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Climate and Landscape Controls on Old-Growth Western Juniper Demography in the Northern Great Basin, USA

Rachel A. Loehman,[1]* Emily K. Heyerdahl,[2] Gregory T. Pederson,[3] and David McWethy[4]

[1]Alaska Science Center, US Geological Survey, 4210 University Drive, Anchorage, Alaska 99508, USA; [2]Rocky Mountain Research Station, Fire Sciences Laboratory, USDA Forest Service, 5775 US West Highway 10, Missoula, Montana 59808, USA; [3]Northern Rocky Mountain Science Center, U.S. Geological Survey, 2327 University Way, Bozeman, Montana 59715, USA; [4]Department of Earth Sciences, Montana State University, 226 Traphagen Hall, Bozeman, Montana 59717, USA

Abstract

Western juniper (*Juniperus occidentalis* Hook.) woodlands have persisted for millennia in semiarid parts of the northern Great Basin, USA, providing critical habitat for plant and animal species. Historical records suggest that the establishment of western juniper is strongly associated with regional climatic variability. For example, the abundance of western juniper pollen and macrofossils measured in lake sediment cores increased rapidly in the mid-1500s, concurrent with a regional increase in winter precipitation. However, little is known about how climatic factors interact with landscape structure to control the spatial distribution of western juniper at fine scales and at lower treelines. We used tree rings to reconstruct a spatially distributed history of establishment for 421 western juniper trees across 130 ha on Horse Ridge in central Oregon. Establishment occurred between 845 and 1961 CE, but most trees established after the mid-1550s. The pronounced sixteenth century pulse of establishment represents a transition from more open wooded shrublands to persistent woodlands and coincides with an increase in cool-season moisture and generally cool summer temperatures. Ancient trees that established before this were limited to certain microsites, suggesting that local topoedaphic conditions influenced juniper woodland demography and distributions, although we could not identify consistent environmental drivers. In the future, warmer and drier growing season conditions and a potential increase in wildfire activity may broadly limit western juniper recruitment and its distribution across the region, but at finer scales landscape features that buffer climate change impacts or provide fire safe niches may serve as refugia.

Key words: dendrochronology; tree rings; arid woodlands; Great Basin; climate; landscape structure; microtopography; refugia; *Juniperus occidentalis* Hook.

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**Corresponding author; e-mail:* rloehman@usgs.gov

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Highlights

- Old-growth western juniper woodlands established under cooler, wetter climates.
- Climate and landscape structure create juniper establishment and survival niches.
- Climatic change and increased wildfire may limit juniper to local refugia.

Introduction

Some of the oldest stands of trees in the intermountain region of the western USA are semiarid woodlands of *Juniperus* species, including western juniper (*Juniperus occidentalis* Hook.) (Chambers and others 1999; Miller and Rose 1999). Ancient western juniper stands—including trees nearly 3000 years in age—are ecologically distinct from more recently established western juniper woodlands that expanded during the twentieth century into areas previously dominated by shrubs and grasses (Miller and Wigand 1994; Chambers and others 1999). Although western juniper woodlands currently occupy more than three million hectares of the northern Great Basin Province (Figure 1a), only three to five percent of these woodlands are considered old growth, that is, greater than 300 years old (Waichler and others 2001). In contrast to more recently established juniper woodlands, old-growth western juniper ecosystems have received little attention (Miller and Rose 1999; Waichler and others 2001; Jacobs and others 2008).

Anthropogenic climate changes are a leading and widespread cause of tree species range shifts and local extinctions, reduced biodiversity, loss of ecosystem resilience, and altered disturbance regimes of a magnitude not previously observed in the long-term ecological record (Root and others 2003; Chen and others 2011; Stevens-Rumann and others 2019). In western North America, much of the research on contemporary climate change impacts on arid woodlands has focused on communities of piñon pine (*Pinus edulis* Engelm.) and one-seeded juniper (*Juniperus monosperma* (Engelm.) Sarg.) (Breshears and others 2005, 2009, 2018). In these ecosystems, hotter droughts and intensified disturbances are a leading cause of increased tree mortality and regeneration failure (Breshears and others 2005; Abatzoglou and Williams 2016; Redmond and others 2018; Davis and others 2019). In contrast to woodlands containing piñon pine, globally the most studied species for drought-induced tree mortality (Breshears and others 2018), the relationships of climate, disturbance, and demography (recruitment, growth, and survival) have not been extensively characterized for western juniper woodlands, which contain a comparatively larger juniper component in the overstory and a distinct herbaceous and shrub composition (Jacobs and others 2008). Much of our understanding of western juniper ecology, establishment history, environmental drivers of biogeographic and demographic patterns, and resilience to disturbance is based on recent studies that provide limited understanding of the long-term ecological dynamics of this species and its vulnerabilities to changing environmental conditions.

Old-growth western juniper communities fill unique and significant biological and ecological roles and provide long-term climate records (Kaufmann and others 1992; Miller and others 1999). Old trees are morphologically distinct, with large, spreading, and irregular canopies, thick, furrowed bark, cavities and hollows on the main stems, and thick and twisted lower limbs that are often covered in fruticose lichens (Waichler and others 2001; Miller and others 2005). This structural complexity is important for wildlife, for example, as roosting sites for western long-eared bats (*Myotis evotis* Allen 1864) (Anthony and Sanchez 2018) and nesting sites for birds, which are more abundant in old-growth than in more recently established stands (Reinkensmeyer and others 2008). Structurally complex old-growth juniper woodlands support higher avian diversity and breeding bird density than are found in sagebrush-steppe and early and late-seral shrub–steppe communities (Reinkensmeyer and others 2007). Ecological interactions and food web relationships are typically more complex in old-growth forests, including enhanced decay processes and nitrogen fixation in snags, downed wood, and decayed portions of living trees, fungal-small mammal relationships, and canopy-supported communities of invertebrates and cryptogams (Moir 1992).

Climate and fire are the major drivers of demographic and spatial patterns of western juniper (Wigand 1987; Miller and Wigand 1994; Chambers and others 1999; Miller and others 2005). Reconstructions of long-term climate, vegetation, and disturbance histories of juniper ecosystems are derived from a variety of proxies, including lake levels and salinity (Cohen and others 2000), tree-rings (Cook and others 2004, 2014), plant pollen and macrofossils (Mehringer and Wigand 1990), and charcoal (Wigand 1987). These records indicate that mild, wet periods in the Holocene (early Holocene, 11,500–8000 years before present [ybp];

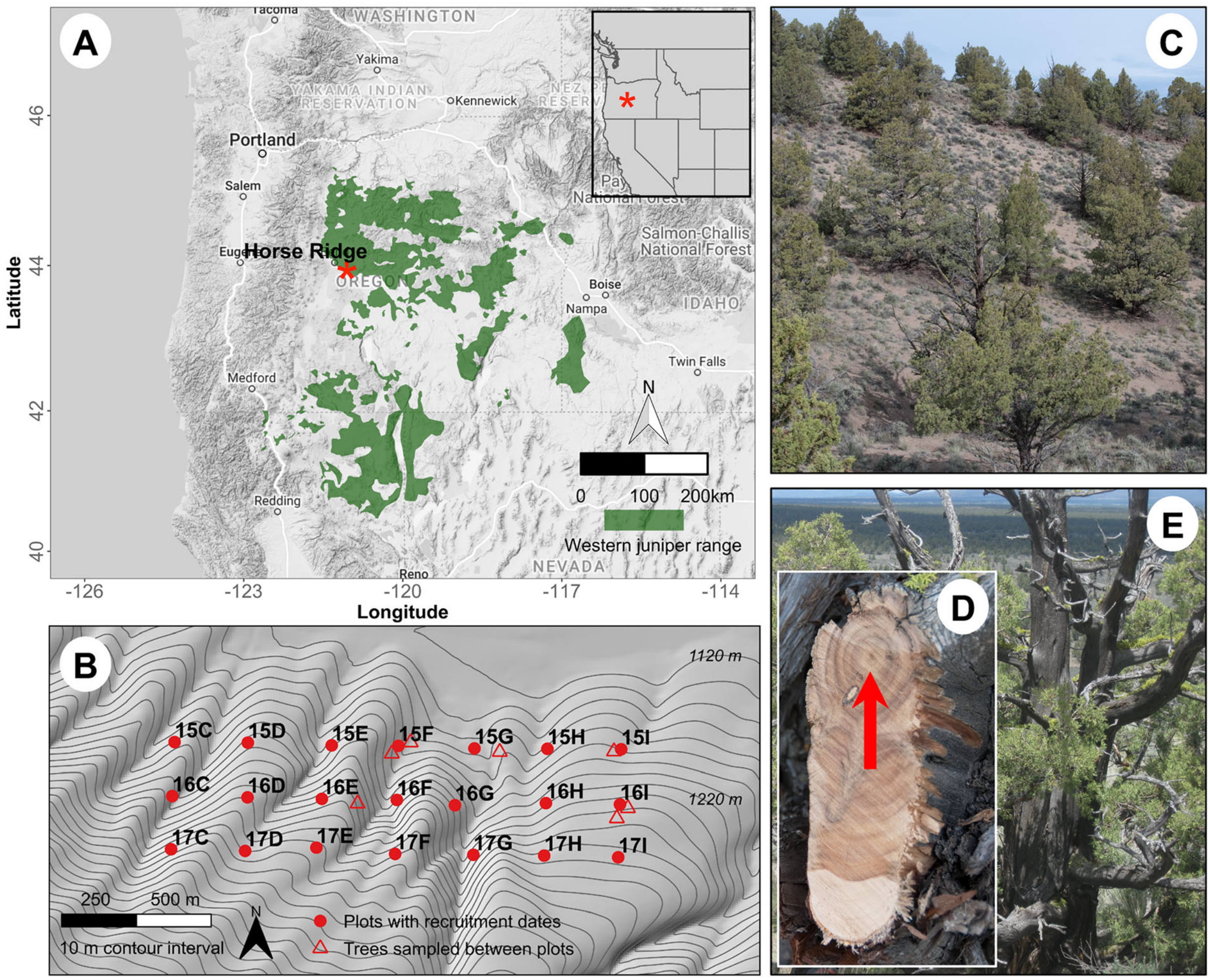

Figure 1. Location of the Horse Ridge study site east of the Cascade Mountains in central Oregon, USA, within the contemporary range of western juniper (*Juniperus occidentalis* Hook., Miller and others 2005), shown in green; basemap provided by Google Earth (**a**); the grid of sampling plots and trees sampled between plots within the complex topography of the site (**b**); low tree density characteristic of the Horse Ridge western juniper woodland study site (**c**); old western juniper often have large basal limbs that we sampled to avoid widespread heart rot (**d**); with an arrow indicating the pith; the presence of dead wood in tree canopies suggests no or limited historical presence of spreading canopy fire at the site (**e**).

Neoglacial, 4500–2500 ybp; Little Ice Age, 550–150 ybp) may have allowed for rapid woodland expansion and downslope movement of western juniper into comparatively drier shrub-steppe communities (Wigand 1987). During the warmest parts of the Holocene (mid-Holocene, 8000–5500 ybp; Post Neoglacial Drought, 2500–1300 ybp) woodland distributions contracted and their northward migration slowed or stopped. Regional declines in western juniper co-occurred with severe drought and major fires during the late Holocene (2500–1500 years ybp; (Mehringer and Wigand 1987; Miller and Wigand 1994).

In contrast to Holocene epoch patterns, recent expansions of western juniper woodlands during the nineteenth century occurred during a period of increasing aridity across the western USA (Mehringer and Wigand 1990; Miller and Wigand 1994; Chambers and others 1999). Proposed drivers of the nineteenth century expansion are a combination of anthropogenic and ecological processes. These include decreased fire frequency as a consequence of fire suppression and grazing impacts on the fine fuel loads that typically sustain surface fires in arid systems, biological inertia, and improved water use efficiency associated with fertilization effects from anthropogenic CO_2 emissions (Knapp and Soulé 1998; Soulé and Knapp 2000; Romme and others 2009). Other studies have highlighted the role of landscape structure in modulating climate effects on recent western juniper growth and on structuring woodland spatial patterns. For example, Knutson and Pyke (2008) found that topographic and edaphic factors influenced drought sensitivity—and, potentially, tree recruitment and mortality—of recently established western juniper woodlands in southern Oregon.

Landscape and environmental controls on old-growth western juniper woodlands are not broadly characterized. Most ancient western juniper trees (> 1000 years) are found in areas where surface fuels are sparse (Miller and Rose 1995, 1999). Historically, wildfire limited conifer encroachment into shrub-grassland communities in the Intermountain West (West 1999; Davies and others 2019) because most fires kill all young western juniper (< 50 years old) and nearly all adult western juniper (Miller and Wigand 1994; Chambers and others 1999). As a result, western juniper woodlands were confined mainly to fuel-limited areas or to fire safe niches, such as productive sites where dense trees limited the growth of understory fuels (Johnson and Miller 2008). However, fire appears not to have played a role in juniper demographic patterns in central Oregon, where uneven-aged stands and presence of old standing wood and down woody debris suggest absence of any major stand-replacing fires within the 450-year plus record (Waichler and others 2001). Weisberg and others (2008) found that although old-growth woodlands were more likely to occur on fire-safe sites, topographic position likely facilitated woodland distribution. In a study of environmental factors influencing the establishment of western juniper in east-central Oregon, rates of tree establishment increased with elevation and decreased with southerly exposure for stands that established in the mid-1800s (Johnson and Miller 2006), indicating the importance of topoclimatic controls on juniper demography.

In the northern Great Basin, much of the inference about long-term patterns of western juniper demography was derived by proxy from two lake sediment cores extracted from Diamond Pond and Fish Lake in the Steens Mountains of southeastern Oregon (Miller and Wigand 1994). These reconstructions document two recent (ca. < 1000 ybp) periods of western juniper expansion in the Great Basin: a mid-1500s gradual expansion into previously xeric sites, attributed to a pattern of stronger winter precipitation that developed about 500 years ago; and a late 1800s expansion facilitated by reduced fire frequency following cessation of Native American intentional burning and removal of fine fuels through grazing (Mehringer and Wigand 1990; Miller and Wigand 1994).

This study was motivated by the lack of information on historical wildfire regimes and demographic controls on western juniper, particularly in old-growth stands in semiarid woodland settings. An understanding of climate and landscape controls on western juniper demographic and spatial patterns informs conservation and management of the species and dependent wildlife populations throughout its range. Western juniper woodlands in various stages of structural development dominate large land areas over broad environmental gradients, but these woodlands are often treated generically in management plans and resources assessments (Waichler and others 2001). For example, tree removal via bulldozing, chaining, prescribed fire, and herbicide application has been implemented to improve capture and storage of water in soils, increase late-season streamflow, and improve rangeland and wildlife habitat (Bates and others 2017; Davies and Bates 2017), but these control measures are based on the premise that western juniper is invasive to shrublands throughout its range (Belsky 1996), rather than a constituent old-growth woodland ecosystem.

Our study of western juniper centers on a low-elevation western juniper woodland site in central Oregon, near the Horse Ridge Research Natural Area (hereafter, Horse Ridge) in the northern Great Basin. Woodlands in this area comprise the most extensive old-growth western juniper woodlands in the species' range (Waichler and others 2001). Horse Ridge is an optimal place to investigate demographic patterns and drivers because the site includes what appeared visually to be spatial variation in tree ages that was different from the pattern on less topographically diverse, nearby areas; thus, it offered the potential for more insights into controls on recruitment, growth, and survival. Horse Ridge lies 200 km from the Steens Mountains site, allowing us to assess whether the climate variables previously identified as drivers of juniper demography were influential at broader, regional scales. The fine-scale topographic variability at Horse Ridge provided a further opportunity to evaluate how local landscape physical characteristics may have moderated regional climate and influenced demographic patterns at these finer scales.

Our objectives were to:

1. Describe spatially distributed, demographic patterns of old-growth western juniper trees using tree rings;
2. Relate spatial and temporal patterns of western juniper demography to potential drivers of climate, wildfire, and landscape structure;
3. Assess the potential vulnerability of old-growth western juniper woodlands to future climate changes, wildfire activity, or other stressors.

We documented a millennial demography of western juniper from a gridded reconstruction of crossdated tree ages; compared demographic patterns to climate reconstructions, including a fine-scale reconstruction of cool-season (Sep–Jun) total precipitation developed for this study; and examined the potential role of wildfire, climate, and landscape structure in influencing patterns of demography using field-measured and derived landscape variables.

Methods

Study Area and Sampling Design

The Horse Ridge study area is a western juniper woodland site located 30 km southeast of Bend, Oregon on land managed by the Prineville District of the Bureau of Land Management (latitude 43° 56′ 16″, longitude − 121° 2′ 56″; Figure 1a, c). The study area lies at 1200 m above sea level on the north face of Horse Ridge, north of the Horse Ridge Research Natural Area (Hall 1972; Schuller and Halvorson 2008). Winters are cold and summers are warm and dry; as summarized from instrumental records (1914–2012) in nearby Bend (elevation 1108 m) mean annual precipitation averages 29 cm, with only 16% falling during summer (Jun–Aug), and monthly temperatures range from an average minimum of − 6 °C in January to an average maximum of 28 °C in July (Western Regional Climate Center 2013). The ridge is composed of old (> 5 mya), primarily basaltic volcanic rocks (MacLeod and others 1982; Geitgey 1992) overlain by nutrient-poor ash soils that developed from tephra ejected by Mount Mazama about 7600 ybp (Geist and Cochran 1991; Egan and others 2015). These soils have low thermal conductivity, but the radiation frosts that are common on the surrounding pumice plateau are not common here because the site is sloped (Schuller and Halvorson 2008). In 1886 CE, George Millican homesteaded just east of Horse Ridge and the surrounding area was densely settled by the early twentieth century (Brogan 1964), but a lack of water has prevented significant domestic livestock grazing on Horse Ridge (Schuller and Halvorson 2008).

We selected our study site to avoid two small, recent prescribed fires near the ridge, but to include areas where some live western juniper trees were felled in 2001 and 2003 and thus could be easily sampled. The site is crossed by a recreational trail but has no roads. Prior to field sampling we mapped a 130-ha grid of 21 plots with a spacing of 250 m to capture the variation in landscape structure arising from a series of small north–south drainages (Figure 1b). Following a field assessment, we moved five of these plots 10 to 50 m to avoid trails or ridges.

Tree Demography

At each plot we used *n*-tree density-adapted sampling to identify the 20 live or dead trees that were closest to plot center and at least 10 cm in diameter at 30 cm height from the ground surface (Jonsson and others 1992; Lessard and others 2002). We computed plot size from the distance of the farthest tree sampled (area of plot = $\pi \times$ [distance from plot center to farthest tree sampled]^2/10,000). This distance varied from 13 to 29 m (20 ± 5 m, average ± standard deviation) resulting in plot sizes of 0.06 to 0.26 ha (0.13 ± 0.07 ha). In each plot, we tallied the small trees we did not sample, that is, those that were at least 30 cm in height, but less than 10 cm in diameter.

Obtaining the recruitment dates of old western juniper trees is challenging because the pith of their main stems is often destroyed by heart rot (Knapp and Soulé 1999). However, individuals of this species often have large, basal limbs lacking heart rot so we sampled full or partial cross sections from the basal limbs of trees with heart rot (Figure 1d). For most trees, we used a chain saw to remove (a) sections from one or two limbs (48% of trees), (b) one or two partial sections from the main stem (26%, mostly from dead trees), or (c) sections from limbs plus the main stem (7%) to test our assumption that basal limbs were similar in age to main stems. From the remaining trees, we used an increment borer to remove a core from the main stem (19%). We also collected wood samples from two stumps and three snags that we encountered between plots because they appeared to be particularly old. We recorded the presence or absence of charred wood on each tree.

We sanded all wood samples until the cell structure was visible with a binocular microscope and assigned calendar years to tree rings by visually crossdating ring widths, assisted by cross-correlation with a measured ring-width chronology for some trees (13%; Holmes 1983). The measured chronology was derived from trees we sampled in our plots, combined with an existing chronology (Meko and others 2001). Some samples could not be crossdated (13%) so we excluded them from analyses requiring precise dates but included them in analyses that did not (for example, modern tree density).

We estimated tree recruitment dates from actual or estimated pith dates at sampling height (30 ± 11 cm high for main stem samples and 26 ± 17 cm for limb samples). For samples that did not intersect pith (19% of crossdated trees), we estimated the number of years to pith geometrically (Applequist 1958; Duncan and Stewart 1991; average correction 10 ± 18 years). We obtained death dates for all dead trees for which we had outside rings from main stem samples. Tree death dates cannot be obtained from limbs of this species because the cambium often dies around all or part of the circumference of a limb before the tree itself dies. We defined old-growth plots as those containing at least one tree that established before 1500 CE, and for each plot calculated old tree density (number of trees establishing prior to 1500 CE per plot area).

Plot Characteristics and Evidence of Fire

We recorded the location, elevation, aspect, and percent slope of each plot in the field, measured soil depth, and visually classified the soil type. We assigned each plot to a slope position (valley bottom, lower slope, middle slope, upper slope, or ridge) relative to the study area as a whole and assigned each plot to a plant association (sensu Driscoll 1964). In a 5.6-m fixed-radius subplot, we recorded the presence of all understory species and visually estimated ground cover in six categories (rock, bare ground, shrubs, perennial grasses, perennial forbs, and annual forbs) by classes ($< 1\%$, > 1–10%, > 10–30%, > 30–50%, > 50–70%, > 70–90%, or > 90–100%) and classified slopes as shallow (0–10%), moderate (11–35%), or steep ($> 35\%$) (Sankey and Germino 2008). We looked for evidence of past fires by examining the boles of all live or dead sampled trees for char and fire scars.

Landscape Characteristics

For each plot, we derived four landscape variables potentially related to tree demography and plant community establishment: classified aspect, topographic position, site exposure, and solar radiation (Wilkinson and Humphreys 2006; Davies and others 2010). We reclassified field-measured aspect to cardinal directions, where $316° > N < 45°$; $46° > E < 135°$; $136° > S < 225°$; and $226° > W < 315°$, to create unique, non-overlapping classes from the circular variable. We calculated a three-position (canyon, slope, or ridge) topographic position index (TPI) for 15-pixel neighborhoods, using the LandFacet Corridor Designer Extension (Jenness and others 2013). The TPI classification reflects the difference between the elevation in a particular cell and the average elevation of the cells around it (neighborhood) and thus represents fine-scale, relative topographic position. We calculated a relative mean site exposure index (SEI) (possible range -100 to 100) that identified cool (lower values) versus warm (higher values) pixels (Johnson and Miller 2006) using map algebra tools, and we determined summer season (Jun–Aug, reference year 1500) solar radiation—a variable that provides a measure of the heat load incident on the variable surface of the site (Fu and Rich 2002). The base data layer for all calculations was a 1/3 arc-second (~ 10 m resolution) digital elevation model (DEM) acquired from the USGS National Elevation Dataset (Gesch and others 2002). All derived variables were calculated using ArcGIS 10.3.1 (Environmental Systems Research Institute 2015) for a 30-m radius circular area around the center of plots, a buffer distance that corresponds to the maximum tree distance from plot center in our study.

Climate Reconstructions

To capture potential seasonal climate responses related to juniper establishment, we used existing millennial-length climate reconstructions of summer temperature and summer Palmer Drought Severity Index (PDSI, Alley 1984) and produced a new tree-ring based reconstruction of cool-season total precipitation (Pederson 2022). The summer (May–Aug) temperature reconstruction data were provided by the last millennium Northern Hemisphere dataset from Anchukaitis and others (2017) and were derived by averaging grid points surrounding our study area (latitude 43.5 to 46.5° and longitude -122 to $-117.5°$). The summer (Jun–Aug) PDSI data were extracted from a grid point 150 km northeast of Horse Ridge (grid point 44, 45°N$-$ 120°W) (Cook and others 2004).

To reconstruct cool-season (Sep–Jun) total precipitation, we used the network of tree-ring chronologies from the Columbia River streamflow reconstruction by Littell and others (2016), extracting all records exhibiting a significant ($p \leq 0.05$) correlation to the gridded 4 km Parameter-elevation Relationships on Independent Slopes Model (PRISM) instrumental precipitation dataset described below. Chronology quality checks are detailed in Littell and others (2016), and standardization was performed using program ARSTAN (version 40c) with an initial detrending based on either a negative exponential curve or negative linear trend fit through the measured ring-width series (see Cook and Holmes 1984; Cook 1985). If the initial detrending equations resulted in a poor growth curve fit, we used a mean line or a cubic spline two-thirds the length of the series. The mean chronology was calculated as the weighted robust mean of the detrended series, and variance stabilization was performed following methods from Briffa (1999) to reduce the influence of decreasing sample size.

Instrumental precipitation calibration data were generated from PRISM (Daly and others 2008) as the average of the 4 × 4 km grid cells of total monthly precipitation across Deschutes County, Oregon. The gridded PRISM precipitation data were checked against the observed precipitation dataset used to drive the variable infiltration capacity (VIC) hydrologic model (Hamlet and others 2005, 2007) and were found to be reasonably homogeneous ($R^2 = 0.703$) over the period tested (1917–2006 CE) considering the different grid sizes and non-equivalent spatial extent. A scatter plot and time series comparing the PRISM and VIC Sep–Jun total precipitation averaged for Deschutes County, Oregon shows very close agreement among the two datasets, with the mean of the VIC dataset slightly higher than the mean of the PRISM dataset (Figure S1).

A total of 20 chronologies were retained after correlation screening for the regression model predictor pool. A subset of 12 of these chronologies then entered into one of three nested reconstruction models (Supplemental Tables S1 and S2). The final cool-season (Sep–Jun) total precipitation reconstruction (Figure S2) was produced by nesting successively longer, but statistically weaker, best-fit multiple linear regression models through time. Additional details on nesting and complete reconstruction procedures are described in Woodhouse and Pederson (2018). Regression models were constructed using a best subsets extensive search criterion within the ''leaps'' package (Lumley 2013), with additional standard dendrochronological analyses and time series functions performed in package ''dplR'' (Bunn 2008, 2010; Bunn and others 2016) in the analytical program R (R Core Team 2020). Selection of the final suite of ''best'' nested models was based on the Mallow's CP statistic, adjusted R^2 values, and results from cross-validation. Models were cross-validated using the leave-one-out and K-folds method in the ''cvTools'' package (Alfons 2012). In the K-folds cross-validation method, a random set of 10 sequential observations was withheld from model fitting for use in prediction testing, with this function then replicated 100 times. Resulting cross-validation statistics provide a mean, median, and full distribution of prediction errors that are displayed in units of root mean squared error of the validation data ($RMSE_v$) (Figure S2, Data S1). Skill ranged from R^2 adj of 0.420 to 0.561, with cross-validation statistics from the leave-one-out and leave-10-out method equivalent producing $RMSE_v$ ranging from 72.25 mm to 80.01 mm (Figure S2, Table S2). The successively longer (but weaker) reconstructions were mean and variance scaled to match the mean and variance of the observed precipitation record, then nested forward and backward in time to generate a single time series of the reconstruction spanning 1000–1991 CE. This approach corrected for artificial variance reduction from regression that arises due to the reduced quality of the longer nested models.

Analysis

After testing for normality and homogeneity of variances we used Welch's two sample *t*-tests (Derrick and others 2017) to test for differences in elevation, slope, summer solar radiation, and site exposure (continuous landscape variables) for plots with old versus young trees, that is, plots with trees that recruited before versus after 1500 CE. To assess the relationship of the density of old trees (non-normally distributed) to categorical landscape variables of aspect, topographic position, slope class, and cover class of bare ground, rock, and perennial grass we used the Kruskal–Wallis test by ranks (Kruskal and Wallis 1952) followed by post hoc Dunn's tests (Dunn 1964) with a Bonferroni correction for variables with significant *p*-values ($p \leq 0.05$) (Zar 1984). To assess the relationship of reconstructed climate variables to juniper establishment we first binned tree establishment dates into 25-year bins beginning with the year 800 CE. An ''establishment pulse'' was then defined as any 25-year bin within which 15 or more trees established into the Horse Ridge population. We defined the peak recruitment phase as the 200-year period 1550–1750 CE, the interval during which the vast majority of the living trees at the site established, with the steepest recruitment curve remaining at or above the 15-tree establishment threshold for each of the 25-year bins (Figure 4d and e). Climate variables were then assessed for significant anomalies over the period of peak recruitment phase (1550–1750 CE) versus the entire record (with 1550–1750 CE removed) by comparing kernel density functions and the means using Welch's unequal variances and sample size *t*-test. As a sensitivity test, this analysis was also re-run on the cool-season precipitation reconstruction with the severe 1612–1660 CE 50-year drought removed from the otherwise wet 200-year peak recruitment phase.

Results

Tree Demography

Most of the 421 western juniper trees in our plots were alive when we sampled them in 2009 (63%) or were felled in 2001 or 2003 (23%). The rest were snags (13%) or logs (1%). Felled trees occurred in 12 plots (8 ± 5 trees per plot). We observed heart rot in at least 25% of all trees. Despite lacking false rings, the western juniper samples we collected were challenging to crossdate because many rings were locally absent, but we obtained recruitment dates or minimum recruitment dates for most trees (87%). Of the 55 trees we were unable to crossdate, most were limb samples (78%). Most were also from live trees (97%). Undated trees occurred in most plots (76%) with an average of three trees per plot (range one to nine trees).

The pith dates we obtained from limbs (45% of trees) were generally similar to those we obtained from main stems (55% of trees). For most of the 15 trees from which we were able to date both types of wood samples, the difference in pith dates was no more than 28 years, with pith dates from the main stem being older than those from limbs for all but one tree. Two trees differed more substantially in pith dates from limb versus main stem samples: 50 and 93 years. At the site level, the chronology of pith dates from main stems was similar to that from limbs (Figure 2).

Tree recruitment was not constant through time. Western juniper trees have been present at our site for at least 1400 years and most of the trees we sampled were pre-settlement; 93% established before 1886 CE, when the first Euro-American settlers homesteaded near Horse Ridge (Miller and others 2005), and only 24 trees recruited after 1870 CE (Figure 4e). A few trees recruited during most decades, with an abrupt increase in recruitment about 500 years before present and peak recruitment (> 15 trees established in a 25-year period) from 1550 through 1750 CE (Figure 4e). Small trees (at least 30 cm in height, but less than 10 cm in diameter) were widespread (4 ± 3 trees in 17 plots) but occurred at low densities (31 ± 33 trees·ha^{-1}) compared to mature trees (130 ± 48 trees·ha^{-1}). The five trees we sampled between plots were among the oldest; they established between 864 and 1145 CE and occurred along the north and east sides of the sampling grid (Figure 5).

Despite the remarkable preservation of dead wood at this dry site, we obtained few tree death dates and they all occurred during the twentieth century (1929–1934 CE; plots 15F, 15H, 15I, 16F, 16G, 16H, and 17H). We sampled 65 snags and logs but obtained death dates for only 11 of them because (a) the samples did not crossdate (four trees), (b) the outside rings had eroded (24 trees), or (c) the samples were obtained from limbs (26 trees).

Plot and Landscape Characteristics

Our 21 plots spanned 150 m in elevation, from 1140 to 1290 m; half faced north (11) and half either west (6) or east (4) (Table 1). Most plots (86%) had moderate slopes (11 to 38% slope) and the rest were steep (40 to 51% slope). Slope position was recorded as valley bottom or lower slope for 19% of plots, middle slope for 52% of plots, and upper slope or ridge for 29% of plots. Plots were positioned in topographic relative positions identified as canyons (24%), slopes (52%), and ridges (24%). Site exposure index (SEI) values ranged from − 34.98 (relatively cooler setting) to 4.91 (relatively warmer setting), with a mean SEI of − 17.25. Summer season solar radiation ranged from 468,404 to 529,885 Wh·m^{-2} (mean 503,762 Wh·m^{-2}), with larger values indicating plots with higher global incident radiation. We found little variation in soil type or vegetation composition across the site. Soils were 42 ± 19 cm deep and classified as moderately deep, frigid, Vitrandic Haploxerolls in all but three plots (15F, 16C, 16G) for which soils were identified as deep to moderately deep mesic Vitritorrandic Haploxerolls (Soil Survey Staff 2019). Western juniper, the only tree species on Horse Ridge, occurred in every plot, as did mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle), Idaho fescue (*Festuca idahoensis* Elmer), and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve ssp. *spicata*). We assigned all plots to Western Juniper/

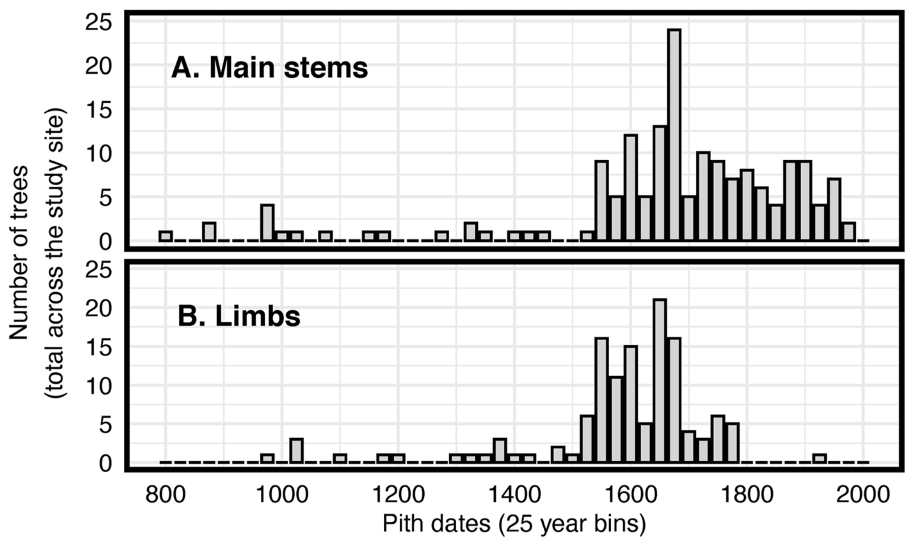

Figure 2. The chronology of tree recruitment we derived from main stem samples (**a**) across the site was similar to the one we derived from limb samples (**b**).

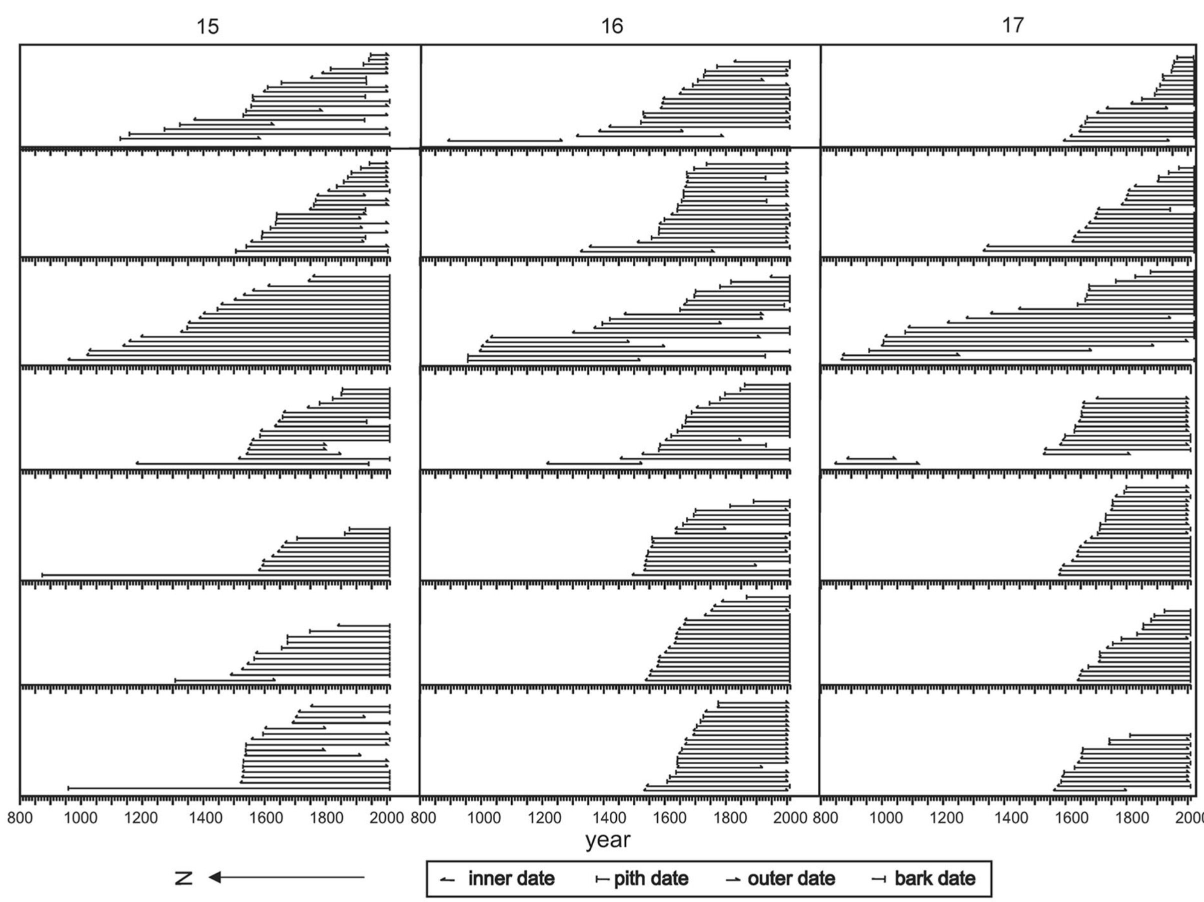

Figure 3. Tree demography by plot. Each panel is from a single plot within our sampling grid, but rotated so that north is to the left. In each panel, horizontal lines represent individual trees, where lines between pith and bark dates indicate tree life span and those between inner and outer dates indicate the tree-ring record that was present or datable for that tree.

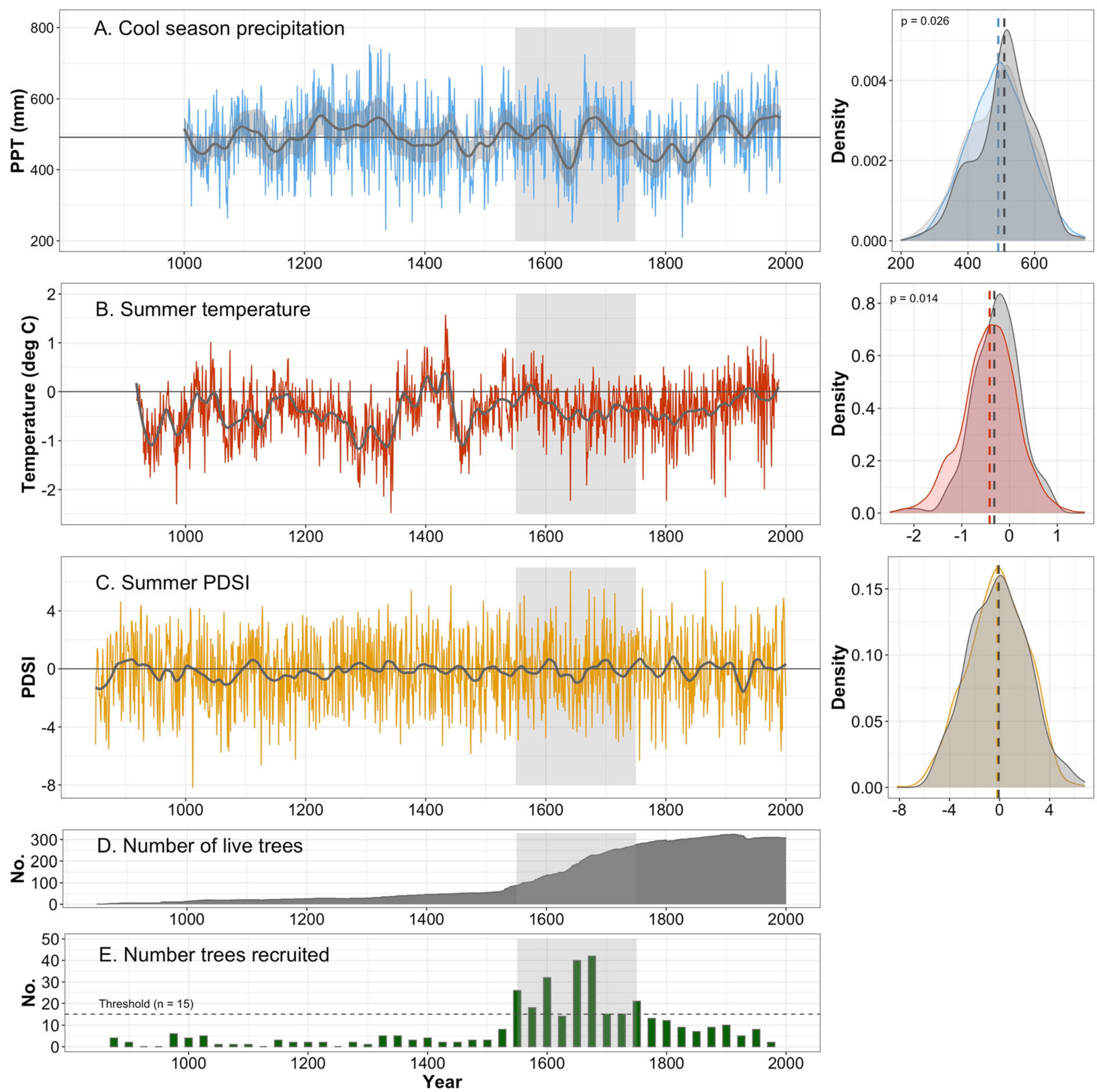

Figure 4. Climate reconstructions and western juniper recruitment at Horse Ridge. All climate series were smoothed with cubic splines that retain 50% of the variance at periods of 50 years. **a** Cool-season (Sep-Jun) total precipitation reconstructed for this analysis, **b** Summer temperature (May-Aug), **c** Summer PDSI (Jun-Aug), **d** Number of live trees, and **e** Recruitment of trees through time, with the dashed line showing the recruitment threshold (> 15 trees established in a 25-year period) defined for this study. For all plots the vertical gray bar highlights the period of peak tree recruitment, from 1550 through 1750 CE. Kernel density plots compare climate conditions during peak tree recruitment (gray density plots) against climate conditions over the remaining period or record (colored density plots) with mean conditions plotted in correspondingly colored dashed vertical lines. For (**a**) cool-season precipitation the dark gray density plot shows the range of conditions omitting the severe drought of 1612–1650 CE, whereas these data are retained in the light gray density plot.

Mountain Big Sagebrush plant associations, most (67%) in the Idaho Fescue-Bluebunch Wheatgrass association and the rest in either the Bluebunch Wheatgrass-Idaho Fescue (19%) or Bluebunch Wheatgrass (14%) associations. Prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.), Sandberg bluegrass (*Poa secunda* J. Presl), and western tansymustard (*Descurainia pinnata* (Walter) Britton) also occurred in all or nearly all plots. Exotic annuals were rare; cheatgrass (*Bromus tectorum* L.)

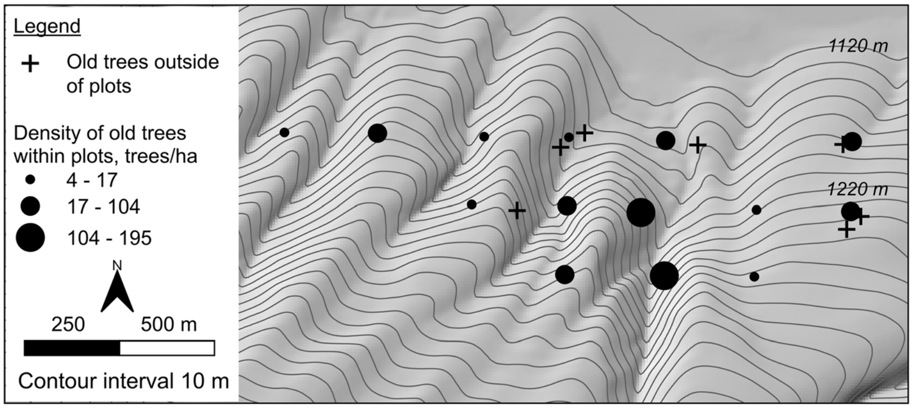

Figure 5. Spatial distribution of old trees (those that recruited before 1500 CE), regardless of whether or not they were alive in 2009. Diameters of plot symbols are proportional to tree density and range from to 4 to 200 trees·ha^{-1}. Old trees sampled between plots are mapped as + 's. Plots lacking old trees are not mapped.

occurred in only nine plots, never covering more than 1% of plot area. Tall perennial grasses covered 20 to 70% of every plot and many plots (13) also included short perennial grasses covering less than 20% of plot area. Shrubs were common but not abundant, occurring in all plots but mostly covering less than 10% of any plot. Perennial and annual forbs occurred in some plots, but always covering an area less than 10%. All plots included at least 30% bare ground, but rock cover was not common (67% of plots with < 10% rock cover, the rest with 10–30%).

Evidence of Fire

We found very little direct evidence of fire at the study site, with evidence of charring in only four trees in three plots (17F, 17G, and 17H) approximately 1 km northeast of the recent prescribed fires. We could not determine when the charring occurred, but two of the trees were alive when sampled (minimum recruitment dates of 1441 and 1791 CE) and two were old logs (tree rings from 885 to 1044 CE and from 845 to 1120 CE). We did not encounter charred trees between plots. We inferred that the presence of dead wood in the canopies of trees indicated an absence of spreading canopy fire at the site (Figure 1e).

Relationships of Tree Demography, Landscape Characteristics, and Climate

Old trees (established before 1500 CE) were not evenly distributed across the landscape (Figure 5), but among landscape variables, only elevation was statistically associated with old tree location: mean elevation of plots containing at least one old tree was significantly lower than for plots with no old trees (Welch's t test, df = 10.959, t = 3.052, p = 0.011) (Figure 6 and Table 1). Half (56%) of the old trees we sampled occurred in a deep draw in plots that are dominated by old trees (Figure 5; 15G, 16G, and 17G). Old and young trees were distributed over similar slope angles (Welch's t test, df = 16.29, t = − 1.12, p = 0.278; Figure 6). There was no difference in site exposure (Welch's t test, df = 11.02, t = 0.5005, p = 0.627) or summer solar radiation (Welch's t test, df = 13.28, t = 1.131, p = 0.278) among plots with old versus young trees. The density of old trees that established within each variable area plot was not significantly different among classes of aspect, topographic position, slope position, or percent cover of bare ground, rock, and perennial grass (Kruskal–Wallis, df = 14, $p \geq 0.05$, H = 14.96, 12.0, 12.89, 16.94, 15.33, 17.09, respectively) (Figure 7).

Tree recruitment at HSE was synchronous with warmer than average summer conditions and high cool-season precipitation. Climate during peak recruitment (1550–1750 CE) had significantly higher cool-season precipitation (mean = + 17 mm and median = + 27 mm) than the long-term mean, omitting the severe drought of 1612–1650 CE, but was not significantly different than climate before or after the period of peak recruitment when the drought period was included (Figure 4a). During the peak recruitment period summer mean conditions were significantly warmer ($p < 0.05$, mean = + 0.01 and median = + 0.014) than mean conditions over the 1070-year period of record due to an anomalously warm period (similar in magnitude to the twentieth century) that occurred just prior to the 1600s in the early stages of the recruitment pulse (Figure 4b). However, mean summer temperatures during peak recruitment

Table 1. Plot and Landscape Characteristics for 21 Gridded Plots Within the Horse Ridge Study Site, Central Oregon, USA

Plot	UTM-E	UTM-N	Plot size (ha)	Num. old trees	Old tree density (trees/ha)	Elevation (m)	Classified aspect	Slope position	Topographic position index	Site exposure index	Summer solar radiation (Wh m^{-2})	Perennial grass cover (%)	Bare ground cover (%)	Rock cover (%)
15C	655,854	4,867,060	0.06	1	17.2	1199	N	Midslope	Slope	− 26.18	486,781.40	30–50	30–50	10–30
15D	656,099	4,867,063	0.06	2	34.4	1211	W	Ridge	Ridge	− 16.92	510,005.82	50–70	30–50	10–30
15E	656,380	4,867,057	0.07	1	14.5	1186	W	Midslope	Slope	− 19.56	492,556.50	30–50	50–70	10–30
15F	656,603	4,867,060	0.23	1	4.3	1160	E	Valley	Canyon	1.50	527,274.79	10–30	70–90	0
15G	656,858	4,867,054	0.13	14	104.0	1142	N	Valley	Slope	− 12.93	516,685.05	30–50	50–70	0
15H	657,102	4,867,058	0.15	0	0.0	1156	W	Middle	Slope	− 18.37	501,369.45	30–50	50–70	1–10
15I	657,349	4,867,062	0.21	5	23.4	1166	N	Middle	Slope	− 14.17	515,182.87	10–30	30–50	0
16C	655,852	4,866,810	0.15	0	0.0	1229	E	Middle	Canyon	4.91	525,384.00	30–50	30–50	10–30
16D	656,104	4,866,810	0.20	0	0.0	1252	N	Ridge	Ridge	− 13.26	522,189.61	30–50	50–70	1–10
16E	656,353	4,866,809	0.09	1	11.7	1231	N	Midslope	Slope	− 30.11	479,348.00	10–30	50–70	1–10
16F	656,604	4,866,810	0.08	2	24.0	1196	W	Midslope	Canyon	− 23.99	478,049.23	30–50	30–50	10–30
16G	656,799	4,866,790	0.06	11	195.0	1200	E	Midslope	Ridge	− 14.15	497,689.16	30–50	30–50	10–30
16H	657,103	4,866,807	0.13	2	15.0	1194	N	Valley	Slope	− 18.33	504,705.45	30–50	50–70	1–10
16I	657,351	4,866,807	0.14	4	28.9	1211	N	Midslope	Slope	− 16.74	513,534.55	10–30	50–70	0
17C	655,854	4,866,563	0.08	0	0.0	1292	N	Ridge	Slope	− 34.98	468,404.10	30–50	50–70	0
17D	656,102	4,866,561	0.23	0	0.0	1281	N	Valley	Canyon	− 18.23	511,770.79	30–50	50–70	0
17E	656,340	4,866,582	0.17	0	0.0	1264	E	Ridge	Ridge	− 9.59	529,885.42	10–30	50–70	1–10
17F	656,604	4,866,559	0.07	2	27.6	1267	W	Ridge	Ridge	− 24.32	496,750.15	30–50	50–70	1–10
17G	656,866	4,866,561	0.07	12	163.2	1217	W	Valley	Canyon	− 25.08	468,695.30	50–70	30–50	10–30
17H	657,103	4,866,563	0.26	2	7.8	1244	N	Midslope	Slope	− 19.05	509,344.15	30–50	50–70	0
17I	657,351	4,866,561	0.18	0	0.0	1245	N	Midslope	Slope	− 12.67	523,387.34	30–50	50–70	0

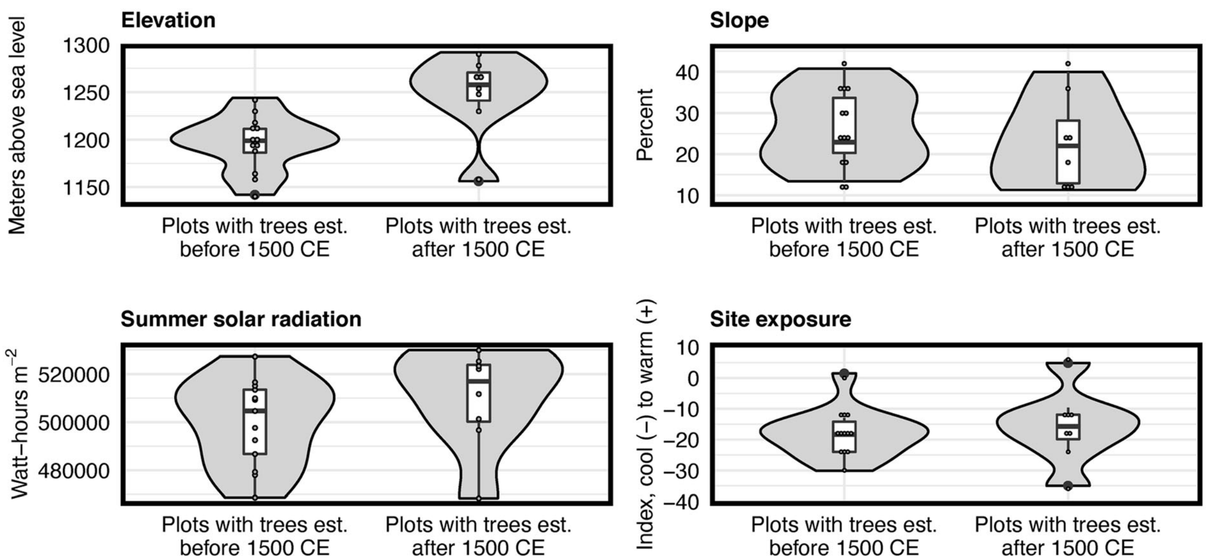

Figure 6. Mean elevation, slope, summer solar radiation, and site exposure for plots with old trees (that is, those that recruited before 1500 CE) versus plots in which all trees established after 1500 CE. Boxplots bound the interquartile range (IQR) divided by the median, whiskers extend to a maximum of 1.5 times the IQR, and circles are data points. Encompassing violin plots indicate kernel probability density, such that the width of the shaded area represents the proportion of the data located there.

were generally cooler than twentieth century temperatures, as was generally the case over the majority of the record. No clear relationships emerge between recruitment and summer PDSI, as all values and decadal anomalies fell well within the mean and distribution of the long-term average conditions (Figure 4c).

Discussion

Demographic Patterns

The primary recruitment and establishment period at Horse Ridge began in the mid-1500s CE and continued through the mid-1700s. This is the only episode of recruitment evident across the site over the past millennium and is coincident with wetter cool-season precipitation and generally warmer average summer temperatures relative to the millennial-length record at the beginning of the recruitment pulse (prior to the substantial cooling during the remainder of the recruitment/establishment event). Horse Ridge did not experience a surge of recruitment consistent with the rapid, late nineteenth century expansion and infilling of western juniper trees that occurred elsewhere in the region (Soulé and Knapp 2000).

We identified only a single episode of tree mortality and infer that it resulted from drought and insects. Most of the 15 trees with death dates (87%) died between 1927 and 1934 CE, and these trees were between 182 and 1069 years old when they died. The drought of the 1920s was the most severe of the past 1500 years (Figure 4c). During this period juniper bark beetles (*Phloeosinus serratus* LeConte, 1868) were observed to aggressively attack and kill living, drought-stressed trees, whereas during subsequent wetter periods attacks were confined to injured or felled trees (Furniss and Carolin 1977). An additional 54 dead trees either died outside the 1920/1930s period or could not be crossdated, so we may have missed other minor episodes of mortality. However, we likely did not miss any major episodes of tree mortality because dead wood is well preserved at this dry site and we found no evidence of fires that might have consumed dead wood.

Our tree demography at Horse Ridge likely suffers less than more mesic sites from the ''fading record'' problem, wherein the completeness of the record decreases with increasing time before present. In less arid settings, trees that die are lost to decay or fire, but we surmise that neither of these factors play a significant role at Horse Ridge, where the preservation of dead trees was remarkable and where we found little evidence of past fires, consistent with a lack of surface fuels. Western juniper trees are long-lived in such dry environments; the oldest live trees at Horse Ridge were over 1000 years old, and individuals of this species attain ages of more than 2000 years elsewhere.

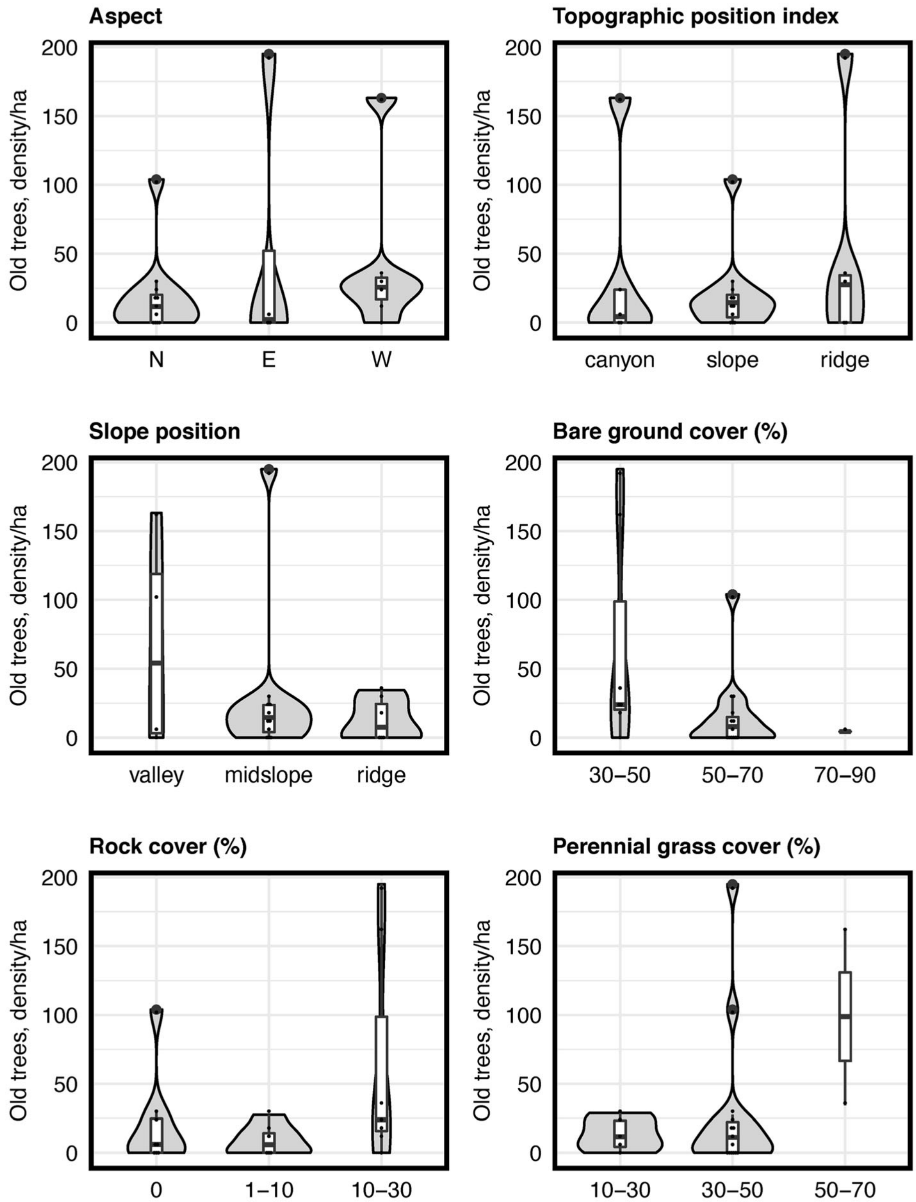

Figure 7. Density of old trees (trees·ha^{-1}) in relation to classified aspect, topographic position index, field-measured slope position, and percent cover of bare ground, rock, and perennial grasses. Boxplots bound the interquartile range (IQR) divided by the median, whiskers extend to a maximum of 1.5 times the IQR, and circles are data points. Encompassing violin plots indicate kernel probability density, such that the width of the shaded area represents the proportion of the data located there.

Climate Drivers of Demography

The initial 1500s increase in recruitment at the study site is a transition from more open wooded shrublands to persistent woodlands (Romme and others 2009), possibly associated with a pattern of stronger winter precipitation that developed in the northern Great Basin about 400–500 years BP (~ 1500–1600 CE) and initiated western juniper expansion (or infill) in the region (Miller and Wigand 1994). Consistent with previous research, we found that pulses of juniper establishment were linked to increases in cool-season precipitation, yet climatic conditions alone did not explain patterns throughout our time series. Our climate reconstruction indicates a significant increase in cool season precipitation (that is, major pluvial) during the period of peak juniper recruitment from 1550–1750 CE versus the long-term mean, excluding a severe drought within that period. However, if climate were the primary driver of western juniper demography and spatial pattern at Horse Ridge, we would have expected to see a nineteenth century pulse of recruitment, as occurred elsewhere in the region, associated with wetter, milder winters (Miller and Wigand 1994; Miller and Rose 1995); widespread tree mortality during the 1920s associated with severe drought; and a more even distribution of old-growth trees across the study site. Based on our cool season precipitation reconstruction, we would also have expected to see a recruitment pulse in the notably wet period from about 1100–1300 CE, but this too is absent from the record.

Landscape and Disturbance Drivers of Demography

Recruitment of trees through time and the spatial pattern of old-growth trees across Horse Ridge were not consistent, and in contrast to the relatively recent expansion of western juniper in many parts of the Great Basin (Johnson and Miller 2008; Miller and others 2008), Horse Ridge has a mix of old and young trees with variable stand density. Although we assessed the potential role of landscape factors such as topography and soil type on spatial-demographic patterns of juniper at Horse Ridge, we detected little influence. As others have noted, the response of long-lived trees to changing climate can be complex, as trees can exhibit sensitivity to both temperature and precipitation signals, often mediated by landscape and topographic controls (Bunn and others 2018; Flake and Weisberg 2019).

The ability of woody plants to survive—and sometimes thrive—as adults in a variety of circumstances is relevant for understanding demography patterns at Horse Ridge and in other, old-growth woodland communities across the western USA. In stable plant communities, the recruitment of new individuals is roughly equal to mortality, in contrast to dynamic communities in which new species replace existing ones (Svejcar and others 2014). At Horse Ridge, rates of recruitment declined past the peak period in the 1500s, suggesting a cover or density threshold for establishment sensu Soulé and Knapp (2000) and Young and Evans (1981). We observed only minor mortality associated with the 1920s drought, possibly because previously established, mature trees were able to survive drought stress. In contrast, substantial drought-caused tree mortality has been documented in southwestern US woodlands (Breshears and others 2005), where differential morality of piñon pines as compared with junipers (95% and 25% mortality for piñon pines and junipers, respectively, McDowell and others 2008; Floyd and others 2009) occurs as a result of species-specific differences in drought-stress tolerance and susceptibility to insect attack (Breshears and others 2009; Gaylord and others 2013).

Regeneration processes (seed production, seed dispersal mechanisms, and seedling establishment) are key determinants of past and contemporary patterns of woodland demography (Chambers and others 1999). Western juniper are submonoecious and produce seeds in most years, beginning at 50–70 years and continuing for centuries (Miller and Rose 1995; Chambers and others 1999). Cone crops are highly variable across sites and years (Miller and others 2005), but little is known about environmental variables related to seed production and development (Chambers and others 1999; Miller and others 2005). Western juniper seeds are surrounded by fleshy fruits, facilitating seed dispersal by animal transport (for example, frugivorous birds and mammals and scatter-hoarding rodents); dispersal also occurs via gravity and overland flow (Miller and others 2005; Dimitri and Longland 2017). Seeds are long-lived and initially dormant, and seed banks are highly persistent in the environment (Chambers and others 1999; Miller and others 2005). Germination occurs over a period of years following seed release and is greatly enhanced by prolonged and cumulative, year-to-year cool-moist stratification (Young and others 1988). Climate and environmental controls on seedling establishment in western juniper are largely unknown, but overstory and understory plant cover may provide favorable conditions for establishment (for example, cooler temperatures, higher relative humidity, and nutrient-rich soils), particularly during periods of increased aridity (Miller and Rose 1995; Chambers and others 1999; Soulé and Knapp 2000).

Patterns of tree density, age structure, and history of establishment in western juniper and other western woodland species have been related to topographic variables such as elevation, insolation, slope, aspect, and landform (Swanson and others 1988; Davis and Goetz 1990; Soulé and Knapp 2000; Lyford and others 2003; Johnson and Miller 2006; Méndez-Toribio and others 2016), including complex spatial patterns in tree demography at local scales produced by interactions of climate and topography (Weisberg and others 2008). However, we found no difference in slope, site exposure, or summer solar radiation among plots with old (pre-1500) versus young trees. Further, the density of old trees within plots did not appear to be influenced by aspect, topographic position, slope position, or ground cover. Plots with old trees were located at lower elevations than plots with post-settlement recruitment, suggesting gravity or overland flow as possible seed dispersal mechanisms to lower slopes; however, in other studies downslope seed dispersal has been documented only for very short (< 2 m) distances from parent trees (Soulé and Knapp 1999).

A decline or change in the characteristics of fire activity about 1500 CE could have initiated a dramatic and continuous increase in the recruitment and establishment of juniper trees. Such a shift in fire activity may have occurred as the result of changes in the spatial arrangement, type, or continuity of fuels caused by plant successional dynamics, herbivory, or changes in the frequency and timing of human-caused or natural ignitions. For example, increased herbivory could have fragmented fine fuels at the relatively arid Horse Ridge site, preventing the spread of fire even if the frequency and timing of ignitions remained constant. However, we found little direct evidence of fire in the preceding period to support this idea. Surface fires, if they had occurred, could have consumed dead and down woody fuel, eliminating evidence of fire, but if fire were an important driver of past tree demography at Horse Ridge, we would have expected to find charring on surface wood and old tree boles, and some fire scars, as western juniper can occasionally scar (Miller and Heyerdahl 2008). Although our lack of evidence of fire limits the support for this explanation, changes in fire activity may provide the most direct and simple causal mechanism linked to the patterns we see in the juniper establishment record. Soil charcoal and phytolith analysis have been used to establish a record of historical fire elsewhere in Great Basin juniper woodlands (Morris and others 2010) and could be used at Horse Ridge to further investigate fire as a potential driver of spatiotemporal demographic patterns.

Conclusions

We suggest that within the arid ecosystems of the Great Basin, western juniper woodlands have persisted under varying climatic conditions and disturbance regimes via a combination of: (1) diverse and complicated evolutionary strategies that buffer periods of unfavorable climate, and (2) recruitment of seedlings into shelter sites, or microrefugia. For long-lived species, once trees are established they become highly resistant to climate extremes and can survive periods of unfavorable climate that would be intolerable for seedlings (Bansal and Germino 2010). In contrast, the regeneration niche for seedlings is typically narrower than the niche for adult survival and reproduction (Grubb 1977). Microrefugia (locally favorable areas for plant establishment and persistence) can serve as important buffers for seedlings against periods of unfavorable climate, as loci for dispersal, and can enhance species persistence (Dobrowski 2011; Serra-Diaz and others 2015). Characteristics of recruitment microrefugia noted for arid environments include low solar exposure during summer (day and night) and leeward wind exposure during winter that generates protective snow cover, topographic shading, lower solar loads, and relatively cool summer temperatures and wetter soils as compared with surrounding locations (Dobrowski 2011; Millar and others 2018; Brodersen and others 2019).

Our Horse Ridge study site is a remarkable and well-preserved example of an old-growth woodland, in part because it has sustained little change in land use since the late 1800s and has experienced minimal disturbance (for example, grazing, wildfires, or silviculture). The site retains much of its historical character, with few invasive exotic plants, no recent changes in fire regime, and without the twentieth century increase in tree density common to other areas within the Great Basin (Svejcar and others 2017). The exception is the eastern edge of the study area where purportedly invasive trees were felled in the early 2000s. However, most of these trees (90%) were over 200 years old when killed, ranging in age from 56 to 730 years. An important measure to preserve and maintain the old-growth woodland at Horse Ridge includes preventing establishment of invasive annual plants that have altered fire regimes in other arid and semiarid ecosystems via changes in the amount, seasonality, and continuity of fine fuels—this may be achieved via restricting grazing and road access, activities that help spread invasive plants (Chambers and Wisdom 2009; Pilliod and others 2017; Bradley and others 2018).

Changing climate may contribute to future loss of old-growth trees and recruitment failure of new cohorts. A recent study in central Oregon identified drought sensitivity of western junipers at lower elevations, particularly for sites with steep slopes and sandy or rocky soils (Knutson and Pyke 2008). In the past century, the northwest region of the USA, including eastern Oregon, has warmed by about 0.7 °C and is projected to warm by 2–5 °C over the coming century, with the greatest warming occurring during summer months (Mote and others 2013). Seasonal precipitation projections are for wetter, warmer winters and drier summers (Snover and others 2003). Episodes of drought-caused mortality that have occurred in western woodlands over the past few decades are indicative of regional-scale response to contemporary climate change (Breshears and others 2005; Allen and others 2010). Understanding species-specific responses to changing climate allows for more robust projections of future ecosystem patterns and vulnerabilities (Remy and others 2019), especially in cases where individual species may exhibit a diversity of adaptations for coping with climate stress (Breshears and others 2009).

Our study of the old-growth western juniper woodland at Horse Ridge provided an opportunity to investigate important unresolved questions focused on the ecology and vulnerabilities of a key semiarid species. Although our study revealed no simple set of climate or landscape drivers of spatiotemporal demographic patterns, we verified the presence of a unique, persistent, old-growth woodland that is largely unimpacted by anthropogenic stressors. A recent assessment identified anthropogenic climate change impacts, long-term management effects, and incorporation of paleoecological data as context for assessing future range shifts as key knowledge gaps and research needs in piñon and juniper woodlands throughout the western USA (Hartsell and others 2020). We suggest that future conservation and management of western juniper and other old-growth woodland ecosystems will benefit from more explicit examination of (1) fire's role in shaping juniper establishment and persistence, (2) environmental controls on seed production and seedling establishment as important determinants of demographic patterns and persistence, and (3) the importance of microrefugia as ecological buffers against predicted warmer, drier future regional climate regimes.

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DATA AVAILABILITY

Our western juniper tree-ring dates and associated metadata are available from the USDA Forest Service Research Data Archive (Loehman and others 2022). The wood samples are available from the LTRR Collection at the Laboratory of Tree-Ring Research, University of Arizona (https://collection.ltrr.arizona.edu/). The reconstruction of cool-season (Sep–Jun) total precipitation for Deschutes County, Oregon (Pederson 2022) is available from the USGS online at https://doi.org/10.5066/P9OC5BBT.

REFERENCES

Abatzoglou JT, Williams AP. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113:11770–11775.

Alfons A. 2012. cvTools: Cross-validation tools for regression models. R package version 0.3.2.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EHT. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Alley WM. 1984. The Palmer drought severity index: Limitations and assumptions. Journal of Climate and Applied Meteorology 23:1100–1109.

Anchukaitis KJ, Wilson R, Briffa KR, Büntgen U, Cook ER, D'Arrigo R, Davi N, Esper J, Frank D, Gunnarson BE, Hegerl G. 2017. Last millennium Northern Hemisphere summer temperatures from tree rings: Part II, spatially resolved reconstructions. Quaternary Science Reviews 163:1–22.

Anthony CR, Sanchez DM. 2018. Roost site selection of western long-eared myotis in a western juniper woodland. The Journal of Wildlife Management 82:618–628.

Applequist MB. 1958. A simple pith locator for use with off-center increment cores. Journal of Forestry 56:141.

Bansal S, Germino MJ. 2010. Variation in ecophysiological properties among conifers at an ecotonal boundary: comparison of establishing seedlings and established adults at timberline. Journal of Vegetation Science 21:133–142.

Bates JD, Svejcar T, Miller R, Davies KW. 2017. Plant community dynamics 25 years after juniper control. Rangeland Ecology & Management 70:356–362.

Belsky AJ. 1996. Viewpoint: Western juniper expansion: Is it a threat to arid northwestern ecosystems? Journal of Range Management 49:53.

Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu M-N. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain western United States and its relationship to fire frequency, seasonality, and ignitions. Biological Invasions 20:1493–1506.

Breshears DD, Carroll CJ, Redmond MD, Wion AP, Allen CD, Cobb NS, Meneses N, Field JP, Wilson LA, Law DJ, McCabe LM. 2018. A dirty dozen ways to die: Metrics and modifiers of mortality driven by drought and warming for a tree species. Frontiers in Forests and Global Change 1:4.

Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J, Anderson JJ, Myers OB, Meyer CW. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences 102:15144–15148.

Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT. 2009. Tree die-off in response to global change-type drought: Mortality insights from a decade of plant water potential measurements. Frontiers in Ecology and the Environment 7:185–189.

Briffa KR. 1999. Interpreting high-resolution proxy climate data—the example of dendroclimatology. Analysis of Climate Variability, . Springer: Berlin, Heidelberg. pp 77–94.

Brodersen CR, Germino MJ, Johnson DM, Reinhardt K, Smith WK, Resler LM, Bader MY, Sala A, Kueppers LM, Broll G, Cairns DM, Holtmeier F-K, Wieser G. 2019. Seedling survival at timberline is critical to conifer mountain forest elevation and extent. Frontiers in Forests and Global Change 2:9.

Brogan PF. 1964. East of the Cascades: Portland. Oregon: Binsford and Mort, Publishers.

Bunn A, Korpela M, Biondi F, Campelo F, Mérian P, Qeadan F, Zang C, Pucha-Cofrep D, Wernicke J. 2016. dplR: Dendrochronology Program Library in R. R Package Version 1(6):4.

Bunn AG. 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26:115–124.

Bunn AG. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28:251–258.

Bunn AG, Salzer MW, Anchukaitis KJ, Bruening JM, Hughes MK. 2018. Spatiotemporal variability in the climate growth response of high elevation bristlecone pine in the White Mountains of California. Geophysical Research Letters 45:13–312.

Chambers JC, Vander Wall SB, Schupp EW. 1999. Seed and seedling ecology of piñon and juniper species in the pygmy woodlands of western North America. Botanical Review 65:1–38.

Chambers JC, Wisdom MJ. 2009. Priority research and management issues for the imperiled Great Basin of the western United States. Restoration Ecology 17:707–714.

Chen I-C, Hill JK, Ohlemuller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Cohen A, Palacios-Fest M, Negrini R, Wigand P, Erbes D. 2000. A paleoclimate record for the past 250,000 years from Summer Lake, Oregon, USA: II. Sedimentology, paleontology and geochemistry. Journal of Paleolimnology 24:151–182.

Cook BI, Smerdon JE, Seager R, Cook ER. 2014. Pan-continental droughts in North America over the last millennium. Journal of Climate 27:383–397.

Cook E, Woodhouse C, Eakin C, Meko D, Stahle D. 2004. Long-term aridity changes in the western United States. Science 306:1015–1018.

Cook ER. 1985. A time series analysis approach to tree ring standardization.

Cook ER, Holmes RL. 1984. Program ARSTAN users manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson 15:50–65.

Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris pp. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

Davies KW, Bates JD. 2017. Restoring big sagebrush after controlling encroaching western juniper with fire: Aspect and subspecies effects. Restoration Ecology 25:33–41.

Davies KW, Petersen SL, Johnson DD, Davis DB, Madsen MD, Zvirzdin DL, Bates JD. 2010. Estimating juniper cover from National Agriculture Imagery Program (NAIP) imagery and evaluating relationships between potential cover and environmental variables. Rangeland Ecology & Management 63:630–637.

Davies KW, Rios RC, Bates JD, Johnson DD, Kerby J, Boyd CS. 2019. To burn or not to burn: Comparing reintroducing fire with cutting an encroaching conifer for conservation of an imperiled shrub-steppe. Ecology and Evolution 9:9137–9148.

Davis FW, Goetz S. 1990. Modeling vegetation pattern using digital terrain data. Landscape Ecology 4:69–80.

Davis KT, Dobrowski SZ, Higuera PE, Holden ZA, Veblen TT, Rother MT, Parks SA, Sala A, Maneta MP. 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proceedings of the National Academy of Sciences 116:6193–6198.

Derrick B, Toher D, White P. 2017. How to compare the means of two samples that include paired observations and independent observations: A companion to Derrick, Russ, Toher and White (2017). The Quantitative Methods in Psychology 13:120–126.

Dimitri LA, Longland WS. 2017. Distribution of western juniper seeds across an ecotone and implications for dispersal. Western North American Naturalist 77:212–222.

Dobrowski SZ. 2011. A climatic basis for microrefugia: The influence of terrain on climate. Global Change Biology 17:1022–1035.

Driscoll RS. 1964. Vegetation-soil units in the central Oregon juniper zone. Pacific Northwest Forest and Range Experiment Station: USDA Forest Service. pp 46–48.

Duncan RP, Stewart GH. 1991. The temporal and spatial analysis of tree age distributions. Canadian Journal of Forest Research 21:1703–1710.

Dunn OJ. 1964. Multiple comparisons using rank sums. Technometrics 6:241–252.

Egan J, Staff R, Blackford J. 2015. A high-precision age estimate of the Holocene Plinian eruption of Mount Mazama, Oregon, USA. The Holocene 25:1054–1067.

Environmental Systems Research Institute (ESRI). 2015. ArcGIS 10.3.1. Redlands. CA.

Flake SW, Weisberg PJ. 2019. Fine-scale stand structure mediates drought-induced tree mortality in pinyon-juniper woodlands. Ecological Applications 29:e01831.

Floyd ML, Clifford M, Cobb NS, Hanna D, Delph R, Ford P, Turner D. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands. Ecological Applications 19:1223–1230.

Fu P, Rich PM. 2002. A geometric solar radiation model with applications in agriculture and forestry. Computers and Electronics in Agriculture 37:25–35.

Furniss RL, Carolin VM. 1977. Western forest insects. Miscellaneous Publication no. 1339. Washington, DC: US Department of Agriculture, Forest Service. 654p.

Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yepez EA, Macalady AK, Pangle RE, McDowell NG. 2013. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. New Phytologist 198:567–578.

Geist JM, Cochran PH. 1991. Influences of volcanic ash and pumice deposition on productivity of western interior forest soils. Harvey AE, Neuenschwander LF, editors. Ogden, UT: Proceedings, Management and Productivity of Western-Montane Forest Soils, USDA Forest Service General Technical Report INT-280.

Geitgey RP. 1992. Pumice in Oregon. Oregon, Department of Geology and Mineral Industries

Gesch D, Oimoen M, Greenlee S, Nelson C, Steuck M, Tyler D. 2002. The National Elevation Dataset. Photogrammetric Engineering and Remote Sensing 68:5–32.

Grubb PJ. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biological Reviews 52:107–145.

Hall FC. 1972. Horse Ridge Research Natural Area. In: Federal Research Natural Areas in Oregon, Washington—a Guidebook for Scientists and Educators, pp. Hr1– Hr7. Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Hamlet AF, Mote PW, Clark MP, Lettenmaier DP. 2005. Effects of temperature and precipitation variability on snowpack trends in the western United States. Journal of Climate 18:4545–4561.

Hamlet AF, Mote PW, Clark MP, Lettenmaier DP. 2007. Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. Journal of Climate 20:1468–1486.

Hartsell JA, Copeland SM, Munson SM, Butterfield BJ, Bradford JB. 2020. Gaps and hotspots in the state of knowledge of pinyon-juniper communities. Forest Ecology and Management 455:117628.

Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69–78.

Jacobs BF, Romme WH, Allen CD. 2008. Mapping ‘‘old’’ vs. ‘‘young’’ piñon-juniper stands with a predictive topo-climatic model. Ecological Applications 18:1627–1641.

Jenness J, Brost B, Beier P. 2013. Land facet corridor designer: Extension for ArcGIS. Jenness Enterprises.

Johnson DD, Miller RF. 2006. Structure and development of expanding western juniper woodlands as influenced by two topographic variables. Forest Ecology and Management 229:7–15.

Johnson DD, Miller RF. 2008. Intermountain presettlement juniper: Distribution, abundance, and influence on postsettlement expansion. Rangeland Ecology & Management 61:82–92.

Jonsson B, Holm S, Kallur H. 1992. A forest inventory method based on density-adapted circular plot size. Scandinavian Journal of Forest Research 7:405–421.

Kaufmann MR, Moir WH, Covington WW. 1992. Old-growth forests: What do we know about their ecology and management in the Southwest and Rocky Mountain Regions. In: Kaufmann MR, Moir WH, Bassett RL, editors. Old-growth forests in the Southwest and Rocky Mountain Regions: Proceedings. Portal, AZ: Rocky Mountain Forest and Range Experiment Station Forest Service U.S. Department of Agriculture. pp 1–11.

Knapp PA, Soulé PT. 1998. Recent *Juniperus occidentalis* (western juniper) expansion on a protected site in central Oregon. Global Change Biology 4:347–357.

Knapp PA, Soulé PT. 1999. Geographical distribution of an 18th-century heart rot outbreak in western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.). Journal of Arid Environments 41:247–256.

Knutson KC, Pyke DA. 2008. Western juniper and ponderosa pine ecotonal climate–growth relationships across landscape gradients in southern Oregon. Canadian Journal of Forest Research 38:3021–3032.

Kruskal WH, Wallis WA. 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47:583–621.

Lessard VC, Drummer TD, Reed DD. 2002. Precision of density estimates from fixed-radius plots compared to n-tree distance sampling. Forest Science 48:1–6.

Littell JS, Pederson GT, Gray ST, Tjoelker M, Hamlet AF, Woodhouse CA. 2016. Reconstructions of Columbia River streamflow from tree-ring chronologies in the Pacific Northwest, USA. Journal of the American Water Resources Association 52:1121–1141.

Loehman RA, Heyerdahl EK, Pederson GT, McWethy D. 2022. Demography of ancient western juniper (Juniperus occidentalis var. occidentalis) trees on Horse Ridge in central Oregon, USA. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2022-0031.

Lumley T. 2013. Package ‘leaps.’ Regression Subset Selection Thomas Lumley Based on Fortran Code by Alan Miller. R package version 3.4.4.

Lyford ME, Jackson ST, Betancourt JL, Gray ST. 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. Ecological Monographs 73:567–583.

MacLeod NS, Sherrod DR, Chitwood LA, Jensen RA. 1982. Geologic map of Newberry Volcano, Deschutes, Klamath, and Lake Counties, Oregon. U.S. Geological Survey Miscellaneous Investigations Series Map I–2455, 2 sheets, scale 1:62,500, pamphlet, 23 p.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologist 178:719–739.

Mehringer PJ, Wigand PE. 1987. Western juniper in the Holocene. Proceedings of the pinyon-juniper conference: USDA Forest Service Intermountain Research Station, General Technical Report INT-215:109–20.

Mehringer PJ, Wigand PE. 1990. Comparison of late Holocene environments from woodrat middens and pollen: Diamond Craters, Oregon. In: Betancourt JL, van Devender TR, Martin PS, Eds. Packrat middens: The last 40,000 years of biotic change, . Tucson, AZ: University of Arizona Press. pp 294–325.

Meko DM, Therrell MD, Baisan CH, Hughes MK. 2001. Sacramento river flow reconstructed to AD 869 from tree rings. Journal of the American Water Resources Association 37:1029–1039.

Méndez-Toribio M, Meave JA, Zermeño-Hernández I, Ibarra-Manríquez G. 2016. Effects of slope aspect and topographic position on environmental variables, disturbance regime and tree community attributes in a seasonal tropical dry forest. Journal of Vegetation Science 27:1094–1103.

Millar CI, Charlet DA, Westfall RD, King JC, Delany DL, Flint AL, Flint LE. 2018. Do low-elevation ravines provide climate refugia for subalpine limber pine (*Pinus flexilis*) in the Great Basin, USA? Canadian Journal of Forest Research 48:663–671.

Miller R, Bates JD, Svejcar TJ, Pierson FB, Eddleman LE. 2005. Biology, ecology, and management of western juniper (*Juniperus occidentalis*). Corvallis, OR: Agricultural Experiment Station, Oregon State University, Technical Bulletin 152.

Miller RF, Heyerdahl EK. 2008. Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: An example from California, USA. International Journal of Wildland Fire 17:245–254.

Miller RF, Rose JA. 1995. Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon. The Great Basin Naturalist:37–45.

Miller RF, Rose JA. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Miller RF, Tausch RJ, McArthur ED, Johnson DD, Sanderson SC. 2008. Age structure and expansion of piñon-juniper woodlands: A regional perspective in the Intermountain West. Fort Collins, CO: USDA Forest Service Rocky Mountain Research Station, Research Paper RMRS-RP-69. 15p.

Miller RF, Tausch RJ, Waichler WS. 1999. Old-growth juniper and pinyon woodlands. Proceedings: ecology and management of pinyon-juniper communities within the interior west. Fort Collins, CO: USDA Forest Service Rocky Mountain Research Station, Proceedings RMRS P-9:375–384.

Miller RF, Wigand PE. 1994. Holocene changes in semiarid pinyon-juniper woodlands: Response to climate, fire, and human activities in the Great Basin. Bioscience 44:465–474.

Moir WH. 1992. Ecological concepts in old-growth forest definition. In: Kaufmann, MR; Bassett, RL; Moir, WH, technical coordinators. Old-growth forests in the Southwest and Rocky Mountain Regions: Proceedings of a workshop. Fort Collins, CO: USDA Forest Service Rocky Mountain Forest and Range Experimental Station, General Technical Report RM-GTR-213. pp 18–23.

Morris LR, Ryel RJ, West NE. 2010. Can soil phytolith analysis and charcoal be used as indicators of historic fire in the pinyon-juniper and sagebrush steppe ecosystem types of the Great Basin Desert, USA? The Holocene 20(1):105–114.

Mote PW, Abatzoglou JT, Kunkel KE. 2013. Climate. In: Dalton MM, Mote PW, Snover AK, Eds. Climate change in the Northwest: Implications for our landscapes, waters, and communities, . Washington, DC: Island Press/Center for Resource Economics. pp 25–40.

Pederson, GT. 2022. Cool season (September-June) total precipitation reconstruction for Deschutes County, Oregon, 1000–1991 CE. U.S. Geological Survey data release, https://doi.org/10.5066/P9OC5BBT.

Pilliod DS, Welty JL, Arkle RS. 2017. Refining the cheatgrass-fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. Ecology and Evolution 7:8126–8151.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Redmond MD, Weisberg PJ, Cobb NS, Clifford MJ. 2018. Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. Journal of Ecology 106:625–639.

Reinkensmeyer DP, Miller RE, Anthony RG, Marr VE, Duncan CM. 2008. Winter and early spring bird communities in grasslands, shrubsteppe, and juniper woodlands in central Oregon. Western North American Naturalist 68:25–35.

Reinkensmeyer DP, Miller RF, Anthony RG, Marr VE. 2007. Avian community structure along a mountain big sagebrush successional gradient. Journal of Wildlife Management 71:1057–1066.

Remy CC, Krofcheck DJ, Keyser AR, Litvak ME, Collins SL, Hurteau MD. 2019. Integrating species-specific information in models improves regional projections under climate change. Geophysical Research Letters 46:6554–6562.

Romme WH, Allen CD, Bailey JD, Baker WL, Bestelmeyer BT, Brown PM, Eisenhart KS, Floyd ML, Huffman DW, Jacobs BF, Miller RF, Muldavin EH, Swetnam TW, Tausch RJ, Weisberg PJ. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. Rangeland Ecology & Management 62:203–222.

Root TL, Price J, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Sankey TT, Germino MJ. 2008. Assessment of juniper encroachment with the use of satellite imagery and geospatial data. Rangeland Ecology & Management 61:412–418.

Schuller R, Halvorson R. 2008. Horse Ridge Research Natural Area: Guidebook supplement 37. Gen. Tech. Rep. PNW-GTR-771. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 25p.

Serra-Diaz JM, Scheller RM, Syphard AD, Franklin J. 2015. Disturbance and climate microrefugia mediate tree range shifts during climate change. Landscape Ecology 30:1039–1053.

Snover AK, Hamlet AF, Lettenmaier DP. 2003. Climate-change scenarios for water planning studies: Pilot applications in the Pacific Northwest. Bulletin of the American Meteorological Society 84:1513–1518.

Soil Survey Staff (2019) Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online: http://websoilsurvey.sc.egov.usda.gov/.

Soulé PT, Knapp PA. 1999. Western juniper expansion on adjacent disturbed and near-relict sites. Journal of Range Management 52:525.

Soulé PT, Knapp PA. 2000. *Juniperus occidentalis* (western juniper) establishment history on two minimally disturbed research natural areas in central Oregon. Western North American Naturalist 60:26–33.

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT. 2019. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.

Svejcar T, Boyd C, Davies K, Hamerlynck E, Svejcar L. 2017. Challenges and limitations to native species restoration in the Great Basin, USA. Plant Ecology 218:81–94.

Svejcar T, James J, Hardegree S, Sheley R. 2014. Incorporating plant mortality and recruitment into rangeland management and assessment. Rangeland Ecology & Management 67:603–613.

Swanson FJ, Kratz TK, Caine N, Woodmansee RG. 1988. Landform effects on ecosystem patterns and processes. BioScience 38:92–98.

Waichler WS, Miller RF, Doescher PS. 2001. Community characteristics of old-growth western juniper woodlands. Journal of Range Management 54:518.

Weisberg PJ, Ko D, Py C, Bauer JM. 2008. Modeling fire and landform influences on the distribution of old-growth pinyon-juniper woodland. Landscape Ecology 23:931–943.

West NE. 1999. Juniper pinyon savannas and woodlands of western North America. In: Anderson RC, Fralish JS, Baskin JM, Eds. Savannas, barrens and rock outcrop plant communities of North America, . New York, New York, USA: Cambridge University Press. pp 288–308.

Western Regional Climate Center. 2013. Cooperative Climatological Data Summaries. https://wrcc.dri.edu/Climate/west_coop_summaries.php

Wigand PE. 1987. Diamond Pond, Harney County, Oregon: Vegetation history and water table in the eastern Oregon desert. The Great Basin Naturalist 46:1–21.

Wilkinson MT, Humphreys GS. 2006. Slope aspect, slope length and slope inclination controls of shallow soils vegetated by sclerophyllous heath—links to long-term landscape evolution. Geomorphology 76:347–362.

Woodhouse CA, Pederson GT. 2018. Investigating runoff efficiency in upper Colorado River streamflow over past centuries. Water Resources Research 54:286–300.

Young JA, Evans RA. 1981. Demography and fire history of a western juniper stand. Journal of Range Management 34:501–506.

Young JA, Evans RA, Budy JD, Palmquist DE. 1988. Stratification of seeds of Western and Utah juniper. Forest Science 34:1059–1066.

Zar JH. 1984. Multiple Comparisons. Biostatistical Analysis 1:185–205.