Climate sensitivity functions and net primary production: A framework for incorporating climate mean and variability

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Abstract. Understanding controls on net primary production (NPP) has been a long-standing goal in ecology. Climate is a well-known control on NPP, although the temporal differences among years within a site are often weaker than the spatial pattern of differences across sites. Climate sensitivity functions describe the relationship between an ecological response (e.g., NPP) and both the mean and variance of its climate driver (e.g., aridity index), providing a novel framework for understanding how climate trends in both mean and variance vary with NPP over time. Nonlinearities in these functions predict whether an increase in climate variance will have a positive effect (convex nonlinearity) or negative effect (concave nonlinearity) on NPP. The influence of climate variance may be particularly intense at ecosystem transition zones, if species reach physiological thresholds that create nonlinearities at these ecotones. Long-term data collected at the confluence of three dryland ecosystems in central New Mexico revealed that each ecosystem exhibited a unique climate sensitivity function that was consistent with long-term vegetation change occurring at their ecotones. Our analysis suggests that rising temperatures in drylands could alter the nonlinearities that determine the relative costs and benefits of variance in precipitation for primary production.

Key words: Bouteloua; *Chihuahuan Desert; climate sensitivity function; climate variability; creosote shrubland; ecotone dynamics; Great Plains grassland; net primary production; Shortgrass steppe; Standardized Precipitation Evapotranspiration Index.*

INTRODUCTION

Understanding patterns and controls on net primary production (NPP) has been a long-standing goal in ecology. Most prior analyses of climatic controls on NPP focus on long-term patterns in average precipitation or temperature. However, climate models consistently project increases in the year-to-year *variance* of precipitation, even when mean trends are ambiguous (Fischer et al. 2013, IPCC 2013). Increased variance in precipitation is likely to interact with warmer average temperatures to accelerate aridity and reduce soil moisture in many ecosystems (Seager et al. 2007). Determining the ecological consequences of interactions between a slow increase in mean temperature and amplified variance in precipitation is thus an important research frontier (Lawson et al. 2015, Vazquez et al. 2016).

Understanding the climatic controls governing NPP within ecosystems is fundamentally important because of the measurable impact of production on the global carbon cycle (Seddon et al. 2016). However, while strong spatial relationships between mean annual precipitation and NPP have been widely documented across ecosystems globally (Sala et al. 1988, Huxman et al. 2004), identifying similarly strong temporal relationships between climate and production within single ecosystems has remained elusive (La Pierre et al. 2011, Reichmann et al. 2013). While recent efforts to narrow the time window of the climate-productivity relationship (Barnes et al. 2016, La Pierre et al. 2016) or include time lags via

antecedent precipitation (Ogle et al. 2015) have improved predictability, temporal relationships typically remain weaker than spatial ones (Sala et al. 2012). Accelerating our understanding of the influence of climate variance has potential to improve this predictability.

Here, we propose a framework to capture ecological responsiveness to both the mean and variance in climate indices. A climate sensitivity function depicts the complex relationship between an ecological response (e.g., NPP) and its climate driver (e.g., precipitation; Fig. 1). Importantly, this function captures the potential for nonlinear responses to climate (see also Hsu and Adler 2014, Yu et al. 2016), which may be common (Knapp et al. 2017), and it departs from the traditional method of characterizing sensitivity as the magnitude of a linear relationship (Munson 2013). When a climate sensitivity function is nonlinear, then changes in the *variance* of a climate index can drive the long-term ecological outcome, *even if mean climate does not change* (Gherardi and Sala 2015)—the mathematical principle of Jensen's Inequality. A monotonically increasing concave function (Fig. 1A) yields net negative effects of increasing variance, because low values of the climate variable (low rainfall) cause large decreases in the ecological response, while high values of the climate variable (high rainfall) cause only small increases. In contrast, a monotonically increasing convex function signals net positive effects of variance (Fig. 1B), where gains during high rainfall years strongly outweigh costs in dry years. If the function changes concavity over a range of climate (Fig. 1C), then climate variance could have positive or negative effects depending on the climate mean, because the climate mean and variance interact. For example, increasing variance may exacerbate declines in NPP during drought periods (concave, Fig. 1C), but then become net beneficial during wet periods

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(convex, Fig. 1C). The degree of nonlinearity will define, in part, the magnitude of the effect of variance on productivity. Observing nonlinear climate sensitivity functions within an ecosystem requires long time series over naturally or experimentally variable climates (Vazquez et al. 2016). Yet, most studies examine only linear relationships.

Climate sensitivity functions may be especially important for understanding ecotone dynamics, where ecosystems can rapidly expand or contract under directional change in abiotic drivers (Peters and Havstad 2006). Climate variance could have large effects on NPP at ecotones if dominant plants reach physiological limits that generate nonlinearities, such as threshold effects. Prior work applied the same nonlinear function across ecosystem types (Hsu and Adler 2014), although recently, Yu et al. (2016) showed that tree versus grass-dominated ecosystems in the Kalahari Desert had different relationships with interannual variance in precipitation.

Here, we used long-term data collected at the confluence of three dryland ecosystems to develop climate sensitivity functions that predict how changes in both climate mean and

variance will interact to control NPP. Drylands provide an excellent test bed to advance general theory on the ecological responsiveness of NPP to non-stationary climate because they are highly ecologically variable and typically more sensitive to climate than mesic ecosystems (Knapp and Smith 2001, Huxman et al. 2004). In addition, future climates in drylands are expected to have greater interannual variance in precipitation (Gutzler and Robbins 2011, Cook et al. 2015) and may experience >40% greater warming than mesic ecosystems (Huang et al. 2017). Assessing the consequences of these dual changes is essential because drylands are key contributors to global carbon fluxes due to their high year-to-year variability in NPP (Ahlstrom et al. 2015) and large terrestrial surface area (~45%), which is rapidly expanding (Huang et al. 2016). We asked if ecosystem-specific differences in climate sensitivity functions corresponded with observed transitions among ecosystems under a changing climate. Our analysis suggests, for the first time, that rising temperatures in drylands could alter the nonlinearities that determine the relative costs/benefits of precipitation variance for net primary production.

METHODS: APPLICATION OF CLIMATE SENSITIVITY FUNCTIONS TO DRYLAND BIOME TRANSITION ZONES

Study site

We developed climate sensitivity functions (CSFs) to explore how aboveground NPP correlated with changes in climate mean and variance across a grassland to shrubland state transition currently playing out in the southwestern US. The Sevilleta National Wildlife Refuge (SNWR), New Mexico, sits at the transition zone between Chihuahuan Desert vegetation to the south and west, and Great Plains grassland to the north and east. Sites in the SNWR are located at endpoints between two broad ecotones, one from blue grama (*Bouteloua gracilis*)-dominated shortgrass steppe (Great Plains grassland) to black grama (*B. eriopoda*)-dominated Chihuahuan Desert grassland. The second ecotone shifts from Chihuahuan Desert grassland to creosotebush (*Larrea tridentata*)-dominated Chihuahuan Desert shrubland (Appendix S1: Fig. S1). Although historically, Chihuahuan Desert shrubland has replaced desert grassland throughout much of the southwestern US (Van Auken 2000), the current ecotone between these systems at the SNWR has been stable for the past two decades (S. L. Collins, *unpublished data*). In contrast, at the grassland ecotone, the competitively inferior black grama (Peters and Yao 2012, Chung and Rudgers 2016) is, enigmatically, replacing its more competitive congener, blue grama (Collins and Xia 2015).

We hypothesized that black grama-dominated Chihuahuan Desert grassland benefits from a combination of high variance in precipitation and hot summer temperatures (convex CSF at high aridity, Fig. 1) relative to blue grama-dominated Great Plains grassland, potentially enabling current expansion of desert grassland. We examined if these combined climate drivers could also explain recent resistance of desert grassland to encroachment by creosotebush shrubs.

Plants

To test these hypotheses, we analyzed long-term NPP data from Chihuahuan Desert grassland, shrubland (since 1999),
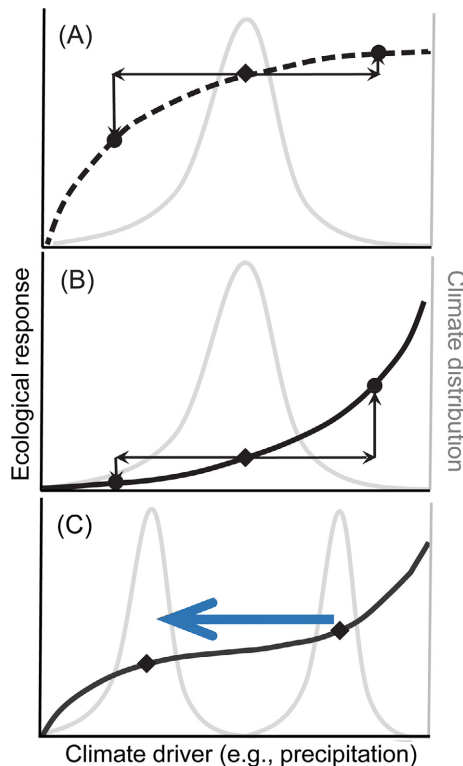

FIG. 1. Types of nonlinear Climate Sensitivity Functions (CSFs). Nonlinear relationships between a climate driver and an ecological response result in asymmetric responses to yearly variation in climate. The ecological response at the mean climate value is indicated with a diamond symbol. For concave functions (A), years that deviate from the mean climate produce larger decreases in the ecological response than increases: increasing climate variance is costly. For convex functions (B), deviations from mean climate produce larger increases than decreases in the ecological response: increasing climate variance is beneficial. A complex CSF (C) demonstrates how the nonlinear ecological response to the climate driver can depend on the value of the mean climate driver, with the large, blue arrow indicating a decrease in the mean over time; this shape is evidence of a mean × variance interaction.

and Great Plains grassland (since 2002). Vascular plant live NPP was estimated for each species using a nondestructive volumetric method (Muldavin et al. 2008) that yields data on species composition and total production (Appendix S1). Volume measurements of all individual plants were recorded at peak biomass (September) each year in permanently located 1-m^2 plots (N ranges from 22 to 106 plots depending on the year and ecosystem; Appendix S1: Tables S1 and S2). Biomass was calculated allometrically via linear regression models with intercepts through the origin; these were developed for each species over multiple years from plants collected outside of the permanent sampling plots (Muldavin et al. 2008).

Climate

Precipitation alone does not override the strong effect of temperature on water availability in dryland ecosystems (Williams et al. 2013). New metrics like the Standardized Precipitation Evapotranspiration Index (SPEI) explicitly incorporate temperature via potential evapotranspiration (Vicente-Serrano et al. 2010). Negative SPEI values indicate more arid conditions. We calculated SPEI for the monsoon season (during which >60% of NPP occurs) using meteorological data from the SNWR during 1989–2015. To determine SPEI, climate variables were recorded at three long-term meteorological stations located in the Great Plains grassland, ecotone between Great Plains and Chihuahuan Desert grassland, and ecotone between Chihuahuan Desert grassland and shrubland. Variables included air and soil temperature, soil moisture, relative humidity, precipitation, solar radiation, and wind speed and direction. We gap-filled missing daily data (e.g., temporary equipment failure) using data from the geographically nearest station within the SNWR. We also obtained monthly average air temperature and monthly accumulated precipitation from 1900 to 2014 for the Socorro, NM, USHCN site (298387, cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html). We calculated potential evapotranspiration using the Thornthwaite method, then determined six-month integrated SPEI ending 30 September (<SPEI> package cran.r-project.org/package=SPEI; R Core Team 2016). Prior analysis of ecosystem flux data from a related study identified that six-month integration, which captures the full monsoon period, explained more variance across ecosystems than three-month or twelve-month integrations.

We determined temporal trends in aridity using Spearman rank correlation between year and either six-month SPEI (30 Sept) or the coefficient of variation (CV) of positivized SPEI, which was determined over non-overlapping, five-year time windows (for Socorro) or four-year windows (for SNWR, to maximize the number of windows).

Climate sensitivity functions

Next, we determined climate sensitivity functions for NPP on SPEI (Appendix S1: Table S1) via model selection procedures (Burnham and Anderson 2002). Because yearly data were repeatedly measured in permanent plots, we included the random effects of both sampling quadrat and year to account for non-independence of observations. Mixed effects models were fit via maximum likelihood using lme in package <nlme>

(Pinheiro et al. 2016, R Core Team 2016). We selected the best model using the AICc criterion and determined marginal and conditional r^2 values using <piecewise SEM> (Lefcheck 2016). Conservatively, we report model averaged coefficients from the set of models with ΔAICc < 10 (CRAN.R-project.org/package=MuMIn; Appendix S1: Table S4). To examine variability in aridity directly, we split datasets into dry (SPEI < 0) or wet periods (>0), and examined the relationship between the mean NPP and CV in SPEI over four-year rolling windows. Plant data (data sets SEV129, SEV182, control plots data from SEV155, SEV176, SEV188, SEV231, SEV297) are available at http://sev.lternet.edu/data. R code and processed data are freely accessible via Rudgers et al. (2017).

RESULTS

Climate change at the SNWR

Aridity during the summer monsoon has fluctuated considerably since 1900 (Fig. 2), with a significant long-term decline in average SPEI ($r = -0.40$, $P < 0.0001$, N = 115). In contrast, the coefficient of variation in aridity has increased ($r = 0.69$, $P = 0.0003$, N = 23 5-year windows), especially since the early 1980s. At the SNWR, mean monsoon SPEI has declined since 1989 ($r = -0.46$, $P = 0.0185$) by -0.04 ± 0.01 SD per year, and CV in aridity has also increased, although not significantly ($r = 0.38$, $P = 0.0725$, N = 23 rolling windows).

Climate sensitivity functions (CSFs)

The potential for the mean and variance of climate indices to influence NPP derives from the specific, nonlinear shape of ecosystem-specific CSFs. Our investigation revealed new differences between two grassland ecosystems that were surprisingly consistent with the observed replacement of Great Plains grassland by Chihuahuan Desert grassland across this ecotone during the past 25 yr (Collins and Xia 2015). In Great Plains grassland, the concave shape of the CSF under dry conditions (Fig. 3A; Appendix S1: Table S3) signaled a cost of variance in aridity, which was also supported by a negative relationship between plant production and the coefficient of variation in
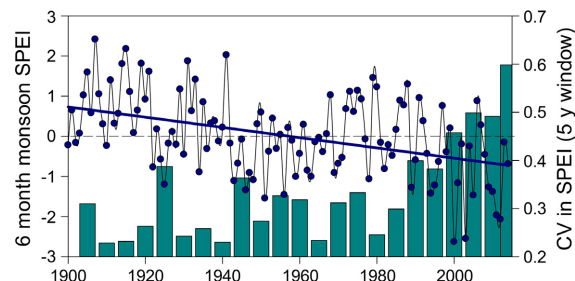

FIG. 2. Temporal trends in the Standardized Precipitation Evaporation Index (SPEI). Negative SPEI values indicate dry and hot conditions for Socorro, NM, about 30 km south of SNWR: Points show the 6-month integrated SPEI over the preceding monsoon season, recorded since 1900. Bars show the coefficient of variation (CV) in the SPEI for non-overlapping 5-yr time windows. The mean SPEI has significantly declined over time ($P < 0.0001$, blue trendline), while the CV in SPEI has significantly increased ($P = 0.0003$).
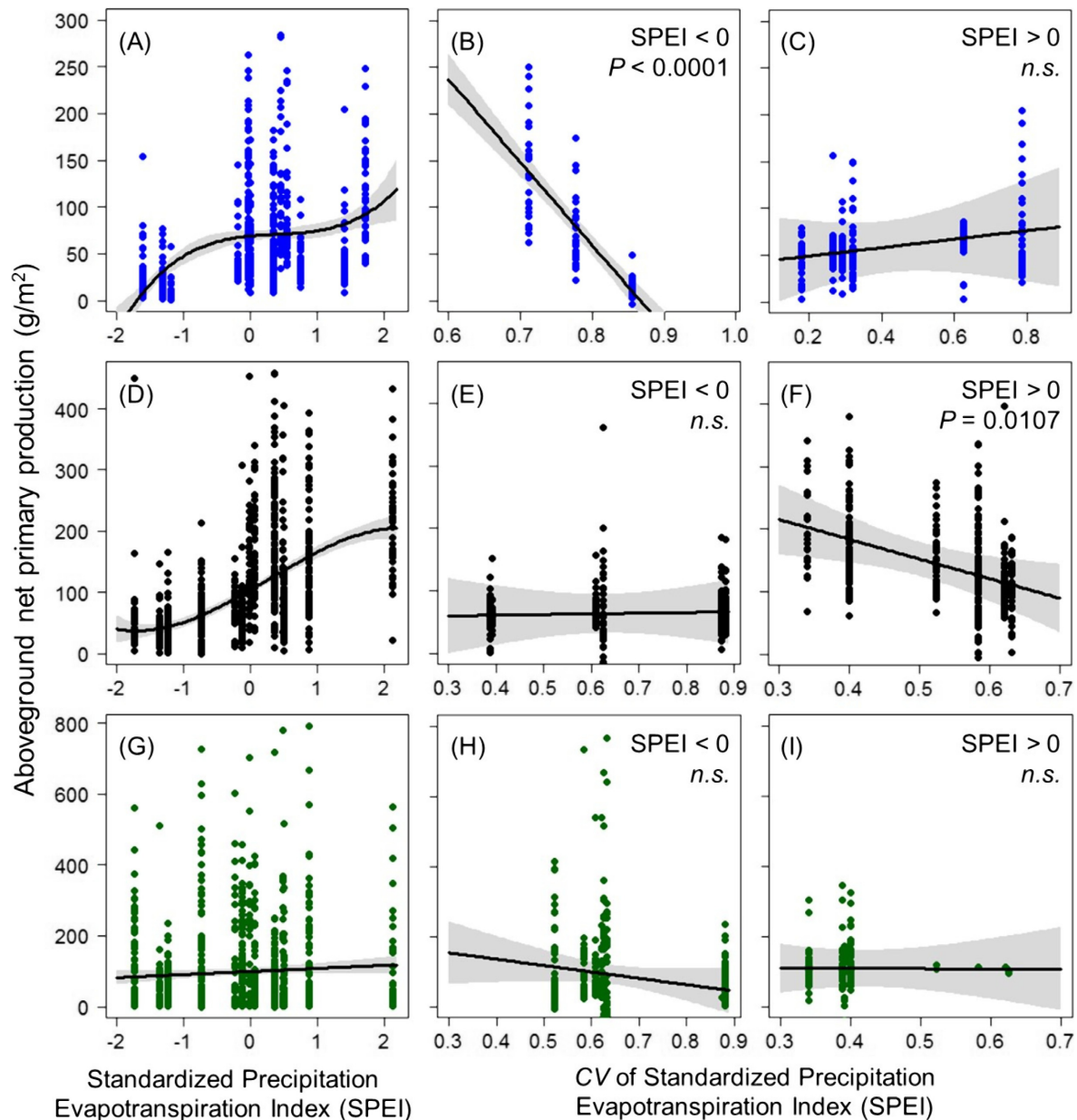
FIG. 3. Climate sensitivity functions for 12–15 yr of aboveground NPP from Great Plains grassland dominated by blue grama (blue points, A), Chihuahuan Desert grassland dominated by black grama (black points, B), and Chihuahuan Desert shrubland dominated by creosotebush (green points, C) in the Sevilleta National Wildlife Refuge, New Mexico. Negative *SPEI* indicates dry and hot conditions. NPP is also plotted against the coefficient of variation (*CV*) in SPEI separately for dry periods (SPEI < 0) and wet periods (SPEI > 0) for each ecosystem (B, C) Great Plains grassland; (E, F) Chihuahuan Desert grassland; (H,I) Chihuahuan Desert shrubland.

SPEI (Fig. 3B, $\beta = -888.0$, $P < 0.0001$). In contrast, the shift to a convex CSF during wet/cool periods at high SPEI suggested possible benefits of variance to NPP, and the *CV* in SPEI was positively, but non-significantly, related to NPP (Fig. 3C, $\beta = 45.3$, $P = 0.46$). Although weaker, the opposite pattern occurred in Chihuahuan Desert grassland (Fig. 3D; Appendix S1: Table S3). Here, the convex CSF suggested this grassland would benefit from variance under aridity, and there was a positive, but non-significant relationship with *CV* (Fig. 3E, $\beta = 10.9$, $P = 0.89$). But, under wetter, cooler conditions, higher *CV* was significantly negatively related to NPP (Fig. 3F, $\beta = -315.0$, $P = 0.0107$). Cubic models (Model 6 in

Appendix S1: Table S1) best fit the relationship between NPP and aridity in both grasslands (Appendix S1: Table S4) and explained 27-30% of variability in NPP relative to the null model (marginal r^2; Appendix S1: Table S3), although the quadratic model was still competitive for the Chihuahuan Desert grassland Appendix S1: Table S4.

In contrast to the grasslands, Chihuahuan Desert shrubland, dominated by the long-lived C_3 shrub creosotebush, was insensitive to climate variance during the monsoon season and lacked significant nonlinearity in the CSF (Fig. 3G–I; *CV* all years: $\beta = 0.32$, $P = 0.57$). This insensitivity held whether we used 3, 6, or 12-month integration for

SPEI. While multiple CSF models fit shrubland data equally well, none explained much variability in NPP (marginal $r^2 \sim 0.02$), and only the linear relationship with SPEI was statistically significant (Appendix S1: Tables S3 and S4).

The complex nonlinearities observed for grasslands can be further explained by decomposing the SPEI aridity index into its component climate drivers: precipitation and temperature. Nonlinear sensitivities for plant production occurred because the influence of monsoon precipitation differed during warm versus cool summers (Appendix S2). In Great Plains grassland, high NPP occurred when summers were cool (maximum summer temperature < average) and precipitation was high; in contrast, high summer temperature plus low precipitation were negatively correlated with NPP (Appendix S3: Tables S1 and S2), corresponding with the hypothesis that high temperatures are driving the increasingly concave shape of the CSF in years with *higher* values of aridity (Fig. 3A). Thus, variance in precipitation may be beneficial only under wet/cool conditions in the Great Plains grassland ecosystem (Appendix S3: Fig. S1B). In contrast, in Chihuahuan Desert grassland, NPP was lower, on average, in wet years with cool summers than in wet years with warm summers. In fact, the relationship flipped from convex under warm summer temperatures, indicating a net benefit of variance Appendix S3: Fig. S1C), to concave when cool (Appendix S3: Fig. S1D), corresponding with the increasingly concave shape of the CSF at high SPEI (Fig. 3B). Collectively, these results suggest that rising mean temperatures may alter the shape and magnitude of the nonlinearities that determine the costs/benefits of precipitation variance, and that the potential for climate mean × variance interactions may differ dramatically among types of ecosystems.

DISCUSSION

The majority of studies investigating NPP and climate in single ecosystems have focused on the strength of linear relationships with current seasonal or annual climate conditions (but see, Hsu and Adler 2014, Yu et al. 2016). We derived non-linear climate sensitivity functions to gain deeper insight into NPP dynamics at ecosystem transition zones. We found nonlinearities that indicated the potential for interannual variation in climate to affect NPP, and for the influence of variance to interact with *average* climate conditions. Of the three ecosystems we examined, the two grasslands had strong nonlinearities with monsoon climate, but the shrubland did not. In both grasslands, NPP was also significantly correlated with the coefficient of variation in aridity, consistent with the importance of variance independently of the mean. The grasslands differed in the conditions under which variance was negatively associated with production. In Great Plains grassland, variance appeared most costly during hot summers, whereas in Chihuahuan Desert grassland, the variance-NPP relationship was most negative during cool summers. Positive effects of variance were statistically less detectable than negative effects, but even sixteen years of data may not be enough to resolve complex nonlinearities in climate sensitivities.

Our results also suggest that new aridity indices can yield insights into future changes in both climate (Fig. 2) and NPP (Fig. 3). As noted by Cook et al. (2015) future climate in the Southwestern and Central U.S. will be driven by changes in both precipitation and temperature. Our analysis of SPEI indicated a larger change in aridity (Fig. 2) than analysis of monsoon precipitation alone, which has not significantly declined since 1900 (Petrie et al. 2014). Although it has garnered the lion's share of attention in the dryland literature, precipitation alone cannot account for the effects of rising temperature, which exacerbate aridity.

New explanations for ongoing ecosystem transitions in drylands

Recent changes in the mean and variance of aridity (Fig. 2) may help explain two ongoing transitions across the northern Chihuahuan Desert to Great Plains ecotone. The first is the expansion of Chihuahuan Desert grassland relative to Great Plains grassland (Collins and Xia 2015). Our detection of nonlinearities (Fig. 3) suggested that increased interannual CV in climate under a changing mean may be an overlooked, but important driver of the Great Plains to Chihuahuan Desert grassland transition. Under arid conditions, Chihuahuan Desert grassland was insensitive or slightly benefited from increased CV (Fig. 3B). In contrast, conditions that were both more arid and more variable were associated with reduced NPP in the Great Plains grassland (Fig. 3A). Thus, greater temporal variance in climate under a changing mean climate may explain the grassland ecotone enigma, where the competitively inferior black grama (Peters and Yao 2012, Chung and Rudgers 2016) appears to be replacing its more competitive congener, blue grama (Collins and Xia 2015).

Like the replacement of Great Plains grassland by Chihuahuan Desert grassland, shrub encroachment by creosotebush into desert grassland is also an ecological conundrum. Although historically Chihuahuan Desert shrubland has replaced desert grassland throughout much of the southwestern US (Van Auken 2000), the current ecotone at the SNWR has been stable over the past two decades (S. L. Collins, *unpublished data*). Desert shrubland was insensitive to year-to-year variance in aridity (Fig. 3G–I), and sensitivity did not increase when we integrated climate over the full year, suggesting that we did not miss a signal from winter precipitation. This result is consistent with prior work that identified monsoon precipitation as a key driver of creosotebush growth (Sponseller et al. 2012). In contrast, Chihuahuan Desert grassland may benefit the most from CV in aridity when average conditions are arid (Fig. 3B), as in the current climate window (Fig. 2). Thus, stability of the grassland/shrubland ecotone may be a logical outcome of historically arid and variable climatic conditions over the past two decades (Fig. 2). Our results also suggest that shrub encroachment will likely not be reversed by ongoing changes in climate mean and variance, assuming these variables continue on their current trajectories (Fig. 2).

Mechanisms of climate sensitivity functions

Understanding mechanisms underlying the shape of climate sensitivity functions could expand the ability to generalize patterns to other ecosystems, worldwide. Species traits could be key to this understanding (reviewed by Lawson et al. 2015). For example, Knapp and Smith (2001) attributed the differential responsiveness of NPP to precipitation to traits such as physiological plasticity and meristem density. Shallow rooting depth could cause a saturating downward

CSF because plants cannot make large gains in biomass following the large rains that infiltrate deep soils (Gherardi and Sala 2015). Dominance by several drought-tolerant plant species could reduce the concavity of an ecosystem's climate sensitivity function. Differences among ecosystems in edaphic factors or other non-climate abiotic variables could also influence the shape of the climate sensitivity function.

At the SNWR, ecosystem responses to changes in climate mean and variance may be linked to key differences in traits among the three dominant species. Black grama is a short-lived (~40 yr), shallow-rooted C_4 grass that can spread rapidly via stolons and occasionally by seeds (Peters and Yao 2012). Its congener, blue grama, is a shallow rooted, caespitose C_4 bunchgrass that may live for more than a century (Gibbens and Lenz 2001). Blue grama seedlings are rare at the SNWR (Peters 2000), and this species spreads primarily by basal tillering (Ravi et al. 2008). Because of these trait differences, black grama may have greater capacity than blue grama to benefit from average years (when SPEI ~ 0) via recruitment and rapid clonal growth, potentially shaping its convex response under high aridity (Fig. 3B). Blue grama, on the other hand, may have limited capacity to benefit from wet years under hot conditions (Fig. 3A; Appendix S3: Fig. S1A), causing biomass to decline as both precipitation variance and temperature increase. Creosotebush is a highly drought resistant (Smith et al. 1997), very long-lived, semi-evergreen, native C_3 shrub that has greatly expanded its regional range during the past 150 yr (Van Auken 2000). Although adult creosotebush are more drought tolerant than black grama (Baez et al. 2013), Pockman and Small (2010) showed that black grama achieved higher leaf-level carbon fixation after moderately sized rain events than did co-occurring creosotebush, indicating that black grama competes better for shallow soil water. Abundant fibrous roots, stoloniferous growth, and seed reproduction should give black grama a competitive advantage over creosotebush because all but the largest rain events increase water in shallow soil, where grass roots dominate over shrub roots (Pockman and Small 2010). The insensitivity of creosotebush to variance in aridity (Fig. 3H) may occur because it can respond equally well to both winter/spring and summer precipitation events (Allen et al. 2008, Sponseller et al. 2012). NPP-climate relationships under monsoon conditions could be additionally influenced by changes in the ratio of winter/spring/monsoon precipitation, which were not captured by our monsoon SPEI metric, and likely deserve future investigation.

Conclusion

Understanding contemporary relationships between climate and NPP remains an important objective if we are to accurately predict how ecosystems will respond to climate in the future. Our results support the contention by Knapp et al. (2017) that NPP is more likely to exhibit a nonlinear rather than linear response within a site over time. We argue, however, against a "one size fits all" approach to fitting the climate-NPP relationship, linear or otherwise. Our results indicate that ecological responses to changes in climate mean and variability will be an ecosystem-specific function, possibly driven by a combination of plant traits and species relative abundance. Thus, we propose that climate sensitivity functions that integrate changes in mean and variance of

integrative climatic indices (such as SPEI) can provide mechanistic insights and predictive capability to forecast ecosystem dynamics under future climate change.

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Supporting Information

Data Availability