Long-term survivorship of single-needle pinyon (Pinus monophylla) in mixed-conifer ecosystems of the Great Basin, USA

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Abstract. We examined stand structure and development of mixed-conifer ecosystems in the south-central Great Basin where pinyon (Pinus monophylla) and juniper (Juniperus osteosperma) are found together with other species, such as ponderosa pine (Pinus ponderosa), with particular emphasis on pre- and post-settlement conditions. Two study sites (Mt. Irish and the Clover Mountains) were selected based on their relative proximity but different topographic conditions and modern fire regime. Vegetation analysis was conducted on 12 0.1-ha plots per site, where all woody stems were mapped, measured, and cored for age determination, as well as on a systematic grid at 175-m intervals where tree measurements and increment cores were obtained. At Mt. Irish the total basal area was 14.5 m² ha⁻¹ and the tree density was 324 stems ha⁻¹, while at the Clover Mountains they were 13.8 m² ha⁻¹ and 342 stems ha⁻¹, respectively. Pre-settlement trees were found throughout each site, with maximum tree ages of 400 years or more, and older individuals being particularly common at Mt. Irish. Density of pinyon pine at both sites more than doubled since the 1800s, with peak survivorship occurring in the early 1900s at Mt. Irish and extending into the mid-1900s at the Clover Mountains. Other tree species, including ponderosa pine, juniper, and white fir (Abies concolor), which have been present over the past few centuries in these stands, have not experienced the large population increase shown by single-needle pinyon, with the exception of ponderosa pine at the Clover Mountains between the late 1800s and early 1900s. Pinyon mortality was <10% at both sites, even after the early 2000s drought, in agreement with other published studies of Pinus monophylla population dynamics. The presence of old individuals across the landscape indicated that pinyon populations have grown in density without invading new areas. Because wildfire regime and land-use changes were not identical between the two study sites, and increases of pinyon-juniper populations have occurred in other Great Basin areas at about the same time, climate was the most likely driver. Therefore, pinyon-juniper woodlands, which have recently experienced dramatic episodes of climate-related dieoffs in regions where Pinus edulis is present, have not been negatively impacted by climate in the Great Basin, where the pinyon species is Pinus monophylla.

Key words: dendroecology; Great Basin; Pinus monophylla; Pinus ponderosa; pinyon-juniper woodlands; ponderosa pine; single-leaf pinyon pine; stand dynamics; tree rings.

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INTRODUCTION

Pinyon-juniper woodlands cover millions of hectares of semi-arid and arid landscapes of western North America (West 1999). These ecosystems are characterized by the presence of two main pinyon species, namely Colorado pinyon (Pinus edulis Engelm.) in the American Southwest (mostly Arizona, New Mexico, Colorado, and Utah), where it covers more than 20 million ha (Cole et al. 2008), and single-needle pinyon (Pinus monophylla Torr. & Frém.) in the Great Basin (mostly Nevada), where it is found over about 7 million ha (Tuell et al. 1979) usually in association with Utah juniper (Juniperus osteosperma (Torr.) Little). In many areas of the Great Basin hydrographic region (as defined by Grayson 2011) pinyon-juniper woodlands have been expanding into adjacent ecosystems, as well as increasing in density over the past century (Tausch et al. 1981, Weisberg et al. 2007, Miller et al. 2008). The increase in woodland area (expansion) and density (infill) has been attributed to multiple factors, both anthropogenic and natural, but primarily to changes in wildfire regimes caused by fire suppression practices and to the introduction of grazing animals associated with Euro-American settlement (Blackburn and Tueller 1970, Miller and Tausch 2001). Other possible factors are recovery from prior disturbance, such as fire or logging related to mining activities (Strachan et al., in press), introduction of exotic species, and the increase in atmospheric carbon dioxide (Romme et al. 2009).

Changes in climate during the instrumental period have contributed to expansion and infill of pinyon-juniper woodlands dominated by P. monophylla (Bradley and Fleshman 2008), which has progressed throughout the Holocene (Miller and Wigand 1994, Grayson 2011). On the other hand, modern climate warming and drying is also considered to be a major contributor to extensive dieback in recent years (Breshears et al. 2005), and to decreased reproduction over the past few decades (Redmond et al. 2012), of pinyon-juniper woodlands where P. edulis is present. Understanding the history of pinyon-juniper woodlands prior to Euro-American settlement is therefore essential to place such modern mortality in a longer context of past tree survival and disturbance history in order to guide management practices (Romme et al. 2003). This is particularly important for the Great Basin to test if landscape-level trends are diverging from the widespread tree mortality either attributed to or predicted from greenhouse warming (van Mantgem et al. 2009, Anderegg et al. 2013).

A number of environmental drivers can either hinder or favor tree populations: climate conditions, wildfire regime, insect outbreaks, blowdowns, and other types of disturbance events can be beneficial or harmful to seedling establishment, while at the same time having similar or opposite effects on radial growth of mature trees (Lloyd and Graumlich 1997). As an example, more nutrients and water are available to seedlings when competition for resources is reduced after the death of larger trees, but new individuals can establish only if seed sources are not eliminated by the disturbance event that removed the canopy. Species interactions also contribute to changes in the demography of plant populations. For example, juniper seedlings are considered to be more drought tolerant than pinyon ones (Nowak et al. 1999), and established junipers can then allow pinyon seedlings to survive by shading them and creating microclimates with a higher relative humidity (Chambers 2001).

The precise role of climate versus disturbance regime, human alteration or other factors in driving woodland expansion or shrinkage is not fully resolved. Pinyon-juniper woodlands were not static landscape features even prior to Euro-American settlement (Betancourt et al. 1993, Cartledge and Propper 1993), and their distribution has varied in the past, following centennial and longer changes in temperature and precipitation (Nowak et al. 1994, Wigand and Rhode 2002). Debate exists even with regard to modern pinyon-juniper encroachment on sagebrush ecosystems, given that woodlands are often simply re-occupying areas that were previously logged for mining and smelting operations (Lanner 1977, Lanner and Frazier 2011). Because management of existing natural resources requires a detailed understanding of woodland dynamics at finer spatial (km-level) and temporal (annual-level) scales than those allowed by most paleoclimatic and paleoecological records, a particularly useful source of information on climatic variability, fire
regime, and species dynamics in the western United States is provided by tree-ring records (Fritts 1976, Swetnam et al. 1999). In pinyon-juniper woodlands, however, fire scars are infrequent even when wildfires are patchy because flames typically reach the crown once the low-hanging branches ignite. Despite the prevalence of localized, high-severity fires in which trees are killed and scars are therefore not formed (Baker and Shinneman 2004), tree-ring dating of fire scars was possible in *P. edulis* stands located at the upper limit of its elevation distribution (Huffman et al. 2008). In relatively pure pinyon-juniper woodlands of the Great Basin, where *P. monophylla* is present, both fire scars (Bauer and Weisberg 2009) and growth patterns (Py et al. 2006) have been used to infer wildfire regime.

Evaluating disturbance effects in pinyon-juniper woodlands is further complicated by the wide variety of fire regimes that have been reported for pre-settlement periods (Baker and Shinneman 2004, Romme et al. 2009). Because fire scars can only record low-severity fire events, age structure can help determine occurrence of high-severity fires, which typically produce stands where the oldest trees are similarly aged (Kipfmueller and Swetnam 2005), although vegetation recovery time may vary considerably. Fire rotation lengths of up to a few centuries were reconstructed for pinyon-juniper woodlands in the American Southwest, where *P. edulis* is present (Floyd et al. 2000, Floyd et al. 2008, Shinneman and Baker 2009). In those environments, fires recorded by ponderosa pines did not generally spread to adjacent pinyon-juniper woodlands (Huffman et al. 2008). Woodlands occupied by *P. edulis* took decades to centuries for recovering from high intensity wildfires (Arnold et al. 1964), and their stand initiation was not always due to fire (Huffman et al. 2008). Overall, one can surmise that pinyon-juniper woodlands are not fire-adapted, in that they do not require fire to regenerate, they cannot reproduce vegetatively after fire, and they have bark and crown characteristics that are not resistant to fire in the first place.

In the Great Basin, where the pinyon species is *P. monophylla*, relatively few fire history reconstructions have been performed to date (Brown et al. 2008, Bauer and Weisberg 2009, Heyerdahl et al. 2011). Despite the overall aridity of this large region, the influence of high mountains on climate allows for cooler and wetter conditions as elevation increases, so that on scattered mountain tops above pure pinyon-juniper stands are mixed-conifer ecosystems, which include not only pinyon and juniper but also ponderosa pine (*Pinus ponderosa* var. *scopulorum* (Engelm.) E. Murr.) and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. var. *concolor*) along with other tree species (Charlet 1996, 2007), such as Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and bristlecone pine (*Pinus longaeva* D.K.Bailey). Few studies to date have focused on long-term stand dynamics and demographic patterns of such mixed-conifer ecosystems, but their conservation requires disentangling the impacts of Euro-American land uses (fire suppression, open-range grazing, wood cutting for early mining operations) from natural events (climate, disturbance) on vegetation dynamics. Fire scars on ponderosa pines growing in mixed conifer associations with pinyon and juniper have already showed that low-intensity fires at relatively high frequencies (mean fire interval < 10 years) were the most common pre-settlement events (Biondi et al. 2011; Kilpatrick et al., in press). In the same areas, assessments of fuel loads and potential fire behavior has uncovered a transition over time from surface to crown fire conditions (Cheek et al. 2012).

As a further contribution to the study of mixed conifer ecosystems in the Great Basin, our primary goal for this research was to analyze woody species dynamics pre- and post-Euro-American settlement. Special consideration was given to examining if *P. monophylla* populations had expanded their distribution and/or increased in density over the past few centuries. Two mountain ranges in Lincoln County, Nevada, were selected to capture a west-to-east increasing trend in fire frequency that was identified from documentary records maintained by federal and state agencies (Dilts et al. 2009). Our study addressed the key question “What is the tree survivorship in high-elevation woodland ecosystems of the North American Great Basin?”, which has immediate implications for understanding the main drivers of semi-arid vegetation dynamics.
MATERIALS AND METHODS

Study areas

The two study areas we sampled are separated by about 90 km of horizontal distance. Mt. Irish (37°38′41″ N, 115°24′04″ W) is located on the western side of Lincoln County, Nevada (Fig. 1), at an elevation of ~2380-2670 m, and is bounded on most sides by rocky cliffs, forming a mesa-like area. Using PRISM (parameter-elevation regression on independent slopes model; Daly et al. 2008) climate data for the study area, obtained from the average of two 2.5-arc minute grid cells, the average total annual precipitation was 28.8 ± 9.6 cm and the average annual temperature was 9.0 ± 0.8°C. Additional details on this site, including its wildfire history pre- and post-settlement, are available in the peer-reviewed literature (Biondi et al. 2011, Cheek et al. 2012). Based on those studies, the year 1860 was chosen as the date of Euro-American settlement for this location.

The Clover Mountain study site (37°27′33″ N, 114°28′02″ W) is located on the eastern side of Lincoln County (Fig. 1), at elevations ranging from 1900 to 2280 m. PRISM climate data were derived from an average of four 2.5-arc minute grid cells giving an average total annual precipitation of 40.8 ± 12.1 cm and an average annual temperature of 9.4 ± 0.9°C. Additional details on this site, including its wildfire history pre- and post-settlement, have already been published (Cheek et al. 2012; Kilpatrick et al., in press). Based on those studies, the year 1900 was chosen as the date of Euro-American settlement for this location.

Field and laboratory methods

A combination of random, opportunistic, and systematic samples were obtained at each study site to measure stand composition, age structure, and spatial relationships. During 2007 and 2008 we sampled 12 0.1-ha plots, half rectangular (50 × 20 m) and half circular (radius of 17.8 m), at each site (Fig. 1). Plot selection was explained by Cheek et al. 2012; for rectangular plots, the long axis direction was randomly determined in the field. All of the woody stems within the plot were mapped using x-y coordinates (for rectangular plots) or polar coordinates (for circular plots). Data collected on each mapped tree included species, height, diameter at base and breast (~1.3 m) height, height to crown base, and crown width. Stems ≥ 2 m in height were recorded as trees, stems < 2 m tall and with base diameter ≥ 5 cm were recorded as saplings, and stems < 2 m tall and with base diameter < 5 cm were recorded as seedlings. Two increment cores were collected from each tree, one from the base and one from breast height as long as stem diameter was ≥3 cm. An attempt was made to intercept the root-shoot collar by taking basal cores on the downslope side of the stem, at an angle rather than horizontally, and/or using a short handle to rotate the borer.

Within each site a systematic sampling design composed of grid points at 175-m intervals was added to provide landscape-level data. At Mt. Irish there were 49 gridpoints, which covered the area encompassed by the 12 plots; at the Clover Mountains there were 68 gridpoints, which covered an area roughly overlapping 10 of the 12 plots (Fig. 1). Physical characteristics of each gridpoint were recorded, including elevation, aspect, and slope. Increment cores were collected from 10 trees within ~20 m of each gridpoint to represent the species distribution while targeting the oldest-looking trees for each species.

In the laboratory, wood increment cores were mounted and sanded using progressively finer sandpaper (from 60 to 600 grit) until the cell walls were visible at 10–30× magnification under a stereo-zoom binocular microscope. Rings were counted because cross-dating was unfeasible due to time constraints (as mentioned in the Results, a total of about 2000 cores was analyzed for this study), non-horizontal cores, and relatively short (<100 years) ring series in many samples. To reduce errors, we grouped tree establishment dates by decade. The majority of the cores did not include the pith, and in those cases stem age had to be estimated. To select the best method for age estimation, wedges were cut from nine pinyon trees, and five simulated cores were drawn on each wedge. One of these simulated cores intercepted the pith, and was used to gauge estimates calculated using the other four. The methods we compared were Applequist’s visual pith locator (Applequist 1958), using concentric circles at 0.50 and 0.25 mm, and Duncan’s formula (Duncan 1989). This latter technique is based on estimating the distance between the
pith and the innermost ring in the core, and then dividing by the average ring width of the innermost rings (for computing this value we used either 5, 10, 15 or 20 rings). Although every method underestimated the true number of missing rings, using Duncan’s formula with the average width of the innermost five rings provided the estimates closest to the true values, and we therefore used this technique for age estimation.

Stem density and basal area were calculated for every conifer species at each plot. Density was calculated separately for trees, seedlings plus saplings, and dead stems; basal area was calculated using live stems with diameter at breast height (DBH) > 0. Values calculated for an entire site used the 10 randomly selected plots as well as all 12 plots. Horizontal and vertical structure profile maps were constructed from the plot data; trees and dead stems were mapped as individual points. Shrubs at Mt. Irish, including mountain-mahogany (Cercocarpus ledifolius Nutt.), were mapped as individual points with no species identification, while at the Clover Mountains they were mapped as polygons because of their greater spatial cover. Vertical profile maps of saplings and trees were generated using the Stand Visualization System (SVS) software (McGaughey 1997) using plant coordinates, species, DBH, height, crown radius, and crown ratio (foliage height divided by tree height). Spatial patterns of seedlings, saplings, trees, or all stems combined were examined by species on plots with at least 10 stems using Ripley’s K-function (Ripley 1976) including edge correction (Hammer et al. 2001).

RESULTS

Horizontal and vertical structure

A total of 2,405 stems were mapped in Mt. Irish plots, which ranged in elevation from 2480 to 2595 m, occurred on various aspects, and on slopes between 4 and 46% (see Table 1 in Cheek et al. 2012). Six randomly selected plots at Mt. Irish included only single-needle pinyon and Utah juniper, one randomly selected plot and one added plot were occupied only by ponderosa pine, and one added plot included ponderosa pine and white fir. The remaining three randomly
selected plots had three or more of these species present (see Table 1 in Cheek et al. 2012). Because 95% of all recorded junipers were *J. osteosperma*, with the rest being *J. scopulorum*, we did not distinguish between the two species in the analysis. Using the 10 randomly selected plots, tree basal area was 12.2 m² ha⁻¹, about half of which was contributed by pinyon (6.1 m² ha⁻¹), 22% (2.7 m² ha⁻¹) by ponderosa pine, 18% (2.2 m² ha⁻¹) by juniper, and 11% (1.3 m² ha⁻¹) by white fir. When using all 12 plots, total basal area increased to 14.5 m² ha⁻¹, with ponderosa and pinyon pine accounting for about 35% each (5.1 m² ha⁻¹), white fir contributing 16% (2.27 m² ha⁻¹), and juniper making up the remaining 14% (2.1 m² ha⁻¹). Total tree density (Tables 1 and 2) calculated from the 10 random plots (333 stems ha⁻¹) did not increase when its value was based on the 12 plots (324 stems ha⁻¹), and pinyon remained the most common species (193 stems ha⁻¹), with juniper having higher density (55 stems ha⁻¹) than ponderosa pine (40 stems ha⁻¹) and white fir (36 stems ha⁻¹).

At the Clover Mountains a total of 1,628 stems were mapped on the plots, which ranged in elevation from 1995 to 2218 m, occurred on various aspects, and on slopes from 20 to 54%. Six of the randomly selected plots were dominated by pinyon, and five of the plots (three randomly located) by ponderosa pine. Although *J. scopulorum* has been found in the area (Charlet 2007), the only junipers we recorded were *J.*

Table 1. Number of pine stems mapped on the 0.1-ha plots sampled at Mt. Irish. For each species, the total number of stems, live or dead, and the total number of increment cores are shown. Live stems are broken down into trees (height ≥ 2 m), saplings (“sap”, height < 2 m and base diameter ≥ 5 cm), and seedlings (“seed”, height < 2 m and base diameter < 5 cm).

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Table 2. Number of fir and juniper stems mapped on the 0.1-ha plots sampled at Mt. Irish. See Table 1 for explanation of column headings.

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osteosperma on two of the pinyon-dominated plots. One randomly located plot had no living trees but was covered by shrubs with a few stumps and logs of ponderosa pine still visible (see Table 1 in Cheek et al. 2012). Based on the 10 randomly located plots, tree basal area was 11.1 m² ha⁻¹ of which about 52% (5.8 m² ha⁻¹) from ponderosa pine, 48% (5.3 m² ha⁻¹) from pinyon pine, and the remaining 0.4% from Utah juniper. Similarly to Mt. Irish, total basal area increased (to 13.8 m² ha⁻¹) when using the 12 plots, with ponderosa pine accounting for about two-thirds of it (9.2 m² ha⁻¹), pinyon pine making up the other one-third (4.6 m² ha⁻¹), and juniper contributing 0.3%. Total tree density (Table 3) based on the 12 plots (342 stems ha⁻¹) was higher than the value calculated from the 10 randomly located plots (314 stems ha⁻¹), and pinyon pine was much more dense (217 stems ha⁻¹) than ponderosa pine (129 stems ha⁻¹).

At both sites, the size (DBH) distribution of pinyon pine was dominated by small stems (DBH < 5 cm), with exponentially fewer individuals in the larger size classes, up to 40–45 cm (Fig. 2) and one tree reaching 46 cm DBH at Mt. Irish. White fir, which was present at Mt. Irish alone, showed an even higher proportion of small sizes (DBH < 5 cm), with density dropping to relatively stable values for all other DBH classes (10–50 cm), and one individual reaching 65 cm DBH. At both sites, ponderosa pine showed a less skewed DBH distribution, with relatively similar density in DBH classes up to 40 cm, and then a few large individuals, reaching the maximum stem DBH (78–79 cm) at both sites (Fig. 2). Juniper at Mt. Irish was characterized by a number of small individuals (DBH < 5 cm) not too much larger than in the bigger size classes (10–40 cm), with only a few individuals reaching up to 60 cm DBH.

At Mt. Irish average base diameter for both pinyon (22.7 cm) and ponderosa (44.1 cm) pine were higher than at the Clover Mountains, where the averages were 18.1 cm for pinyon and 30.6 cm for ponderosa pine. On the other hand, pinyon pines at the Clover Mountains were taller (4.4 m) than at Mt. Irish (3.8 m), and ponderosa pines were of similar average height (11.3 m at Mt. Irish and 12.0 m at the Clover Mountains). The relationship between stem DBH and height (Fig. 3), when represented by an exponential function through the origin, explained a larger amount of variance for ponderosa pine than for other species at both sites. In addition, pinyon and ponderosa pines of a given DBH were generally taller at the Clover Mountains than at Mt. Irish.

At both sites, the density of stems <2 m in height (i.e., saplings and seedlings) was higher than tree density (Tables 1–3). At Mt. Irish the average was 1193 stems ha⁻¹ (decreasing to 973 stems ha⁻¹ for the 10 random plots), with individual plot values ranging from 450 to 3240 stems ha⁻¹. At the Clover Mountains, where trees were about as dense as at Mt. Irish, seedling and saplings were also about as abundant when their density was computed using the 10 random plots (1004 stems ha⁻¹). When using all 12 plots, the density of saplings and seedlings at the Clover Mountains would have appeared to be less than

<table>
<thead>
<tr>
<th>Plot</th>
<th>Single-needle pinyon pine</th>
<th>Ponderosa pine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tree</td>
<td>Sap</td>
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<td>12</td>
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<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>268</td>
<td>54</td>
</tr>
</tbody>
</table>

Table 3. Number of pine stems mapped on the 0.1-ha plots sampled at the Clover Mountains. See Table 1 for explanation of column headings.
at Mt. Irish, with an average of 870 stems ha$^{-1}$, and a range of 0–2260 stems ha$^{-1}$ for individual plots. Very few ponderosa pine (1%) and juniper (2%) seedlings were found at Mt. Irish, whereas pinyon pine seedlings (54% of the total) were found in all 12 plots, including those without any pinyon trees, although in those plots pinyon seedlings accounted for the lowest percentages (Tables 1 and 2). White fir accounted for 43% of all seedlings, but one added plot contributed disproportionately to this value, as fir seedlings on that single plot accounted for almost 25% of all observed seedlings at Mt. Irish. Ten Clover Mountains plots included pinyon pine seedlings, and even though ponderosa pine seedlings were present on seven plots, only one included more than two seedlings (Table 3).

Tree mortality was quantified by recording the presence of dead stems, which were found on every plot at both sites (Tables 1–3). Approximately 5% of all pinyon pines at Mt. Irish and 9% at the Clover Mountains were dead. Dead ponderosa pine stems were roughly a quarter of the species’ total density at both sites. No dead juniper stems were found at the Clover Mountains, whereas 15% of juniper stems at Mt. Irish

![Diameter at breast height (DBH) distribution of tree species at the two study sites. The minimum size for inclusion in the dataset was a stem height of 2 m, so that DBH was >0 cm.](image-url)
were dead. About 3\% of white fir stems at Mt. Irish were dead. At Mt. Irish live trees were found on all plots and gridpoints (Tables 1–2), while at the Clover Mountains there were areas dominated by shrubs with no trees currently present (Table 3). At such treeless areas in the northern section of the study site, living trees were once present as shown by large ponderosa pine logs on plot 9 (maximum log diameter of 28, 40, and 47 cm) and at a gridpoint \( \sim 50 \) m southeast of plot 9 (maximum log diameter of 80 cm). Three other nearby gridpoints without living trees also had logs and remnants of charred wood, showing that at one time trees were present, but fire had killed them. This evidence, in combination with fire scar data, was used by Kilpatrick et al. (in press) to suggest that the 1946 wildfire occurred with localized high severity. Visualization of plot data allowed for a graphical representation of stand horizontal and vertical structure, including both live and dead trees, and for a glimpse of spatial relationships.
between species and plant types (Appendix: Figs. A1 and A2).

Species clustering was examined for all sizes as well as separately for trees and seedlings but not saplings because they were <10 per plot per species. At Mt. Irish the seven plots that included at least 10 single-needle pinyon trees were characterized by a random spatial distribution. Pinyon pine seedlings were clustered at seven plots and randomly distributed at the other five plots. A random spatial distribution was identified for juniper and ponderosa pine trees and seedlings at each plot. White fir had a clustered distribution on four of five plots with >10 stems; the remaining plot had a random spatial distribution. Clustering was observed at three plots for white fir seedlings while trees were randomly located on two plots. At the Clover Mountains, ponderosa pine showed a mix of random and clustered distributions. Clustering was observed at the six plots with at least 10 single-needle pinyon trees, either for seedlings alone or for trees and seedlings combined. When only pinyon trees were considered, clustering occurred on two plots while the other four showed a random spatial distribution.

Age structure and survivorship

We analyzed a total of 936 cores from Mt. Irish, of which 464 were collected at the plots (Tables 1 and 2) and 472 at the gridpoints. Of the plot cores, 64% were from pinyon pine, 13% from juniper, 12% from white fir, and 11% from ponderosa pine. The same order of magnitude was found for the gridpoint cores from juniper (14%) and white fir (12%), while pinyon pine was less (56%) and ponderosa pine was more (18%) represented. The oldest single-needle pinyon had an estimated pith age greater than 700 years, and pre-settlement pinyon pines were identified all over the study area. At the plots, pinyon pines began increasing in number by more than 10 trees per decade in the mid-1800s, and survivorship reached a maximum in the first few decades of the 1900s (Fig. 4), although the rate of increase varied between individual plots. After that period, which corresponds to a well-known pluvial (Woodhouse et al. 2005), the number of pinyon trees establishing at the site decreased gradually to pre-mid 1800s levels. Gridpoint data (Fig. 4) showed a less prolonged peak, with a maximum in the first decade of the 1900s. Pinyon density started increasing by more than 10 trees per decade in the early 1700s, more than a century earlier than at the plots, which may be due in part to the selective targeting of larger trees at the gridpoints. At the gridpoints, as mentioned above for the plot data, the number of
newly established pinyons decreased in number during the 1900s, reaching pre-1700s levels at the end of the 20th century.

No such remarkable expansion in density over time was uncovered for the other conifer species at Mt. Irish (Fig. 4). Juniper trees, which reached a maximum estimated age of about 600 years, were present in every plot. Their survivorship, either from plot or gridpoint cores, increased only slightly since the 1780s, with minor peaks in the 1850s and early 1900s. Ponderosa pine, whose maximum estimated age reached about 600 years, showed a relatively steady survivorship at the plots and at the gridpoints, although less so at the plots, especially in the last 200 years. White fir, with a maximum estimated age greater than 500 years, showed a relatively stable survivorship at the gridpoints, slightly increasing since the 1700s. At the plots the survivors increased in the early 1900s, as did pinyons and junipers. An early 1900s slight increase in survivorship was also recorded for ponderosa pines at the gridpoints (Fig. 4).

Fig. 5. Survivorship age structure of conifer species sampled at the Clover Mountains study site: (left) from the 12 0.1-ha plots; (right) from the 68 grid points. The graph was drawn using the same method used for Fig. 4.

For the Clover Mountains we analyzed 1,027 cores, of which 459 from the plots (Table 3) and 568 from the gridpoints. Pinyon pine accounted for the majority of cores, 66% from the plots and 77% from the gridpoints. Ponderosa pine made up the remaining 34% of plot cores and 21% of gridpoint cores, while Utah juniper was only cored at the gridpoints (2%). The oldest pinyon pine had an estimated pith age of 365 years, and pre-settlement pinyons were found throughout the study area. Plot data showed pinyon pine survivorship reaching above 10 trees per decade in the 1830s, then progressing to a maximum in the 1960s (Fig. 5), and returning to pre-1830s value at the end of the 20th century. At the gridpoints (Fig. 5) the peak in survivorship was less pronounced but it began increasing above 10 trees per decade about 50 years earlier (since the 1780s), resulting in sustained establishment well before Euro-American settlement. The highest levels of successful establishment were again recorded during the early 1900s, and then declined with time until the present.

The oldest ponderosa pine at the Clover Mountains had an estimated age of 570 years.
At the plots (Fig. 5), ponderosa pine exhibited two survivorship peaks, a minor one (not exceeding 10 trees per decade) in the late 1700s, which was mostly derived from one of the two added plots, and a major one in the late 1800s. Of the 155 ponderosa pines sampled at the plots, 78% became established during the 1860–1930 period. Afterwards, successful establishment decreased smoothly, reaching pre-late 1700s levels by the mid-1900s. This late 1800s-early 1900s survivorship peak was also observed in the gridpoint data (Fig. 5). The number of Utah juniper samples (12 total with ages extending over almost 350 years) was too small to reliably infer any changes in survivorship through time.

The relationship between age and size (either DBH or height) was even more variable than that found between DBH and height. For pinyons at Mt. Irish, a relatively small DBH range (30–40 cm) corresponded to widely different ages (100–500 years) and heights (3–10 m). At the Clover Mountains this variability was less pronounced, also because of fewer old-growth pinyon pines, particularly in the northern portion of the study area, but pinyons with DBH of 30–40 cm could still have ages of 100–300 years and heights of 5–13 m. In other words, the connection between tree age and size was affected by groups of trees that were similarly aged, but that varied greatly in both height and DBH. Only for ponderosa pine at Mt. Irish the growth rate remained fairly constant through time, resulting in almost linear age-height and age-DBH relationships (Bradley 2009).

**Discussion**

The Clover Mountains study area is on average about 400 m lower than the Mt. Irish one, and it would be expected to be drier based on orographic effects on climate generally found over the Great Basin (Houghton et al. 1975). Instead, the Clover Mountains receives higher precipitation than Mt. Irish (average annual total of 41 vs. 29 cm) according to PRISM model results, while temperature is very similar (average annual mean of about 9°C). This somewhat unexpected climatic feature is most likely the reason for the presence of ponderosa pine at the Clover Mountains. At that site, based on elevation alone, juniper should be a major species, but it was rarely found, although its abundance increased at lower elevations, outside of the area occupied by ponderosa pine. Juniper was the second densest species at Mt. Irish, where also a montane species such as white fir occurred in association with the other conifers. While not included at any of the plot or grid point locations, bristlecone pine is also present at Mt. Irish (D. Charlet personal communication), where it reaches a maximum DBH of 84 cm (K. Rock, personal communication).

The reported density of pinyon-juniper woodlands throughout the Great Basin varies from a maximum of 885 trees ha\(^{-1}\) in west-central Utah to a minimum of 344 trees ha\(^{-1}\) in central Nevada (Miller et al. 2008). Other studies found 850 trees ha\(^{-1}\) in southwest Utah (Tausch and West 1988), 750 trees ha\(^{-1}\) in east-central Nevada (Blackburn and Tueller 1970), and 537 trees ha\(^{-1}\) in southwest Idaho (Miller et al. 2008). Based on the six plots including only pinyon and juniper stems, the density of pinyon-juniper stands at Mt. Irish was 410 stem ha\(^{-1}\) and at the Clover Mountains it was 425 stem ha\(^{-1}\). These similar values, which fall in the lower half of the range of published densities, are likely related to the general character of our target ecosystems, which belongs to the mixed conifer assemblage more than the pure pinyon-juniper type.

Single-needle pinyon was the most common species at both sites, accounting for approximately 60% of all trees, but was minimally affected by mortality, even after the early 2000s drought. Less than 10% of all mapped pinyon pines at our sites were dead, whereas in pinyon-juniper ecosystems of northern Arizona dominated by *P. edulis* and *J. monosperma* (Engelm.) Sarg., pinyon mortality reached more than 50% after the 1996 and 2002 dry years (Mueller et al. 2005). Soil properties (Peterman et al., in press) and stand characteristics, combined with the effect of pinyon ips (*Ips confusus* Leconte) outbreaks (Floyd et al. 2009), have influenced how the adverse impact of drought was recently manifested in *P. edulis* populations. At our study sites, density of *P. monophylla* more than doubled since the 1800s, with peak survivorship occurring in the early 1900s at Mt. Irish and extending into the mid-1900s at the Clover Mountains. Plot and gridpoint data clearly indicate that although there has been an increase in survivorship of
single-needle pinyon since Euro-American settlement, that species existed across the landscape long before settlement, hence pinyon has enlarged its density (i.e., infilling), rather than invading adjacent ecosystems.

The rise of pinyon-juniper woodlands throughout the Great Basin has occurred at approximately the same time, but there are some regional differences in species dynamics. In the northern Great Basin, woodland spread was driven by *Juniperus occidentalis* Hook. (Burkhardt and Tisdale 1976, Miller and Rose 1999, Miller et al. 2008), given that pinyon does not occur north of a southwest to northeast boundary roughly corresponding to the Truckee River–Humboldt River axis (Charlet 1996). In the southern Great Basin expansion and infill are primarily due to enhanced pinyon pine survivorship with no corresponding juniper proliferation (Blackburn and Tueller 1970, Tausch et al. 1981, Tausch and West 1988), and the same pattern was found at our study sites. In the central Great Basin and over a 30-year period, the area of pinyon-juniper woodland increased by 11% over relatively coarse, ecotonal scales (0.4 ha) but by 33% over single-tree scales (20 m²) because of infilling processes (Weisberg et al. 2007). Regardless of the species involved, survivorship episodes display coherent features throughout the Great Basin. The age structure data of *P. monophylla* at Mt. Irish is similar to that of *J. occidentalis* in Idaho (Miller et al. 2008) and of *P. monophylla* in southwestern Utah (Tausch and West 1988), while at the Clover Mountains it resembles that of pinyon-juniper woodlands in the Shoshone Mountains from central Nevada (Miller et al. 2008).

Tree age distributions at Mt. Irish were consistent with a pre-settlement fire regime characterized by frequent low-severity events (Biondi et al. 2011), as trees older than 200 years were found at most plots and gridpoints. Such old-growth individuals are also consistent with a long fire rotation. Reconstructed fire events did not coincide with groups of similarly aged trees except for plot 10, where all trees in the plot but a single juniper established after 1836, and a ponderosa pine located about 50 m away recorded a fire in 1836. A somewhat different fire regime at the Clover Mountains, with less frequent events that occasionally had patchy high severity, was consistent with our data. Five gridpoints without current tree coverage and two gridpoints with trees that established after 1946 were located between fire-scarred trees that had recorded the 1946 event (Kilpatrick et al., in press). Similarly, the 1862 fire, which was identified as having higher severity at that site (Kilpatrick et al., in press), preceded a pulse of ponderosa pine survivorship observed at two plots and 10 gridpoints. Methodologically, fire scars document low-severity fires, while stand age structure can provide evidence of high-severity fires (Kipfmueller and Swetnam 2005), and at both study sites the fire scar and vegetation data were in agreement with one another with regard to fire regime.

Due to the low numbers of ponderosa pine and juniper seedlings at both sites, only pinyon pine and white fir seedlings could be tested for clustering. The lack of highly coherent spatial patterns was not surprising given their multiple, interacting drivers. The seed dispersal mechanism of pinyon is mostly scatter-hoarding by birds and rodents, leading to clusters of reproduction. Single-needle pinyon seedlings are also known to avoid interspaces, and instead favor the microclimates that exist under other trees and shrubs (Chambers 2001). White fir seeds are dispersed by the wind, which would potentially lead to random or dispersed distributions, but seedling establishment is likely due to locally favorable conditions, which results in clustered distributions. At our study sites, spatial arrangements were driven by the presence of seedlings at the plots, i.e., when seedlings were clustered, the plot overall was clustered, most likely because seedlings often outnumbered trees and saplings. On the other hand, the spatial distribution of trees alone did not necessarily correspond with that of the seedlings or the plot as a whole. Trees were randomly distributed on most plots, suggesting that while seedlings may have established in groups, most of the group components did not survive to become trees, breaking down the original clusters to produce a random tree distribution.

Using current age structure to interpret historic species dynamics implies that only survivorship can be determined, making it impossible to know if greater survivorship is due to increased regeneration, decreased mortality, or a combination of both. Whatever the cause, it is evident
from the plot data that species dynamics have changed over time leading to greater pinyon pine survivorship between the mid-1800s and at least the mid-1900s. Observed tree ages may not fully represent the youngest individuals, given their small size and therefore difficulty of obtaining datable increment cores. As a consequence, recent decreases in survivorship may in part be a reflection of this sampling bias. Age structure of single-needle pinyon followed similar patterns at the two sites, whereas ponderosa pine ages differed between them. At Mt. Irish ponderosa pine survivorship was relatively stable through time (Fig. 4), whereas at the Clover Mountains it intensified in the late 1800s and then peaked in the late 1800s-early 1900s (Fig. 5). Episodic establishment in ponderosa pine stands has been reported for the American Southwest and Colorado Plateau, with changes in disturbance and climate regimes being the likely causes (White 1985, Savage et al. 1996, Mast et al. 1998, Brown and Wu 2005).

The period since Euro-American settlement during the late 19th and early 20th century coincides with a period of wetter conditions in the Great Basin (Biondi et al. 2011), possibly associated with the end of the Little Ice Age (Grayson 2011). Roughly at the same time, the reduction in wildfire frequency uncovered at both study areas (Biondi et al. 2011; Kilpatrick et al., in press) was the main factor that allowed the increased survivorship of pinyon and ponderosa pine. After the early-2000s drought, and despite the greater density they acquired over the past century, the pinyon-juniper populations we studied have not experienced the dramatic mortality observed where *P. edulis* is present. Our findings, which at first could be deemed relevant only for mixed-conifer ecosystems, are in close agreement with another recent study of relatively pure pinyon-juniper woodlands in central Nevada (Greenwood and Weisberg 2008), showing a 7% mean tree mortality in 217 plots spread over a 3250-km² area that included 11 mountain ranges and covered elevations from 1600 to 2500 m. Given that pinyon-juniper woodlands have recently experienced dramatic, drought-related dieoffs in regions where *P. edulis* is present, whereas they have remained at low mortality levels in the Great Basin, where the pinyon species is *P. monophylla*, modern climatic changes must have impacted pinyon populations differently in this region as compared to the Colorado Plateau and the North American Monsoon System region.

**CONCLUSION**

The similar timing of multiple changes, from climate episodes to wildfire regime, from logging to grazing, makes it difficult to determine if there is a main cause for augmentation of pinyon-juniper woodlands, or if a combination of forcings are responsible (Romme et al. 2009). Because similar temporal dynamics of expansion and infill are found throughout the Great Basin, climate is the most likely factor for imparting synchronous patterns in this sparsely populated region. On the other hand, at roughly the same time, Euro-American occupation of these lands involved discovery of ore bodies with associated mining and charcoal production, followed by establishment of ranches and towns to support the mining (Paher 1970, Hulse 1971, Carlson 1974), and such activities impacted pinyon-juniper woodlands throughout the region (Lanner and Frazier 2011; Strachan et al., in press). At our study sites, since wildfire regime and land-use changes were not identical, the most likely driver for a large pulse in single-needle pinyon survivorship within these mixed-conifer ecosystems remains climate. Any future management activity should consider that current woodland conditions are the result of both natural and anthropogenic factors, and that pre-settlement pinyons are found across the landscape in mixed conifer ecosystems of the Great Basin.

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**LITERATURE CITED**


Dilts, T. E., J. S. Sibold, and F. Biondi. 2009. A weights-of-evidence model for mapping the probability of


References


Fig. A1. An example of the visualization used to represent the horizontal and vertical stand structure based on the data collected at the study sites. This graph shows plot 1 at Mt. Irish: shrubs were relatively rare, so that they were mapped as points without reporting the species.
Fig. A2. An example of the visualization used to represent the horizontal and vertical stand structure based on the data collected at the study sites. This graph shows plot 1 at the Clover Mountains: only the species legend is shown since the stem size and vertical shape symbols are the same as in Fig. A1. Shrub cover was relatively abundant, so that it was mapped as polygons and reported by species for Gambel oak (*Quercus gambelii* Nutt.) and manzanita (*Arctostaphylos* spp.).