Spatial and ecological variation in dryland ecohydrological responses to climate change: implications for management

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Abstract. Ecohydrological responses to climate change will exhibit spatial variability and understanding the spatial pattern of ecological impacts is critical from a land management perspective. To quantify climate change impacts on spatial patterns of ecohydrology across shrub steppe ecosystems in North America, we asked the following question: How will climate change impacts on ecohydrology differ in magnitude and variability across climatic gradients, among three big sagebrush ecosystems (SB-Shrubland, SB-Steppe, SB-Montane), and among Sage-grouse Management Zones? We explored these potential changes for mid-century for RCP8.5 using a process-based water balance model (SOILWAT) for 898 big sagebrush sites using site- and scenario-specific inputs. We summarize changes in available soil water (ASW) and dry days, as these ecohydrological variables may be helpful in guiding land management decisions about where to geographically concentrate climate change mitigation and adaptation resources. Our results suggest that during spring, soils will be wetter in the future across the western United States, while soils will be drier in the summer. The magnitude of those predictions differed depending on geographic position and the ecosystem in question: Larger increases in mean daily spring ASW were expected for high-elevation SB-Montane sites and the eastern and central portions of our study area. The largest decreases in mean daily summer ASW were projected for warm, dry, mid-elevation SB-Montane sites in the central and west-central portions of our study area (decreases of up to 50%). Consistent with declining summer ASW, the number of dry days was projected to increase rangewide, but particularly for SB-Montane and SB-Steppe sites in the eastern and northern regions. Collectively, these results suggest that most sites will be drier in the future during the summer, but changes were especially large for mid- to high-elevation sites in the northern half of our study area. Drier summer conditions in high-elevation, SB-Montane sites may result in increased habitat suitability for big sagebrush, while those same changes will likely reduce habitat suitability for drier ecosystems. Our work has important implications for where land managers should prioritize resources for the conservation of North American shrub steppe plant communities and the species that depend on them.

Key words: Artemisia tridentata; climate impacts; drought; dryland; ecohydrology; sagebrush; Sage-grouse Management Zone; shrub steppe; soil water availability; water balance.

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INTRODUCTION

Drylands, which cover ~40% of global terrestrial surface area, are defined by low and highly variable precipitation regimes of generally small event sizes and are particularly vulnerable to climate change (Lauenroth and Bradford 2009, Wang et al. 2012). The consequences of climate change for dryland ecosystems is determined by temperature and precipitation, which interact with vegetation structure and soil texture and depth to determine the availability of water, which is often the primary limiting resource (Sala et al. 1992, Loik et al. 2004). Here, we focus on big sagebrush ecosystems, important mid-latitude drylands that cover a large portion of the United States, which are characterized by soil water recharge in winter and early spring, followed by a dry soil period during the growing season (Schlaepfer et al. 2012a). In this region, temperature is projected to increase on average by 5.5°C by the end of the 21st century under representative concentration pathway RCP8.5, while predictions for precipitation are more uncertain, with potential increases or decreases of 10% possible (IPCC 2013, Anderegg and Diffenbaugh 2015). Palmquist et al. (2016) explored climate change impacts on water balance for big sagebrush ecosystems using a process-based soil water simulation model and found that on average soils may be wetter in the future during the late fall to early spring due to projected increases in cold-season precipitation, but will likely dry out more rapidly and remain drier for a longer portion of the growing season, due to shifts in transpiration, evaporation, and groundwater recharge to earlier in the year. These results reflect region-wide expectations for big sagebrush ecosystems, but do not capture the important spatial variability in ecohydrological responses to climate change that may emerge in response to gradients of precipitation, temperature, elevation, topography, and soil properties across the western United States (Miller et al. 2011, Chambers et al. 2014a).

Anticipated future changes in precipitation and temperature are expected to vary across the western United States. Some of the variability in future precipitation projections are related to latitude, as multi-model means and ensemble predictions suggest increases in winter precipitation for the northern half of the western United States, but decreases in southern latitudes (Abatzoglou and Kolden 2011, IPCC 2013, Anderegg and Diffenbaugh 2015). Future temperature regimes may also exhibit a spatial pattern across latitude, with potentially larger increases in temperature in the northern portion of the western United States (Abatzoglou and Kolden 2011). In addition, future climatic regimes will likely be contingent on elevation, with anticipated increases in precipitation at higher elevations and decreases at lower elevations (IPCC 2013). The ratio of precipitation falling as snow and the duration of snowpack is predicted to decrease across much of the western United States, but particularly for lower elevations in the southwestern United States (Brown and Mote 2009, Klos et al. 2014, Palmquist et al. 2016). Collectively, these changes may result in considerably drier conditions in the southwest United States (Diffenbaugh et al. 2008, Abatzoglou and Kolden 2011, Anderegg and Diffenbaugh 2015), which are already being realized (Seager et al. 2007) and potentially wetter conditions in the northeastern portion of the western United States (Maloney et al. 2014, Melillo et al. 2014).

In addition to spatial variability of future climatic impacts, we expect that big sagebrush ecosystems may differ in their response to climate change due to differences in their ecology. There are three primary big sagebrush ecosystems found in the western United States: Intermountain Basins Big Sagebrush Shrubland (SB-Shrubland), Intermountain Basins Big Sagebrush Steppe (SB-Steppe), and Intermountain Basins Montane Sagebrush Steppe (SB-Montane; USGS 2011, Schlaepfer et al. 2012a). These ecosystems are characterized by shifts in the dominant big sagebrush sub-species and are differentiated by their climatic niches, soil properties, and geography (Miller et al. 2011). SB-Montane ecosystems, dominated by Artemisia tridentata ssp. vaseyana, may have greater resilience and resistance to environmental stress and disturbance because of greater resource availability and more suitable conditions for plant growth and survival, while warm, dry big sagebrush communities dominated by Artemisia tridentata ssp. wyomingensis and ssp. tridentata (SB-Steppe, SB-Shrubland) may have lower resilience and resistance to disturbance and invasion (Chambers et al. 2007, 2014a, b, Miller et al. 2011,
As such, we expect that these three ecosystems will have different responses and capacities to withstand perturbations in the face of changing precipitation and temperature regimes, with the consequence that ecohydrological responses, management implications, and the resulting management actions will vary across them (Davies et al. 2006, Davies and Bates 2010).

Understanding the spatial pattern of future climate predictions and their ecological impacts is critical from a land management perspective (Diffenbaugh et al. 2008). Land managers have limited resources and need guidance on where to spatially concentrate those resources for climate change mitigation and adaptation. An additional concern of land managers who are making decisions in the face of climate change is whether “high-quality” sites will continue to be of high quality in the future. Decisions on where to concentrate resources now in anticipation of future changes may be informed by spatial changes in habitat suitability and identification of areas that are most vulnerable to climate change (Manier et al. 2013). In the big sagebrush region, much of the ongoing conservation and management efforts are focused on greater sage-grouse (Centrocercus urophasianus). Big sagebrush is the most important sagebrush species for greater sage-grouse habitat (Miller et al. 2011); however, big sagebrush plant communities currently differ in their capacity to provide suitable habitat (Davies et al. 2006, Davies and Bates 2010). As such, a key need of land managers is to understand whether current habitat will continue to be suitable in the future and what implications the future spatial pattern of habitat will have for greater sage-grouse conservation and management (Homer et al. 2015).

We used two approaches to quantify the impacts of altered climate on variability in future ecohydrology. First, we explore the variability of future ecohydrological responses across the three big sagebrush ecosystems found in the western United States. Second, we quantified the spatial variability in future ecohydrological responses across the seven Sage-grouse Management Zones (MZs) in the western United States. Specifically, we asked the following questions: (1) How are changes in future big sagebrush ecohydrology related to climatic gradients? (2) How will climate change impacts on ecohydrology differ in magnitude and variability across sites for big sagebrush ecosystems? and (3) What is the spatial pattern of climate change impacts on big sagebrush ecohydrology and what are the anticipated impacts within Sage-grouse Management Zones? We explored these potential changes for mid-century (2030–2060) for RCP8.5 (IPCC 2013) using a process-based water balance model for 898 big sagebrush sites across the western United States using site-specific climate information, vegetation parameters, and soil properties for multiple soil layers. We focused on analyzing changes in soil water availability and ecological drought from current conditions to mid-century, as we believe these ecohydrological variables are most relevant in big sagebrush ecosystems and may inform land management decisions about where to geographically concentrate climate change mitigation and adaptation resources in the coming decades. We believe the first step in designing climate change mitigation is to understand the spatial and seasonal variability in future soil water availability, which is often the key driver of aboveground plant community structure in big sagebrush ecosystems, on which greater sage-grouse depend, in addition to minimum winter temperature and snow cover (Schlaepfer et al. 2012c, 2015). As such, our work has the ability to inform conservation and management action at broad spatial scales in a large portion of the United States. In addition, we use an unique approach to summarize sub-continental changes in ecohydrology in response to changing climatic conditions at regional scales at which management decisions and management actions are made. We believe this approach will be of interest to applied scientists and practitioners working in other ecosystems that span large spatial extents, by providing a framework to implement local and regional conservation and management action.

**Methods**

**Study area and site selection**

We used 898 sites described in Schlaepfer et al. (2012a) and Palmquist et al. (2016), which are located within a 3.1 x 10^6 km^2 region of the western United States (Fig. 1). We chose these sites randomly from land cover data from regional gap analysis programs (GAP, grid cells of...
30 m²), which were classified as big sagebrush ecosystems (USGS 2011). Our 898 sites span the three big sagebrush ecosystems found in the western United States: SB-Shrubland (n = 357), SB-Steppe (n = 348), and SB-Montane (n = 193; Fig. 1).

SB-Shrubland ecosystems are located primarily in the southern portion of the big sagebrush ecosystem range (Fig. 1) and occur in wide, flat basins on deep fertile soils (Schultz 2006, Miller et al. 2011). SB-Steppe ecosystems occupy the northern latitudes of the western United States (Fig. 1), occur on warm, dry valley and foothills sites, and are thought to be the driest of the big sagebrush ecosystems (Schultz 2006, Miller et al. 2011). SB-Montane ecosystems occupy upland sites, which tend to be at higher elevation and are often cooler and wetter than either SB-Shrubland or SB-Steppe (Schultz 2006, Miller et al. 2011), although there is considerable evelational overlap between all three (Chambers et al. 2014b; Appendix S1). SB-Montane ecosystems are often more species rich with greater plant biomass (Davies and Bates 2010). SB-Shrubland is dominated primarily by A. tridentata ssp. tridentata with lesser amounts of A. tridentata ssp. wyomingensis, SB-Steppe is co-dominated by A. tridentata ssp. tridentata and A. tridentata ssp. wyomingensis, while A. tridentata ssp. vaseyana is the dominant in SB-Montane sites. MAT of the SB-Shrubland sites is 7.6°C (range = 1.8–16°C), 7.2°C (range = 1.2–11.7°C) for SB-Steppe, and 4.0°C (range = −1.7° to 8.7°C) for SB-Montane. Mean annual precipitation (MAP) increases with elevation, with greater amounts of precipitation in SB-Montane (479 mm) relative to SB-Shrubland (295 mm) and SB-Steppe (324 mm).

Seven Sage-grouse Management Zones have been designated in the western United States by the Western Association of Fish and Wildlife Agencies to encompass populations of greater sage-grouse in regions with similarities in climate, elevation, topography, geology, soils, and floristics (West 1983, Miller and Eddleman 2001, Manier et al. 2013). We use them to explore both the spatial pattern of future ecohydrological changes and the implications of those changes for plant community structure, habitat quality for greater sage-grouse, and management action. A total of 858 of our 898 sites fall within one of the seven Sage-grouse Management Zones: MZ 1: Great Plains (n = 152), MZ 2: Wyoming Basins (n = 158), MZ 3: Southern Great Basin (n = 145), MZ 4: Snake River Plain (n = 249), MZ 5: Northern Great Basin (n = 99), MZ 6: Columbia Basin (n = 30), and MZ 7: Colorado Plateau (n = 25; Fig. 1). Thus, our results summarizing future ecohydrology for the three ecosystems use all 898 sites, while our results for Management Zones utilize 858 sites. For each MZ, we summarize the proportion of sites that are SB-Shrubland, SB-Steppe, and SB-Montane (Fig. 1).

SOILWAT simulation modeling

We quantified changes in ecohydrology at each of our 898 sites using SOILWAT, a process-based soil water balance model (Parton 1978, Sala et al. 1992, Lauenroth and Bradford 2006), which has been modified and validated for big sagebrush ecosystems, by incorporating modules for
hydraulic redistribution, snow, multiple vegetation types, and phenology and biomass as a function of climate (Schlaepfer et al. 2012a, b, Bradford et al. 2014a). SOILWAT uses site-specific daily precipitation and temperature data, site-specific monthly climate conditions (relative humidity, wind speed, cloud cover), site-specific monthly vegetation parameters for multiple plant functional types (total aboveground biomass, litter, living aboveground biomass, active root depth profile), and site-specific soil properties from multiple layers to model all components of daily water balance. This includes interception by vegetation and litter, evaporation of intercepted water, bare-soil evaporation, infiltration, groundwater recharge, transpiration from each soil layer, and available soil water for plants to use. Our modeling approach allows for changes in vegetation based on climate, such that vegetation parameters under current conditions (1980–2010) and future conditions (2030–2060) varied due to differences in climate between those time periods. Although vegetation parameters varied across sites and time periods, monthly parameters were held constant for each site during a simulation run for a given time period.

We extracted site-specific current and future weather data for all 898 sites to run SOILWAT simulations for 1980–2010 and 2030–2060. Current temperature and precipitation data was extracted from 1/8-degree gridded, daily weather data for 1980–2010 (Maurer et al. 2002). Monthly estimates of relative humidity, wind speed, and cloud cover were obtained from the Climate Maps of the United States (http://cdl.nccdc.noaa.gov/cgi-bin/climaps/climaps.pl). To obtain future daily weather data for each site, we extracted temperature and precipitation data for each GCM from the “Downscaled CMIP3 and CMIP5 Climate and Hydrology Projects” archive at http://gdo-dcp.ucar.edu/downscaled_cmip_projections/ (Maurer et al. 2007) and then applied the hybrid-delta downscaling method, which uses historic daily weather data with monthly future predictions to obtain future daily forcing (Hamlet et al. 2010, Dickerson-Lange and Mitchell 2014). In addition, we extracted site-specific soil data for each soil layer (sand %, clay %, volume of gravel, bulk density, soil depth) for all 898 sites from the NRCS STATSGO database (1-km² grids; Miller and White 1998). To obtain site-specific parameters for the relative composition of C3 and C4 grasses and shrubs as well as monthly aboveground biomass, monthly live biomass, monthly litter, and monthly root depth distributions, we used the methods provided in Bradford et al. (2014b) and applied by Palmquist et al. (2016), which relate climate conditions to vegetation and seasonal biomass. Specifically, the composition of plant functional types (shrubs, C₃ grasses, C₄ grasses) was calculated for each of the 898 sites based on current climate and re-calculated for future climate (Paruelo and Lauenroth 1996). Mean monthly aboveground total biomass, monthly live biomass, and monthly litter were calculated based on site-specific precipitation and temperature, which collectively influence biomass and growing season length. Transpiration coefficients were calculated separately for each plant functional type based on the amount of root biomass within each soil layer (Schenk and Jackson 2003).

We simulated ecosystem water balance using current conditions (1980–2010) and future climatic conditions (2030–2060) from 10 GCMs for RCP8.5 (see Palmquist et al. 2016, Table S1 for list of GCMs). We selected GCMs which performed well in the western United States (Rupp et al. 2013) and which were representative of the families of GCMs in existence (Knutti et al. 2013). Although we ran SOILWAT simulations for 10 GCMs, we focus on summarizing predictions for the median GCM, which was identified individually for each of the 898 sites. To identify the median GCM prediction for each site, we sorted the 30-year mean annual values for the 10 GCMs and then averaged values 5 and 6 after sorting. We identified and calculated the median GCM prediction for each climatic and ecohydrological variable separately for 1980–2010 and 2030–2060. To characterize the uncertainty for each ecohydrological variable, we indicate how many of the GCMs agree on the direction of the change predicted by the median.

**Statistical analysis**

We first summarized the key climatic variables that have previously been identified as important in influencing big sagebrush ecohydrology (Lauenroth and Bradford 2012, Schlaepfer et al. 2012a, b).
This included current and predicted future mean annual precipitation (mm) and temperature (°C), which were derived from GCM output. We also characterized climatic variables that reflect the type, timing, and size of current and future precipitation events: current cold-season precipitation (CSP; October–March), change in CSP, current annual snow/precipitation ratio, change in snow/precipitation ratio, current CSP/total precipitation ratio (CSP ratio), change in CSP ratio, current number of precipitation events, change in number of precipitation events, current fraction of precipitation events in the 0–5 mm size class, and change in the fraction of 0–5-mm precipitation events.

To examine the impact of altered climate on soil water dynamics, we quantified several key ecohydrological variables in big sagebrush ecosystems (Schlaepfer et al. 2012a). This included: annual total transpiration (T, mm), annual total evaporation (E, mm), annual total evapotranspiration (AET, mm), annual T/AET ratio, annual groundwater recharge (GR, mm), and mean available soil water (ASW, mm, greater than −3.9 MPa) in spring and summer for top and bottom soil layers. Lastly, we summarized several variables that characterize changes in the length and timing of dry periods in the future, which we believe will inform land management decisions: aridity index (annual precipitation/annual potential evapotranspiration; UNEP 1992, Maestre et al. 2012) and the number of dry days (less than −3.9 MPa) for both top and bottom soil layers on an annual basis and separately for spring (March, April, May) and summer (June, July, August). We used −3.9 MPa as a cutoff for both ASW and dry days, as big sagebrush can extract some soil water up to this point; thereafter, the risk of cavitation increases leading to reduced hydraulic conductivity (Kolb and Sperry 1999).

To address how climate change will impact big sagebrush ecohydrology (question 1), we explore which geospatial (latitude, longitude, elevation) and climatic variables influence future changes in each ecohydrological variable across all 898 sites in the western United States. We conducted principal components analysis (PCA) to determine the main axes of variation in our geospatial and climatic data set and to reduce the dimensionality of that data set. PCA was implemented using the prcomp function after centering and scaling the data to have unit variance. The first three PCs explain 70% of the variation in the climatic and geospatial data set. The first three PCs explain 70% of the variance (PC1 = 34%, PC2 = 22%, PC3 = 14%). PC1 represents a gradient of precipitation, capturing amount, type, event size, and timing (Table 1; Appendix S2), while PC2 largely represents a temperature gradient, but also captures aspects of precipitation. PC3 is harder to interpret, with

| Climatic or geospatial variable | PC1  | PC2  | PC3  |
|--------------------------------|------|------|------|
| Longitude                      | 0.18 | −0.39| 0.11 |
| Latitude                       | 0.18 | −0.14| −0.46|
| Elevation                      | −0.21| −0.22| 0.41 |
| MAP (mm)                       | −0.27| −0.30| −0.20|
| Change in MAP (mm)             | −0.33| 0.01 | −0.13|
| MAT (°C)                       | 0.14 | 0.39 | −0.09|
| Change in MAT (°C)             | 0.05 | −0.36| 0.24 |
| Cold-season precipitation (mm) | −0.38| −0.03| −0.13|
| Change in cold-season precipitation (mm) | −0.31| 0.01 | −0.35|
| Cold-season precipitation/total precipitation ratio | −0.29| 0.32 | 0.00 |
| Change in cold-season precipitation/total precipitation ratio | 0.11| 0.00 | −0.49|
| Snow/precipitation ratio       | −0.33| −0.17| 0.07 |
| Change in snow/precipitation ratio | 0.33| −0.14| −0.16|
| Number of precipitation events | −0.09| −0.28| −0.24|
| Change in number of precipitation events | 0.02| −0.27| −0.11|
| Fraction of precipitation events, 0–5 mm | 0.27| 0.17 | 0.08 |
| Change in fraction of precipitation events, 0–5 mm | 0.24| −0.27| −0.06|

Note: The first three PCs explain 70% of the variation in the climatic and geospatial data set.
latitude, change in CSP, change in CSP ratio, and the number of precipitation events loading negatively on PC3 and elevation and change in MAT loading positively (Table 1; Appendix S2). To determine which climatic axes were related to future ecohydrology, we extracted the axis scores for the first three PCs axes and calculated Pearson correlation coefficients ($r$) between them and the ecohydrological variables of interest: absolute change in ASW in top and bottom layers for both spring and summer, and absolute change in mean number of dry days in top and bottom layers in spring and summer.

To understand how future ecohydrology may vary across the three big sagebrush ecosystems (question 2), we summarize median absolute and percent changes in all climatic and ecohydrological variables described above for each ecosystem. To quantify the spatial variability in future water balance changes across the 898 sites in the western United States (question 3), we summarize median absolute and percent changes in climate and ecohydrology for all variables described above for each of the seven Sage-grouse Management Zones. We present percent changes to indicate how the absolute change values we report relate to current magnitudes. All statistical analyses were performed in R v.3.2.2 (R Development Core Team 2015).

**RESULTS**

**Climate change impacts on ecohydrology for all sites**

PC1 represents a precipitation gradient with high PC1 values corresponding to low-elevation sites in the northeastern portion of our study area (MZ 1) that currently have a precipitation regime characterized by a large fraction of small events, falling mostly in the warm season. These sites are expected to have decreases to small increases in precipitation in the future (Appendix S2). In contrast, high-elevation sites (low PC1 values), which are already defined by dominantly CSP of large event sizes, will continue to increase in precipitation in the future, but with a smaller fraction falling as snow. Sites with high PC2 axis scores tend to be at low elevation with relatively dry, hot climates that are defined by few cold-season precipitation events. These sites can be found in the west and southwest (MZs 3, 5, and 6) and are predicted to have small temperature increases, along with decreases in the number of precipitation events, but increases in the size of those events (Appendix S2). Sites with high PC3 values are found at southern and southeastern high-elevation sites (MZs 2 and 7) where the future will be much warmer with fewer precipitation events and less cold-season precipitation.

Our simulations indicate the amount and timing of available soil water (ASW) will likely change by mid-century. ASW in both top and bottom soil layers was predicted to increase in the spring months, but decrease in summer for most sites. Absolute changes in ASW in spring were negatively correlated with PC1 (top layers: $r = -0.23$, bottom layers: $r = -0.48$) and PC2 (top layers: $r = -0.61$, bottom layers: $r = -0.38$), suggesting ASW is likely to increase the most in high-elevation sites that currently have and are predicted to have greater amounts of cold-season precipitation in the future (Fig. 2A, B). In contrast, absolute changes in summer ASW for top layers were positively correlated with PC1 ($r = 0.5$), PC2 ($r = 0.41$), and PC3 ($r = 0.13$), suggesting the largest decreases in summer ASW are expected in mid-elevation sites located in the central and west-central regions, which are currently warm and dry and are predicted to have relatively small increases in future precipitation (Fig. 2C; Appendix S3). For bottom layers, absolute changes in summer ASW were correlated with PC1 ($r = 0.5$) and PC2 ($r = 0.3$), again suggesting that sites with the greatest reduction in summer soil water will be warm, dry sites (Fig. 2D; Appendix S2).

For most sites, absolute changes in the number of future spring dry days were predicted to be small (median predictions ~ 0), especially for bottom soil layers. For those sites that will change, the greatest increases in spring dry days are predicted for dry, hot sites at low elevation in the southwest United States (PC2 $r = 0.43$, PC1 $r = -0.27$). In contrast, most sites may have increases in the number of summer dry days in the future. Absolute changes in summer dry days for top layers were weakly negatively correlated with PC2 ($r = -0.26$) and PC3 ($r = -0.21$), suggesting greater increases for sites that will become considerably warmer in the future; these sites tend to be at higher latitudes and elevations and further east (Appendices S2 and S4).
Predictions were similar for bottom soil layers, with absolute change in summer dry days weakly negatively correlated with PC1 ($r = -0.13$), PC3 ($r = -0.11$), and PC2 ($r = -0.09$; Appendix S4).

Absolute changes in AET were negatively correlated with PC1 ($r = -0.41$) and weakly positively correlated with PC2 ($r = 0.09$), suggesting sites further west with greater water inputs and warmer temperatures in the future will have greater water loss through AET. Changes in GR were strongly negatively correlated with PC1 ($r = -0.76$) and negatively correlated with PC3 ($r = -0.3$): Increases in GR are expected for sites with predicted future increases in precipitation (Table 1; Appendix S2).

Fig. 2. Absolute changes in mean daily spring and summer ASW for all 898 sites for top and bottom soil layers. All values presented are for the median GCM and were calculated from 1980–2010 to 2030–2060. Each panel is plotted according to the two most important PC explaining variation in that ecohydrological variable across all 898 sites in the western United States.
Climate change impacts on ecosystem ecohydrology

All results reported here reflect the median GCM of the 10 GCMs examined for RCP8.5, unless otherwise specified. Future changes in median MAP were relatively consistent across ecosystems, with increases predicted for SB-Shrubland (9%), SB-Montane (7%), and SB-Steppe (5%; Fig. 3A; Appendix S5). More precipitation will be falling in the cold season, with no differences in the magnitude of these changes across ecosystems (Appendix S6). The number of precipitation events is predicted to decrease, particularly for SB-Shrubland, with fewer events in the 0–5 mm size class for all ecosystems. Despite increased precipitation in the future, less precipitation will be falling as snow: Reductions in snow/precipitation ratio were slightly greater for SB-Shrubland (39%), compared with SB-Steppe (28%) and SB-Montane (27%; Appendix S6). Absolute changes in MAT by mid-century were large, but especially so for SB-Steppe and SB-Montane (Fig. 3B).

Differences in the magnitude of percent changes in ASW emerged across ecosystems: Top soil layers will likely be slightly wetter in SB-Steppe (15%) and SB-Montane (15%) during the spring, relative to SB-Shrubland (3%), while the greatest increase in spring ASW in bottom layers was for SB-Montane (22%), compared

Fig. 3. Changes in MAP (A), MAT (B), GR (C), and AET (D) from 1980–2010 to 2030–2060 for each big sagebrush ecosystem. Values shown are the median (black horizontal line), first and third quartiles (ends of the box), range (ends of the whiskers), and outliers (points) across all sites for each ecosystem for the median GCM. The number of GCMs that agree on the direction of the median change across sites is shown just above the x-axis.
with SB-Steppe (16%) and SB-Shrubland (13%; Fig. 4A, B). During the summer, SB-Shrubland had slightly larger predicted decreases in ASW for top layers (39%, relative to the other ecosystems), although all had predicted decreases of 31–39% (Fig. 4C). For bottom layers, SB-Shrubland and SB-Montane had slightly larger decreases in summer ASW than SB-Steppe (Fig. 4D). There was considerable variation within each ecosystem in the magnitude of changes in ASW, particularly for SB-Shrubland (Fig. 4). In contrast to percent changes in ASW, SB-Montane ecosystems consistently had greater absolute increases in spring ASW and greater decreases in summer ASW than the other ecosystems (Appendix S7).

The median prediction for the number of spring dry days suggests little change in top layers (SB-Shrubland: 0.5 d, SB-Steppe and SB-Montane: 0) and no change in bottom layers (0 for all ecosystems; Fig. 5A, B; Appendix S8). However, increases and decreases were projected for some sites for each ecosystem, particularly for SB-Shrubland. Absolute and percent changes in the number of summer dry days were consistently larger for both top and bottom soil layers.

Fig. 4. Percent change in ASW from 1980–2010 to 2030–2060 for each big sagebrush ecosystem in spring for top and bottom soil layers (A, B) and summer for top and bottom soil layers (C, D). Values shown are the median (black horizontal line), first and third quartiles (ends of the box), and range (ends of the whiskers) across all sites for each ecosystem for the median GCM. Outliers are not shown here. The number of GCMs that agree on the direction of the change in the median value reported is shown just above the x-axis.
for SB-Montane (16% and 24% increase for top and bottom, respectively), relative to SB-Steppe (9% and 13% increase) and SB-Shrubland (3% and 6% increase; Fig. 5C, D; Appendix S8). On average, all GCMs agree that summer dry days will increase for SB-Montane in the future. However, there were decreases predicted for some sites in each ecosystem: SB-Shrubland (top layers: 20%, bottom layers: 14%), SB-Steppe (top layers: 5%, bottom layers: 6%), and SB-Montane (top layers: 5%, bottom layers: 2%). Consistent with our findings for the number of summer dry days, the aridity index for SB-Montane and SB-Steppe was projected to decrease slightly in the future, suggesting drier conditions, while the aridity index for SB-Shrubland was projected to increase slightly (Appendix S6).

Actual evapotranspiration (AET) will likely increase in the future for all ecosystems (4–7%), although slightly less for SB-Steppe (Fig. 3D; Appendix S5). Most of the increase in AET is the result of increased transpiration (T), as evaporation (E) was predicted to change only by +1–2 mm (Appendix S6). Changes in T were relatively
consistent across ecosystems, as were changes in E and T/AET ratio (Appendix S6). However, there was considerable variation in the direction and magnitude of changes in AET, T, E, and T/AET across sites within each ecosystem (Fig. 2D; Appendix S6). Percent changes in GR were similar across all ecosystems (SB-Shrubland: 18%, SB-Steppe: 15%, SB-Montane: 14%; Fig. 3C), but the median predicted absolute change was higher for SB-Montane (Appendix S5). Most sites, regardless of ecosystem, were predicted to have increases in GR (SB-Shrubland: 84%, SB-Steppe: 95%, SB-Montane: 84%), due to predicted increases in MAP (Fig. 3A, C; Appendix S6).

Spatial patterns of climate change impacts on ecohdrology: management zone responses

Most GCMs agreed that MAP will increase in each MZ, most of which will be falling in the cold season (Fig. 6A; Appendix S9). Increases in MAP are projected to be greatest for MZ 3: Southern Great Basin (11%) and lowest for MZ 1: Great Plains (3%; Fig. 6A). However, decreases in MAP were predicted for a small percentage of sites in

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**Fig. 6.** Changes in MAP (A), MAT (B), GR (C), and AET (D) from 1980–2010 to 2030–2060 for each Sage-grouse Management Zone. Values shown are the median (black horizontal line), first and third quartiles (ends of the box), range (ends of the whiskers), and outliers (points) across all sites for each Management Zone for the median GCM. The number of GCMs that agree on the direction of the change in the median value reported is shown just above the x-axis.
each MZ except the Snake River Plain and Columbia Basin: MZ 1 (8%), MZ 2 (1%), MZ 3 (1%), MZ 5 (7%), and MZ 7 (12%). Less precipitation will be falling as snow for all sites, but those reductions are expected to be particularly high in the south and western portions of the range (MZs 3–7; Appendix S9). Fewer precipitation events are expected rangewide, especially for the western half of the study area (MZs 3–6), which in tandem with reductions in the fraction of 0- to 5-mm events suggest fewer, larger precipitation events in the future (Appendix S9). Increases in MAT are predicted to be greatest in the east (MZs 1–4), relative to the west (MZs 5 and 6; Fig. 6B). For top soil layers, the eastern and central regions of the big sagebrush distribution (MZs 1–4) are expected to have increases in spring ASW, especially MZ 1 (22%) and MZ 2 (24%; Fig. 7A; Appendix S5). In contrast, the northwestern United States (MZs 5 and 6) is expected to experience a 1% decline in ASW (with sites experiencing both increases and decreases in ASW), while the median prediction for the Colorado Plateau suggested slightly reduced spring ASW (2%; Fig. 7A). For bottom soil layers, the median prediction suggested increases in spring ASW for all MZs, but especially for MZ 1 (20%), MZ 2 (27%), MZ 3 (18%), and MZ 4 (17%; Fig. 7B). All MZs are expected to have somewhat large reductions in the amount of ASW in the summer (27–50%), with the largest decreases expected for the Northern Great Basin (Fig. 7C, D; Appendix S5). There was consistently more variability in the magnitude of changes in spring and summer ASW for sites within MZs 2–5, compared with other MZs.

The south and southwestern regions (MZs 3–6) are expected to have little change in the number of spring dry days in top layers in the future (0–1 d; Fig. 8A). In contrast, the Great Plains and Wyoming Basins will likely have slightly fewer spring dry days (−2.5 and −0.5 d, respectively), while spring dry days are predicted to increase for the Colorado Plateau (+1.5 d; Fig. 8A). For all MZs, the median prediction for change in spring dry days for bottom layers was zero, although a small fraction of sites in each MZ may increase or decrease by mid-century (Fig. 8B; Appendix S8). The number of summer dry days was projected to increase for almost all MZs for both top and bottom soil layers (Fig. 8C, D), suggesting soils will be drier for a longer portion of the growing season in the future across most of the big sagebrush region. The one exception was bottom soil layers in MZ 7 (median prediction = 0). Increases in summer dry days for top and bottom layers were greater for the Great Plains (13% and 20%) and Wyoming Basins (11% and 11%) and smallest for the Southern Great Basin (2.5% and 3.5%) and the Colorado Plateau (4% and 0%). Absolute and percent changes in summer dry days were consistently greater for bottom soil layers than for top soil layers within each MZ (Fig. 8C, D; Appendix S8). Change in the aridity index suggests the central region of the big sagebrush distribution will become slightly wetter in the future on an annual basis, while the Great Plains, Wyoming Basins, Northern Great Basin, and Colorado Plateau will become slightly more arid (Appendix S9).

Actual evapotranspiration will likely increase more or less uniformly across all the MZs, with the smallest increases in the Great Plains (9 mm, 3%), relative to the other MZs (14–20 mm, 5–7%; Fig. 6D). GR will likely increase on average across all MZs, but particularly for the southern and western portions of the big sagebrush distribution (16–31%, MZs 3–7), relative to the eastern MZs (7–12%, Great Plains and Wyoming Basins; Fig. 6C). The magnitude of GR increases in each MZ largely mirrors the changes in MAP predicted for mid-century (Fig. 6A, C).

**Discussion**

Our simulation results for changes in ASW and dry days suggest that during spring, soils will be wetter in the future across most sites in the big sagebrush region. In contrast, soils in the summer will be drier, with increases in summer dry days and decreases in summer ASW expected for most sites. Percent changes in summer ASW were considerable and represent decreases of between 27% and 50%, depending on the region in question. The magnitude of these changes differed across the distribution of big sagebrush ecosystems. The largest increases in spring ASW are expected for high-elevation...
SB-Montane sites and the eastern and central regions of the big sagebrush distribution (MZs 1–4; Figs. 4 and 7; Appendices S3, S7, and S11), with no large changes in the number of spring dry days predicted for most sites (Figs. 5 and 8; Appendices S3, S8, and S11). The largest decreases in summer ASW were projected for warm, dry mid-elevation SB-Montane sites in the central and west-central portions of our study area (MZs 4 and 5), which are projected to have only small increases in MAP in the future (Figs. 4 and 7; Appendices S3, S7, and S11). The number of dry days both in the top and bottom soil layers during the summer was projected to increase rangewide, but particularly for SB-Montane and SB-Steppe sites in the eastern and northern portions of our study area (MZs 1, 2, and 4; Figs. 5 and 8; Appendix S11). Collectively, these results suggest that most sites will be drier in the future during the summer months, but especially mid- to high-elevation sites in the northern half of our study area.

Fig. 7. Percent changes in available soil water from 1980–2010 to 2030–2060 for each Sage-grouse Management Zone in spring for top and bottom soil layers (A, B) and summer for top and bottom soil layers (C, D). Values shown are the median (black horizontal line), first and third quartiles (ends of the box), range (ends of the whiskers), and outliers (points) across all sites for each Management Zone for the median GCM. The number of GCMs that agree on the direction of the change in the median value reported is shown just above the x-axis.
Ecosystem responses to altered climate

SB-Montane ecosystems responded differently to climate change than the drier ecosystems: increases in spring soil moisture and decreases in summer soil moisture were both greatest for SB-Montane sites. Although these sites were predicted to become drier during the summer, habitat suitability for big sagebrush in SB-Montane sites may increase in the future due to warmer winter temperatures, which is a key factor that limits big sagebrush regeneration at high elevations (reviewed by Schlaepfer et al. 2014).

Fig. 8. Absolute changes in the number of dry days from 1980–2010 to 2030–2060 for each Sage-grouse Management Zone in spring for top and bottom soil layers (A, B) and summer for top and bottom soil layers (C, D). Values shown are the median (black horizontal line), first and third quartiles (ends of the box), range (ends of the whiskers), and outliers (points) across all sites for each Management Zone for the median GCM. The number of GCMs that agree on the direction (+, −, 0) of the change in the median value reported is shown just above the x-axis. For bottom layers in spring, all GCMs agree with the median prediction of 0.
In addition, SB-Montane sites are currently the most mesic (Schultz 2006, Miller et al. 2011) and the magnitude of decreases in ASW predicted by mid-century will likely not put these sites outside the range of suitability for big sagebrush (Schlaepfer et al. 2012b). However, warmer temperatures and wetter winter and spring conditions could also result in SB-Montane sites becoming increasingly suitable for invasive, annual, cold-season grasses (e.g., cheatgrass, *Bromus tectorum*), which are currently constrained by minimum winter temperatures and limited in their distribution and abundance at high elevations (Chambers et al. 2007, Concilio et al. 2013, Compagnoni and Adler 2014).

SB-Steppe and SB-Shrubland responded similarly and will likely continue to become drier in the future. Although the changes predicted for these ecosystems were smaller than for SB-Montane, they will perhaps be more ecologically significant, leading to potential negative impacts on big sagebrush regeneration and survival. Despite smaller reductions in summer ASW, SB-Steppe and SB-Shrubland will continue to be the driest ecosystems in the future (Appendix S1), which may make these portions of the big sagebrush region more vulnerable to drought-related mortality and increased fire frequency. Our findings are consistent with other studies that have suggested mesic big sagebrush communities have greater resistance and resilience to climate change, disturbance, and invasion, than the drier ecosystems, due to underlying differences in temperature, moisture, productivity, and native plant diversity (Davies et al. 2006, 2012, Miller et al. 2011, Chambers et al. 2014a, b).

**Sage-grouse management zone responses to altered climate**

Our simulation results suggest that the largest increases in summer dry days and decreases in summer ASW in the future are expected for the northern half of the big sagebrush region (MZs 1, 2, 4, and 5), but especially for the Snake River Plain (MZ 4) and Northern Great Basin (MZ 5). This is concerning as these MZs contain the core populations of greater sage-grouse, have the highest reported bird densities, and encompass substantial greater sage-grouse habitat (Connelly et al. 2004, Manier et al. 2013). These regions may become drier and potentially more vulnerable by mid-century, despite predicted increases in precipitation and wetter winter and spring soil conditions. However, warmer temperatures, particularly in the northern portion of our study area, may increase habitat suitability in some cases, such as on mesic sites. In contrast, smaller changes in soil water are expected for the Southern Great Basin (MZ 3), the Columbia River Basin (MZ 6), and the Colorado Plateau (MZ 7). These areas are already the hottest and driest portions of the big sagebrush region, with very little stored water that could be subject to additional evaporative loss in the future and as such, changes in ASW and dry days are expected to be smaller. Despite smaller changes, sites in MZ 3, MZ 6, and MZ 7 will remain among the driest (Appendix S1), underscoring the potential for elevated vulnerability for plant communities in the southwestern United States (Gremer et al. 2015, Schlaepfer et al. 2015) to increased drought intensity and frequency (Seager et al. 2007, Abatzoglou and Kolden 2011, Anderegg and Diffenbaugh 2015). Throughout the range of big sagebrush, our findings of increases in summer dry days and decreases in ASW are consistent with other studies that have projected increased aridity in the future across much of the western United States (Seager et al. 2007, Rehfeldt et al. 2012). However, our results provide new insights by considering spatial patterns using relevant conservation and management units (MZs) and by also considering differences in responses among sites within the same region, according to their underlying ecological conditions (Appendix S11).

**Management implications**

Changes in the magnitude of timing of soil water availability forecasted here will likely influence disturbance regimes, invasion dynamics, and their interactions in the future. Range-wide, our simulations suggest wetter spring and winter conditions, which could benefit cheatgrass’s life history strategy (Prevéy and Seastedt 2014, Bradley et al. 2016) and in tandem with warming temperatures could open up new parts of the big sagebrush range (e.g., high elevations, higher latitudes), and result in increased fire activity (Westerling et al. 2006). Our simulations indicate that the dry ecosystems (SB-Steppe, SB-Shrubland) will become drier in the future,
perhaps making them even more fire-prone and less resistant and resilient to cheatgrass invasion following fire, with implications for restoration success (Chambers et al. 2007, 2014a, b, Davies et al. 2012). Currently, SB-Montane sites may be more resistant and resilient to fire and invasion, but will likely become more vulnerable in the future, with implications for habitat quality and the fire-return interval in higher elevation sites. In addition, we expect that the eastern and northern portions of our study area, where cheatgrass is not currently as ubiquitous and abundant as it is in the Great Basin (Bradley et al. 2016), will become more susceptible to cheatgrass invasion in the future, due to warmer and wetter winter and spring conditions.

Our results suggest climate change adaptation and management actions should differ according to the ecosystem and geographic location in question. SB-Montane ecosystems currently provide important summer and fall habitat for greater sage-grouse (Connelly et al. 2000, Walker et al. 2016), but could also begin to provide more suitable winter habitat in the future, depending on future temperature regimes and snow conditions. In contrast, the drier ecosystems (SB-Shrubland, SB-Steppe) will likely continue to provide important winter habitat for greater sage-grouse and other wildlife (Homer et al. 1993, Connelly et al. 2000), but may provide sub-optimal habitat during the summer months in the future due to drier conditions. Davies et al. (2006) found that some SB-Steppe sites did not currently meet the vegetation requirements in recently developed greater sage-grouse habitat guidelines (Connelly et al. 2004) and our results suggest this trend may continue. Collectively, our results and the work of others suggest new areas of habitat suitability for big sagebrush, primarily in high latitudes and high-elevation sites, and decreased habitat suitability at low elevations in the southwest United States (Shafer et al. 2001, Schlaepfer et al. 2012c, 2015).

SB-Montane sites will potentially provide new, suitable habitat for greater sage-grouse in the future, while current habitat at low to mid-elevations in the Southern Great Basin, Colorado Plateau, and Columbia River Basin may be too dry to support adequate regeneration, productivity, and plant diversity for greater sage-grouse in the future. As such, management may benefit from concentrating resources in portions of the big sagebrush region that may now be too cold to provide year-round habitat for greater sage-grouse and perhaps placing less priority on conservation of dry, low-elevation sites that will have decreased suitability in the future for big sagebrush. These insights may help target conservation and management efforts for multiple agencies in big sagebrush ecosystems across their spatial extent in the western United States to enhance the abundance of big sagebrush habitat in the context of global environmental change.

Finally, we present a spatial framework for summarizing sub-continental climate change impacts at the spatial scales at which management and conservation is implemented, in our case Sage-grouse Management Zones. We believe this approach could be useful for managers summarizing climate change impacts in a variety of ecosystems that span broad spatial extents to generate information to guide managers acting at local to regional scales. In addition, we believe our work has implications for understanding how ecohydrology in other mid-latitude shrub steppe ecosystems (e.g., Patagonia, Central Asia) may respond to changing climatic conditions.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1590/full