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Research Article

Are regional precipitation–productivity relationships robust to decadal-scale dry period?

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Abstract

Precipitation (PPT) is the primary climatic determinant of plant growth and aboveground net primary productivity (ANPP) for many of the world's major terrestrial ecosystems. Thus, relationships between PPT and productivity can provide insight into how changes in climate may alter ecosystem functions globally. Spatial PPT–ANPP relationships for grasslands are found remarkably similar around the world, but whether and how they change during periods of extended climatic anomalies remain unknown. Here, we quantified how regional-scale PPT-ANPP relationships vary between an extended wet and a dry period by taking advantage of a 35-year record of PPT and NDVI (as a surrogate for ANPP) at 1700 sites in the temperate grasslands of northern China. We found a sharp decrease in the strength of the spatial PPT–ANPP relationship during an 11-year period of below average PPT. We attributed the collapse of this relationship to asynchrony in the responses of different grassland types to this decadal period of increased aridity. Our results challenge the robustness of regional PPT–productivity if aridity in grasslands is increased globally by climate change.

Keywords grassland, net primary productivity, precipitation–productivity relation, drought, climate change, NDVI

降水–生产力的空间关系是否稳定不变？

摘要：降水是全球陆地生态系统中植被生长和净初级生产力的主要驱动因素。因此，探究降水和生产力关系有助于深入了解气候变化如何改变生态系统功能。降水–生产力的空间关系在全球不同草地上非常相似，但在连续多年气候异常的情况下，这种关系是否会发生变化以及如何变化尚不清楚。本研究利用利用中国北方温带草地长达10年低于多年平均降水的时期，基于遥感植被指数数据，量化了区域尺度上降水–植被生产力关系在持续多年的干湿期之间将如何变化。结果表明，在连续10年的干期，降水–生产力空间相关性急剧下降，而该空间关系的下降主要是由于不同草原类型对干旱的响应在空间上存在高度的异质性，即不同生态系统对干旱的响应程度存在差异。因此，如果未来气候变化进一步加剧全球草地的干旱，那么基于历史时期(平水期)得到的降水–生产力空间关系推测区域尺度植被生产力可能导致误差。

关键词：草地，净初级生产力，降水–生产力关系，干旱，气候变化，植被指数

INTRODUCTION

Precipitation (PPT) is the primary climatic determinant of plant growth and aboveground net primary productivity (ANPP) for the world's major grasslands, as well as many other terrestrial ecosystems (Knapp *et al.* 2017; Running *et al.* 2004; Sala *et al.* 2012). Variations in mean annual PPT spatially can account for >50% of the variation in mean ANPP among grassland sites (e.g. Bai *et al.* 2008; Guo *et al.* 2012; Hu *et al.* 2010; Sala *et al.* 2012). PPT is also the major climatic factor controlling the interannual variations in ANPP in grasslands (Hu *et al.* 2018; Knapp *et al.* 2017). Thus, relationships between precipitation and productivity (PPT–ANPP) can provide insight into how changes in climate may alter ecosystem functions (Huxman *et al.* 2004).

PPT–ANPP relationships can be derived from responses of ANPP to interannual variation in PPT at a particular location (temporal model) or by combining ANPP data from multiple sites across regions that encompass a substantial PPT gradient (spatial model). In theory, temporal models are superior to spatial models in providing near-term (e.g. several years) insight for ecosystem responses to climatic fluctuations (Adler *et al.* 2020; Knapp *et al.* 2017). However, most findings suggest that the temporal PPT–ANPP relationships are inconsistent among ecosystems and usually too weak to make predictions (Huxman *et al.* 2004; Sala *et al.* 2012). In addition, the temporal model fails to take into account shifts in species composition, which a critical factor determining ANPP dynamics over long term. Therefore, as the well-known space-for-time substitution method, spatial models are alternative approaches employed for predicting ANPP response to PPT change, especially for predicting the responses over long term (e.g. decades or more) with shifts in species composition and biogeochemistry (Adler *et al.* 2020; Hu *et al.* 2010; Huxman *et al.* 2004; Knapp *et al.* 2017).

As reported, the spatial PPT–ANPP relationships in grasslands are remarkably robust in North America (R^2 = 0.94, Sala *et al.* 1988), China (R^2 = 0.76, Bai *et al.* 2008) and South Africa (R^2 = 0.83, Forrestal *et al.* 2017). The reported robust spatial relationship implicitly convey an information that the spatial model is universal and stable. However, the spatial models are typically derived under climates near historical averages. It remains unclear if these relationships will change through time with projected increases in climate variability and extremity (IPCC 2013). Grassland ecosystems differ dramatically in drought sensitivity as well as responses to alterations in PPT attributes (Heisler-White *et al.* 2009; Knapp *et al.* 2015; Maurer *et al.* 2020), which thus should alter the spatial PPT–ANPP relationships. However, how or if the spatial PPT–ANPP relationships will be altered by climate change is unknown.

Here, we assessed how the regional-scale PPT–ANPP relationship in the temperate grasslands of northern China was impacted by an extended dry period. We took advantage of a 35-year record (1981–2015) of PPT and NDVI (a surrogate for ANPP) for this ca.1.2 million km^2 region, focusing on an extended dry period (11 of 13 years with below average PPT) that followed a 17-year period of slightly above average PPT.

Hypothesis

Assuming the spatial model is the most robust (i.e. highest in the R^2) under long-term mean climate condition, we used this unique dataset to assess two alternative hypotheses: (i) ecosystems in this region would all respond similarly to this dry decade so that the strength (R^2) of PPT–ANPP relationship would remain relatively unchanged despite overall reductions in ANPP (Fig. 1, Cases 1 and 2). In Case 1, all ecosystems exhibit high resistance to rainfall reduction (no change in ANPP) and the degree of rainfall reduction is similar among sites. In Case 2, all ecosystems exhibit a similar sensitivity to rainfall reduction. Alternatively, (ii) grassland ecosystems across this region could respond independently or asynchronously so that the regional-scale PPT–ANPP relationship would be weakened (Fig. 1, Cases 3 and 4). In Case 3, all ecosystems exhibit high resistance to rainfall reduction and the degree of rainfall reduction is spatially heterogeneous. In Case 4, all ecosystems exhibit diverge sensitivities (i.e. spatial asynchrony [SA]) to rainfall reduction. We also assessed alterations in precipitation-use efficiency (PUE = ANPP/PPT) as an extra indicator to identify potential mechanisms of the change. For example, if responses to a dry period are asynchronous across sites, we would predict that both the regional mean and cross-site differences in PUE would increase (Fig. 1, Cases 3 and 4).

MATERIALS AND METHODS

Study region

The study area is the temperate grassland region in Inner Mongolia, China. Representative of the vast Eurasian grasslands, this region is dominated

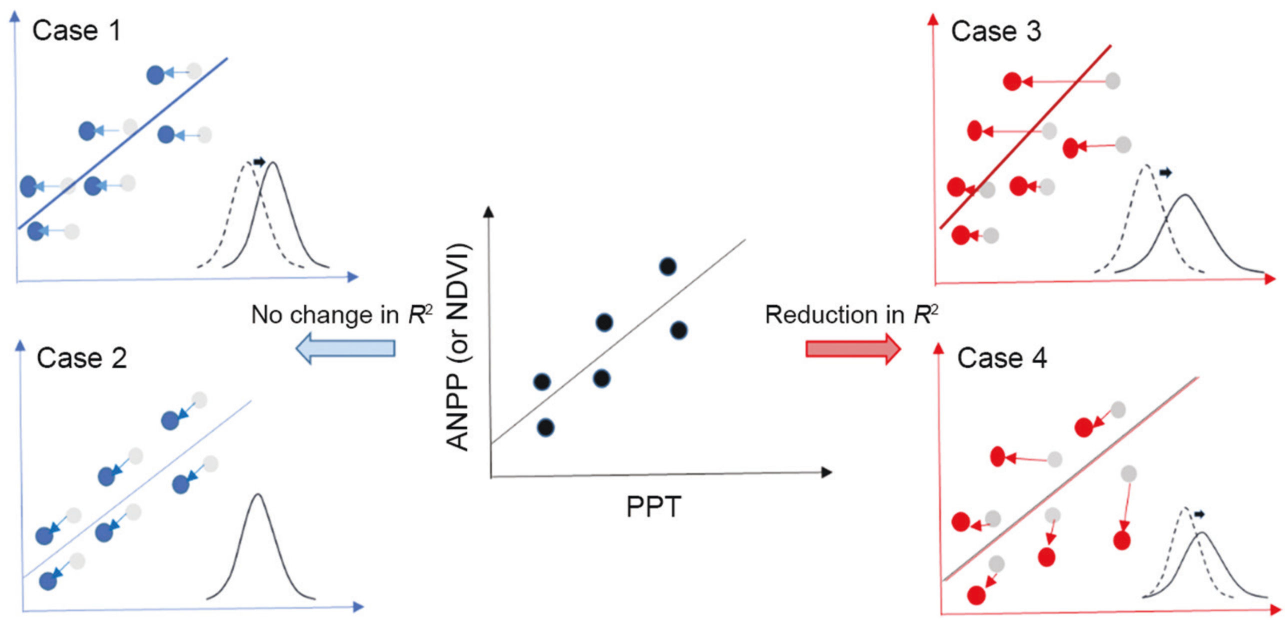

Figure 1: Possible mechanisms that could alter the robustness of the spatial PPT–ANPP relationship and cross-site frequency distribution of PUE (depicted as curves in the lower right of the four cases) when experiencing regional drought conditions. In Case 1 (upper left), all sites illustrate high resistance to drought (i.e. little reduction in productivity), and experience similar amount of PPT reduction. The R^2 of PPT–ANPP relationship will not change and the cross-site average PUE will increase. In Case 2 (lower left), vegetation productivity decreases similarly as a result of PPT reduction at all sites, resulting in no change in the spatial R^2, as well as the cross-site average PUE. In Case 3 (upper right), all sites illustrate high resistance to drought but experience diverse amounts of PPT reduction, resulting in decrease in the spatial R^2. In addition, since the sites manifest different magnitudes of increase in PUE, not only the overall average, but the cross-site variance of PUE will increase. In Case 4 (lower right), productivity at the sites decrease asynchronously in response to drought, resulting in a decrease in the spatial R^2 and an increase in cross-site variance in PUE. Note that the overall average in PUE may increase or decrease in the 4th case. The negative effects of SA of PPT and productivity (NDVI in this study) on the spatial R^2 can be seen in Supplementary Fig. S1.

by three intergrading grassland types, i.e. the xeric desert steppe, the semi-arid typical steppe and the mesic meadow steppe (Fig. 2). Mean annual PPT in the region ranges from *ca*. 100 to 500 mm and mean annual temperature ranges from −3 to 9 °C (DAHV and GSAHV 1996). Most plant species are C_3 owing to the relatively cool climate. Dominant species of the meadow steppe are *Stipa baicalensis*, *Leymus chinensis*, *Filifolium sibiricum* and *Stipa grandis*. The typical steppe is dominated by *S. grandis*, *L. chinensis*, *S. krylovii*, *Cleistogenes squarrosa* and *Agropyron cristatum*. And the desert steppe is dominated by *Stipa klemenzii*, *Agropyron desertorum*, *Stipa gobica*, *Cleistogenes songorica* and *Artemisia frigida*.

Datasets

NDVI data were derived from Advanced Very High Resolution Radiometer, Global Inventory Modeling and Mapping Studies (AVHRR GIMMS, 8 × 8 km^2 in resolution, 1982–2015). The dataset is a 10-day compiled product, which had been subjected to correction in order to reduce the effects of residual clouds, atmospheric perturbations, variable illumination and viewing geometry. August is generally when peak aboveground biomass occurs in the study region, thus we calculated monthly NDVI by averaging the three 10-day NDVI compilations in this month as a proxy of ANPP.

Relative long-term (1980–2015) climate data including monthly PPT, air temperature, solar radiation and wind speed were obtained from the database of the China Meteorological Administration for nearly 750 meteorological stations distributed throughout this grassland region. We used the Anusplin software package (Hutchinson 2014) to interpolate and derive spatially continuous climate data at an annual basis with a thin plate smoothing spline interpolation method at 8 × 8 km^2 resolution, which was consistent with the spatial resolution of the NDVI dataset. In addition, we calculated potential evapotranspiration (PET, the algorithm adopted by the United Nations Environmental Programme (UNEP)) with this gridded climate dataset and hence annual aridity index, the ratio of PPT to PET. Finally,

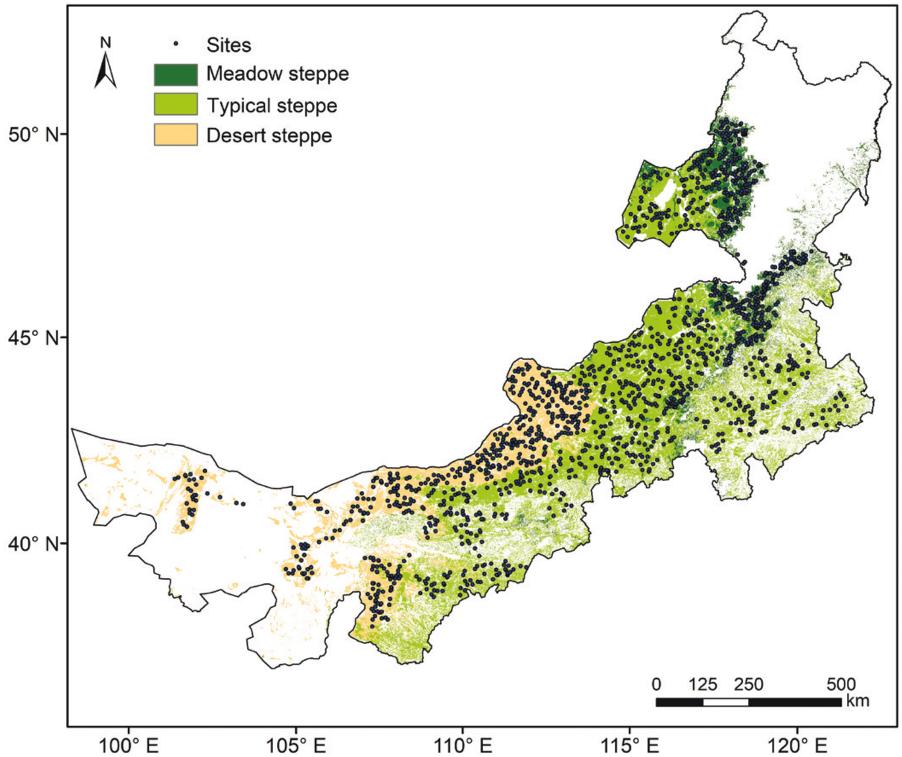

Figure 2: Study region and spatial distribution of sampling sites for analysis.

we used daily PPT data from the 47 meteorological stations located in the study region to calculate other PPT characteristics, e.g. total PPT in growing season and in June–July, mean size of rainfall events for the entire year or just the growing season, and number of rainfall events exceeding 5, 10 and 20 mm.

Data processing

We sampled 500 sites for the desert steppe, 700 for the typical steppe and 500 sites for the meadow steppe in the region (Fig. 2). This sampling design reflected the proportional area covered by the grassland types. The 1700 sites were randomly sampled to make sure they were evenly distributed in the study region and represented most climatic conditions (Guo *et al.* 2012). All subsequent analyses were based on the data from these sites. With PPT and NDVI at all sites in the region, linear regression analysis was conducted to derive the spatial R^2 and slope for the spatial PPT–NDVI relationship. Note that exponential regression analysis may be used for deriving the spatial R^2 for a specific ecosystem type (see results), in which case the spatial R^2 was larger than the linear model. A 5-year moving window was employed to assess the temporal dynamics of the spatial R^2 and slope, and the mean of PPT and NDVI for the 5 years in each window were used to establish the linear function. One reason we used 5-year moving window approach was to dampen extreme annual variations and facilitate identifying decadal trends. Another reason was to identify a 'dry' (and 'wet') year to calculate SA of changes in PPT and NDVI across sites (see details below).

To clarify which mechanisms may alter the spatial R^2 in dry years, we derived a metric to quantify the SA of *changes* in PPT and NDVI across sites in the study region. SA_{PPT} was calculated to quantifying the cross-site variability in PPT change (Cases 1 and 3 in Fig. 1):

$$SA_{PPT} = \mathrm{std}\left(\frac{\Delta\ PPT}{PPT_{base}}\right) \quad (1)$$

where std means standard deviation of relative changes in precipitation among the 1700 sites. PPT_{base} is the mean annual precipitation in a period. ΔPPT indicates the differences of precipitation between PPT_{base} and the minimum (or maximum) annual PPT within the 5 years, indicating change in PPT in the driest (or wettest) year. High SA_{PPT} indicates high spatial asynchrony in the PPT change across sites (Case 3) and low SA_{PPT} indicates low spatial asynchrony (Case 1).

We can yield only one value of SA_{PPT} if compare the PPT in the normal period and a dry period, which cannot be used directly to identify the mechanism. In addition, it is also possible that the spatial R^2 declines in wet years with similar potential mechanisms illustrated in Fig. 1. Therefore, using the data of a moving 5-year window of the study period, we calculated SA_{PPT} for both the dry (the driest year) and wet (the wettest year) conditions, respectively. Further, the asymmetry of PPT response, i.e. the ratio of SA_{PPT} in dry and wet years was calculated to identify potential mechanism:

$$A_{\mathrm{ppt}} = \frac{\mathrm{SA}_{\mathrm{PPT\_dry}}}{\mathrm{SA}_{\mathrm{PPT\_wet}}} \tag{2}$$

One value of A_{ppt} was derived within each 5-year window for the entire study region or for each grassland type. If $A_{ppt} > 1$, the SA due to PPT reductions in dry years is larger than that PPT increase in wet years, and the spatial R^2 of ANPP–PPT relation would be lower in dry years than that in wet years.

The second metric SA in vegetation response to rainfall change (Cases 2 and 4 in Fig. 1) was calculated as

$$\mathrm{SA}_{\mathrm{veg}} = \mathrm{std}\left(\frac{\Delta\ \mathrm{NDVI}/\mathrm{NDVI}_{\mathrm{base}}}{\Delta\ \mathrm{PPT}/\mathrm{PPT}_{\mathrm{base}}}\right) \tag{3}$$

where $NDVI_{base}$ is the base NDVI, and here is the mean annual peak NDVI within the 5-year window. ΔNDVI indicates the difference between $NDVI_{base}$ and the NDVI in the year with maximum or minimum PPT. The term in the parenthesis in Equation (3) indicates the degree of response in NDVI to changes in PPT. SA_{veg} describes the SA in NDVI in response to PPT. High SA_{veg} indicates high spatial asynchrony in vegetation responses (Case 4) and low SA_{veg} indicates low spatial asynchrony in the response (Case 2).

Asymmetry of vegetation response, i.e. the ratio of SA_{veg} in dry and wet years was calculated as

$$A_{\mathrm{veg}} = \frac{\mathrm{SA}_{\mathrm{veg\_dry}}}{\mathrm{SA}_{\mathrm{veg\_wet}}} \tag{4}$$

One value of A_{veg} was derived within each 5-year moving window for the entire study region or for each grassland type. If $A_{veg} > 1$, the SA in NDVI in response to dry periods is larger than that in response to wet periods, which implies the spatial R^2 of ANPP–PPT relation would be lower in dry years than wet years.

RESULTS

We first show the temporal dynamics of PPT through 1982–2015, with a focus on the degree of PPT reduction during the 1999–2011 dry period. We then investigate how the strength (i.e. R^2) of the spatial PPT–NDVI relation changed during the dry period. At last, we explored the mechanism underlying the change of the spatial R^2 from the angle of PUE and SA in PPT and NDVI.

The climate in the study region was characterized with three distinct periods. The region experienced slightly wetter than average conditions from 1982 to 1998 (6.8% or 20 mm yr^{-1} above average), followed by a decade of dry conditions from 1999 to 2011 (11 of 13 years with below average PPT, 16.5% or 49 mm yr^{-1}), with recovery of PPT beginning in 2012 (Fig. 3). Similarly, other PPT characteristics, e.g. growing season PPT, and the number of rainfall events >5, 10 and 20 mm all declined in the dry period (Supplementary Fig. S1).

Corresponding to the temporal dynamics of PPT, the R^2 of the spatial PPT–productivity relationship showed distinct temporal phases (Fig. 4). The 5-year moving average of the spatial R^2 was significantly correlated with that of annual PPT ($P < 0.01$, $R^2 = 0.64$). Specifically, the spatial R^2 was high and relatively stable during the wet period. But it decreased abruptly during the dry period and recovered in the following wet period (Fig. 4). Using the aridity index as well as PPT characteristics, we also identified a reduction of the spatial R^2 during the decadal dry period (Fig. 4 and Supplementary Fig. S2). This suggests that air temperature and the other PPT characteristics were not covarying in ways that would cause the spatial relationship between PPT and NDVI to change.

Considering the wet (1982–1998) and the dry period (1999–2011) separately, we regressed mean annual PPT and NDVI for each period. For the entire region (Fig. 5a), the spatial relationship was weaker during the dry period ($R^2 = 0.71$) in comparison to the wet period ($R^2 = 0.84$). In addition, the slope was also significantly steeper for the decadal dry period ($P < 0.01$). A similar pattern was evident for the spatial PPT–NDVI relationships during the dry period within each grassland type, with a reduction of R^2 more than 0.3 units, suggesting that the explanatory power of PPT on the spatial variations in NDVI largely declined (Fig. 5b–d). However, no significant difference in slopes was found between the two periods for each grassland type ($P > 0.05$).

As Fig. 6 illustrates, the PUE (ratio of NDVI to PPT) in the dry period (1999–2011) was 0.0018 NDVI mm^{-1}, which was higher than that in the wet period (0.0016 NDVI mm^{-1}, $P < 0.05$). In addition, the cross-site variance of PUE during the dry period (0.0007) was significantly larger than that in the wet period (0.0003, P < 0.05). All grassland types also showed the same phenomenon, i.e. increase in both the magnitude and cross-site variance during the dry period (Fig. 6c–h). These results indicate that an extended period of low PPT increased ecosystem PUE, but in a pattern that was spatially asynchronous. Changes in PUE during the dry period were consistent with mechanisms 3 and 4 in Fig. 1. This implies that the reduction in spatial R^2 and increase in regional PUE during the dry period may be caused by either spatially asynchronous changes in PPT or NDVI.

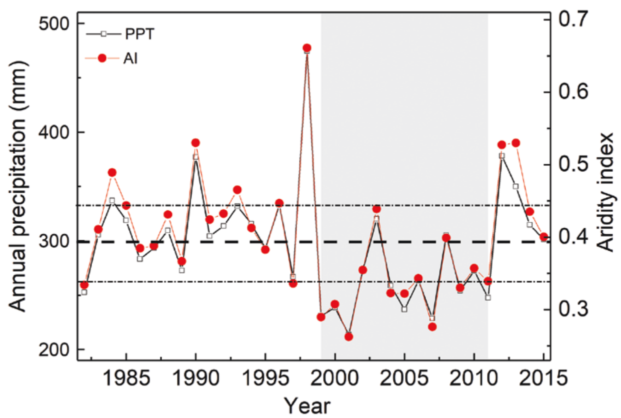

Figure 3: Annual PPT and aridity index (the ratio of PPT to PET) for the grassland region of Inner Mongolia in northern China for the period 1982–2015. The dashed lines indicate mean (±std) annual PPT in 1982–2015 and the gray shading denotes the dry period (1999–2011).

To further clarify which mechanism (3 and 4 in Fig. 1) caused the reduction of R^2 during the dry period, we assessed the asymmetry metrics developed in this study. Our results indicated that the average asymmetry in changes of PPT, A_{ppt} (mean of the 30 values based on 5-year window calculations in 1982–2015) was <1 across most of the region (Fig. 7a). In addition, the average A_{ppt} for each grassland type was <1 (P < 0.05). This suggests that the SA in changes of PPT was due to PPT increases being greater than decreases, implying the spatial R^2 should decrease in wet years but not in dry years. In other words, SA in PPT change is likely not the reason for the reduction in spatial R^2 during the drought period. In contrast, A_{veg}, the metric quantifying the SA of NDVI change, was >1 across the region (P < 0.05), except for some sites located in the desert steppe, suggesting that the SA in vegetation responses to rainfall changes was greater in drought than in wet years in most of the region (Fig. 7b). This means that the spatial asymmetry in vegetation response was likely the key mechanism causing the reduction in spatial R^2 during the decadal dry period.

DISCUSSION

Shift of the spatial PPT–NDVI relationship in the dry period

We assessed the spatial PPT–NDVI relationship across the temperate grasslands of northern China during extended periods of slightly above- and well-below average PPT. During a decadal dry period, the slope

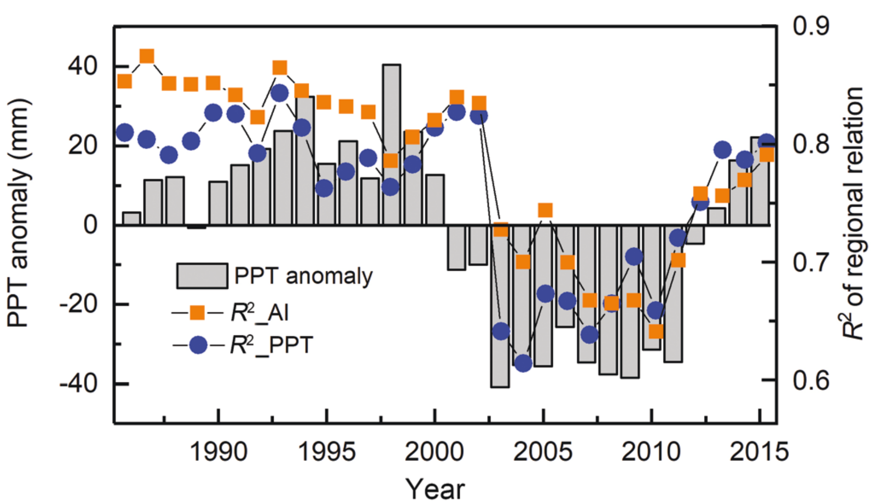

Figure 4: Temporal dynamics of PPT anomalies, i.e. the difference between annual PPT and average annual PPT during the study period, and the R^2 of the regional relationship between NDVI and annual PPT (or aridity index, the ratio of annual PPT to PET). The data are 5-year moving averages, thus values in a year (e.g. 1985) indicate the averages of previous 5 years (1981–1985).

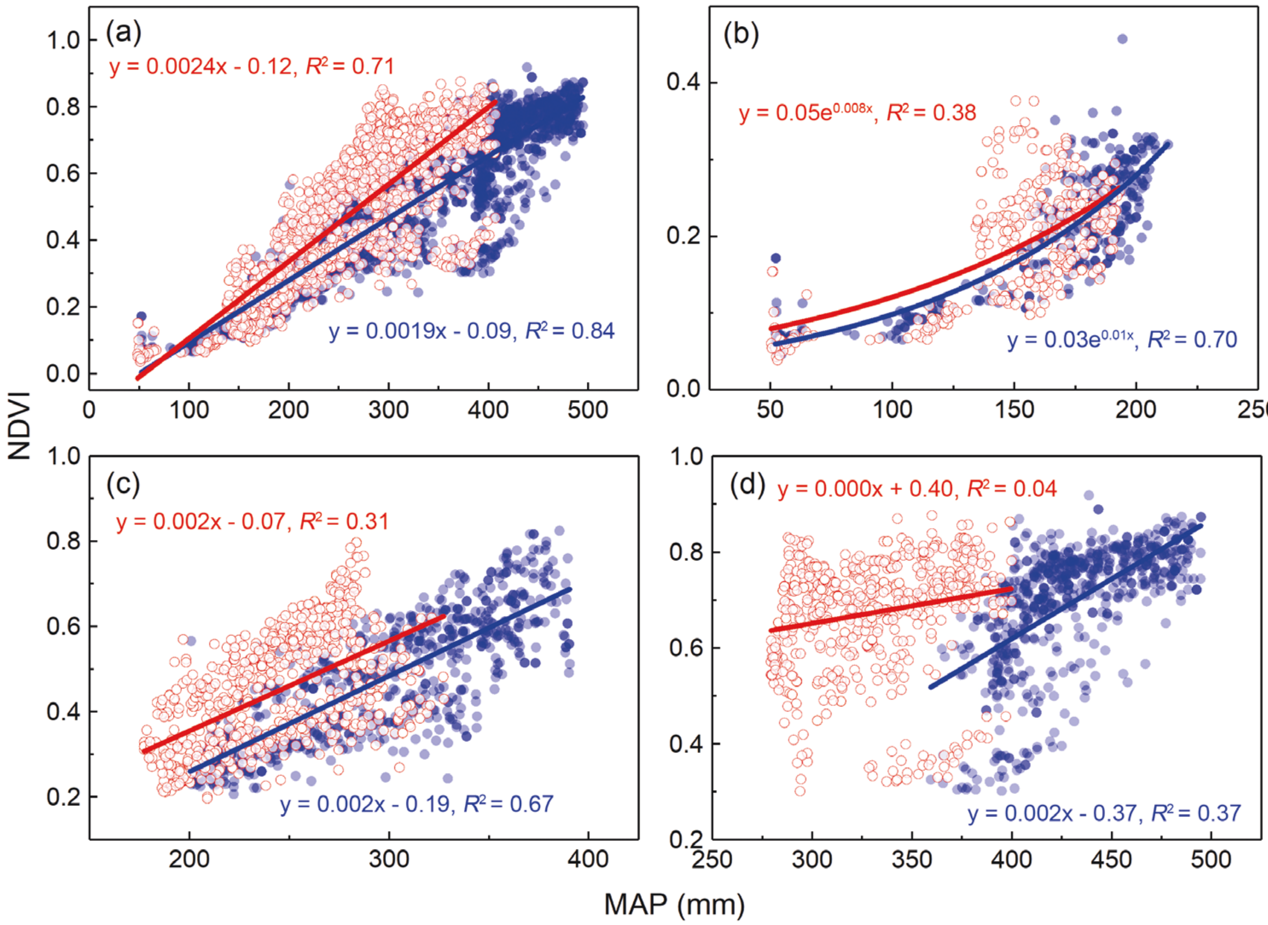

Figure 5: Comparisons of the spatial PPT–NDVI relationship during the wet period (1982– 1998, in blue) and decadal dry period (1999–2011, in red) for the entire region (**a**) and different grassland types (**b**: desert steppe, **c**: typical steppe, **d**: meadow steppe). The fitted lines are significant at the level of 0.05 except case of meadow steppe in the dry period (d).

of the regional PPT–NDVI relationship increased but the variation in productivity explained by PPT declined sharply. This result partially contrasts with previous analyses. Past studies have suggested the slope of regional relationships would increase and also that the variation explained by PPT would be greater as ecosystem functions converged under severe water limitation (Bai *et al.* 2008; Huxman *et al.* 2004). We investigated other climatic factors, e.g. air temperature, attributes of PPT patterns, that may affect the spatial relationship during dry periods. For example, increasing air temperatures may increase the degree of water limitation, which may weaken the PPT–productivity relationship (Epstein *et al.* 1997; Hu *et al.* 2007). In addition, shifts in PPT attributes such as evenness of the distribution of rainfall during the growing season, or the size and distribution of individual events may affect the PPT–productivity relationship independent of PPT amount (Fay *et al.* 2003; Guo *et al.* 2015; Heisler-White *et al.* 2008). However, we also observed a sharp reduction in the spatial R^2 during the dry period when we substituted the aridity index, which incorporates the effect of air temperature (Fig. 3a). This suggests that air temperature contributed little to the change in R^2 of the spatial PPT–productivity relationship. In addition, using indices of PPT characteristics of rain events instead of total rainfall also yielded a reduction of the R^2 during the dry period (Supplementary Fig. S3). Thus, we conclude that the decline in R^2 of the spatial PPT–productivity relationship is not due to variations in other characteristics of PPT.

Mechanism of the shift of PPT–NDVI relationship

Further, our analyses suggest that the spatial heterogeneity of vegetation responses to PPT change, rather than the spatial heterogeneity in PPT change itself, plays a key role in altering the spatial relationship. We show that vegetation responses to

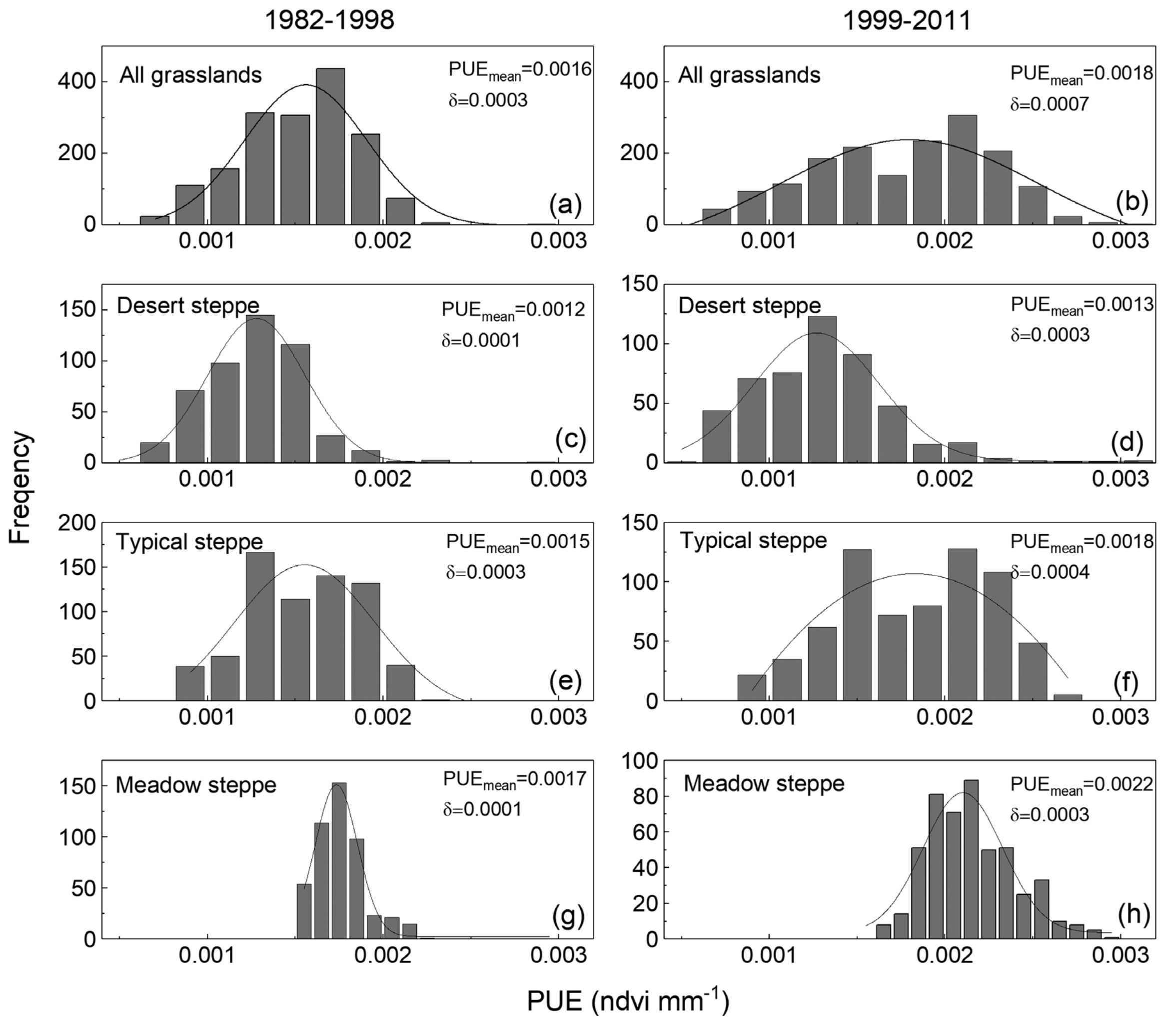

Figure 6: Frequency distributions of PUE for all grasslands (**a**, **b**), desert steppe (**c**, **d**), typical steppe (**e**, **f**) and meadow steppe (**g**, **h**) in the study region during wet (1982–1998, a, c, e, g) and dry (1999–2011, b, d, f, h) periods. Both the mean PUE and the standard deviation (δ) of the regressed Gaussian functions are significantly different between the two periods ($P < 0.05$). Higher δ indicates a larger range of PUE across the pixels.

dry years are more spatially asynchronous compared with responses to wet years (i.e. A_{veg} >1). This implies that these grasslands are functionally similar under wet conditions but are differentially sensitive to dry periods. A possible mechanism is plants in grasslands employ more diverse strategies when coping with drought stress. For example, the study of Craine *et al.* (2013) indicates that the capacity of physiological drought tolerance varies in a range of as large as 10-fold in global grassland species. In addition, spatial heterogeneity in soil texture and nutrients may contribute to the spatially asynchronous responses of vegetation during dry conditions. For example, soils that vary in texture and nutrient availability would result in difference degrees in soil water availability in dry years, and thus different degrees of water stress for communities (Epstein *et al.* 1997; Fay *et al.* 2015). Note that the plant species are mostly C_3 in our study region, thus we cannot conclude that the strength of the spatial PPT–NDVI relation would decline to a similar degree beyond C_3 grasslands. The generally greater water stress experienced normally by C_4 grasslands might result in the spatial relationship being less sensitive to extended dry periods.

Implications

The spatial PPT–productivity relationship has been used previously to predict regional and global levels of productivity, e.g. the Miami model (Hu *et al.* 2010; Leith 1975). In addition, the spatial relationship has been used to predict the trajectory of changes in ecosystem productivity in response to climate change via space-for-time approaches (Sala *et al.* 2012). Our analyses indicate that using these spatial relationships to predict

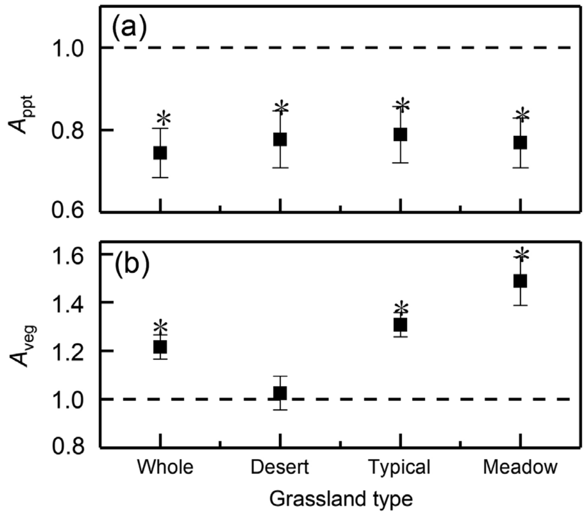

Figure 7: Spatial asymmetry in changes of PPT (**a**) and in the NDVI response (**b**) across the study region and the different grassland types. Asterisks indicate values are significantly <1.0 (a) or >1.0 (b) at the level of 0.05 (*t* test).

the future may be difficult if global climate change leads to increases in aridity or the occurrence of extended dry periods, both predicted by a range of climate change scenarios (IPCC 2013). In case of temporal model, when considering years with extremely climate condition, the PPT–ANPP relation was inconsistent with the near-universally used linear models (Knapp *et al.* 2017). Our finding suggests that such kind of inconsistence also exist in the spatial model, which is conventionally considered stable and robust (Sala *et al.* 2012). This highlights the importance of further investigating the mechanism controlling the function of ecosystem under extreme climate conditions.

CONCLUSIONS

Based on a 35-year remotely sensed vegetation index, we investigated the temporal dynamics of regional (spatial) PPT–productivity relationship in the temperate grasslands in northern China. We found a sharp decrease of the strength (R^2) of the spatial relationship during a decadal dry period relative to a previous wet period, driven we contend, by substantial SA in responses of different grassland ecosystems. Thus, the spatial PPT–productivity relationship is not as robust temporally as it is among global grasslands. Caution should be exercised if spatial PPT–productivity relationships are used to predict future ecosystem productivity, or verify model projections, given expectations that extended periods of PPT anomalies will become more frequent in the future for grasslands globally.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Theoretical demonstration of the effects of spatial asynchrony of changes in precipitation (**a**) and NDVI (**b**) on the spatial R^2 of PPT–NDVI relationship.

Figure S2: Temporal dynamics of precipitation within different periods (**a**), average of rainfall size in different periods (**b**) and the number rainfall events above 5, 10 and 20 mm (**c**).

Figure S3: Temporal dynamics of the spatial R^2 between NDVI and annual precipitation (PPT), precipitation in growing season (PPTgs), precipitation in June–July (PPTjj), average size of rainfall events in whole year (AvgRainEvent) and growing season (AvgRainEvent), number of rainfall events above 5 mm (NumRain5), 10 mm (NumRain10) and 20 mm (NumRain20), respectively.

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Conflict of interest statement. The authors declare that they have no conflict of interest.

REFERENCES

Adler PB, White EP, Cortez MH (2020) Matching the forecast horizon with the relevant spatial and temporal processes and data sources. *Ecography* **43**:1729–1739.

Bai Y, Wu J, Xing Q, *et al.* (2008) Primary production and rain use efficiency across a precipitation gradient on the Mongolia Plateau. *Ecology* **89**:2140–2153.

Craine JM, Ocheltree TW, Nippert JB, *et al.* (2013) Global diversity of drought tolerance and grassland climate-change resilience. *Nat Clim Change* **3**:63–67.

DAHV (Department of Animal Husbandry and Veterinary, Ministry of Agriculture) and GSAHV (General Station of Animal Husbandry and Veterinary, Ministry of Agriculture) (1996) *Rangeland and Resources of China*. Beijing, China: China Science and Technology Press.

Epstein HE, Lauenroth WK, Burke IC. (1997) Effects of temperature and soil texture on ANPP in the U.S. Great Plains. *Ecology* **78**:2628–2631.

Fay PA, Carlisle JD, Knapp AK, *et al.* (2003) Productivity responses to altered rainfall patterns in a C_4-dominated grassland. *Oecologia* **137**:245–251.

Fay PA, Prober SM, Harpole WS, *et al*. (2015) Grassland productivity limited by multiple nutrients. *Nat Plants* **1**:15080.

Forrestel EJ, Donoghue MJ, Edwards EJ, *et al*. (2017) Different clades and traits yield similar grassland functional responses. *Proc Natl Acad Sci U S A* **114**:705–710.

Guo Q, Hu Z, Li S, *et al*. (2012) Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: effects of mean annual precipitation and its seasonal distribution. *Glob Change Biol* **18**:3624–3631.

Guo Q, Hu Z, Li S, *et al*. (2015) Contrasting responses of gross primary productivity to precipitation events in a water-limited and a temperature-limited grassland ecosystem. *Agric For Meteorol* **214**:169–177.

Heisler-White JL, Knapp AK, Kelly EF (2008) Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia* **158**:129–140.

Heisler-White JL, Blair JM, Kelly EF, *et al*. (2009) Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Glob Change Biol* **15**:2894–2904.

Hu Z, Fan J, Zhong H, *et al*. (2007) Spatiotemporal dynamics of aboveground primary productivity along a precipitation gradient in Chinese temperate grassland. *Sci China Ser D Earth Sci* **50**:754–764.

Hu Z, Yu G, Fan J, *et al*. (2010) Precipitation-use efficiency along a 4500-km grassland transect. *Glob Ecol Biogeogr* **19**:842–851.

Hu Z, Shi H, Cheng K, *et al*. (2018) Joint structural and physiological control on the inter-annual variation in productivity in a temperate grassland: a data-model comparison. *Glob Change Biol* **24**:2965–2979.

Hutchinson MF (2014) *Anusplin Version 4.3*. Canberra, Australia: Centre for Resource and Environmental Studies, The Australian National University.

Huxman TE, Smith MD, Fay PA, *et al*. (2004) Convergence across biomes to a common rain-use efficiency. *Nature* **429**:651–654.

IPCC (2013) *Climate Change 2013. The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press, p. 1535.

Knapp AK, Carroll CJ, Denton EM, *et al*. (2015) Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia* **177**:949–957.

Knapp AK, Ciais P, Smith MD (2017) Reconciling inconsistencies in precipitation-productivity relationships: implications for climate change. *New Phytol* **214**:41–47.

Leith H (1975) Modeling the primary productivity of the world. In Lieth H, Whittaker RH (eds). *Primary Productivity of the Biosphere*. Berlin, Germany: Springer Press.

Maurer GE, Hallmark AJ, Brown RF, *et al*. (2020) Sensitivity of primary production to precipitation across the United States. *Ecol Lett* **23**:527–536.

Running SW, Nemani RR, Heinsch FA, *et al*. (2004) A continuous satellite-derived measure of global terrestrial primary production. *BioScience* **54**:547–560.

Sala OE, Parton WJ, Joyce LA, *et al*. (1988) Primary production of the central grassland region of the United States. *Ecology* **69**:40–45.

Sala OE, Gherardi LA, Reichmann L, *et al*. (2012) Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philos Trans R Soc Lond B Biol Sci* **367**:3135–3144.