>-N influenced temporal stability by changing SD of NDVI, with aridity strengthening the positive relationship between NH<sub>4</sub><sup>+</sup>-N and SD of NDVI at high aridity level. To further disentangle contributions from aridity, ammonia, the interaction between aridity and ammonia, and species richness on temporal stability, the variation partitioning analysis for the multiple linear regression showed that the interaction between aridity and NH<sub>4</sub><sup>+</sup>-N alone explained most of the variance (14.3%; Supporting information) of temporal stability compared to aridity (3.8%), NH<sub>4</sub><sup>+</sup>-N (11.6%) or species richness (< 0.1%) alone or jointly.

## Discussion

In this study, we investigated the influence of aridity and its interaction with soil fertility on temporal stability of community productivity at a larger spatial scale along a natural gradient. Studies related to how global change drivers impact temporal stability of community productivity were usually based on manipulated experiments at a single site with limited variance in environmental conditions (Xu et al. 2015, Ma et al. 2017, Huang et al. 2020). Therefore, these studies were not able to assess how aridity and soil fertility impact community stability along natural gradients at a larger spatial scale. Here, we combined remote-sensing based estimates

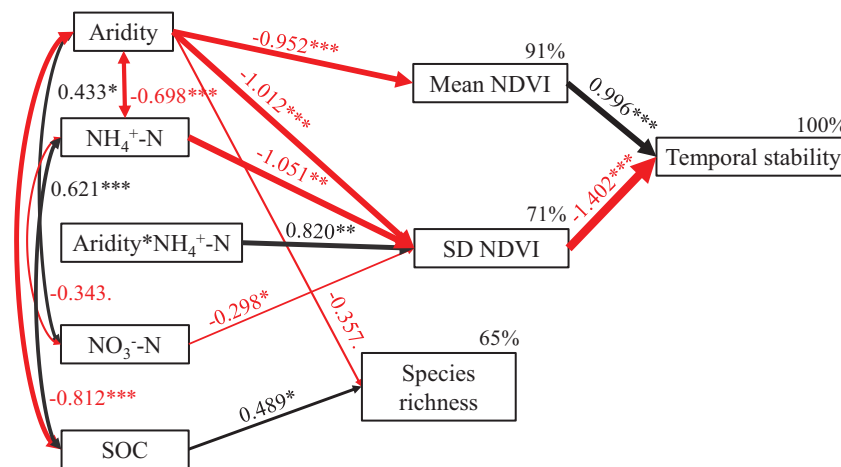


Figure 6. Structural equation models for the causal links among aridity, soil fertility and temporal stability of plant productivity and its two components in all sites (n = 30). Red and solid lines: significant negative; Black and solid lines: significant positive. Numbers on arrows are standardized path coefficients (scaled by their mean and standard deviation), and asterisks indicate statistical significance (\*\*p < 0.01; \*\*p < 0.01; \*p < 0.05; .p < 0.1). Percentages next to endogenous variables indicate the variance explained by the model (R<sup>2</sup>). Overall model: Fisher's C = 22.489, p = 0.758, AIC = 56.489, d.f. = 28. NO<sub>3</sub><sup>-</sup>-N = nitrate nitrogen; NH<sub>4</sub><sup>+</sup>-N = ammonia nitrogen; SOC = soil organic carbon.



of primary productivity with observed measures of biodiversity in natural communities within their real-world ranges of environmental conditions. We demonstrated the interactive effects of aridity and ammonium ( $\text{NH}_4^+\text{-N}$ ) on temporal stability. The relationship between ammonium and temporal stability of NDVI shifted from positive to negative due to increased standard deviation of NDVI with increasing aridity. Species richness was not related to temporal stability because it influenced the mean and standard deviation of NDVI proportionally, and soil fertility outweighed the effect of species richness in the SEM.

Productivity can both impact and respond to soil fertility. Previous studies have proposed a causality of productivity on soil fertility (Li et al. 2020), and of soil fertility on productivity (Chen et al. 2021). Here, we focused on how productivity changes as a function of soil fertility and aridity. Consistent with the study of Hu et al. (2021) in grasslands in northern China, aridity was negatively related to soil nutrient availability including soil organic carbon, ammonium ( $\text{NH}_4^+\text{-N}$ ) and available phosphorus. This may be because of reduced litter inputs and soil microbial activity under arid conditions (Hu et al. 2021). Inconsistent with the result of Hu et al. (2021), but consistent with results from many arid and semi-arid ecosystems (Hook and Burke 1995, Erskine et al. 1996, Cookson et al. 2006), our results show that aridity was positively related to nitrate ( $\text{NO}_3^-\text{-N}$ ). The accumulated nitrate in arid conditions can happen due to several reasons. First, nitrate in the soil can increase because of the decrease in plant absorption with less root in aridity (Deng et al. 2021). Second, soil microorganisms like ammonia-oxidizing archaea may dominate and carry out nitrification due to their high resistance to water and nutrient stress conditions (Delgado-Baquerizo et al. 2013a). Third, nitrate accumulation can arise from a decrease in soil microorganisms related to denitrification and nitrogen emission ( $\text{N}_2$  or  $\text{N}_2\text{O}$ ) because of limited soil water availability (Dannenmann et al. 2008). Our results showed that nitrate is a strong predictor of temporal stability (Fig. 5, Supporting information). Although plants prefer ammonium due to lower uptake energetic cost compared to nitrate (Salsac et al. 1987), ammonium can cause soil acidification and associated species loss (van den Berg et al. 2008, Midolo et al. 2019). Nitrate addition may moderate soil acidification and species loss induced by ammonium, because plants release hydroxide through nitrate uptake (van den Berg et al. 2008). Plants prefer nitrate to balance the electric charge from cations such as potassium ( $\text{K}^+$ ) and calcium ( $\text{Ca}^{2+}$ ) (Boudsocq et al. 2012). Therefore, nitrate is likely to stabilize community productivity by decreasing standard deviation of productivity (Supporting information, Fig. 6).

Studies based on nitrogen addition experiments reported a negative impact of nitrogen on temporal stability of productivity (Xu et al. 2015, Zhang et al. 2016, Hautier et al. 2020, Huang et al. 2020). We found a negative relationship of ammonium with temporal stability of productivity at high aridity, but the opposite pattern at low aridity (Fig. 3a). This was attributed to the positive effect of ammonium on the standard deviation of NDVI at high aridity, but

the opposite pattern at low aridity (Fig. 3c). Our findings at low aridity contrast with previous evidence showing the negative effect of nitrogen on temporal stability (Xu et al. 2015, Zhang et al. 2016, Hautier et al. 2020, Huang et al. 2020). This suggests that manipulated experiments may not directly transpose to natural communities. One potential explanation is that the simulated gradients in experimental studies are much larger compared to the gradient found in our natural ecosystems. For example, nitrogen addition experiments in an alpine meadow (Huang et al. 2020) and a temperate grassland (Zhang et al. 2016) span a range of nitrogen addition treatments between 0 and  $15 \text{ g m}^{-2} \text{ year}^{-1}$ , and 0 and  $50 \text{ g m}^{-2} \text{ year}^{-1}$  respectively. It leads to maximally higher levels of soil ammonium ( $45.35 \pm 6.2 \text{ mg kg}^{-1}$  in the alpine meadow, Zhang et al. 2020b;  $87.52 \pm 17.0 \text{ mg kg}^{-1}$  in the temperate grassland, Li et al. 2020) and nitrate ( $17.63 \pm 2.7 \text{ mg kg}^{-1}$  in the alpine meadow, Zhang et al. 2020b;  $97.90 \pm 33.6 \text{ mg kg}^{-1}$  in the temperate grassland, Li et al. 2020) in these experiments compared to those found in our natural gradient at low aridity (ammonium:  $13.01 \pm 1.27 \text{ mg kg}^{-1}$ ; nitrate:  $13.43 \pm 1.93 \text{ mg kg}^{-1}$ ). Higher nitrogen especially higher ammonium is likely to lead to more species loss and low temporal stability regardless of aridity. The relationship of ammonium with temporal stability of productivity depending on aridity in our study may be because aridity changes plant–plant interactions as predicted by the stress-gradient hypothesis (Bertness and Callaway 1994). The stress-gradient hypothesis proposes that positive biotic interactions (i.e. facilitation) are unusually common forces in harsh environmental conditions (e.g. arid conditions) because primary space-holders frequently buffer neighbors from potentially limiting stresses (Bertness and Callaway 1994, Armas et al. 2011). That is, at low aridity, species competition for nutrients is strong. For example, increased precipitation could increase competition between woody and herbaceous plants (Xu et al. 2015). Competition and species asynchrony may increase as ammonium increases, thereby leading to a decrease in temporal standard deviation of productivity. Consistent with a previous study conducted in Inner Mongolia grassland, the proportion of shrubs in the communities increases with aridity in our study (Supporting information). Shrubs can increase nutrient availability and have facilitative effects on their neighbor herbaceous vegetation (Segoli et al. 2012). We inferred that the facilitative effects of shrubs on herbaceous vegetation may increase at high aridity, and competition and species asynchrony may decrease as ammonium increases, thereby leading to a stronger increase in temporal standard deviation of productivity.

Similar to previous studies (García-Palacios et al. 2018, Li et al. 2020), we found a marginally significant interaction between aridity and species richness on mean of NDVI (Supporting information). This indicates that at high aridity (and low species richness), adding an additional species to the community is related to a higher increase in mean of NDVI compared to adding an additional species at low aridity (and high species richness). It may also support the stress-gradient hypothesis (Bertness and Callaway 1994) given that the

relative species richness of shrubs increased with aridity in our study (Supporting information), thus the facilitative effects of shrubs on herbaceous vegetation increased. Although facilitative interactions were strong in arid conditions, species richness and productivity were lower under arid compared to less arid conditions because few species can tolerate the abiotic stress with insufficient water and nutrients (Fraser et al. 2015).

In our study, species richness was not related to temporal stability along the aridity gradient. This resulted because the increase in mean NDVI with species richness was proportional to the increase in standard deviation in the linear models (Fig. 2e–f). However, our SEM showed that species richness was not related to temporal stability, mean or standard deviation of NDVI (Fig. 6). This suggests that aridity and soil fertility outweighed species richness and explained additional variance of temporal stability and its two components compared to species richness. However, soil fertility and species richness were strongly correlated with aridity in our study (Supporting information). The effects of species richness or ammonia on temporal stability depended on aridity (Supporting information). However, the results of variation partitioning analysis further identified the confounding and separate variance in temporal stability explained by aridity, ammonia, the interaction between aridity and ammonia, and species richness. The results confirmed that aridity and ammonia outweighed the effect of species richness on temporal stability, with the interaction between aridity and ammonia explaining the largest variance of temporal stability (Supporting information). This is inconsistent with many studies reporting a positive relationship between species richness and temporal stability in response to manipulated global changes (Hautier et al. 2020, Valencia et al. 2020), but consistent with the results from Dee et al. (2022) showing that most observational studies found no relationship between biodiversity and ecosystem functioning. It may be because species richness may not fully represent plant diversity over large areas, and the fact that landscape properties, including dispersal, are more likely to be related to ecosystem functioning (Manning et al. 2019). Besides, confounding variables like soil fertility can influence the causal relationship between biodiversity and ecosystem functioning (Dee et al. 2022). Our result that species richness was not related to temporal stability is also inconsistent with the results of many studies at large spatial scales (Oehri et al. 2017, García-Palacios et al. 2018, Gilbert et al. 2020). For example, a recent worldwide dryland study showed that species richness may have a greater stabilizing role under arid conditions (García-Palacios et al. 2018). However, in these studies based on large scales along aridity gradients, like the study of García-Palacios et al. (2018), soil fertility (i.e. soil organic carbon) was not considered. It is unknown whether the soil fertility will outweigh biodiversity in affecting temporal stability. Finally, abrupt decays of soil fertility and plant richness occurred at aridity of around 0.69 and 0.83, respectively (Berdugo et al. 2020). There may be more of our sampling sites experiencing soil nutrients reduction (10 sites with aridity more than 0.69) than that experiencing species loss (five sites with aridity more than 0.83),

making soil nutrients more influential predictors for ecosystem functioning.

However, the productivity of the shrubs was likely to be overestimated in our study. Because the total above-ground biomass at each site was badly correlated with NDVI ( $R^2=0.02$ ; Supporting information), but the variance explained by the linear model increased to 0.47 after excluding the shrub biomass at each site (Supporting information).

Our results highlight the role of soil fertility instead of species richness in influencing temporal stability and its two components at a larger spatial scale in aridity. Specially, ammonium was more positively related to standard deviation of NDVI and more negatively related to temporal stability of productivity at arid conditions. Our study investigated the interaction effects of aridity and soil fertility on temporal stability in naturally assembled communities and their corresponding environmental gradients, and suggests that to gain a deeper understanding of the relationship between biodiversity and ecosystem stability, it is necessary to investigate in the ‘real-world’ ecosystem considering both biotic and abiotic aspects including biodiversity, climate factors and soil fertility.

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#### Author contributions

**Mengjiao Huang:** Conceptualization (equal); Formal analysis (equal); Writing – original draft (lead); Writing – review and editing (equal). **Job de Vries:** Investigation (equal); Writing – review and editing (equal). **Shurong Zhou:** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Investigation (equal); Writing – review and editing (equal). **Yann Hautier:** Conceptualization (equal); Formal analysis (equal); Writing – review and editing (equal).

#### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m905qfv46> (Huang et al. 2023).

#### Supporting information

The Supporting information associated with this article is available with the online version.

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