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Key Points:

- Convergence of hillslope topography contributes to higher ecosystem net primary productivity across the majority of the western United States
- Hillslope convergence reduces ecosystem sensitivity to climate, especially within semiarid regions
- Ecosystems in flat, arid environments are the most vulnerable to drought-induced reductions in productivity

Supporting Information:

- Supporting Information S1

Correspondence to:

Z. H. Hoylman,
zhoymal@gmail.com

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The Topographic Signature of Ecosystem Climate Sensitivity in the Western United States

Zachary H. Hoylman^{1,2}, Kelsey G. Jencso^{1,2}, Jia Hu³, Zachary A. Holden⁴, Brady Allred^{2,5}, Solomon Dobrowski², Nathaniel Robinson⁵, Justin T. Martin⁶, David Affleck², and Carl Seielstad^{2,7}

¹Montana Climate Office, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA,

²W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA, ³School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA, ⁴USDA Forest Service, Northern Region, Missoula, MT, USA, ⁵Numerical Terradynamic Simulation Group, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA, ⁶Department of Ecology, Montana State University, Bozeman, MT, USA,

⁷National Center for Landscape Fire Analysis, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA

Abstract It has been suggested that hillslope topography can produce hydrologic refugia, sites where ecosystem productivity is relatively insensitive to climate variation. However, the ecological impacts and spatial distribution of these sites are poorly resolved across gradients in climate. We quantified the response of ecosystem net primary productivity to changes in the annual climatic water balance for 30 years using pixel-specific linear regression (30-m resolution) across the western United States. The standardized slopes of these models represent ecosystem climate sensitivity and provide a means to identify drought-resistant ecosystems. Productive and resistant ecosystems were most frequent in convergent hillslope positions, especially in semiarid climates. Ecosystems in divergent positions were moderately resistant to climate variability, but less productive relative to convergent positions. This topographic effect was significantly dampened in hygric and xeric climates. In aggregate, spatial patterns of ecosystem sensitivity can be implemented for regional planning to maximize conservation in landscapes more resistant to perturbations.

Plain Language Summary: It is well known that gradients in elevation and aspect can have a significant influence on the degree of water and energy available for plant growth and the sensitivity of ecosystems to wet or dry time periods. Little work has examined how hillslope topography and downslope movement of water to zones of convergent terrain can impact plant available water and vegetation growth. We quantified ecosystem response to the climatic water balance (ecosystem sensitivity) across a 30-year record and at a 30-m resolution across the western United States. Our results show that vegetation in zones of hillslope convergence, where moisture from upslope tends to accumulate, is less sensitive to droughts, especially in semiarid settings. Divergent hillslope positions were moderately sensitive to climate and less productive relative to convergent positions. Ecosystem response to topography was dampened in especially wet or dry climates due to significant moisture surplus or moisture deficit, respectively. These distributed measurements of ecosystem sensitivity are important considerations when describing local ecosystem-climate relationships and for identifying management priorities across landscapes. Zones of resistant vegetation are more likely to persist through future droughts, influencing the greater ecosystem's response to climate change.

1. Introduction

Identifying the sensitivity of ecosystems to climate is an important consideration in conservation planning (Keppel et al., 2015) and may provide a means to promote climate adaptation (Morelli et al., 2016). Areas of reduced ecosystem sensitivity to climate are likely to support the persistence of climate refugia (Ashcroft, 2010; Dobrowski, 2011; Rull, 2009) and influence climatic connectivity as species move in response to increasing dryness (Carroll et al., 2018; Dobrowski et al., 2013; Dobrowski & Parks, 2016). Therefore, a suggested strategy for conservation and management efforts is to identify factors that contribute to the sensitivity of vegetation to drought and longer term climatic change in order to leverage natural ecosystem resistance (Keppel et al., 2015; Morelli et al., 2016).

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Research across the globe has documented productivity-climate relationships associated with regional differences in variables such as temperature, precipitation, radiation, and cloud cover (Churkina & Running, 1998; Schuur, 2003; Seddon et al., 2016; Vicente-Serrano et al., 2013; Vicente-Serrano et al., 2018). However, the sensitivity of ecosystem net primary productivity (NPP) to climate within a given region may also be explained by complex topographic gradients that contribute to lateral flows of energy and water, but at hillslope scales. In many semiarid ecosystems, productivity is constrained by subsurface moisture availability to plants, which is determined by the partitioning of regional climate into runoff, evapotranspiration (actual evapotranspiration [AET]), and subsurface storage (Eagleson, 1978; Rodriguez-Iturbe, 2000). Topographically driven hydrologic processes (e.g., lateral flows of soil water and groundwater; Dingman, 2015) and atmospheric processes (e.g., cold air drainage, vapor pressure deficit-soil moisture feedbacks, and radiation shading; Entekhabi et al., 1996; Frey et al., 2016) modify climatic partitioning of moisture across complex landscapes, producing heterogeneous patterns of plant available water.

Striking differences in subsurface moisture content and atmospheric vapor pressure can emerge across distances of meters due to topographic convergence and divergence in the landscape (e.g., topoclimates/microclimates; Hoylman et al., 2019). Additionally, the hydraulic properties of soil resulting from physical and geochemical soil processes (Brubaker et al., 1993; Seibert et al., 2007), weathering of parent material (Clair et al., 2015; Gabet et al., 2006), and indirect biophysical feedbacks (Dietrich & Perron, 2006; Yetemen et al., 2010) can also influence the storage and release of water to vegetation between upslope and downslope positions. Therefore, at the scale of hillslopes, vegetation can experience a large range of moisture availability and microclimates, which deviate significantly from regional climate conditions due to topographic position.

Vegetation responds to hillslope scale variations in moisture (Hoylman et al., 2018; Istanbulluoglu et al., 2008; Ivanov et al., 2008; Swetnam et al., 2017), creating zones where ecosystems may be buffered from climatic moisture limitations. The degree of buffering is determined collectively by the topographic properties of the landscape (flat vs. convergent, single drainage vs. highly dissected), seasonal delivery of water and energy (climatic water and energy balance), and the physiological responses by vegetation within the ecosystem itself. Areas of reduced ecosystem-climate sensitivity may only exist where regional climatic conditions promote the occurrence of requisite hydrological and meteorological processes (e.g., microclimates, enhanced soil moisture, and near surface groundwater tables) that facilitate establishment, growth, and productivity (McLaughlin et al., 2017).

Here we examine the spatial expression of ecosystem climate sensitivity across the western United States. To characterize ecosystem sensitivity, we computed pixel-specific linear regressions (30-m pixel resolution) between the climatic water balance (deficit = potential evapotranspiration [PET] – AET; Stephenson, 1998) and Landsat-derived ecosystem NPP (Robinson et al., 2018) using 30 years of record (1986–2015). The standardized slope of this relationship represents ecosystem sensitivity and is a simple metric that considers both annual climatic water availability and the resulting plant growth. To isolate the effect of topography, we quantified distributions of ecosystem sensitivity within intervals of the local climatic water balance and hillslope topography (from divergent to flat to convergent). Our results highlight the importance of topography for hillslope scale variations in moisture, creating zones where ecosystems are buffered from climate. Together, these analyses provide important information for the conservation and management of ecosystems from hillslope to regional scales.

2. Materials and Methods

2.1. Ecosystem Productivity Data

We utilized gridded datasets of annual NPP that were produced for the continental United States at a 30-m grid resolution from 1986 to 2015 (Robinson et al., 2018; Figures 1a and 2a and 2b). NPP was calculated using the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD17 algorithm (Running et al., 2004; Sims et al., 2008; Smith et al., 2016). Gross primary productivity was calculated using the daily fraction of photosynthetically active radiation estimates from Landsat surface reflectance products (Feng et al., 2012; Masek et al., 2006; Vermote et al., 2016), meteorological data from gridMET (Abatzoglou, 2013), land cover classifications from the National Land Cover Database (NLCD; Homer et al., 2007; Homer et al., 2015; Fry et al., 2011), and optimized biome-specific parameters (Robinson et al., 2018). NPP was calculated

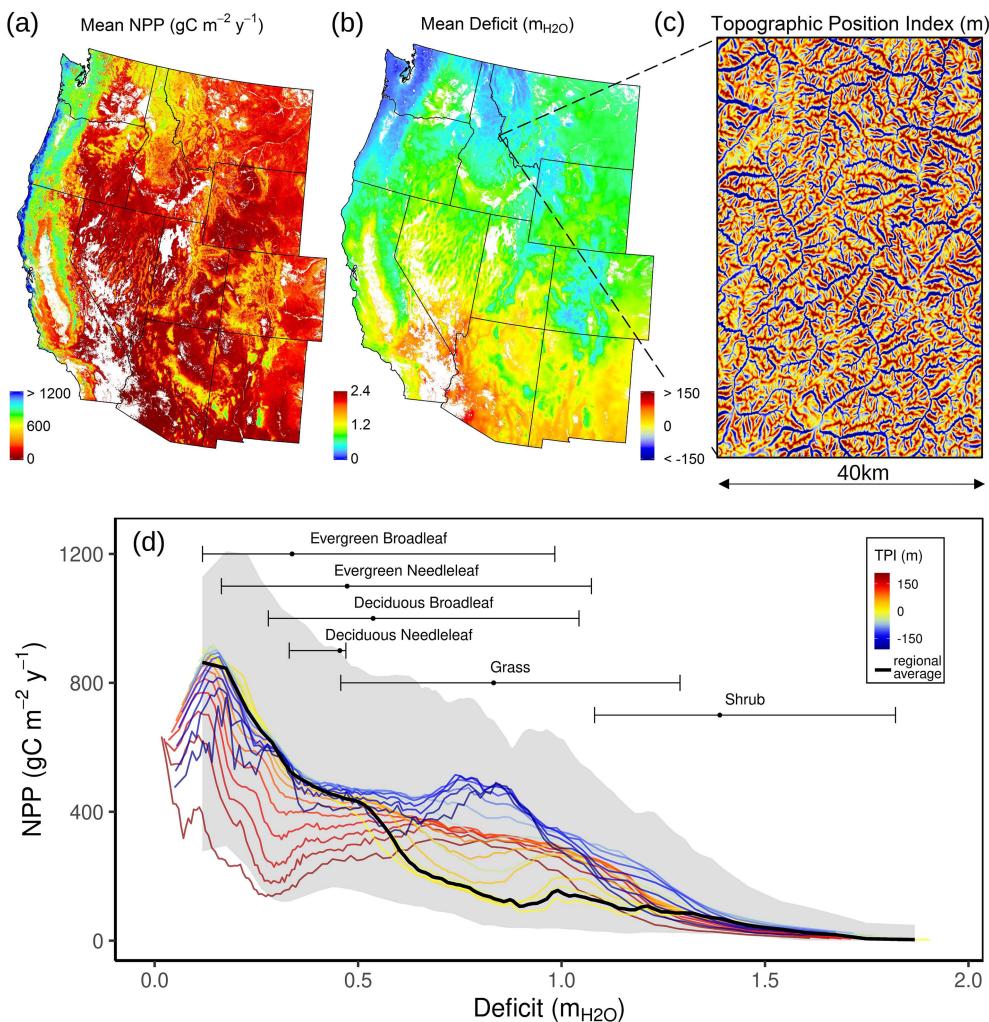


Figure 1. (a) The average annual net primary productivity (NPP) and (b) climatic water deficit (deficit = potential evapotranspiration – actual evapotranspiration) for the western United States calculated using annual data from 1986 to 2015. An example region from Montana shows (c) the topographic position index (TPI) of a mountainous region. The negative TPI values represent convergent topographic positions and positive values represent divergent positions. The white regions represent agricultural, urban, and nonvegetated lands that were removed from analysis. (d) The relationship between the climatic water deficit and ecosystem NPP for the western United States. We discretized the entire western United States into 100 quantiles of the deficit. For each deficit quantile the median (black line) and 5th and 95th quantiles (grey ribbon) of NPP are shown. The effect of topography was quantified by repeating this analysis on discrete deficit regions defined by the TPI (lines color coded by red-blue color gradient). The lines transitioning from red to yellow to blue indicate a gradient from divergent to flat to convergent landscape positions. The 5th and 95th deficit quantiles associated with each plant functional type are represented by the horizontal bar and the median value is represented by the scatter point on each horizontal bar.

as the sum of the daily differences between GPP and maintenance respiration, minus annual growth respiration.

2.2. Climatic Water Balance Data

The climatic water balance imparts a strong control over the spatial distribution of plant functional types and is an important driver of ecosystem productivity. We used daily estimates of PET and AET output from a 8 arc-second ($\sim 250 \text{ m}$) gridded soil water balance model, evaluated from 1986 to 2015 (Holden et al., 2019), to calculate the climatic water deficit (deficit = PET – AET). We then calculated the total annual deficit for each year, which represents the unmet atmospheric demand for moisture. Using the nearest neighbor method, we resampled the 250-m deficit dataset to match the NPP grid resolution (30-m) in Google Earth Engine (GEE; Gorelick et al., 2017). This climatic water balance is topographically resolved with respect

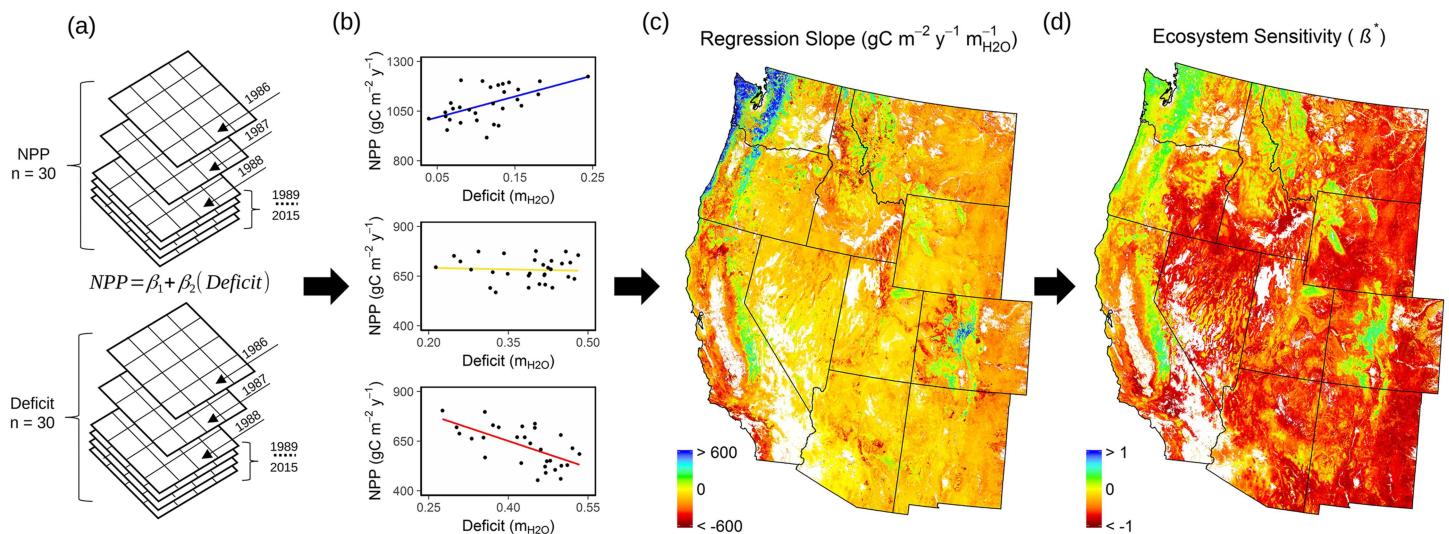


Figure 2. (a) Diagram showing how pixel-specific regressions are computed across the spatial grid. (b) Scatter plots showing example regressions between the climatic water deficit (deficit = potential evapotranspiration – actual evapotranspiration) and annual net primary productivity (NPP) for three 30-m pixels across 30 years. (c) The spatial distribution of regression slopes for each pixel across the western United States. (d) The spatial distribution of standardized regression slopes (β^* , ecosystem sensitivity) computed using the pixel-specific deficit and NPP distributions. Ecosystem sensitivity accounts for differences in NPP and deficit variance to compare the response of NPP to annual climate dynamics across ecosystems. Negative ecosystem sensitivity values represent ecosystems where NPP declines during times of water limitation, while values close to zero represent insensitive ecosystems. Positive sensitivity values are representative of ecosystems that show increases in NPP during years with increased climatic water deficits and higher PET.

to elevation effects on precipitation, aspect effects on incident radiation, and shading effects from adjacent terrain but does not incorporate lateral flow of water in the subsurface.

2.3. Landscape Topography Characterization

Surface topography has been identified as an important factor driving water movement in the subsurface (Dingman, 2015; Moore et al., 1991) and is used commonly to describe probabilistic soil moisture distributions (Grayson et al., 1997; Western et al., 1999; Western et al., 2004). In addition, topographic gradients are known to affect atmospheric conditions and the development of microclimates (Chen et al., 1999; Frey et al., 2016; Hoyleman et al., 2019; Young et al., 1997). To approximate the summed effect of topographically driven hydrological processes that can occur in complex terrain, we extracted digital elevation models derived from the Shuttle Radar Topography Mission dataset (Farr et al., 2007) at a 30-m resolution and conducted terrain analysis over the domain. We selected the topographic position index (TPI; Weiss, 2001) to describe the distribution of topographic positions across the western United States. The TPI was calculated at a 30-m grid resolution using a 1,000-m circular focal radius to preserve hillslope to watershed scale gradients in topographic relief (Figure 1c). The TPI is calculated as:

$$TPI = z_0 - \bar{z}$$

$$\bar{z} = \frac{1}{n_A} \sum_{i \in A} z_i$$

where z_0 is the elevation of a pixel, \bar{z} is the focal mean elevation of pixels in an area (A) defined as the area within a 1,000-m radius of pixel z_0 , and n_A is the number of pixels in A . The TPI is a topographic metric, which considers the relative difference in elevation of a pixel with respect to the focal mean of the surrounding pixels (topographic position). Progressively negative TPI values represent toe-slope and valley bottom topographic positions (i.e., convergent topographic positions), while progressively positive TPI values represent sideslope and ridgeline positions (i.e., divergent topographic positions). The TPI has been used to describe landforms across complex terrain (Weiss, 2001), spatial variability of soil N_2O and CO_2 fluxes (Arias-Navarro et al., 2017), and patterns of vegetation productivity, biomass, and forest structure across watersheds (Hoyleman et al., 2018; Swetnam et al., 2017).

2.4. Plant Functional Type

To remove unwanted land cover types from the analysis and determine how plant functional types related to ecosystem sensitivity, we used the 2015 annual MCD12Q1.006 MODIS Land Cover Type 5, Plant Functional Type scheme (Friedl & Sulla-Menashe, 2015) resampled to a 30 m using nearest neighbor procedures in GEE. We removed all cereal and broadleaf croplands, urban and built-up lands, permanent snow and ice, nonvegetated lands, and water bodies from the analysis. Therefore, the ecosystems we characterized in this analysis were composed of evergreen needleleaf trees, evergreen broadleaf trees, deciduous needleleaf trees, deciduous broadleaf trees, grasses, and shrublands.

2.5. Statistical Analysis:

2.5.1. Pixel-Specific Linear Regression

For each 30-m pixel across the western United States we calculated linear regressions between the climatic water deficit and NPP to describe the local productivity-climate relationship (regression slope: β_2) using gridded time series from 1986 to 2015 (Figures 2a–2c). We used linear regressions due to computational limitations in response to the very large number of pixel-specific regressions considered (30-year annual time series of NPP and deficit at 2,870,751,368 locations). These simple regressions do not capture potential nonlinear behaviors between vegetation growth, mortality, and the climatic water deficit. Statistical models were computed using GEE (Gorelick et al., 2017). We did not remove regressions with nonsignificant slope coefficients (i.e., p -values > 0.05) in order to preserve pixels with slopes close to 0 (insensitive pixels; see Figure 2b). Instead, to assess the performance of each linear regression, we calculated the root-mean-square error of each linear regression to describe the pixel-specific regression error (Figure S1 in the supporting information). We then normalized the linear regression slopes (Figure 2c) to account for different distributions of NPP and deficit at each pixel by calculating standardized regression coefficients (β^* ; Bring, 1994):

$$\beta^* = \beta_2 \times (\sigma_{\text{deficit}} / \sigma_{\text{NPP}})$$

where β^* is the standardized regression slope (Figure 2d, considered ecosystem sensitivity), β_2 is the original regression slope (Figure 2c), σ_{deficit} is the standard deviation of the pixel-specific deficit distribution, and σ_{NPP} is the standard deviation of the pixel-specific NPP distribution. This normalization was necessary to conduct cross-pixel comparisons of regression slopes (for example for bordering pixels with differing vegetation types). Vegetation type, density, and cover directly influence the NPP distribution of a pixel and thus, the raw regression slope. By accounting for spatial variation in NPP (and deficit) magnitude and variance we can compare ecosystem sensitivity across locations with differing climatic and physiological characteristics.

2.5.2. Regional Analysis

Spatiotemporal gradients in the climatic water balance exhibit a strong control over global vegetation distributions (Stephenson, 1998; Woodward, 1987) and serve as a biologically meaningful representation of the climatic drivers of productivity (Vicente-Serrano et al., 2015). In order to quantify the effect of regional climate gradients on average ecosystem NPP and the sensitivity of ecosystem NPP to the annual water balance (ecosystem sensitivity; β^*), we aggregated NPP and ecosystem sensitivity values for the western United States into 100 bins that were determined by the 30-year mean climatic water deficit. Each bin consisted of 1% of the domain area (100 deficit quantiles, $\sim 25,836 \text{ km}^2$ in each bin) from which the median value, 5th and 95th quantiles of NPP, and ecosystem sensitivity (β^*) were calculated. We compared these measures of response to the median deficit value for a deficit bin (Figures 1d and 3a). To assess how spatial patterns of dominant plant functional types varied within the regional continuum of ecosystem sensitivity, we calculated the climatic conditions which were associated with each plant functional type. To do so, we calculated the median (Figures 1d and 3a; black scatter point) and 5th and 95th deficit quantiles (Figures 1d and 3a; horizontal bars) experienced by each plant functional type across the western United States.

2.5.3. Topographic Position Analysis

We evaluated how spatial patterns of NPP and ecosystem sensitivity (β^*) were affected by hillslope scale gradients in topographic position by extracting NPP, ecosystem sensitivity, and climatic water deficit grids that were aligned with discrete classes of the TPI. Classes of TPI were determined using equal 20-m

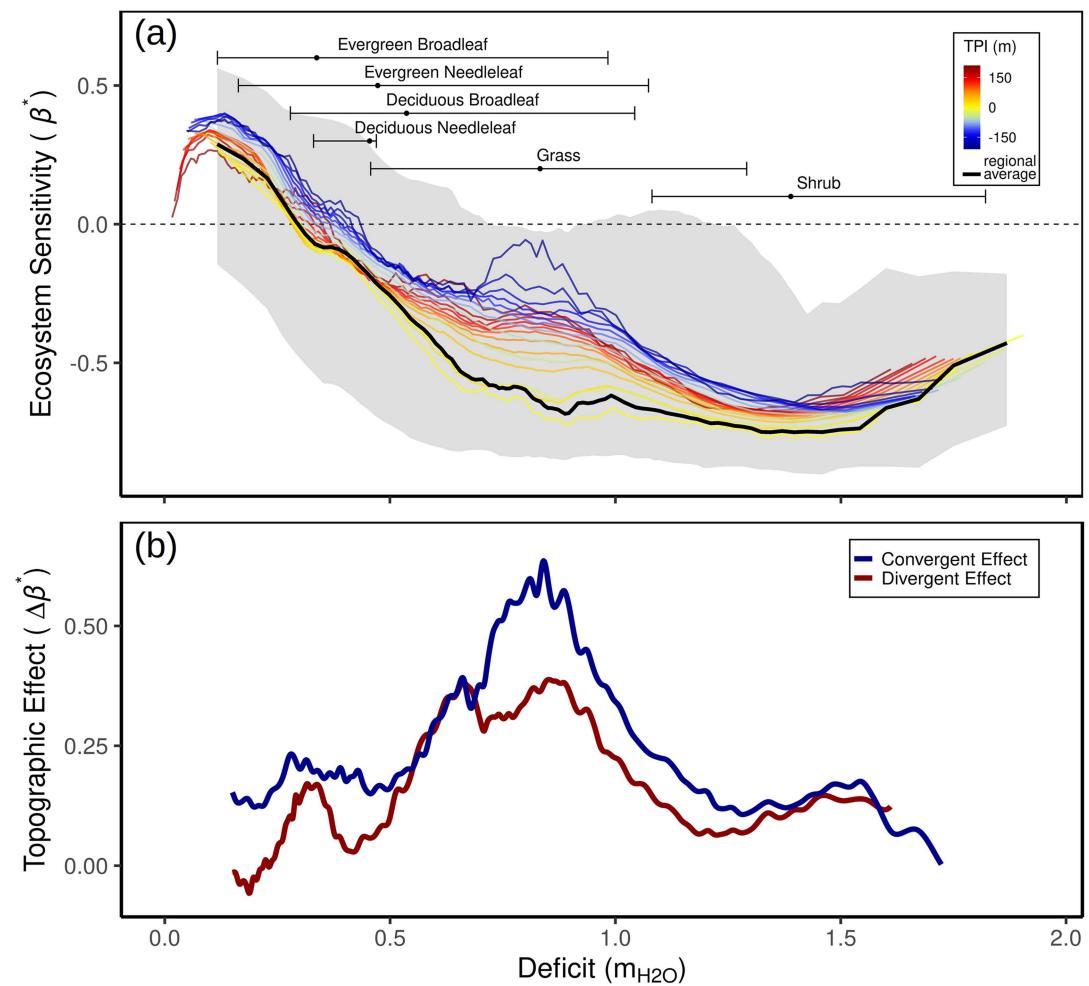


Figure 3. (a) The relationship between the climatic water deficit (deficit = potential evapotranspiration – actual evapotranspiration) and ecosystem sensitivity (β^*) for the western United States. We discretized the entire western United States into 100 quantiles of the deficit. For each deficit quantile the median (black line) and 5th and 95th quantiles (grey ribbon) of ecosystem sensitivities are shown. The effect of topography was quantified by repeating this analysis on discrete deficit regions defined by the TPI (lines color coded by red-blue color gradient). The lines transitioning from red to yellow to blue indicate a gradient from divergent to flat to convergent landscape positions. The 5th and 95th deficit quantiles associated with each plant functional type are represented by the horizontal bar, and the median value is represented by the scatter point on each horizontal bar. (b) The relative influence of topography on ecosystem sensitivities was calculated as the difference in ecosystem sensitivity (β^*) between flat, highly convergent and highly divergent positions within a given deficit region.

breaks that ranged from TPI values of less than -190 m to greater than 190 m . Once we extracted grids associated with each TPI class, we replicated the regional analysis described above for each TPI class; we aggregated the data into 100 quantile bins based on the TPI-specific climatic water deficit distribution. Within each TPI-specific deficit bin, we calculated the median NPP and ecosystem sensitivity (β^*) value (Figures 1d and 3a).

To quantify the relative effect of topography on ecosystem sensitivity across the western United States deficit gradient, we calculated the difference in ecosystem sensitivity ($\Delta\beta^*$; Figure 3b) between the flat TPI class ($10 > \text{TPI} > -10$; Figure 3a; yellow line) and the most convergent/divergent TPI class (Figures 3a and 3b; $-190 > \text{TPI}, 190 < \text{TPI}$; dark blue, dark red lines respectively). To do so, we interpolated these two lines into equal intervals of the deficit using a spline function and calculated the difference between the convergent/divergent and flat median sensitivity values across the deficit gradient.

3. Results

The complexity of ecosystem climate sensitivity across the western United States was strongly influenced by the spatial alignment of the climatic water balance and local hillslope topography (Figures 3a and 3b). Across most regions of the west, we found a reduced sensitivity of NPP to annual climate fluctuations (ecosystem sensitivity) and greater rates of NPP across sites with convergent topography (Figures 1d and 3a and 3b). We also observed a reduction in ecosystem sensitivity along divergent hillslope positions, although rates of NPP in these locations were substantially lower than convergent sites (Figures 1d and 3a and 3b). Importantly, the effect of topography on ecosystem productivity was contingent on local aridity. Semiarid ecosystem productivity (absolute rate and sensitivity) was the most responsive to topographic effects (Figures 3a and 3b; $0.6 \text{ m} < \text{deficit} < 1.0 \text{ m}$), and these climatic regions represent 43.8% of the western United States landscape. Here, vegetation in flat topographic positions was the most sensitive to annual fluctuations in the climatic water balance ($10 > \text{TPI} > -10$; $640,715 \text{ km}^2$), vegetation in divergent positions was less sensitive ($\text{TPI} > 100$; $\sim 9,738 \text{ km}^2$), and vegetation in convergent positions was the least sensitive ($\text{TPI} < -100$; $\sim 8,126 \text{ km}^2$; Figures 3a and 3b). The topographic effect was substantially lower in mesic/hygric (deficit $< 0.6 \text{ m}$) or arid sites ($1.0 \text{ m} < \text{deficit} < 1.5 \text{ m}$). Finally, topographic position had little influence on ecosystem climate sensitivity in xeric locations with average deficits $> 1.5 \text{ m}$, although divergent positions tended to be slightly less sensitive than the regional average.

The majority of the western United States exhibited negative ecosystem climate sensitivities, representing reduced NPP during dry years and water-limited ecosystem response. Water-limited conditions tended to occur where the annual climatic water deficit was greater than 0.3 m (Figures 1b, 2d, and 3a). Hygric areas with deficits less than 0.3 m were aligned with positive ecosystem sensitivities (Figure 3a), representing increasing NPP with increasing annual deficit. These areas were generally located in mountainous terrain (e.g., Sierra Nevada Range and Rocky Mountain Range) and in coastal climatic regions (e.g., Washington/Oregon coast and the Olympic Peninsula) characterized by energy-limited ecosystems. Ecosystems were the most sensitive to annual variations in the climatic water balance in regions with deficits of $\sim 1.5 \text{ m}$; however, in xeric climates (deficit $> 1.5 \text{ m}$), ecosystem-climate sensitivity decreased (* trended toward 0).

Vegetation land cover type was related to the 30-year mean deficit of a pixel (Figure 3a). Generally forest ecosystems were present in regions with less than $\sim 1\text{-m}$ deficit, while grasslands were present from $\sim 0.5\text{-}$ to 1.3-m deficit and shrublands were present from $\sim 1.1\text{-}$ to 1.8-m deficit (Figure 3a). Evergreen needleleaf and evergreen broadleaf land cover types dominated ecosystems in the most hygric portions of the western United States and exhibited the most positive ecosystem sensitivity to the deficit. The most negative ecosystem sensitivity occurred at the transition from grass to shrub dominated landscapes where the deficit was $1.3\text{--}1.5\text{m}$.

4. Discussion

There has been a need to characterize “where and when, across the diverse and dynamic environments of the globe” we can expect hydrological processes associated with topography (e.g., groundwater, shallow soil moisture, and microclimates) to be relevant for predictions of the carbon balance (Fan et al., 2019; McLaughlin et al., 2017). We found that vegetation in convergent zones were generally the least sensitive to climate (in water-limited settings) or had the greatest positive response to dryness (in energy-limited settings) across the majority of the western United States (Figure 3a). However, the relative importance of topography for ecosystem sensitivity varied across gradients in the climatic water balance. Our analysis provides strong evidence that topography has the greatest effect on ecosystem sensitivity in semiarid climates but little effect in especially wet or dry regions (Figure 3b). To our knowledge, this finding has never been quantified and reported at this scale or level of detail. Our results also highlight that vegetation in divergent topographic positions are less sensitive to climatic variability, albeit to a lesser degree than vegetation in convergent positions (Figures 3a and 3b). Vegetation in flat positions was the most sensitive to climate, except in energy-limited regions where the climatic water deficit was low (deficit < 0.3).

Our results reflect the strong gradients in moisture associated with topographic positions that buffer ecosystems from regional climate dynamics (Hoyleman et al., 2018; Hoyleman et al., 2019; Ivanov et al., 2008;

Swetnam et al., 2017). We posit that semiarid regions experience transient to prolonged shallow subsurface flow (e.g., Jencso et al., 2009) in convergent locations, thereby enhancing soil moisture and reducing ecosystem water limitations along downslope positions (Hawthorne & Minitat, 2018; Hwang et al., 2012; Maxwell & Condon, 2016). Atmospheric microclimates also occur in convergent landscape positions and contribute to feedbacks that reduce evaporative fluxes from the soil (Entekhabi et al., 1996; Hoyleman et al., 2019) and prolong the buffering effect produced by soil moisture and groundwater movement in the near surface rooting zone. In these locations, enhanced soil moisture buffers ecosystem water use (i.e., transpiration) from climate (Hawthorne & Minitat, 2018) and prolongs the growing season in more convergent hillslope positions (Hoyleman et al., 2018; Hoyleman et al., 2019; Martin et al., 2017). Weathered bedrock has also been shown to be a significant moisture storage reservoir, especially along upslope divergent positions (Rempe & Dietrich, 2018). Morphological adaptation of vegetation along divergent positions may exploit this moisture by extending roots deep into the weathered bedrock (Fan et al., 2017). Thus, “rock moisture” may sustain plant water demand during drought and contribute to reduced ecosystem sensitivity on divergent hillslope positions (Figures 3a and 3b).

The relatively small percentage of the western United States ecosystem with positive slopes (12.4%; Figures 2d, 3a, and S2a) are indicative of locations where energy availability (radiant energy, temperature, growing season length, and thus annual PET) as opposed to water availability was a dominant climatic driver of ecosystem productivity (Schuur, 2003; Churkina et al., 2005; Seddon et al., 2016; Figure 3a). In these climatic regions, flatter areas had higher rates of productivity compared to divergent or convergent hillslope positions (Figure 1d), likely due to greater exposure and therefore daily photosynthetically active radiation. The topographic effect on ecosystem sensitivity was reduced in this energy-limited environment due to more homogeneous moisture availability across all landscape positions (Figures 3a and 3b). Positive relationships between NPP and the deficit (i.e., ecosystem sensitivity values greater than 0 across the deficit gradient; dashed line in Figure 3a) may also reflect ecosystem water usage from near-surface reservoirs such as persistent regional groundwater tables (Fan et al., 2013; Fan et al., 2017). Biogeochemical and biological factors (such as nutrients, biological competition, and species richness; Mittelbach et al., 2001; LeBauer & Treseder, 2008) also contribute to spatial patterns of NPP and the associated sensitivity to climate, especially where water limitations do not dominate. These energy-limited ecosystems may become a greater sink for atmospheric carbon as climate increases annual PET across the west (Fu & Feng, 2014).

The dominance of negative ecosystem sensitivities across the majority of the western United States (i.e., deficit > 0.3 m; Figure 3a; 87.6% of the land area) agrees with previous work and provides further evidence that water is a significant limitation for ecosystem productivity across the region (Littell et al., 2008; Seddon et al., 2016; Vicente-Serrano et al., 2013). In general, ecosystems became more sensitive to annual climatic fluctuations (* decreased) as the climatic water deficit became more arid and the deficit increased (Figure 3a). The increasing sensitivity of NPP to the climatic water balance indicates that these ecosystems become increasingly opportunistic[vulnerable] to moisture availability[limitation] as they are located in progressively drier climates. Importantly, in moderately water-limited regions (semiarid), vegetation in zones of topographic convergence had the highest rates of NPP (Figure 1d) and were the least sensitive to variability in the climatic water balance (Figure 3a).

Ecosystem-climate sensitivity decreased (* trended toward 0) where shrubs became the dominant plant functional type over grasses (Figure 3a) in xeric climates (deficit > 1.5 m). This inflection may reflect species traits more adapted to arid environmental conditions and rapidly changing water availability (Chaves et al., 2003), although NPP in these regions remained very low (Figure 1d). Drought tolerance has been observed in shrubs and can be attributed to seasonal modification to leaf water relations and gas exchange capacity that result in positive leaf turgor in times of extreme soil water deficits (Reynolds et al., 1999). Shrub drought avoidance has also been observed in species with deep rooting depths, preventing prolonged stomatal closure during drought (Hinckley et al., 1983).

Analysis of ecosystem sensitivity to climate can identify those ecosystems vulnerable to water stress, providing a context for identifying areas more likely to experience drought-induced declines in productivity and species shifts. As regional climatic water deficits become progressively more arid throughout the century (Barnett et al., 2005; Ficklin & Novick, 2017; Fu & Feng, 2014; IPCC, 2013; Leung et al., 2004) we expect the climate sensitivity of western United States ecosystems to increase, resulting in greater vulnerability to drought induced stress and decreased NPP (e.g., shifting right along Figures 1d and 3a). Exceptions to this

generality may arise in hygric or xeric regions where significant moisture surpluses (hygric) and physiological adaptations (xeric) will likely slow ecosystem responses to a changing water balance.

5. Limitations and Implications

Our results show a clear effect of local landscape topography and the importance of its distribution within a given region for quantifying ecosystem sensitivity to drought (Figures 3a and 3b). We did not explicitly characterize the active hydrological processes that occurred across varying topographic settings of the western United States climate gradient. Instead, we inferred key processes from the wealth of experimental and theoretical hydrology studies that have documented the importance of landscape topography for water redistribution and storage in the subsurface and near-surface atmosphere (Beven & Kirkby, 1979; Hoylman et al., 2019; Jencso et al., 2009; Rasmussen et al., 2015; Troch et al., 2003; Western et al., 2004), contributing to the persistence of plant available water in convergent settings (Fan et al., 2017; Hawthorne & Miniat, 2018; Maxwell & Condon, 2016; Moeslund et al., 2013; Tai et al., 2017) and in some cases, divergent settings (Fan et al., 2017; Rempe & Dietrich, 2018).

Hydrological processes and their persistence are highly dependent upon the topography, soil, geology, vegetation, anthropogenic modification, and the amount of water and energy available in a given landscape (Wagener et al., 2007). In the future, it will be important for ecological studies to explicitly identify and incorporate the spatial distribution of active hillslope hydrology processes, and their potential to change with climate shifts, if we are to fully predict ecosystem trajectories in water-limited landscapes (Fan et al., 2019; Simeone et al., 2018; Tai et al., 2017). One potential way forward is to perform site-specific analysis across the ecosystem sensitivity gradient (Figures 2d and 3a) using field-based hydrology approaches (e.g., Martin et al., 2017; Hawthorne & Miniat, 2018; Hoylman et al., 2019) or distributed ecohydrology modeling frameworks that couple the water and carbon cycles (e.g., Maneta & Silverman, 2013; Simeone et al., 2018; Tague & Band, 2004)

We present a simple and mappable empirical method to identify ecosystems that are buffered from annual climate fluctuations (e.g., Figure S2a), an important consideration when describing local ecosystem-climate relationships and for identifying conservation and management priorities across scales (Morelli et al., 2016). It is well known that factors such as climate and climate change, combined with topography, soil types, nutrient availability, and disturbance regimes, are central drivers of the state and potential trajectory of ecosystems (Box, 1996; Delcourt et al., 1982; McCarty, 2001). Ultimately, plant species must “migrate” in response to climate change, as they can only survive, compete, and reproduce within the range of climate and resource availability to which they are physiologically adapted. By combining gridded climatic water balance data with measures of biological response (i.e., ecosystem NPP) we can assess the potential for plant communities to persist across differing landscape positions into the future. While the zones of resistant vegetation identified here represent a small fraction of the landscape (Figure S2a), their persistence through future droughts effects the greater ecosystem response to climate change. Topographically buffered vegetation will be more likely to sustain ecosystem species assemblages outside of their regional distribution (Dobrowski, 2011; McLaughlin et al., 2017; Rull, 2009) and influence the migration corridors of ecotones as PET and AET partitioning changes into the future (Allen & Breshears, 1998).

Decision-makers often have to prioritize options for action on the ground. Site-specific analyses that map vegetation sensitivity (Figures 2d and S2a) allow for better prioritization, given limited resources. Our approach takes a first step toward classification of sensitive ecosystems across the entirety of the western United States using simple linear models. The root-mean-square error of the linear regressions tended to be larger in areas with high rates of NPP, which generally align with areas with positive slopes (Figures 2d and S1) and energy limitations. For site-specific analysis it would be possible to incorporate more complex statistical models that would better characterize potential nonlinear behaviors between productivity and water availability due to physiological differences across plant types, where the climatic water balance is not a significant constraint on NPP, or where mortality events occur in response to extreme events. Importantly, it is possible to overlay maps of ecosystem sensitivity with maps of other features, vulnerabilities, management potential, historical legacies, and land ownership (Frazier et al., 2014; Morelli et al., 2016). Indices of ecosystem sensitivity/vulnerability should not be dependent upon generalized characteristics of the ecosystem, but stressor-specific environmental indicators that include information on local

exposure pathways, ecosystem sensitivity, and the potential adaptive capacity (Beroya-Eitner, 2016; De Lange et al., 2010). Following identification of conservation or management targets, improved management options may be identified.

6. Conclusion

Our results show that hillslope topography exerts a strong control over spatial patterns of primary productivity and ecosystem sensitivity to climate. The relative effect of topographic convergence and divergence on ecosystem productivity varied across the western United States climate gradient. Under water-limited conditions, vegetation in convergent terrain was generally less sensitive to climate variability and more productive than vegetation in flat and divergent landscape positions, especially in semiarid environments. Vegetation in divergent terrain was also less sensitive to climate than vegetation in flat positions, but comparatively less productive and more sensitive than vegetation in convergent terrain. Conversely, topography had little effect on ecosystem sensitivity to climate in hygric and xeric environments where climatic drivers were extreme (e.g., larger moisture surplus or deficit respectively). This work provides a mappable approach for regional planning to maximize conservation in landscapes more resistant to perturbations.

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