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Conifer radial growth response to recent seasonal warming and drought from the southwestern USA[☆]

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ABSTRACT

Future droughts are expected to become more severe and frequent under future climate change scenarios, likely causing widespread tree mortality in the western USA. Coping with an uncertain future requires an understanding of long-term ecosystem responses in areas where prolonged drought is projected to increase. Tree-ring records are ideally suited for this task. We developed 24 tree-ring chronologies from 20 U.S. Forest Service Forest Inventory and Analysis (FIA) plots in the southwestern USA. Climate variables were derived from the PRISM climate dataset (800-m grid cells) to capture the bimodal precipitation regime of winter snow and summer monsoonal rainfall, as well as warm-season vapor-pressure deficit (VPD) and winter minimum temperature. Based on mixed linear models, radial growth from 1948 to 2013 for four conifer species (*Pinus edulis*, *Juniperus osteosperma*, *Pinus ponderosa*, and *Picea engelmannii*) responded negatively to warm-season VPD and positively to cold-season precipitation. *Pinus* spp. benefited from warm-season precipitation linked to the North American monsoon, and *Pinus* spp. and *J. osteosperma* radial growth increased with warmer cold-season minimum temperature. However, warmer cold-season minimum temperatures countered the beneficial influence of cold-season precipitation for radial growth in *Pinus* spp. and *J. osteosperma*, while *P. engelmannii* was unaffected. Also, enhanced drying effects of warm-season VPD associated with decreased cold-season precipitation negatively affected radial growth of *Pinus* spp. and *P. engelmannii*. Of the four conifer species studied, *Pinus* spp. are most affected by droughts since 1948, while *P. engelmannii* and *J. osteosperma* appear to be more resilient. Investigating seasonal climate responses and interaction effects on radial growth in areas impacted by severe drought helps identify species that may be particularly at risk from climate change impacts in the Anthropocene.

1. Introduction

Drought negatively impacts tree species and is projected to become more frequent in many regions, including the southwestern USA (“Southwest”), under future climate scenarios (Stocker et al., 2014). Conifer species have experienced landscape-wide drought-related mortality events over the last few decades (van Mantgem et al., 2009; Allen et al., 2010), especially during the early millennial drought peaking in 2002 (Breshears et al., 2005; Shaw et al., 2005). However, some tree species and forests are more drought-resilient than others

(McDowell et al., 2008), and can possibly lead to repopulation of drought-stricken areas.

Inter- and intra-annual trends in seasonal climate contribute to the overall health and response of forests after severe drought. For instance, high precipitation in the Southwest during 1978–1995 allowed for rapid radial growth, making trees more susceptible to mortality through beetle infestation and associated pathogens during the drought years that followed (Breshears et al., 2005; Swetnam & Betancourt 1998). Across the extra-tropical Northern Hemisphere, years with anomalous climatic water deficit, a measurement of drought stress first proposed

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by Stephenson (1990), cause drought legacy effects in radial growth for a few years to follow (Anderegg et al., 2015).

In the Southwest, the major drivers of annual radial growth of conifers from a range of elevations are warm-season vapor pressure deficit (VPD) and cold-season precipitation (Williams et al., 2013), with deficits of cold-season precipitation typically defining drought conditions. Moreover, climatic conditions prior to droughts affect resistance and recovery of radial growth during post-drought years (Peltier et al., 2016). These relationships are derived largely from tree ring records from the early 20th century, with the number of records decreasing sharply for the past few decades (Williams et al., 2013). Refining understanding of how climate drives forest response in more recent years is vital, especially considering the projected increase of temperature and aridity in the Southwest (Seager et al., 2007; Udall & Overpeck, 2017).

Much of the Southwest is defined by a bimodal precipitation regime with peaks during both the cold- and warm-season, the latter due to the North American monsoon (Douglas et al., 1993; Higgins et al., 1999; Vera et al., 2006). Dry periods with warm temperatures and high VPD are particularly acute in late spring prior to the initiation of the monsoon and again in early fall after the monsoon and before cold-season precipitation (Williams et al., 2013). A climate variable often overlooked when investigating drought in this region is cold-season minimum temperature, which plays a major role on snowpack duration, stream runoff, and snow-to-rain transition (Knowles et al., 2006; Pederson et al., 2013). A rise in cold-season temperatures can increase snowmelt in early spring leading to enhanced drought stress on vegetation during the summer and to higher frequency of wildfires in forests of the western USA (Westerling et al., 2006). Increased cold-season temperatures could also lead to a quicker snow-to-rain transition as 21st century abrupt climate change continues. Thus, cold-season minimum temperature is an important variable to consider in relation to cold-season precipitation when evaluating radial growth responses to climatic variability across elevations and latitudes.

The objective of our study was to understand recent drought impacts on dominant conifer species, with a focus on radial growth during the instrumental monitoring period starting in 1948. More specifically, our main goal was to test if and to what extent seasonal (e.g. warm-versus cold-season) climate variables and their interactions affected annual radial growth in relation to the bimodal precipitation regime of the Southwest. We addressed these goals by collecting tree cores from 20 sites for four conifer species across the Southwest. Site chronologies were developed from ring-width records to provide indices of annual radial growth, which we analyzed in the context of their climatic drivers.

2. Materials and methods

Conifer tree species dominate the mid-to-upper elevation landscapes in the spatially heterogeneous Southwest (i.e., Arizona, New Mexico, Colorado, and Utah). Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) is most abundant near the upper treeline, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) dominates the mid-elevations, and two-needled pinyon pine (*Pinus edulis* Engelm.) coexists with Utah juniper (*Juniperus osteosperma* (Torr.) Little) at the lower end of the conifer range (Vankat, 2013).

2.1. Tree-Ring sampling and laboratory analysis

We sampled 20 U.S. Forest Service Forest and Inventory Analysis (FIA; Gillespie, 1999; Shaw, 2017) plot locations in summer 2014 throughout the states of Arizona, New Mexico, Utah, and Colorado (Fig. 1). These plots were selected from a set of 120 candidates from the FIA database using the following criteria: (1) the stand type was classified by FIA during a previous plot visit as pinyon/juniper woodland, ponderosa pine, Engelmann spruce, or Engelmann spruce/subalpine fir

(i.e., stands dominated by one of the focal species), (2) the plot was scheduled for re-measurement by FIA during the 2014 field season (i.e., previously measured in 2004, except in the case of New Mexico plots which were last measured in 1999), and (3) located on public land. The candidate plots were further screened using recent aerial photography to eliminate plots that were disturbed by fire or harvesting activities since the last plot visit, and to identify plots that were within 1 km of accessible roads. The final sample of 20 was intended to cover the full range of latitude and elevation, and therefore climatic variation, on sites occupied by the target forest types within the area of interest.

Ten trees per species representing a range of sizes were selected within or near (< 5 m horizontal distance) each FIA plot. After measuring stem diameter at breast height (~1.4 m), two tree cores were extracted with an increment borer on opposite sides of the main stem in a direction parallel to the slope contours. In the laboratory, tree cores were mounted, sanded, and visually cross-dated (Stokes & Smiley, 1968) with the assistance of nearby tree-ring chronologies from the International Tree-Ring Data Bank (Grissino-Mayer & Fritts, 1997). Tree cores were then scanned and each ring was measured to the nearest 0.001 mm with the WINDENDRO2012 measurement system. Ring-width series were quality controlled using the COFECHA software (Grissino-Mayer, 2001). All tree-ring chronologies were based on a minimum of ten cores dating back to 1948, and sixteen cores as the maximum. Tree cores were measured back to 1940 unless the tree was younger than 66 years.

Raw ring-width measurements were first detrended by fitting a cubic smoothing spline with a 50% frequency response for a 40-year period (Cook and Peters, 1981) to standardize age-growth trends among FIA plots. We further “pre-whitened” the detrended ring-width series to remove time-series auto-correlation (Biondi and Swetnam 1987) using the auto-regressive model in the dendrochronology program library (dplR) that is part of the R software environment (Bunn et al., 2014). The arithmetic mean of annual ring width indices was calculated for each species to build plot-level, species-specific tree-ring chronologies. Empirical measures including expressed population signal, Gini coefficient, and 1st-order autocorrelation were used to quantify the strength of dendroclimatic signals (Wigley et al., 1984; Biondi & Qeadan, 2008; Box & Jenkins, 1976).

2.2. Seasonal climate variables

We calculated seasonal climate variables using monthly climate data from the Parameter-Regression at Independent-Slopes Model (PRISM) dataset with 800-m spatial grid cells (Daly et al., 2008). Cold-season precipitation was defined by mean monthly precipitation from previous November to current March, which is consistent with previous studies (Williams et al., 2013). July-September precipitation has been used to define the temporal range of monsoon precipitation (Romme et al., 2009), and thus, we used mean monthly precipitation for the July-September period to quantify warm-season precipitation.

To investigate the interaction of seasonally derived temperature variables with the bimodal precipitation regime, we calculated warm-season VPD and cold-season minimum temperature. Warm-season VPD was given by the mean monthly VPD of six months, antecedent VPD conditions for three months from the previous year of annual radial growth (August-October) and three months from the current year (May-July) (Williams et al., 2013). Cold-season minimum temperature was defined by mean monthly minimum temperature from the previous November to the current March. We additionally considered growth-season maximum temperature (April-October mean maximum monthly temperature), antecedent VPD (previous August-October), and current VPD (May-July) as independent variables, which were highly correlated with warm-season VPD. Pearson’s linear correlation coefficient was calculated between each tree-ring chronology and seasonal climate variable to investigate site-specific radial growth response to seasonal climate variables.

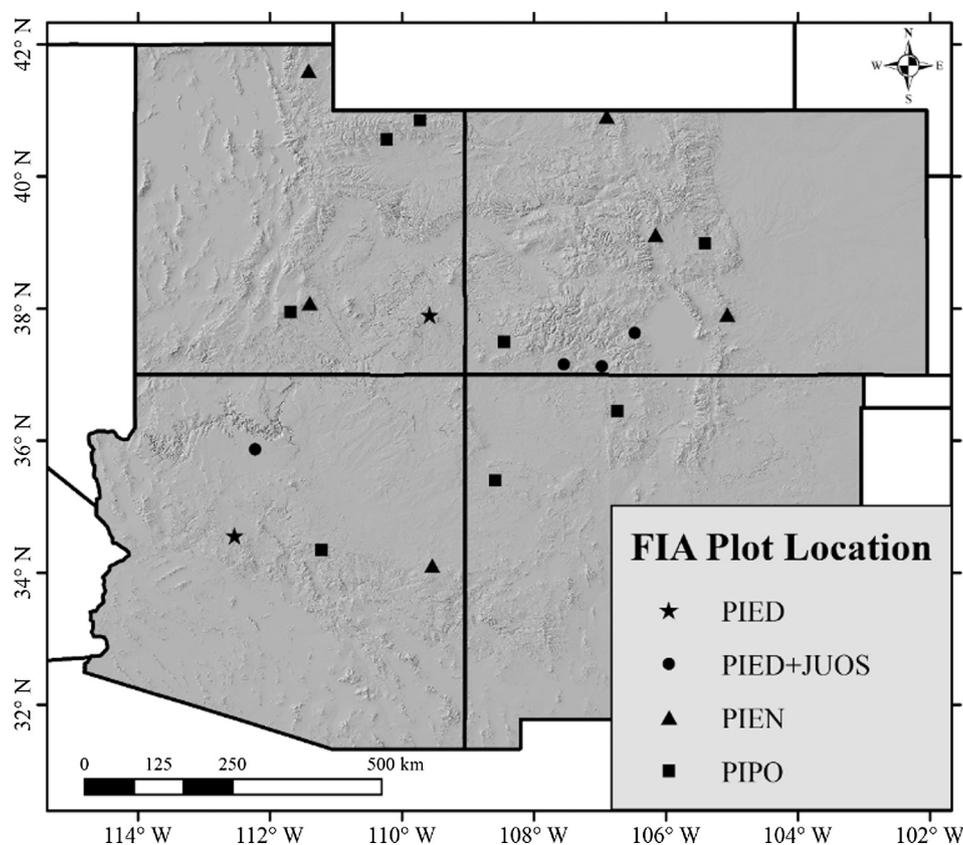


Fig. 1. Geographical location of the study areas (Forest Inventory and Analysis National Program plots). Tree cores were extracted for *Pinus edulis* (PIED), *Juniperus osteosperma* (JUOS), *Picea engelmannii* (PIEN), and *Pinus ponderosa* (PIPO).

2.3. Linear mixed-effects models

To quantify seasonal climate interactions that affect radial growth, we analyzed the site-level, pre-whitened tree-ring chronologies (response variable) via a linear mixed-effects model for each conifer species from 1948 to 2013. We included the main effects of every seasonal climate variable, and the two-way interactions between: (1) cold-season precipitation and minimum air temperature, (2) warm-season precipitation and VPD, and (3) cold-season precipitation and warm-season VPD (FDSI seasons). We decided to use warm-season VPD because it had a higher correlation with more tree-ring chronologies than growth-season maximum temperature (Supp. Information Table 1). The climate variables were standardized (expressed as Z-scores) prior to including them in the linear mixed-effects models. A plot random effect was included to account for spatial variability beyond what could be explained by the climate variables. Significance tests for regression coefficients used the Satterthwaite approximation for degrees of freedom. Analyses were performed using the lme4 package (Linear Mixed-Effects Models using ‘Eigen’ and S4) for the R software environment (Bates et al., 2015; R Development Core Team, 2017).

3. Results

3.1. Dendroclimatic signals

Tree-ring chronologies had relatively uniform sample depth, from 12 to 15 ring-width series per year at all sites (Table 1, Fig. 2). The average DBH varied among species, with ponderosa pine having the largest average DBH (44.5 ± 14.2 cm), followed by Engelmann spruce (36.4 ± 9.6 cm), Utah juniper (30.0 ± 13.0 cm), and two-needled pinyon-pine (29.7 ± 10.3 cm). Because four plots had both two-needled pinyon pine and Utah juniper, a total of 24 chronologies were

developed. The shortest chronology was 70 years long (Utah juniper in a Colorado plot), while the longest ones were 89 years long (ponderosa pine at two Colorado plots).

Dendrochronological statistics for the 24 tree-ring chronologies were acceptable for the purpose of reconstructing responses to seasonal climate variables (Table 1). The expressed population signal (Wigley et al., 1984) for each tree-ring chronology was ≥ 0.855 , except for AZ2J (0.737). First-order autocorrelation was relatively low (between -0.185 and 0.128). The Gini coefficient for the tree-ring chronologies varied significantly among species according to ANOVA tests (F -value = 19.11, $p < .001$). JUOS had the highest mean Gini coefficient (0.211 ± 0.032), followed by PIPO (0.151 ± 0.037) and PIED (0.149 ± 0.023). PIEN had the lowest mean Gini coefficient (0.072 ± 0.021). ANCOVA results comparing Gini coefficients among species with mean climatic water deficit, latitude, longitude, and elevation had no significant relationships. Only the Gini coefficient among species remained significantly different (F -value = 7.16, $p < .01$).

Correlation between annual ring width indices and seasonal climate variables varied by species (Fig. 3 and Supp. Table 1). Twenty-one tree-ring chronologies were significantly negatively correlated with warm-season VPD. Three out of six Engelmann spruce tree-ring chronologies had no significant correlations with warm-season VPD (Fig. 3a). All two-needled pinyon pine and Utah juniper tree-ring chronologies, seven out of eight ponderosa pine, and four out of six Engelmann spruce tree-ring chronologies were significantly correlated with cold-season precipitation (Fig. 3b). Two tree-ring chronologies, one two-needled pinyon pine in Utah and one Engelmann spruce in Arizona, were negatively correlated with cold-season minimum temperature (Fig. 3c). No tree-ring chronologies had a significant correlation with warm-season precipitation (Fig. 3d).

When climatic variables were included together in a linear mixed-effects model, all tree-ring chronologies responded negatively to warm-

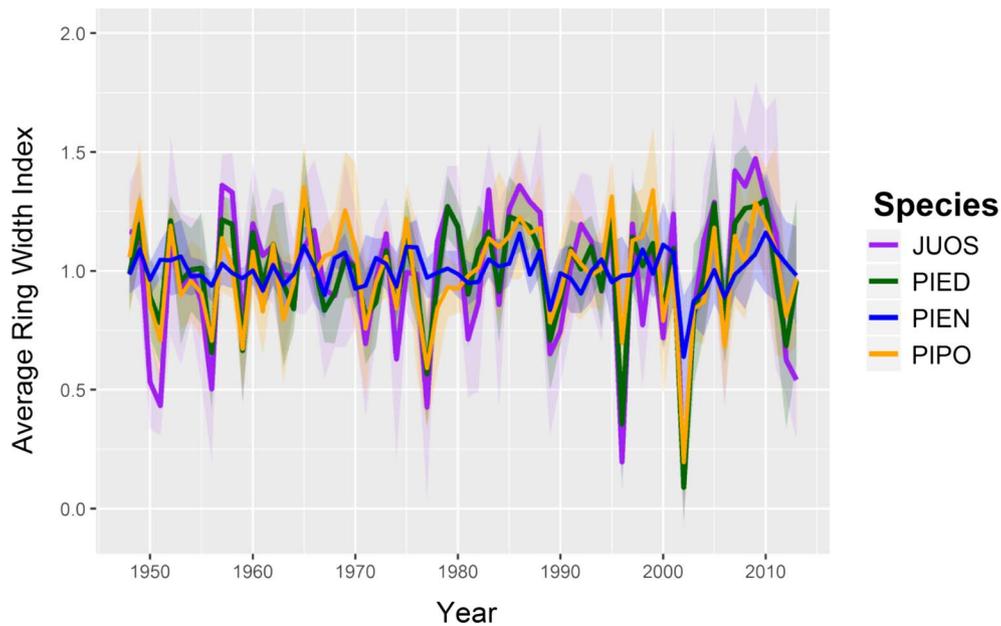


Fig. 2. Regional average tree-ring chronologies (1948–2013) per species included in this study (JUOS = 4, PIED = 6, PIEN = 6, and PIPO = 8; see Fig. 1 for species codes). Shaded areas represent ± 1 standard deviation.

season VPD and positively to cold-season precipitation (Table 2 and Suppl. Info. Modeling Results). Ponderosa pine radial growth had the most negative response to warm-season VPD, followed by Utah juniper, two-needled pinyon pine, and Engelmann spruce. Utah juniper radial growth responded most positively to cold-season precipitation, followed by two-needled pinyon pine, ponderosa pine, and Engelmann spruce. Ponderosa pine radial growth responded most positively to cold-season minimum temperature, followed by two-needled pinyon pine, and Utah juniper. Ponderosa pine radial growth was most positively influenced by warm-season precipitation, with two-needled pinyon pine also responding positively to warm-season precipitation.

We found the strongest interaction effect between cold-season minimum temperature and cold-season precipitation in two-needled pinyon pine radial growth followed by ponderosa pine and Utah juniper

(Fig. 4b,c,d). For the three species, the beneficial effect of cold-season precipitation on radial growth decreased with increasing cold-season minimum temperature. The strongest interaction effect between warm-season VPD and cold-season precipitation was found in two-needled pinyon pine radial growth followed by ponderosa pine and Engelmann spruce. Therefore, decreasing cold-season precipitation increases the harmful effects of warm-season VPD for *Pinus* spp. radial growth, followed by Engelmann spruce (Fig. 4e,f,h).

4. Discussion

4.1. Seasonal climate radial growth responses

We investigated conifer tree-ring records for the Southwest

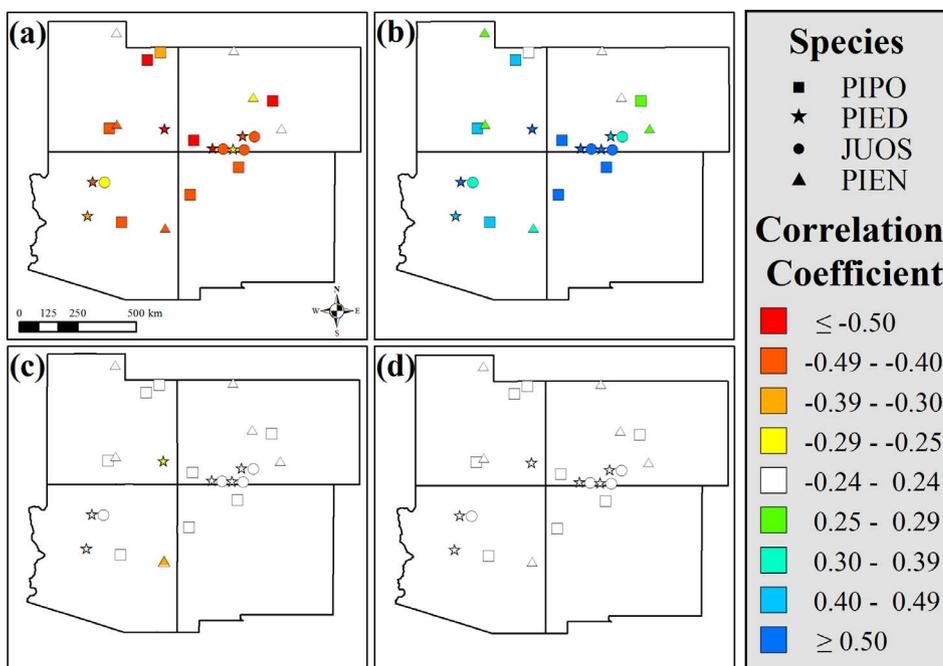


Fig. 3. Pearson's r correlation coefficient between PRISM (800-m grid cells) seasonal climate variables and pre-whitened tree-ring chronologies from 1948 to 2013. Seasonal climate variables include: (a) warm-season (previous August–previous October and May–July of growth year) vapor-pressure deficit, (b) cold-season (previous November through March of growth year) precipitation, (c) warm-season (July–September of growth year) precipitation, and (d) cold-season minimum temperature. Symbols with no color are not significant ($p > .05$).

Table 1
Tree-ring chronology summary statistics for 24 tree-ring chronologies from the Southwest.

FIA Plot	Species	Elevation (m)	Length (yrs)	Time span	[†] LAR	^{**} %LAR	Number of tree rings	Trees	Cores	Cores to 1948	Min/Max index	[†] EPS	[#] G	^{##} A ₁
AZ1	PIED	1815.4	74	1940–2013	16	1.56	1029	10	15	14	0.002/1.776	0.888	0.131	0.029
AZ2P	PIED	1876.4	78	1936–2013	42	4.53	927	9	13	12	0.002/1.686	0.914	0.188	-0.163
AZ2J	JUOS	1876.4	74	1940–2013	54	6.23	867	7	12	11	0.288/1.827	0.737	0.203	-0.185
CO1P	PIED	2699.8	74	1940–2013	31	2.93	1059	10	15	13	0.240/1.411	0.94	0.14	0.01
CO1J	JUOS	2699.8	70	1944–2013	50	4.78	1047	10	15	15	0.001/1.865	0.967	0.246	0.128
CO2P	PIED	2236.2	73	1941–2013	20	1.96	1022	9	14	14	0.004/1.432	0.934	0.132	-0.05
CO2J	JUOS	2236.2	74	1940–2013	29	2.61	1110	10	15	15	0.006/1.633	0.956	0.171	0.008
CO3P	PIED	2155.9	85	1929–2013	12	1.01	1190	10	14	14	0.002/1.420	0.938	0.137	-0.079
CO3J	JUOS	2155.9	75	1939–2013	43	4.02	1070	10	15	14	0.002/1.738	0.941	0.224	0.015
UT1	PIED	2286.9	74	1940–2013	62	5.59	1110	10	15	15	0.215/1.614	0.918	0.168	-0.145
AZ3	PIPO	1670.9	74	1940–2013	20	2.02	989	10	14	12	0.014/1.571	0.894	0.13	-0.075
CO4	PIPO	2564.0	89	1925–2013	36	2.70	1335	10	15	15	0.174/1.749	0.963	0.19	-0.022
CO5	PIPO	2322.9	74	1940–2013	9	0.89	1015	10	14	12	0.158/1.554	0.957	0.143	-0.041
NM1	PIPO	2328.2	75	1939–2013	8	0.84	957	9	13	13	0.195/1.788	0.974	0.211	0.007
NM2	PIPO	2472.0	76	1938–2013	5	0.52	960	10	13	13	0.313/1.445	0.927	0.146	-0.071
UT2	PIPO	2518.3	77	1937–2013	26	2.11	1232	10	16	16	0.046/1.548	0.946	0.156	0.009
UT3	PIPO	2639.9	74	1940–2013	16	1.45	1107	10	15	15	0.051/1.570	0.93	0.138	-0.067
UT4	PIPO	2468.8	74	1940–2013	5	0.52	962	10	13	13	0.447/1.415	0.907	0.092	-0.064
AZ4	PIEN	2787.3	80	1934–2013	0	0.00	1005	10	15	10	0.531/1.676	0.932	0.112	-0.153
CO6	PIEN	3128.8	89	1925–2013	3	0.24	1246	10	14	15	0.321/1.316	0.918	0.6	-0.028
CO7	PIEN	2679.6	73	1941–2013	0	0.00	1084	10	15	15	0.731/1.326	0.855	0.056	0.025
CO8	PIEN	3451.3	74	1940–2013	0	0.00	1110	10	15	15	0.539/1.269	0.934	0.057	-0.027
UT5	PIEN	2574.7	73	1941–2013	0	0.00	1095	10	15	15	0.631/1.306	0.915	0.076	-0.021
UT6	PIEN	3264.0	74	1940–2013	1	0.09	1101	10	15	15	0.535/1.243	0.908	0.068	-0.016

* LAR = number of locally absent tree rings.

** LAR (%) = percentage of absent rings.

[†] EPS = expressed population signal.

[#] G = Gini coefficient.

^{##} A₁ = first-order autocorrelation.

Table 2
Regression coefficient estimates (± std. error) for linear mixed-effects models.

Climate variable	JUOS	PIED	PIEN	PIPO
Warm-season VPD	-0.204 ± 0.048 ^{***}	-0.181 ± 0.028 ^{***}	-0.034 ± 0.01 ^{***}	-0.234 ± 0.022 ^{***}
Warm-season precipitation	-0.001 ± 0.022	0.029 ± 0.014 [*]	0.003 ± 0.01	0.038 ± 0.014 ^{**}
Warm-season interaction Term	-0.003 ± 0.021	0.003 ± 0.014	0.009 ± 0.008	0.01 ± 0.012
Cold-season minimum temperature	0.096 ± 0.047 [†]	0.086 ± 0.032 ^{**}	0.011 ± 0.01	0.103 ± 0.026 ^{***}
Cold-season precipitation	0.197 ± 0.025 ^{***}	0.149 ± 0.015 ^{***}	0.029 ± 0.009 ^{**}	0.133 ± 0.018 ^{***}
Cold-season interaction term	-0.078 ± 0.038 [*]	-0.116 ± 0.022 ^{***}	0.005 ± 0.008	-0.087 ± 0.022 ^{***}
FDSI [†] Seasons interaction term	0.059 ± 0.042	0.121 ± 0.024 ^{***}	0.024 ± 0.01 [*]	0.077 ± 0.022 ^{***}

* $p < .05$.

** $p < .01$.

*** $p < .001$.

[†] The Forest Drought Severity Index (FDSI) seasons include warm-season VPD and cold-season precipitation.

(Arizona, New Mexico, Utah, and Colorado) without favoring sites with water-limiting conditions, such as those that would traditionally be selected in dendrochronological studies (Fritts & Swetnam, 1989). The International Tree-Ring Data Bank (ITRDB) is an open-access database (Grissino-Mayer & Fritts, 1997) that has been used extensively for climate impact analysis (e.g., Williams et al., 2013) and drought evaluation (Griffin & Anchukaitis, 2014). However, tree-ring chronologies in the ITRDB usually end prior to the 2000s droughts, as was the case for our four conifer species, whose representation declined from fifty chronologies reaching the year 2002 to two ending in 2007, and with only one including the year 2013 (ITRDB, 20 July 2017, <https://www.ncdc.noaa.gov/paleo-search/>).

Our results confirm the importance of warm-season (previous August-previous October and May-July of growth year) VPD and cold-season (previous November through March of growth year) precipitation for radial growth of conifer species abundant in the Southwest (Williams et al., 2013). We also investigated other seasonal climate variables and their interactions with these two well-developed variables to better understand conifer species response to drought in the Southwest. The arrival of warm-season precipitation brings relief to the

Southwest from dry early-summer conditions, and *Pinus* spp. are adapted to take advantage of this precipitation within the extent and populations of our study. *Pinus* spp. isohydric ecophysiological traits maintain stomatal conductance for a longer duration than Utah juniper during drought conditions (McDowell et al., 2008) and could more readily use warm-season precipitation after extended dry periods early in the growth season. However, warm-season precipitation originating from the North American monsoon is projected to decrease in June and July and increase in September (Cook and Seager, 2013), possibly prolonging the early-summer drought-like conditions that stress conifer species (Williams et al., 2013). The relief that the North American monsoon brings to the semi-arid Southwest is on the forefront of dendroclimatological research and is an important climatic driver in forest composition and structure of Southwest conifer forests.

In general, increasing cold-season minimum temperature could extend the growth season of conifers in the Southwest. When analyzing cold-season minimum temperature as a sole independent variable, its positive effect on radial growth was likely due to the extension of the growth season. However, for *Pinus* spp. and Utah juniper, which are located in mid-to-low elevations where soil moisture is recharged by

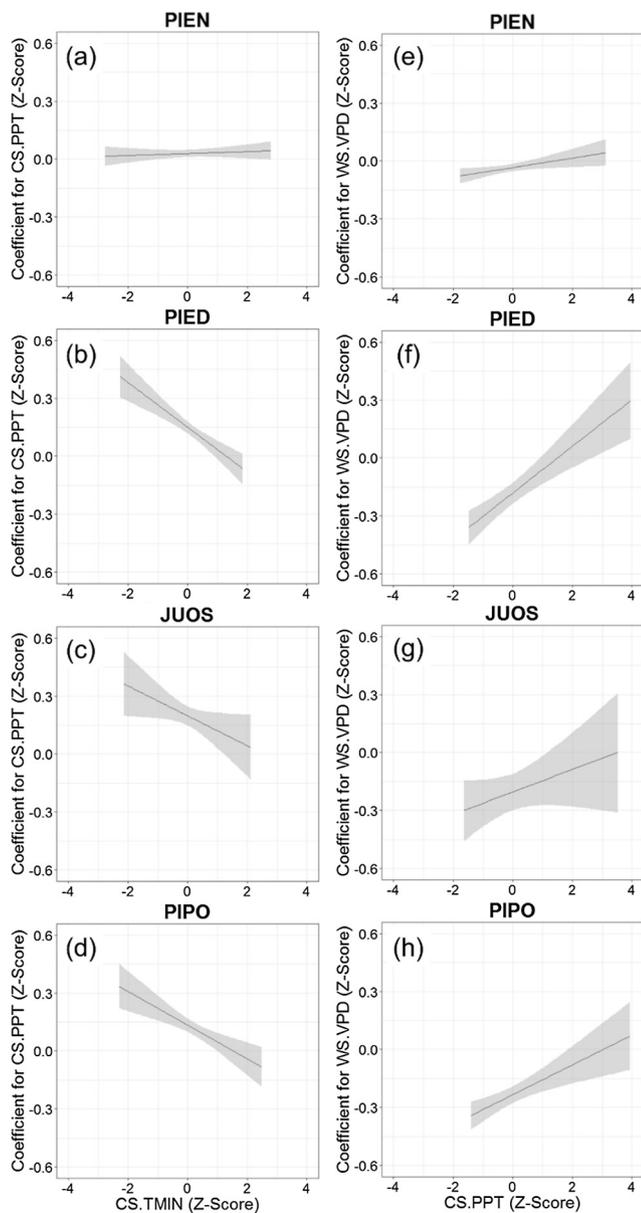


Fig. 4. Two-way interactions based on the linear mixed-effects models (see methods for modeling approach). The interaction of how cold-season minimum temperature (CS.TMIN) influences the effect of cold-season precipitation (CS.PPT) on radial growth for each conifer species is displayed (Fig. 4a,b,c,d); as well as the interaction of how cold-season precipitation influences the effect of warm-season VPD (WS.VPD) on radial growth for each species (Fig. 4e,f,g,h). See Fig. 1 for species code.

melting snow, warmer cold-season minimum temperatures inhibited the beneficial growth effect of cold-season precipitation. Higher minimum temperature during the cold-season plays a major role in the snow-to-rain transition influencing snowpack duration and spring runoff (Knowles et al., 2006). If growth season starts earlier in the year and snowpack duration decreases, then the available soil moisture provided by cold-season precipitation runoff may dissipate earlier and increase the stressful warm-season VPD drought-like conditions in mid-to-low elevation forests. *Pinus* spp. are most strongly affected by these stressful interaction effects, followed by Utah juniper and Engelmann spruce. Engelmann spruce is unaffected or may benefit from earlier access to available soil moisture due to increasing minimum temperatures at higher elevations and latitudes. In addition, DeLucia and Smith, (1987) found that photosynthetic rates of Engelmann spruce declined as minimum soil and air temperature decreased through the growth season. Cold-season minimum temperature warming trends could heat

topsoil earlier and maintain warm temperatures later in the growth season, increasing radial growth in Engelmann spruce populations.

Minimum temperatures during the cold-season may have a greater impact on radial growth than maximum temperature in a future warming climate because late winter/early spring daily minimum temperatures are increasing faster than maximum temperatures in the western USA (Bonfils et al., 2008; Barnett et al., 2008). This relationship is most noticeable when comparing the greater increase of minimum temperature versus maximum temperature between the 1950s drought and early 2000s drought in the Southwest (Breshears et al., 2005). Also, warmer cold-season minimum temperatures could lead to less over-winter mortality in biotic pathogens leading to increased stress and mortality (Bentz et al., 2010; McDowell et al., 2008). Cold-season minimum temperature is a possibly overlooked variable in dendroclimatological studies that could increase drought stress, particularly in mid-to-low elevation conifers, while potentially accelerating radial growth in conifers at higher elevations.

4.2. Management implications

The main driver of radial growth sensitivity to seasonal climate fluctuations depends greatly on the species. Regional-to-stand level abiotic variables, including climatic water deficit, latitude, longitude, and elevation did not explain differences in ring-width variability and the climatic effect sizes. Therefore, it is important to consider the different responses of these species within their forest types in the context of forest management strategies to shifting precipitation regimes and increasing drying effects (Ganey and Vojta, 2011; Floyd et al., 2009).

According to our analysis, Engelmann spruce present in subalpine forests is the least sensitive conifer species and should be considered less exposed to drought stress among the four conifer species. The low sensitivity of Engelmann spruce is likely due to minimal water stress it experiences at high elevations. Other conifer species found in subalpine forests in the Southwest are likely to be less affected by drought than conifers found at mid-to-low elevations. However, the southernmost population we sampled in Arizona responded negatively to increasing cold-season minimum temperature and warm-season VPD. Populations of Engelmann spruce isolated on desert mountain ranges in the Sonoran Desert have experienced greater stress than the populations farther north and may be at higher risk from spruce beetle outbreaks (O'Connor et al., 2015). Allowing for other conifer species to regenerate at lower elevation ecotones on these desert mountains could lead to establishment of more drought- and fire-resistant species to maintain soil stability in upper-elevation watersheds (Truettner et al., 2018).

Ponderosa pine was affected by the highest number of seasonal climate variables indicating that it might possess the most adaptive plasticity to changing precipitation regimes. For instance, ponderosa pine was most negatively affected by warm-season VPD, but also benefited the most from warm-season precipitation. Ponderosa pine is the dominant conifer species at mid-elevations in the Southwest and likely experiences the highest variability of seasonal climate fluctuations. Extensive genetic studies of ponderosa pine have successfully distinguished different haplotypes of ponderosa pine that respond differently to cold-season precipitation and warm-season precipitation (Shinneman et al., 2016; Potter et al., 2015). As ponderosa pine populations and evolutionary trajectories are better understood (Lesser et al., 2013; Frankham, 2010), populations adapted to projected climatic changes over the next hundred to two hundred years could even be considered for assisted migration experiments.

Pinyon-juniper woodlands found at the lowest elevations of forested areas in the Southwest are likely threatened the most by desertification and rapidly spreading invasive species like cheatgrass (*Bromus tectorum*) (Charlet, 2008). The anisohydric, drought-tolerant ecophysiological traits of Utah juniper could be responsible for its highly variable radial growth response compared to the other conifer species. The ecophysiological response of Utah juniper to drought is quicker than two-

needed pinyon pine (McDowell et al., 2008) and ponderosa pine. Utah juniper could act as a transition species that could maintain forest structure as more drought-intolerant species' ranges shift due to increased warm-season VPD and cold-season minimum temperature. Encroachment of pinyon-juniper woodlands in northern areas of the Southwest can often be considered as natural regeneration due to extensive deforestation of the late 19th century due to railroad and mining activities (Charlet, 2008; Lanner and Frazier, 2011), as well as natural migration into warming valley bottoms (Nowak et al., 1994).

Our 20 FIA plot locations do not represent the entire distribution of the four conifer species we studied. Difficulties with cross-dating limited our dataset to four Utah juniper tree-ring chronologies mostly on the northern edge of the North American monsoon. Utah juniper tree-ring chronologies found in northern or southern sites would better represent this species' response to fluctuations in precipitation regimes. Analysis of cell anatomical features associated with earlywood and latewood radial growth might further elucidate responses to warm-season precipitation. For instance, latewood growth in ponderosa pine populations in Arizona and New Mexico is responsive to precipitation from the North American monsoon (Griffin et al., 2013; Leavitt et al., 2011), while other populations are more responsive to VPD conditions during the monsoon (Kerhoulas et al., 2017). In addition, other direct and indirect factors including soil properties, competition, slope, and aspect related to the FIA plot locations may confound the effects of the seasonal climate parameters we used in our analysis.

Management suggestions from our study results are not entirely novel (Clark et al., 2016), but policy needs to progress quickly if forests in the western USA are to withstand the impacts of 21st century abrupt climate change (Williams and Dumroese, 2013). Large-scale replanting projects using proper genetic varieties of conifer species in areas of range shifts could be considered so that forest managers have options to maintain forests not only in the Southwest, but possibly in the northern Rocky Mountains and surrounding areas. Future projections of the distribution of conifer species in the Rocky Mountains are dire (Bell et al., 2014), and management plans facing these projected drastic range shifts (Millar et al., 2007) should be at the forefront of forest and rangeland management policies.

5. Conclusion

Tree-ring chronologies help natural resource managers and forest researchers understand thresholds of climate change leading to vegetation change (Froyd & Willis, 2008; Swetnam & Betancourt, 1998). The ranges of many conifer species have shifted during past abrupt climate changes, with tree species generally moving upwards in elevation and northerly with warming climates (Cole, 1990; Anderson et al., 2000). Species' range margins have already experienced shifts in the 20th century (Allen & Breshears, 1998) and are projected to continue changing over the 21st century (Notaro et al., 2012; Bell et al., 2014). Our analysis of seasonal climate responses in tree-ring chronologies from the Southwest strengthen concerns of *Pinus* spp. being at particular risk of mortality in their southernmost ranges, while Engelmann spruce and Utah juniper were found to be more resilient.

Tree-ring chronologies provide information on terrestrial carbon cycling and water use efficiency prior to instrumental monitoring data (Babst et al., 2014), as well as insight on drought impacts on the global carbon cycle, which are generally not captured in contemporary Earth system models (Anderegg et al., 2015). If warming trends continue to enhance the drying effects of warm-season VPD and cold-season minimum temperatures, water-use efficiency and photosynthetic rates may decrease in ponderosa and two-needled pinyon pine. This decrease could further limit the carbon sink capacity of forest ecosystems in the Southwest (Schwalm et al., 2012).

Investigating seasonal climate responses and interaction effects on radial growth in areas impacted by severe drought helps identify species that may be particularly at risk from climate change impacts in the

Anthropocene.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.01.044>.

References

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Gonzalez, P., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259 (4), 660–684.
- Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proc. Natl. Acad. Sci.* 95 (25), 14839–14842.
- Anderegg, W.R., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Wolf, A., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349 (6247), 528–532.
- Anderson, R.S., Betancourt, J.L., Mead, J.I., Hevly, R.H., Adam, D.P., 2000. Middle- and late-Wisconsin paleobotanical and paleoclimatic records from the southern Colorado Plateau, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 155 (1), 31–57.
- Babst, F., Bouriaud, O., Papale, D., Gielen, B., Janssens, I.A., Nikinmaa, E., Grünwald, T., 2014. Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites. *New Phytol.* 201 (4), 1289–1303.
- Barnett, T.P., Pierce, D.W., Hidalgo, H.G., Bonfils, C., Santer, B.D., Das, T., Cayan, D.R., 2008. Human-induced changes in the hydrology of the western United States. *Science* 319 (5866), 1080–1083.
- Bates, D., Maechler, Martin, Bolker, Ben, Walker, Steve, 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48.
- Bell, D.M., Bradford, J.B., Lauenroth, W.K., 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.* 23 (2), 168–180.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience* 60 (8), 602–613.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res.* 64 (2), 81–96.
- Biondi, F., Swetnam, T.W., 1987. Box-Jenkins models of forest interior tree-ring chronologies. *Tree-Ring Bull.* 47, 71–95.
- Bonfils, C., Santer, B.D., Pierce, D.W., Hidalgo, H.G., Bala, G., Das, T., Mirin, A., 2008. Detection and attribution of temperature changes in the mountainous western United States. *J. Climate* 21 (23), 6404–6424.
- Box, G.E., Jenkins, G.M., 1976. *Time Series Analysis: Forecasting and Control*, revised ed. Holden-Day.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Anderson, J.J., 2005. Regional vegetation die-off in response to global-change-type drought. *PNAS* 102 (42), 15144–15148.
- Bunn, A.G., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Mudelsee, M., Qeadan, F., Schulz, M., Zang, C., (2014). *dplR: Dendrochronology Program Library in R*. < <http://CRAN.R-project.org/package=dplR> > .
- Charlet, D.A. (2008). *Shah-Kan-Daw: Anthropogenic Simplification of Semi-Arid Vegetation Structure*.
- Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., Jackson, S.T., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biol.* 22 (7), 2329–2352.
- Cole, K.L., 1990. Reconstruction of past desert vegetation along the Colorado River using packrat middens. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 76 (3), 349–366.
- Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull.* 41, 45–53.
- Cook, B.I., Seager, R., 2013. The response of the North American Monsoon to increased greenhouse gas forcing. *J. Geophys. Res.: Atmosph.* 118 (4), 1690–1699.
- Daly, C., Halbleib, M., Smith, J.L., Gibson, W.P., Doggett, M.K., Taylor, G.H., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* 28 (15), 2031–2064.
- Delucia, E.H., Smith, W.K., 1987. Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. *Can. J. For. Res.* 17 (6), 527–533.

- Douglas, M.W., Maddox, R.A., Howard, K., Reyes, S., 1993. The Mexican monsoon. *J. Climate* 6 (8), 1665–1677.
- Floyd, M.L., Clifford, M., Cobb, N.S., Hanna, D., Delph, R., Ford, P., Turner, D., 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands. *Ecol. Appl.* 19 (5), 1223–1230.
- Frankham, R., 2010. Challenges and opportunities of genetic approaches to biological conservation. *Biol. Conserv.* 143 (9), 1919–1927.
- Fritts, H.C., Swetnam, T.W., 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* 19, 111–188.
- Froyd, C.A., Willis, K.J., 2008. Emerging issues in biodiversity & conservation management: the need for a palaeoecological perspective. *Quat. Sci. Rev.* 27 (17), 1723–1732.
- Ganey, J.L., Vojta, S.C., 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona USA. *For. Ecol. Manage.* 261 (1), 162–168.
- Gillespie, A.J.R., 1999. Rationale for a national annual forest inventory program. *J. Forest.* 97 (12), 16–20.
- Griffin, D., Woodhouse, C.A., Meko, D.M., Stahle, D.W., Faulstich, H.L., Carrillo, C., Leavitt, S.W., 2013. North American monsoon precipitation reconstructed from tree-ring latewood. *Geophys. Res. Lett.* 40 (5), 954–958.
- Griffin, R.D., Anchukaitis, K.J., 2014. How unusual is the 2012–2014 California drought? *Geophys. Res. Lett.* 41, 9017–9023.
- Grissino-Mayer, H.D., Fritts, H.C., 1997. The international tree-ring data bank: an enhanced global database serving the global scientific community. *Holocene* 7 (2), 235–238.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.*
- Higgins, R.W., Chen, Y., Douglas, A.V., 1999. Interannual variability of the North American warm season precipitation regime. *J. Climate* 12 (3), 653–680.
- Kerhoulas, L.P., Kolb, T.E., Koch, G.W., 2017. The influence of monsoon climate on latewood growth of southwestern ponderosa pine. *Forests* 8 (5), 140.
- Knowles, N., Dettinger, M.D., Cayan, D.R., 2006. Trends in snowfall versus rainfall in the western United States. *J. Climate* 19 (18), 4545–4559.
- Lanner, R.M., Frazier, P., 2011. The historical stability of Nevada's pinyon-juniper forest. *Phytologia* 93 (3), 360–387.
- Leavitt, S.W., Woodhouse, C.A., Castro, C.L., Wright, W.E., Meko, D.M., Touchan, R., Ciancarelli, B., 2011. The North American monsoon in the USA Southwest: potential for investigation with tree-ring carbon isotopes. *Quat. Int.* 235 (1), 101–107.
- Lesser, M.R., Parchman, T.L., Jackson, S.T., 2013. Development of genetic diversity, differentiation and structure over 500 years in four ponderosa pine populations. *Mol. Ecol.* 22 (10), 2640–2652.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Yezpez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178 (4), 719–739.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17 (8), 2145–2151.
- Notaro, M., Mauss, A., Williams, J.W., 2012. Projected vegetation changes for the American Southwest: combined dynamic modeling and bioclimatic-envelope approach. *Ecol. Appl.* 22 (4), 1365–1388.
- O'Connor, C.D., Lynch, A.M., Falk, D.A., Swetnam, T.W., 2015. Post-fire forest dynamics and climate variability affect spatial and temporal properties of spruce beetle outbreaks on a Sky Island mountain range. *For. Ecol. Manage.* 336, 148–162.
- Nowak, C.L., Nowak, R.S., Tausch, R.J., Wigand, P.E., 1994. Tree and shrub dynamics in northwestern Great Basin woodland and shrub steppe during the Late-Pleistocene and Holocene. *Am. J. Bot.* 265–277.
- Potter, K.M., Hipkins, V.D., Mahalovich, M.F., Means, R.E., 2015. Nuclear genetic variation across the range of ponderosa pine (*Pinus ponderosa*): phylogeographic, taxonomic and conservation implications. *Tree Genet. Genomes* 11 (3), 38.
- Pederson, G.T., Betancourt, J.L., McCabe, G.J., 2013. Regional patterns and proximal causes of the recent snowpack decline in the Rocky Mountains USA. *Geophys. Res. Lett.* 40 (9), 1811–1816.
- Peltier, D., Fell, M., Ogle, K., 2016. Legacy effects of drought in the southwestern United States: a multi-species synthesis. *Ecol. Monogr.* 86, 312–326.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Romme, W.H., Allen, C.D., Bailey, J.D., Baker, W.L., Bestelmeyer, B.T., Brown, P.M., Miller, R.F., 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon–juniper vegetation of the western United States. *Rangeland Ecol. Manage.* 62 (3), 203–222.
- Schwalm, C.R., Williams, C.A., Schaefer, K., Baldocchi, D., Black, T.A., Goldstein, A.H., Scott, R.L., 2012. Reduction in carbon uptake during turn of the century drought in western North America. *Nat. Geosci.* 5 (8), 551–556.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Li, C., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316 (5828), 1181–1184.
- Shaw, J.D., 2017. Introduction to the special section on forest inventory and analysis. *J. Forest.* 115 (4), 246–248.
- Shaw, J.D., Steed, B.E., DeBlander, L.T., 2005. Forest inventory and analysis (FIA) annual inventory answers the question: what is happening to piñon-juniper woodlands? *J. Forest.* 103 (6), 280–285.
- Shinneman, D.J., Means, R.E., Potter, K.M., Hipkins, V.D., 2016. Exploring climate niches of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) haplotypes in the western United States: implications for evolutionary history and conservation. *PLoS One* 11 (3), e0151811.
- Stephenson, N., 1990. Climatic control of vegetation distribution: the role of the water balance. *Am. Nat.* 135 (5), 649–670.
- Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M.M., Allen, S.K., Boschung, J., Midgley, P.M., 2014. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of IPCC the Intergovernmental Panel on Climate Change*.
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago.
- Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Climate* 11 (12), 3128–3147.
- Truettner, C., Cole, K.L., Anderson, R.S., D'Andrea, R.M., Peters, M., Jarrad, Z., Cobb, N.S., 2018. Past, present, and fate of spruce-fir forests on desert mountain ranges in Arizona, USA. *Ecol. Evol.* (submitted for publication).
- Udall, B., Overpeck, J., 2017. The twenty-first century Colorado River hot drought and implications for the future. *Water Resour. Res.* 53 (3), 2404–2418.
- Van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323 (5913), 521–524.
- Vankat, J., 2013. *Vegetation Dynamics on the Mountains and Plateaus of the American Southwest*. Springer Science & Business Media.
- Vera, C., Higgins, W., Amador, J., Ambrizzi, T., Garreaud, R., Gochis, D., Nogues-Paegle, J., 2006. Toward a unified view of the American monsoon systems. *J. Climate* 19 (20), 4977–5000.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western USA forest wildfire activity. *Science* 313 (5789), 940–943.
- Wigley, T.M., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Climate Appl. Meteorol.* 23 (2), 201–213.
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Dean, J.S., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Climate Change* 3 (3), 292–297.
- Williams, M.I., Dumroese, R.K., 2013. Preparing for climate change: forestry and assisted migration. *J. Forest.* 111 (4), 287–297.