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LETTER

Sensitivity of primary production to precipitation across the United States

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Abstract

Primary production, a key regulator of the global carbon cycle, is highly responsive to variations in climate. Yet, a detailed, continental-scale risk assessment of climate-related impacts on primary production is lacking. We combined 16 years of MODIS NDVI data, a remotely sensed proxy for primary production, with observations from 1218 climate stations to derive values of ecosystem sensitivity to precipitation and aridity. For the first time, we produced an empirically-derived map of ecosystem sensitivity to climate across the conterminous United States. Over this 16-year period, annual primary production values were most sensitive to precipitation and aridity in dryland and grassland ecosystems. Century-long trends measured at the climate stations showed intensifying aridity and climatic variability in many of these sensitive regions. Dryland ecosystems in the western US may be particularly vulnerable to reductions in primary production and consequent degradation of ecosystem services as climate change and variability increase in the future.

Keywords

Drought, ecosystem function, interannual variability, photosynthesis, remote sensing.

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INTRODUCTION

Primary production provides the energetic basis and material substrate for nearly all heterotrophs, including humans, and is a critical component of the many services that ecosystems provide (Millennium Ecosystem Assessment 2005; Haberl *et al.* 2014). Variation in primary production over time thus has important consequences for overall ecosystem functioning, and for the stability and value of production-derived ecosystem services. In particular, primary production is a key regulator of the global carbon cycle (Melillo *et al.* 1993), yet we do not have a reliable benchmark for assessing the sensitivity of terrestrial primary production to year-to-year changes in precipitation across broad geographic extents. Biomes contribute differentially to global primary production and therefore, affect the global carbon budget differentially. For example, tropical forests dominate the annual global carbon sink, whereas semi-arid and arid regions contribute the most to interannual variability of the carbon sink (Ahlström *et al.* 2015). Additionally, regional- or continental-scale changes in climate, like prolonged droughts, can potentially impact the global carbon budget by shifting the regional carbon balance from a sink to a source (Davidson *et al.* 2012; Brienen *et al.* 2015) or vice versa (Poulter *et al.* 2014). Thus, quantifying the sensitivity of primary production to climatic variation at large spatial scales is essential for predicting how the global carbon cycle will respond to future climatic conditions.

Common measures of primary production, such as gross primary production (GPP) and net primary production (NPP), are very responsive to climate. For example, a well-documented spatial relationship exists between mean annual precipitation (MAP) and annual NPP (Rosenzweig 1968; Sala *et al.* 1988; Knapp & Smith 2001; Huxman *et al.* 2004a). However, temporal relationships between annual precipitation and NPP are less consistent (Lauenroth & Sala 1992; Hsu *et al.* 2012; Sala *et al.* 2012; La Pierre *et al.* 2016; Knapp *et al.* 2017). Climate is becoming increasingly variable, resulting in more frequent, longer droughts and more extreme precipitation events (Fischer *et al.* 2013; Singh *et al.* 2013), and models predict that these trends will continue into the future (Diffenbaugh *et al.* 2008; Intergovernmental Panel on Climate Change 2013; Wuebbles *et al.* 2014). Furthermore, precipitation amounts are increasing in some regions of the conterminous United States (US) and decreasing in others, whereas temperatures are increasing across the continent (Wilbanks & Bilello 2014; Anderegg & Diffenbaugh 2015).

Previous analyses have demonstrated differential sensitivity among terrestrial ecosystems to year-to-year changes in precipitation, or to measures of aridity that also include temperature (Knapp & Smith 2001; Huxman *et al.* 2004a; Hsu *et al.* 2012; Sala *et al.* 2012; Ponce Campos *et al.* 2013; Biederman *et al.* 2016). Therefore, the impacts of climate change on ecosystem processes such as primary production will be the product of year-to-year changes in precipitation and temperature, and ecosystem sensitivity to these drivers. Previous studies of ecosystem sensitivity to climate have typically used isolated ground-based observations of primary production (Knapp & Smith 2001; Huxman *et al.* 2004a; Hsu *et al.* 2012;

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Sala *et al.* 2012) or experimental manipulations (Heisler-White *et al.* 2009; Plaut *et al.* 2013; Rowland *et al.* 2018) over relatively short spatial and temporal scales. These efforts, while valuable, do not yield detailed, spatially distributed, measures of ecosystem sensitivity to climate that can be used for continental-scale comparisons or for the validation of distributed biome and carbon cycle models.

Here, we present a comprehensive analysis that, for the first time, integrates precipitation, temperature, and proxies for primary production to understand ecosystem sensitivity to climate across the conterminous U.S. We used 1218 century-long weather station records from the U.S. Historical Climate Network (USHCN; Menne *et al.* 2009) to measure long-term trends in climate across the continent. We paired the latter portion of these climate records with sixteen years of recent satellite-derived proxies for primary production, including the Normalised Difference Vegetation Index (NDVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor, a robust and widely used surrogate for primary production (Huete *et al.* 2002; Running *et al.* 2004; Pettorelli *et al.* 2005; Nestola *et al.* 2016). With these data, we were able to calculate the sensitivity of primary production to interannual variation in climate at broad spatial and temporal scales. We hypothesised that trends towards a more arid and variable climate, particularly in the western US, would intersect with high ecosystem sensitivity to precipitation and aridity, thus highlighting ecosystems with greater potential vulnerability to climate change. We interpolated the climatic trends and ecosystem sensitivity values calculated at the USHCN stations across the conterminous US, and grouped our analyses within the ecoregions defined by the National Ecological Observatory Network (NEON, see Fig. S1 for reference), which are similarly sized and defined by biophysical and climatic characteristics (Hargrove & Hoffman 2004; Keller *et al.* 2008). With this analysis, we can identify which regions of the US are experiencing the greatest changes in climate, those that are most responsive to climate variation, and thus, which regions may be more vulnerable to climate change.

MATERIAL AND METHODS

Selection of a primary production proxy and justification

In this study, we focus on the NDVI spectral vegetation index as our main proxy for primary production, and for this, we used a 16-year (2000–2015) NDVI data set from the satellite-based MODIS sensor (Running *et al.* 2004; Spruce *et al.* 2016). Vegetation indices like NDVI are highly correlated to primary production across spatial scales and are commonly used to estimate quantities such as vegetation biomass, productivity and phenology (Pettorelli *et al.* 2005). For example, satellite NDVI has been used for decades as an estimator of biomass accumulation and aboveground NPP in grassland ecosystems (Tucker *et al.* 1985; Paruelo *et al.* 1997; Nestola *et al.* 2016; Chen *et al.* 2019). The strong relationship between NDVI, which is calculated as the ratio of red to near-infrared reflectance, and absorbed photosynthetically active radiation (fPAR) is also well supported in the literature (Pettorelli *et al.* 2005). To test our assumption that NDVI is correlated to primary production across our study area, we fit a regression relationship between the multi-year mean of ground-observed NPP data from 11 of the sites in Huxman *et al.* (2004a), and the average of 16 years (2000–2015) of satellite-derived NDVI for these same sites, and found a highly significant linear correlation ($R^2 = 0.72$; Fig. S2), indicating that MODIS NDVI values adequately represent ground-based measurements of NPP.

The generally reliable relationship between remotely sensed vegetation indices and primary production has led to the creation of algorithmic data products that combine spectral measurements with models of vegetation light-use efficiency and climate data to yield estimates of GPP and NPP (Running *et al.* 2004; Kolby Smith *et al.* 2015) and their response to climatic variability (Nemani *et al.* 2003). These products, however, show bias in low- and high-biomass ecosystems (Turner *et al.* 2006a), and dampen the interannual variability observed in many biome types. This is particularly evident in drylands, which are known to be highly sensitive to year-to-year changes in precipitation (Turner *et al.* 2006b; Anav *et al.* 2015; Verma *et al.* 2015; Biederman *et al.* 2017). In fact, MODIS satellite vegetation indices, in raw, seasonally-integrated or annually-integrated form, are more direct measures of vegetation activity, and therefore, frequently estimate primary production metrics (such as NPP, GPP and NEE) as well or better than algorithmic MODIS NPP and GPP products (Rahman *et al.* 2005; Sims *et al.* 2006; Verma *et al.* 2014).

Satellite vegetation indices do have drawbacks, however. MODIS NDVI is known to asymptotically saturate at values greater than 0.9 (Huete *et al.* 2002). This phenomenon is important in forests with high fractions of evergreen foliage, such as the Amazon basin, and may reduce observed interannual variability in NDVI, which in turn may lead to underestimation of ecosystem sensitivity to climate (Sims *et al.* 2006). When we examined the distribution of raw MODIS NDVI values across our study area, we found that only 0.03% of all values were greater than 0.9, so we do not believe our estimates of variability in primary production are biased by NDVI saturation in regions with high biomass or productivity. For these reasons, along with the strong correlation with ground-based measurements of NPP within our study area (Fig. S2), we opted to focus on annually integrated NDVI ($NDVI_{int}$, described below) as a proxy for primary production in this study.

To confirm the generality of our NDVI results, we conducted analyses of three additional MODIS satellite proxies for primary production: MOD17 NPP and GPP (Robinson *et al.* 2018), and annually-integrated values of the Enhanced Vegetation Index (EVI; Didan 2015). The NPP and GPP data sets are algorithmic primary production products, while EVI is a vegetation index with a more linear response that is less susceptible to saturation at high biomasses compared to NDVI (Huete *et al.* 2002; Rahman *et al.* 2005). These three data sets were examined for sensitivity to precipitation variability using the same methods as for MODIS NDVI. Additional methodological details are described in the "Confirmatory analysis with other MODIS proxies" section of the Supporting Information.

NDVI time series

We extracted time series of NDVI from a smoothed and gap-filled MODIS NDVI data set distributed by the Oak Ridge National Lab DAAC service (Spruce *et al.* 2016). This data set provides 250 m resolution NDVI data for the conterminous US every 8 days from 2000 through 2015. Quality control procedures for this data set have reduced the impact of clouds and other radiometric aberrations. The NDVI vegetation index is unitless, ranging from 0 to 1, with higher values indicating greater leafy biomass and photosynthetic potential.

From this data set, we calculated the mean NDVI value of a 100 square km area surrounding each of the 1218 USHCN stations (1681 pixels centred around station coordinates) at each observation time, yielding an 8-day mean NDVI time series for each station across the full 16-year period. This spatial averaging scheme incorporates natural, agricultural, and urban areas surrounding each station, allowing us to correlate NDVI with climate across the full range of existing vegetation and land-use. These 8-day time series were reduced to monthly frequency using the mean of all observations per month. For comparison to standardised aridity indices, we also generated a standardised monthly NDVI data set by calculating the z-score of 8-day NDVI time series (zNDVI; $z = \frac{(x-\mu)}{\sigma}$, where x = NDVI observed at a given time, μ = the station mean of NDVI, and σ = the standard deviation of NDVI) for each station before reducing to monthly frequency. Both NDVI and zNDVI were further reduced to annually integrated values (by calendar year) when calculating primary production sensitivity metrics.

Long-term and interannual climate variation

We retrieved USHCN data from the publicly available data archive of the U.S. National Oceanic and Atmospheric Administration (NOAA; ftp://ftp.ncdc.noaa.gov/pub/data/ushcn/v2.5/). The USHCN network is a subset of the Cooperative Observer Program weather station network with long, bias-corrected surface temperature and precipitation records that are suitable for assessing continental-scale climatic change (Menne *et al.* 2009). We found that the USHCN network had a minimum record length of 106 years, spanning from 1912, or earlier, to 2017, with a maximum of 22.67 years missing (< 15.26% missing data). We reduced these daily data to monthly values of mean daily air temperature and monthly cumulative precipitation for our analyses.

Primary production responds to available water from precipitation and atmospheric demand for water, the latter of which is partly a function of temperature (Park Williams *et al.* 2012). Consequently, we calculated an aridity index that integrates both precipitation and temperature, the Standardised Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano *et al.* 2010), and examined its relationship to primary production in our study. The full, 100 + year, monthly climate records from all USHCN stations were used to calculate SPEI with a 12-month integration period. We then examined long-term trends and variability in aridity across the conterminous US using SPEI. Long-term trends in SPEI were estimated by linear regression using the 'tslm' function in the *forecast* package in R (R Core Team 2018), which estimates trend coefficients matching the frequency of the data. Similarly, to quantify long-term trends in SPEI variability at each station, we fit 'tslm' models to the 5-year moving-window coefficient of variation (CV) of its SPEI time series. Trends in SPEI and SPEI CV were interpolated across the conterminous US (in Fig. 4a and b) using the 'autoKrige' function in the *automap* package in R (R Core Team 2018).

Ecosystem sensitivity metrics

Monthly time series of NDVI, zNDVI, precipitation and SPEI overlapped between 2000 and 2015, which allowed us to derive two ecosystem sensitivity metrics using linear mixed-effects models. The first of these metrics relates NDVI to precipitation, while the second relates zNDVI to aridity (as SPEI). To derive the first metric, we summed monthly NDVI and precipitation, by calendar year, for each year from 2000 to 2015 and assigned them to be the dependent and independent variables, respectively, in a linear mixed-effects model (the $NDVI_{int}$:Precip model; Table S1). We used the independent variable coefficients (the sum of fixed and random slopes) from this model as our metric of ecosystem sensitivity to precipitation (e.g. Huxman *et al.* 2004a; Knapp *et al.* 2015a). The units of this sensitivity metric are, therefore, the change in annually integrated primary production ($NDVI_{int}$) per unit of change in annual precipitation. We derived the second metric, ecosystem sensitivity to aridity, in a similar manner, but first z-transformed the NDVI measurements (zNDVI) for each USHCN station. Because SPEI is a standardised measure of the variability in climate at each USHCN site, transformation of NDVI to zNDVI was necessary to calculate sensitivity values with a comparable range of variability across all sites. The relationship between zNDVI and SPEI, was then estimated with annually integrated zNDVI (by calendar year) as the dependent variable and annual 12-month SPEI as the independent variable in another linear mixed-effects model (the $zNDVI_{int}$:SPEI model; Table S2). The units of $zNDVI_{int}$ sensitivity to aridity derived from these models (the SPEI coefficients in the model) are, therefore, the change in annually integrated primary production ($zNDVI_{int}$), per unit of change in annual SPEI.

After being fit to the data, each sensitivity model had uncertainty (residual variance) indicating how well year-to-year changes in precipitation or aridity explain variation in primary production. We quantified this uncertainty at the random effects level, i.e. by USHCN station, using the root mean square error (RMSE) statistic. Model estimates of ecosystem sensitivity to precipitation and aridity, and the corresponding uncertainty of these estimates, were then interpolated among sites and mapped across the conterminous US in Fig. S4. To yield uncertainty statistics comparable across locations and models, RMSE statistics for all USHCN stations were first normalised by the range in observed sensitivity values (NRMSE = $RMSE/(y_{max}-y_{min})$). All spatial interpolations were done with the 'autoKrige' function in the *automap* package for R (R Core Team 2018).

The $NDVI_{int}$: Precip model and the $zNDVI_{int}$:SPEI model were each selected from a separate pool of 18 candidate models (Tables S1 and S2). Each of the 18 candidate models for both sensitivity metrics contained all possible combinations of a set of fixed effects, random effects, and correlation structures. Candidate models always included the independent variable (precipitation or aridity) as a fixed effect. Candidate models that included NEON domain as a fixed additive and/or interactive effect were included in the model selection. Independent variables and the y-intercept were allowed to have random effects varying by weather station, NEON domain, or weather station nested within NEON domain. Candidate models with and without autoregressive (AR1) correlation structures were included. The models we selected as our two ecosystem sensitivity models had the lowest Bayesian Information Criterion (BIC) statistic among the candidates (Tables S1 & S2).

RESULTS

At the regional scale, primary production increased with mean annual precipitation (MAP), reaching a plateau at around 1000 mm MAP ($NDVI_{int} = c * \left(1 - e^{k*P_{ann}}\right)$, Efron's $R^2 = 0.55$, $P < 0.001$ for c and k; Fig. 1). We also found that temporal relationships between primary production and precipitation within NEON domains were weaker (i.e. explain a smaller fraction of the variability) and shallower (i.e. have lower slopes) than the overall spatial relationship between primary production and precipitation across domains (Fig. 1). These temporal relationships, however, were related to MAP. Across the conterminous US, the sensitivity of primary production to precipitation decreased nonlinearly from deserts and grasslands to savannahs and forested domains (Efron's $R^2 = 0.52$, $P < 0.001$; Fig. 2). Primary production not only responds to precipitation, but also to changes in temperature that alter atmospheric demand for water. Indeed, we found that primary production was sensitive to annual variation in aridity, quantified as SPEI, and that this sensitivity declined nonlinearly with MAP in a pattern similar to precipitation sensitivity ($\text{Sensitivity} = c * \left(e^{-MAP}\right)$, Efron's $R^2 = 0.39$, $P < 0.001$; Fig. S3).

We used a simple spatial interpolation technique (i.e. kriging) to map the 1218 ecosystem sensitivity estimates, and their corresponding uncertainty values, as a continuous surface across the conterminous US (Fig. 3). Ecoregions in which primary production showed the highest sensitivity to variations in precipitation included the Central Great Plains and the Desert Southwest followed by the Great Basin and the Southern Rockies/Colorado Plateau regions that had somewhat more moderate sensitivity to precipitation (Fig. 3; Table S3). Sensitivity of NDVI to precipitation and aridity were near zero for most of the eastern US as well as the Pacific Northwest (Figs. 3 and S3; Table S3). In most of the study area, uncertainties for both sensitivity metrics, estimated as NRMSE, were inversely related to the sensitivity values themselves (Fig. S4), meaning that estimates of primary production sensitivity to precipitation and aridity were more uncertain in mesic regions of the continental U.S. Spatial patterns of ecosystem sensitivity to precipitation were generally consistent within the Great Plains and Desert Southwest domains, and there were steep boundaries in the degree of sensitivity at the borders of these domains (Fig. 3).

The three additional satellite-derived proxies for primary production largely confirmed continental-scale patterns in sensitivity to precipitation that were observed with MODIS NDVI (Fig. S5a–c). MODIS EVI, NPP and GPP were all generally more sensitive to year-to-year precipitation variation in the western US. The MODIS NPP and GPP data sets reported lower sensitivity in regions with low plant biomass and productivity when compared with the spectral vegetation indices (NDVI and EVI).

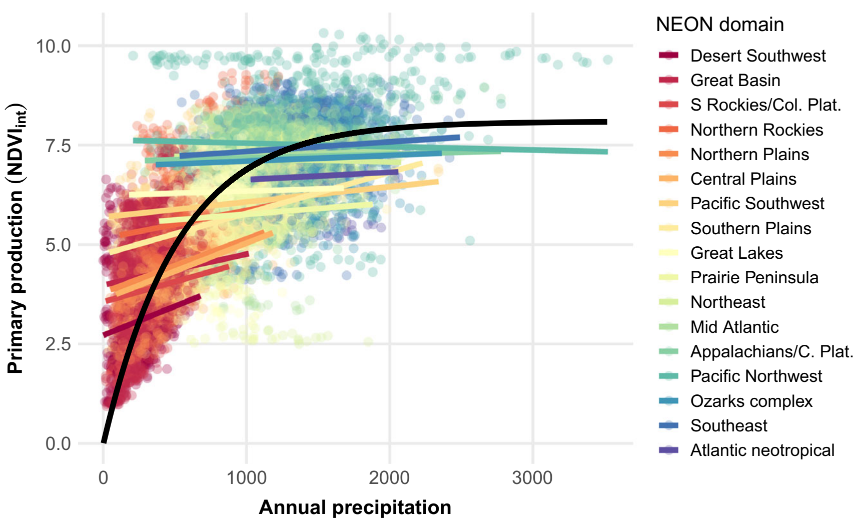

Figure 1 Primary production ($NDVI_{int}$) response to annual precipitation at 1218 USHCN stations distributed across the conterminous US. Each point represents primary production and precipitation data for one year at one station. Points are coloured by the NEON domain (see Fig. S1). Linear models representing the mean temporal relationship between primary production and annual precipitation, derived from a mixed-effects model relating the two variables at USHCN stations from years 2000 through 2015, are plotted as lines coloured by the NEON domain (model P-value for annual precipitation < 0.001). A nonlinear model representing the spatial pattern in the primary production to precipitation relationship (unrelated to our linear ecosystem sensitivity models) is plotted in black ($NDVI_{int} = c * \left(1 - e^{k*P_{ann}}\right)$, Efron's $R^2 = 0.55$, $P < 0.001$ for c and k).

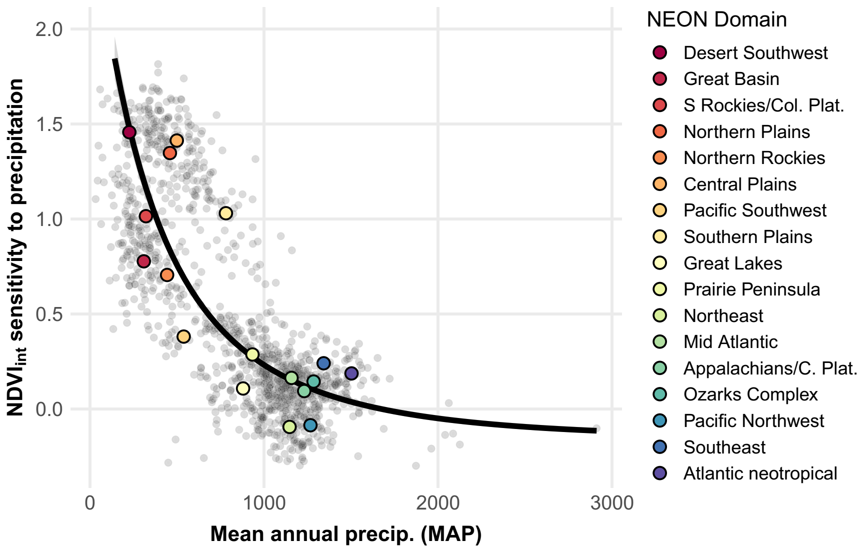

Figure 2 Sensitivity of primary production ($NDVI_{int}$) to precipitation derived from a mixed-effects model relating the two variables at USHCN stations from years 2000 through 2015 (model *P*-value for annual precipitation < 0.001). The y-axis units represent the change in annual primary production ($NDVI_{int}$) per meter of change in precipitation. The sensitivity values of individual USHCN stations (fixed + domain random + station random effects) are shown as grey points and the sensitivity values of NEON domains (fixed + domain random effects) are shown as coloured points (see Fig. S1 for reference). A nonlinear model fit to individual station sensitivities is shown in black ($NDVI_{int} : prcp = c * \left(e^{-MAP}\right)$, Efron's $R^2 = 0.52$, $P < 0.001$).

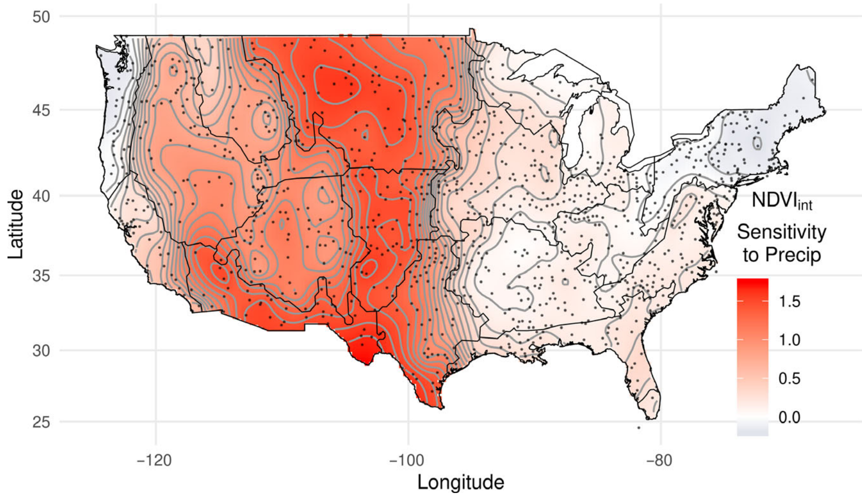

Figure 3 A map of the sensitivity of primary production to precipitation across the conterminous US sensitivity index was calculated for each USHCN station as the temporal relationship between annual primary production ($NDVI_{int}$) and annual precipitation, as described in Fig. 2. These values were then interpolated between stations using kriging. All USHCN station locations are plotted as small black points, with the boundaries of NEON domains outlined in black.

Sensitivity estimates from NPP and GPP were especially low in the arid Desert Southwest domain, and high in the Central and Northern Plains. Conversely, MODIS EVI showed high sensitivity in the Desert Southwest, Central and Southern Plains, and comparatively low sensitivity in the Northern Plains ecoregion. These three proxies also confirmed greater uncertainty in more mesic, less sensitive NEON domains (Fig. S5d–f). Patterns of sensitivity in Pacific Northwest and northeastern US domains were similar between MODIS EVI and NDVI data (Figs 3 and Fig. S5, panel A), suggesting that NDVI saturation was minimal in high-biomass regions of our study area.

Based on temporal patterns of SPEI at the 1218 USHCN stations, aridity has increased significantly since the early 20th century across the western portion of the conterminous US. (Fig. 4a; Table S3). These changes were largest in the Desert Southwest, Southern Rockies and Colorado Plateau and Great Basin domains. During the same period, variability in SPEI (the 5-year CV of SPEI) increased significantly in many regions of the western US. (Fig. 4b; Table S3). In contrast, variability in SPEI has decreased in the eastern US during the past century. Thus, regions where primary production is most sensitive to climate have become more arid and more variable

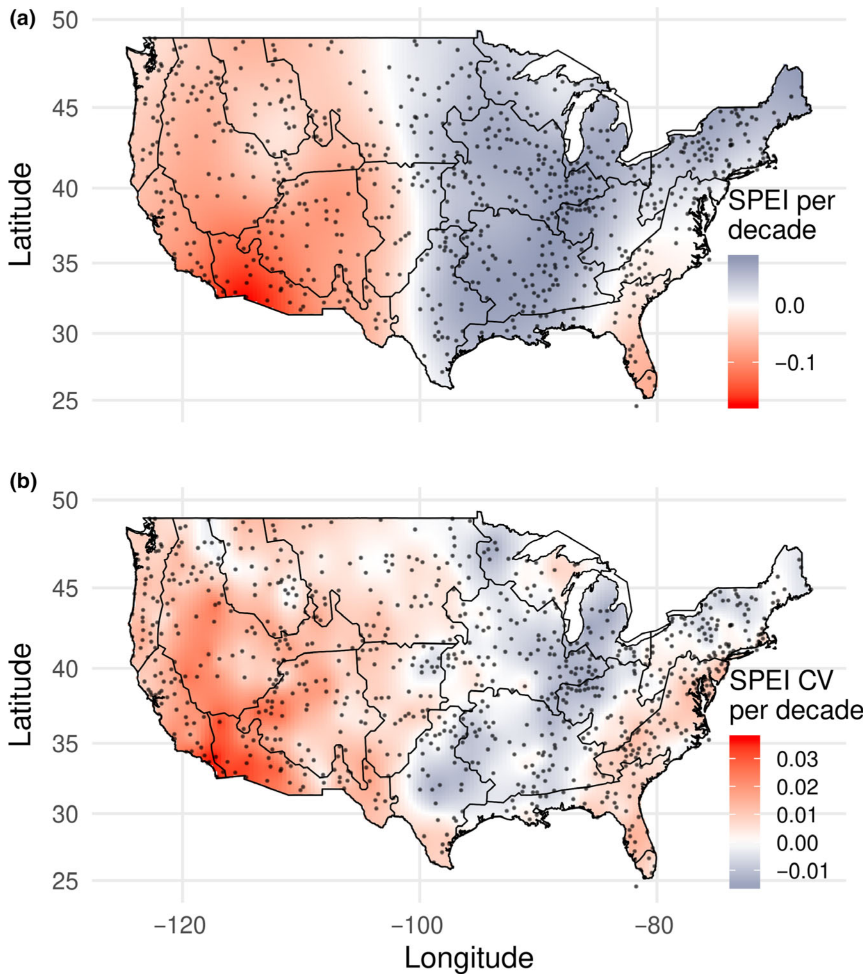

Figure 4 Aridity trends across the conterminous US since 1900. Panel (a) shows trends in SPEI and panel (b) shows trends in SPEI coefficient of variation (CV; 5-year rolling window calculation). Individual trends, that is, the slope coefficients of linear models fit to the time series data, were calculated at each USHCN station and were then interpolated between stations using kriging. Note that negative trends in SPEI indicate intensifying aridity, and positive trends in SPEI CV indicate increasing climatic variability. Significance of trends varied among USHCN stations and only stations with significant trends are indicated by points on the map. NEON domain boundaries are outlined in black.

over time, whereas climate in the eastern US, where the sensitivity of primary production is generally lower, has become more mesic and more stable over time (Table S3).

DISCUSSION

Overall, we found a nonlinear spatial relationship between MAP and NDVI (Fig. 1), consistent with prior analyses based on smaller numbers of observations of ground-based NPP (Rosenzweig 1968; Huxman *et al*. 2004a; Sala *et al*. 2012) or net ecosystem production (NEP; Biederman *et al*. 2016), both of which provide an important source of empirical support for our satellite-derived estimates of productivity. In addition, we found that within site relationships between annual precipitation and primary production were weaker than the spatial relationship across sites (Fig. 2). Decreased sensitivity to precipitation change observed within sites, relative to the spatial model, results from multiple causes, including lags in NPP response as a function of species composition (Sala *et al*. 2012; Isbell *et al*. 2013) and legacy effects (Reichmann *et al*. 2013). Collectively, our results demonstrate that ecosystems exhibit systematic increases in the magnitude of primary production and decreases in the sensitivity of primary production to year-to-year changes in precipitation, along continental-scale precipitation gradients. Together, these observations reinforce previous studies made across ecosystems (Huxman *et al*. 2004a; Biederman *et al*. 2016), but include a much broader range of individual sites and ecosystem types, many of which are representative of ecosystems globally (e.g. deciduous forest, grasslands, drylands, conifer forests).

Some of the most sensitive ecoregions, such as the Central Great Plains and the Desert Southwest, overlap with continental climate change hotspots previously identified in climate model studies (Diffenbaugh *et al*. 2008; Anderegg & Diffenbaugh 2015). These ecoregions are predicted to experience increases in aridity (Seager *et al*. 2007; Gutzler & Robbins 2010) leading to more frequent, longer and more severe droughts (Cook *et al*. 2015) by the end of the 21st century. Consistent with recent studies of continental US warming and drying trends (Anderegg & Diffenbaugh 2015; Lehner *et al*.

2018), our analysis identified several ecoregions, including the Desert Southwest, Great Basin and Southern Rockies/Colorado Plateau, where high sensitivity of primary production converges with strong trends in aridity in the past century (Figure S6). If climatic shifts towards greater aridity and variability continue throughout the rest of the 21st century, as is predicted by global climate models, these ecoregions will be at risk of significant declines in both productivity and vegetation cover. Indeed, climate-driven ecosystem transitions involving shifts in dominant vegetation type and overstory tree mortality are already evident and predicted to continue across the Desert Southwest (Breshears *et al.* 2005; van Mantgem *et al.* 2009; Scott *et al.* 2010; Park Williams *et al.* 2012).

Changes in annual precipitation explain a larger fraction of the variability in primary production (Efron's $R^2 = 0.52$) than does SPEI (Efron's $R^2 = 0.39$). We suggest that the somewhat higher explanatory power of precipitation over SPEI is related to differences in the range and scale of variation of precipitation and temperature from one year to the next (Mowll *et al.* 2015). Indeed, precipitation exhibits higher interannual variability than abiotic drivers such as temperature or wind speed (Okin *et al.* 2018). Nevertheless, it is critical to consider future changes in aridity, which are driven by increases in global surface temperature in response to elevated levels of atmospheric CO_2. Over long timescales, precipitation exhibits limited trends across many regions, while warming trends are widespread and consistent (Diffenbaugh & Field 2013; Anderegg & Diffenbaugh 2015). This is particularly evident across the southwestern US, where warming temperatures have increased atmospheric demand for water, and thus aridity (Fig. 4a), despite no change in mean annual precipitation (Gutzler & Robbins 2010).

In addition to mean precipitation and aridity, changes in climatic variability over time are likely to have significant effects on primary production. Several observational studies demonstrate that the timing and magnitude of precipitation events, or variability in aridity, are important controls on NPP (Huxman *et al.* 2004b; Heisler-White *et al.* 2009; Hsu *et al.* 2012; Rudgers *et al.* 2018). For example, Rudgers *et al.* (2018) found that changes in both mean and variability in SPEI were strongly related to differential, nonlinear responses of NPP in Great Plains versus Chihuahuan Desert grassland ecosystems. Under periods of lower aridity, precipitation variability favoured NPP of Great Plains grassland, whereas variability favoured Chihuahuan Desert grassland as aridity increases. Furthermore, a recent global study found that precipitation variability enhanced above-ground NPP (ANPP) for ecosystems with MAP less than 300 mm per year, but in ecosystems with MAP > 300 mm per year, interannual precipitation variability decreased ANPP (Gherardi & Sala 2019). To keep our analysis consistent across sites, and with prior analyses, we used linear ecosystem sensitivity models that did not estimate the nonlinear effects of climatic variability on primary production (see also Felton *et al.* 2019). However, residual variance in the sensitivity model we fit to SPEI, which integrates climatic variability over the prior year, suggests that nonlinear models might better estimate the response of some regions to changes in aridity. Importantly, our long-term analysis of climate trends among 1218 weather stations showed significant 20th and early 21st century increases in both mean aridity and climatic variability, including the current ecotone region between the Central Plains and Desert Southwest domains (Figs 4a and b).

One of the most striking patterns from our analysis is the clear differentiation between increasing "mesicness" in the eastern US and increasing aridity and variability in the western US over the past century (Figs 4a and b). Interannual variability and directional change in arid and semi-arid ecosystems and consequent effects on NPP have clear implications for the global carbon budget. For example, a recent global carbon sink anomaly was driven by semi-arid ecosystems in the Southern Hemisphere in response to La Niña conditions that caused extended periods of increased precipitation (Poulter *et al.* 2014; Haverd *et al.* 2016). Climatic variability also exacerbates the risk of vegetation mortality. Ecosystems require time to recover from drought or other extreme climatic events, and as the frequency, severity, or duration of such events increases, recovery may become unattainable in many ecosystems (Schwalm *et al.* 2017). Thus, as the climate system produces greater and more frequent extremes, the potential to see nonlinear effects on primary production increases. Though our study does not specifically address such nonlinearities, theoretical and experimental studies of NPP suggest that saturating climate–productivity relationships may lead to hydraulic limitation or ecosystem state changes under high or low precipitation extremes, respectively (Knapp *et al.* 2017; Wilcox *et al.* 2017). Therefore, increased climatic variability has the potential to affect both year-to-year variations in the global carbon budget, as well as the overall size of the terrestrial carbon sink (Gherardi & Sala 2019).

Historically, limited site-level data on ecosystem functioning has prevented a comprehensive understanding of which ecosystems are most sensitive to, and potentially vulnerable to, climate change. Comparative analyses of ecosystem sensitivity to climate have also been hampered by methodological inconsistencies, including differences in the magnitude of climatic variability, response metrics and the spatial and temporal scales of analysis (Knapp *et al.* 2015b). These data gaps and comparability issues create challenges for synthesis and generality regarding how ecosystems have responded to changes in precipitation and temperature in the past and how those responses can be used to forecast dynamics under future climate. Global estimates of ecosystem sensitivity to climate using global biome models and remote-sensing data highlight the sensitivity of boreal, arctic and tropical regions (Nemani *et al.* 2003; Piao *et al.* 2009; Seddon *et al.* 2016), but are coarse in resolution and have granted little attention to sparsely vegetated arid and semi-arid regions. Coupling remote-sensing vegetation dynamics with spatially dense measurements of climate allowed us to generate an integrative measure of ecosystem sensitivity to climate variation that we could then map in great detail across a large section of North America (Fig. 3).

Assessing historical patterns in ecosystem sensitivity to climate provides a strong foundation for predicting and comparing ecosystem responses to future changes in climate at the continental scale. Yet, while historical sensitivity is not necessarily the same as future sensitivity due to the limitations of extrapolating past observations into the climate of the future, the work presented here suggests important baseline trends that can be used as guidelines of future ecosystem responses. It is also important to note that sensitivity does not always imply vulnerability since we know that resistance to change (sensitivity) and the ability to recover from change (resilience) are not necessarily related (Isbell *et al*. 2015). Many ecosystems already experience considerable variability in environmental drivers. Moreover, documenting the degree to which ecosystems differ in their sensitivity to climate does not necessarily elucidate the mechanisms behind those differences. Hypotheses range from nutrient limitation, time lags, legacy effects, variation in ecosystem-level hydraulic patterns (e.g. isohydricity) and variable responses among different vegetation functional types such as annuals, perennial grasses shrubs or trees (Sala *et al*. 2012; Konings *et al*. 2017). Therefore, multiple approximations, such as simulation modelling, remotely sensed-derived data (as reported here) and coordinated distributed experiments are needed to determine mechanisms driving differential sensitivities of ecosystem processes to climate variability (Borer *et al*. 2013; Fraser *et al*. 2013).

Our study greatly extends the analysis of ecosystem sensitivity to year-to-year changes in precipitation both within sites and across the conterminous US, thereby firmly establishing the generality of these spatial and temporal relationships between climate and ecosystem primary production. Of greater significance, we have generated for the first time a map of ecosystem sensitivity to interannual variability of precipitation at the continental scale that can be used as a benchmark against which models and future mechanistic or empirical analyses can be based. Sensitivity of primary production to climate variability differs substantially among biotic regions, and is the highest in regions that are already transitioning to a more arid and variable climate. This pattern is most notable in dryland and grassland ecosystems of the western US. These same sensitive regions are predicted to experience severe climate extremes by 2100 (Cook *et al*. 2015), likely inhibiting their ability to provide essential ecosystem services needed by a growing human population (Reynolds *et al*. 2007). We suggest that climate change research and mitigation efforts identify and focus on areas that are highly sensitive to climate variability and are changing rapidly under multiple drivers of global environmental change.

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DATA ACCESSIBILITY STATEMENT

All raw data used in this study are public. Weather station data came from NOAA's public USHCN archive at ftp://ftp.ncdc.noaa.gov/pub/data/ushcn/v2.5/ on 2017-05-21 (ushcn.v2.5.5.20170521). The MODIS NDVI and EVI data sets are available at https://dx.doi.org/10.3334/ORNLDAAC/1299 and https://doi.org/10.5067/MODIS/MOD13Q1.006 respectively. MODIS NPP and GPP products (Robinson *et al*. 2018) are available as Google Earth Engine ImageCollection IDs UMT/NTSG/v2/MODIS/NPP and UMT/NTSG/v2/MODIS/GPP. The R code used in data processing, formal analysis, statistics, and figure creation is published, along with key-derived data sets, at Figshare (https://doi.org/10.6084/m9.figshare.c.4780313).

AUTHORSHIP

All authors conceived of the research. GM, AH and RB assembled the data and performed exploratory data analysis. GM performed formal analysis with input from other authors. SC, OS and GM wrote the manuscript with direct contributions from other authors. All authors reviewed and edited the manuscript.

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

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