

108 years of change in spatial pattern following selective harvest of a *Pinus ponderosa* stand in northern Arizona, USA

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Abstract

Questions: How did an initial tree harvest in 1894 influence the spatial and temporal patterns of *Pinus ponderosa* recruitment? How do these patterns compare to our understanding of *P. ponderosa* stand dynamics prior to Euro-American settlement? How might spatial pattern information, particularly with respect to patch characteristics, inform current restoration and management practices?

Location: A 2.59-ha permanent sample plot in the Fort Valley Experimental Forest, Flagstaff, Arizona. The plot was selectively harvested in 1894 and measured in 1909 and 2002.

Methods: We used historical stem-map and ledger data, contemporary data, and dendrochronological techniques to reconstruct stand structure (tree size, age, location) in three scenarios: (1) unharvested (1909), (2) harvested (1909), and (3) contemporary (2002). We used Clark and Evans' R, Ripley's $K(t)$ univariate analysis, and correlogram analysis to assess the spatial pattern in each scenario. We also used Ripley's $K_{12}(t)$ bivariate analysis and tree age data to examine spatial and temporal recruitment patterns as observed in the contemporary scenario.

Results and Conclusions: The unharvested stand was aggregated at scales up to 28 m. The selective harvest accentuated the spatial patchiness of the stand in 1909 and changed spatial patterns by homogenizing tree size within patches. By 2002, the stand was a single patch dominated by small trees. Post-harvest recruitment patterns were not spatially random; *Pinus* seedlings initially established in natural grass openings and then proceeded to fill-in stump patches created by harvesting. Knowledge of spatial pattern should be explicitly incorporated into restoration activities in these forests.

Keywords: Clark and Evans' R; Fort Valley Experimental Forest; Gap model; Moran's I; Neyman-Scott Process; Recruitment pattern; Residual stand; Ripley's K ; Woolsey permanent plots.

Nomenclature: Kearney & Peebles (1951); McDougall (1973).

Abbreviations: QMD = Quadratic mean diameter; BA = Basal area; CSR = Complete spatial randomness; NND = Nearest neighbor distance; TPH = Trees per ha; DRC = Diameter at root collar.

Introduction

Plant spatial patterns observed today are the net result of interactions among prior processes such as regeneration, competition, and mortality (Dale 1999; Youngblood et al. 2004). Analyses of changes in spatial pattern can increase our understanding of plant community dynamics (Levin 1992; Dale 1999; Fortin & Dale 2005) and the consequences of management activities such as fire exclusion, grazing, and thinning (Foster et al. 2003) on these processes. Thus, analyses of spatial patterns could increase our ability to understand and predict future stand development.

Much has been written about the dramatic structural and functional changes that *Pinus ponderosa* var. *scopulorum* forests of the southwestern United States have undergone since Euro-American settlement (Covington & Moore 1994; Fulé et al. 1997; Mast et al. 1999, Allen et al. 2002; Moore et al. 2004), but few studies have focused on spatial patterns. Furthermore, tree spatial data deemed essential for understanding heterogeneity in contemporary and historical stand structures (Youngblood et al. 2004; Boyden et al. 2005) are often inadequate or lacking. A review of the literature revealed three studies (Cooper 1960; White 1985; Biondi et al. 1994) that quantified spatial patterns in southwestern *P. ponderosa* forests, while four other studies examined *P. ponderosa* spatial patterns in other regions of the United States (Mast & Veblen 1999; Harrod et al. 1999; Youngblood et al. 2004; Boyden et al. 2005).

The dramatic structural changes in these forests suggest that the underlying processes may also have changed over time. For example, presettlement tree seedlings likely concentrated in and around the established tree patches because frequent surface fires, grass competition, and drought greatly reduced the likelihood of seedling establishment elsewhere. Mortality of individual trees may have produced small recruitment sites, and frequent surface fires would have acted as a thinning agent on the pine seedling patches, most likely resulting in small,

uneven-aged groups of trees or patches (White 1985; Fulé et al. 2002; Stephens & Fry 2005). In comparison, post-settlement stand development has been highly affected by the lack of surface fires, and is generally thought to follow a 'gap' model (Watt 1947; Stephens & Fry 2005) where even-aged patches of seedlings originate in forest openings created by disturbance (Cooper 1960, 1961; White 1985; Fulé et al. 2002). *P. ponderosa* seedlings establish in groups (or patches), often in the immediate vicinity of older trees (Pearson 1923), and may be more abundant northeast of seed trees, where environmental conditions are less harsh (Pearson 1942; Haase 1981). In addition, regeneration persists at higher densities on limestone- than basalt-derived soils (Heidmann et al. 1982; Goodwin 2004), is episodic in nature (Pearson 1950; Savage & Swetnam 1990; Savage et al. 1996; Mast et al. 1999; Allen et al. 2002; Bailey & Covington 2002; Brown & Wu 2005), and is limited by drought and competition with herbaceous vegetation (Pearson 1942; 1950; Schubert 1974; Kolb & Robberecht 1996).

One type of disturbance in post-settlement times is management activities such as the intensive harvesting that occurred during the last century. Understanding how these past management activities have influenced contemporary forest spatial patterns will allow managers to better understand the consequences of their decisions (Foster et al. 2003; Taylor 2004). Our objective was to use historically stem-mapped tree data to describe spatial patterns over a 108-year period in a pure *P. ponderosa* stand in northern Arizona. We addressed three questions: 1. How did an initial tree harvest in 1894 influence the spatial and temporal patterns of *P. ponderosa* recruitment? 2. What are the contemporary patterns of tree recruitment and how do they compare to our understanding of pre-settlement *P. ponderosa* stand dynamics? 3. How might this spatial pattern information, particularly with respect to patch characteristics, inform current restoration and management practices?

Methods

Study site

The study site is located 10 km NW of Flagstaff, Arizona on the Fort Valley Experimental Forest within the Coconino National Forest (35°15.94' N, 111°44.99' W). *Pinus ponderosa* is the only tree species on the site, and the understory vegetation is predominantly perennial bunchgrasses. The site is within a vegetation unit that comprises 7% (56 000 ha) of Coconino National Forest (Terrestrial Ecosystem Unit 582; Miller et al. 1995). The elevation is 2240 m. Soils are derived from Tertiary basalt flows and cinders, and are classified as a complex of fine, smectitic

Typic Argiborolls and Mollic Eutroborolls, primarily with clay loam and stony clay textures (Kerns et al. 2003). Mean annual temperature is 7.5 °C and mean annual precipitation is 570 mm, following a monsoonal precipitation pattern with half of the precipitation as rain in July and August, and half as winter snow.

Our site, known as COCS1A (2.59 ha, 160 m × 160 m), was established in 1909 as part of a network of permanent plots used to quantify *P. ponderosa* growth at the tree and stand levels (Pearson 1923, 1933; Moore et al. 2004). Secondary objectives of the original study were to compare the effects of different harvesting and slash disposal practices on stand dynamics and to determine the effects of herbaceous competition, soil, and disturbance events (timber harvesting, livestock grazing, fire, and pest outbreaks) on *P. ponderosa* regeneration (Woolsey 1911, 1912; Pearson 1923, 1933; Moore et al. 2004). COCS1A was selectively harvested in 1894; 8 to 10 mature (> 200 years old) trees per ha were retained as a regeneration source (Pearson 1923; Nyland 1996). Beginning in 1909, the plot was fenced to exclude livestock.

All live trees ≥ 9.14 cm (3.6 inch) diameter at breast height (DBH; 1.37 m above ground level) were measured and stem-mapped at plot establishment. Tree condition, DBH, and other variables were recorded in a ledger that is housed in the Fort Valley Experimental Forest Archives (Rocky Mountain Research Station, USDA Forest Service, Flagstaff, AZ). The residual tree density, as measured in 1909, was 52 trees per ha (TPH). A thinning in 1941 removed 16 TPH (mean DBH: 48.7 cm, SD = 21.4 cm) and left a residual stand density of 401 TPH.

Data collection

Historical and contemporary field methods are detailed by Moore et al. (2004), who also report on stand structure changes within a 1-ha subplot of this and other permanent plots throughout Arizona and New Mexico. For our study, we measured the entire 2.59 ha plot because a larger spatial extent was needed for analyses of spatial patterns. All live and dead tree structures, including stumps, snags, and wind-fallen trees that grew to at least breast height, were measured. Spatial coordinates of all tree structures were obtained with a surveying laser.

To examine recruitment patterns, all tree structures were designated in the field as either pre-harvest (center date ≤ 1894 at 40 cm above ground) or post-harvest (center date > 1894). Live trees given a pre-harvest age designation were cored at 40 cm above the ground, as were 20% of the post-harvest trees. Trees were re-cored up to 3 times if they missed the pith, and the best core was selected. Increment cores were mounted, surfaced, and crossdated using standard dendrochronological techniques (Stokes & Smiley 1996; Swetnam & Dieterich

1985). When the increment core failed to intercept the pith, or where the pith was rotten, the number of years from the innermost ring to the pith was estimated with a pith locator (Appelquist 1958). Of the 493 trees cored, only six could not be dated to center. The average number of years from the innermost ring to the pith was 4.4 years (SD = 3.3; $n = 154$). Our age estimates do not account for the time required for seedlings to grow to a 40 cm height, which can range from 3 to 10 years (Sackett 1984; Cormier 1990) in this area.

Stand structural scenarios

We examined the spatial patterns of three stand structural scenarios: (1) ‘unharvested’ (1909 stand structure as it would have been if selective harvesting had not occurred in 1894); (2) ‘harvested’ (actual 1909 stand structure); and (3) ‘contemporary’ (actual 2002 stand structure). We restricted our attention to trees ≥ 9.14 cm DBH because detailed historical data were not collected for smaller trees. In total, our dataset contained 219 trees for the unharvested scenario, 134 for the harvested scenario, and 1487 for the contemporary scenario. All tree spatial coordinates were obtained during contemporary measurements. The historical stem map was used to verify that trees and stumps present at plot establishment were located correctly.

To compare stand structure and spatial patterns among scenarios, we used the location (x-y coordinates), historical stem-map, and DBH of all trees and stumps (reconstructed) in each scenario. DBH data for the contemporary scenario were obtained during contemporary measurements, and data for the harvested scenario were obtained from the 1909 stem map and plot ledger. For the unharvested scenario, we also needed to account for the trees that were harvested in 1894. Decomposition rates are slow in this area (Jenny et al. 1949; Hart et al. 1992; Covington & Moore 1994), and most windfall and stumps from the 1894 harvest are still present on the site. We measured the current DRC of each stump, using evidence of past tree size such as rings of residual bark at the soil line, sapwood, and/or immovable rocks (designating a permanent root collar boundary) to aid in the measurement. A regression model was used to predict DBH from DRC for each harvested tree ($r^2 = 0.96$, $SE_{\text{residuals}} = 1.18$, $n = 192$; Sánchez Meador 2006).

Describing tree spatial patterns

We used univariate point pattern analyses to determine whether trees were distributed uniformly, randomly (also called complete spatial randomness or CSR), or aggregated (Upton & Fingleton 1985; Legendre 1993). Clark and Evans’ R (Clark & Evans 1954) is a nearest

neighbor distance (NND) index that has been reported in other studies of southwestern *P. ponderosa* forests (Cooper 1961; White 1985); we used it to permit direct comparisons with these results. It examines the distribution associated with distance from a randomly selected tree to its first nearest neighbor. We corrected for edge effects and used z -tests to determine whether spatial distributions were significantly ($\alpha = 0.05$) non-random.

Ripley’s $K(t)$ function (Ripley 1976, 1977, 1981) is a second-order statistic that examines the spatial pattern of pairs of points within t radial lag distances. It does not aggregate spatial data and therefore can quantify the intensity (density of points per unit area) of pattern at multiple scales (Upton & Fingleton 1985; Dale 1999). We used 2-m lag distances and a maximum lag distance of 80 m (half the minimum dimension of the plot; Boots & Getis 1988) to reduce the error induced by edge effects. Visual interpretation was simplified using a square root, variance-stabilizing transformation of $K(t)$ to $L(t) - t$ (Besag 1977). The observed values were tested for significance at $\alpha = 0.05$ using 99 Monte Carlo permutations (Upton & Fingleton 1985). Clark and Evans’ R and Ripley’s $K(t)$ were implemented using an online spatial package (Reich & Davis 1998) in S-Plus 6.1 (Insightful Corp., Seattle, WA, 2002).

Depending on whether patches are even- or uneven-aged, variability in tree size within patches should be low or high, respectively. This hypothesis was tested for each scenario by using Moran’s I (Moran 1950; Legendre & Legendre 1998) to examine spatial autocorrelation in DBH. As recommended by Legendre & Legendre (1998), each correlogram was tested for global significance and individual lag distances were tested ($\alpha = 0.05$, Bonferroni corrected to account for the number of distance classes) only when the global test was significant. The lag distance was set to 5 m so that results were directly comparable with Biondi et al. (1994), which was conducted nearby and utilized correlogram analysis to examine spatial patterns. Spatial autocorrelation analysis was implemented in the *R* software environment (v.2.2.0; R development Core Team 2005) using the *spdep* package (Bivand & Gebhardt 2000).

Lastly, we quantified the number and size of patches for each scenario. The lag distance and value of $L(t)$ at the point of maximum divergence from CSR was used to estimate the initial values for patch size and patch intensity (Reich & Davis 1998; Boyden et al. 2005). A Neyman-Scott point process (Neyman 1939; Neyman & Scott 1958) was then fit to observed point patterns (assuming stationarity) using least squares techniques (Diggle 2003; Batista & Maguire 1998; Reich & Davis 1998) and optimized estimates of patch density and mean patch size were computed.

Describing tree recruitment patterns

We were specifically interested in where and when seedlings established relative to unharvested trees, natural grass openings in the stand, and openings created by harvesting. We hypothesized that pine seedlings would first establish in natural grass openings and then in openings created by harvesting. We used Ripley's $K_{12}(t)$ bivariate point pattern analysis (Lotwick & Silverman 1982; Rowlingson & Diggle 1993; Diggle 2003) to examine the spatial patterns of regeneration (second population) given the spatial pattern of established trees (first population). This statistic is computed and interpreted as the Ripley's $K(t)$ statistic, except that distances are calculated between points from different populations and confidence envelopes are formed by holding the locations of established trees constant while simulating 99 toroidal shifts of the recruited tree locations. Two analyses were conducted, one with unharvested trees as the first population and the other with cut stumps as the first population. Analyses were implemented using *R* v.2.2.0 and the *splancs* package (Rowlingson & Diggle 1993; Bivand & Gebhardt 2000).

To visualize when and where recruitment occurred, we examined tree age distribution over the entire plot. We used semivariogram analysis and kriging (Isaaks & Srivastava 1989) to obtain a smooth map of trees ages and to aid in the interpretation of tree establishment dates and spatial pattern. On the resulting map, individual tree establishment dates are interpolated across the site (on a 5 m × 5 m grid) and smoothed contours delineate areas

with similar establishment dates. Closer contours indicate greater variation in establishment dates. These analyses were implemented using *R* v. 2.2.0 and the *geoR* package (Ribeiro & Diggle 2001).

To test if these specific tree cohorts were an artifact of our center date estimation methods, we examined a subset of full post-harvest data set (≥ 1894 ; $n = 277$ with 44% estimated to be within 5 years of center) to determine if our age structure was dominated by a single cohort (ca. 1919, as reported by Savage et al. 1996) and represented a true range of establishment dates.

Results

Tree spatial patterns

The 1894 harvest of *Pinus ponderosa* removed approximately one third of the trees and two-thirds of the stand basal area (Table 1). Most of the retained trees were in the southern and easterly portions of the plot, and were smaller in size than those removed by the harvest (Fig. 1). By 2002, tree density had increased six-fold and basal area had more than doubled compared to unharvested conditions.

Live trees were significantly aggregated under all scenarios (Table 1; Fig. 1), but were most strongly aggregated in the harvested scenario. Trees were much closer together in the contemporary scenario (mean NND = 1.9 m) than in 1909 (mean NND = 4.5 m and 3.9 m in the unharvested and harvested scenarios, respectively).

Table 1. Stand-level structural and spatial data for trees ≥ 9.14 cm DBH for unharvested (1909), harvested (1909), and contemporary (2002) scenarios.

Attribute	Unharvested	Harvested	Contemporary
Structural			
Diameter at Breast Height (cm)			
Mean \pm SD	44.0 \pm 18.1	35.6 \pm 13.4	26.1 \pm 13.3
Minimum	9.5	10.2	9.1
Maximum	105.0	76.2	86.6
Density (TPH ¹)	85	52	575
Basal Area (m ² /ha)	15.1	5.8	38.6
QMD ² (cm)	47.6	38.0	29.3
Spatial			
Nearest Neighbor Distance (m)			
Mean \pm SD	4.5 \pm 3.7	3.9 \pm 3.6	1.9 \pm 1.2
Median	3.3	2.6	1.6
Minimum	0.9	1.0	0.0
Maximum	16.2	19.2	11.9
Clark & Evans R	0.83 ³	0.55 ³	0.90 ³
Patch			
Density (PPH ⁴)	58.0	14.5	.6
Size ⁵ (ha)	0.02	0.03	-.6

¹TPH = trees per hectare; ²QMD = quadratic mean diameter; ³Clark & Evans R = index of dispersion; ⁴PPH = patches per hectare; ⁵Size = area of the smallest polygon that encloses all trees in the plot. The contemporary scenario exhibited an inhomogeneous clustered pattern, which violates the assumptions of the Neyman-Scott model and therefore could not be estimated.

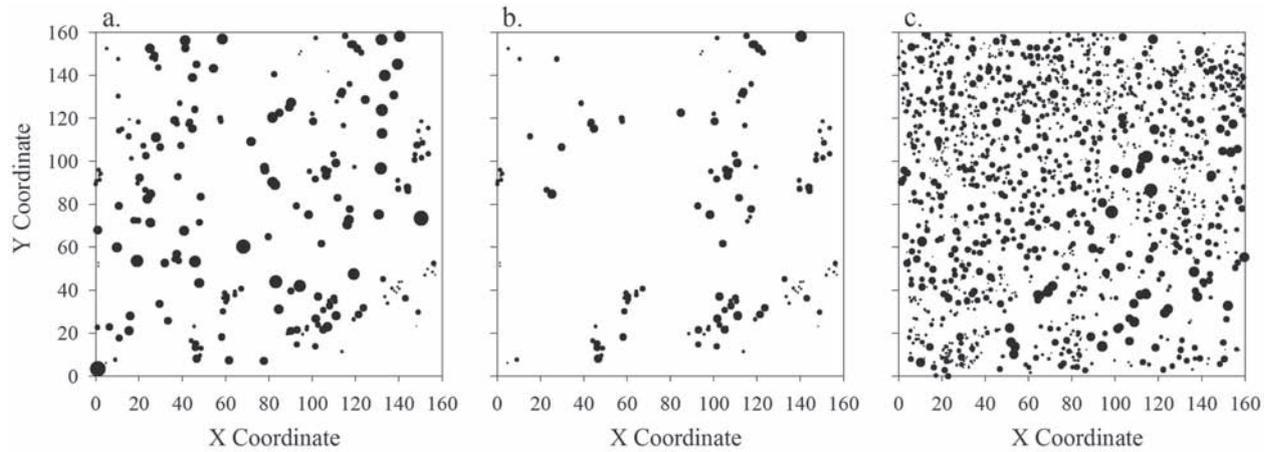


Fig. 1. Stem maps of live trees ≥ 9.14 cm DBH for three scenarios: **(a)** unharvested (1909; $n = 219$), **(b)** harvested (1909; $n = 134$), and **(c)** contemporary (2002; $n = 1,487$). Point size is proportional to stem diameter and on a different scale from tree coordinates for visual clarity.

In the unharvested and harvested scenarios, the data exhibited a distinct peak in aggregation at 6 to 8 m lag distances (Fig. 2a,b), indicating that patches averaged 0.02 ha to 0.03 ha in size (Table 1). Harvesting increased the magnitude of this peak and also increased the scale at which aggregation was observed (Fig. 2b). In the contemporary scenario, distinct small patches were not discernable and trees were aggregated at all spatial scales tested (Fig. 2c).

Trees of similar size were positively autocorrelated for all three scenarios ($p \leq 0.001$, 0.026 , and ≤ 0.001 for unharvested, harvested, and contemporary, respectively). Significant autocorrelation occurred at short distances in

1909 (lags up to 15 m in the unharvested scenario, 5 m in the harvested scenario) and at much greater distances in 2002 (lags up to 30 m) (Fig. 3). Autocorrelation statistics were much more variable in the harvested than unharvested scenario (Fig. 3a, b).

The 1894 harvest reduced patch density by seventy five percent with a corresponding patch size increase of 0.01 ha (Table 1). In the contemporary scenario, the observed point pattern no longer exhibits stationarity (visible in the NW-SE density gradient; see Fig. 1c) violating this assumption of the Neyman-Scott clustered point process. As a result, contemporary patch density and size could not be estimated.

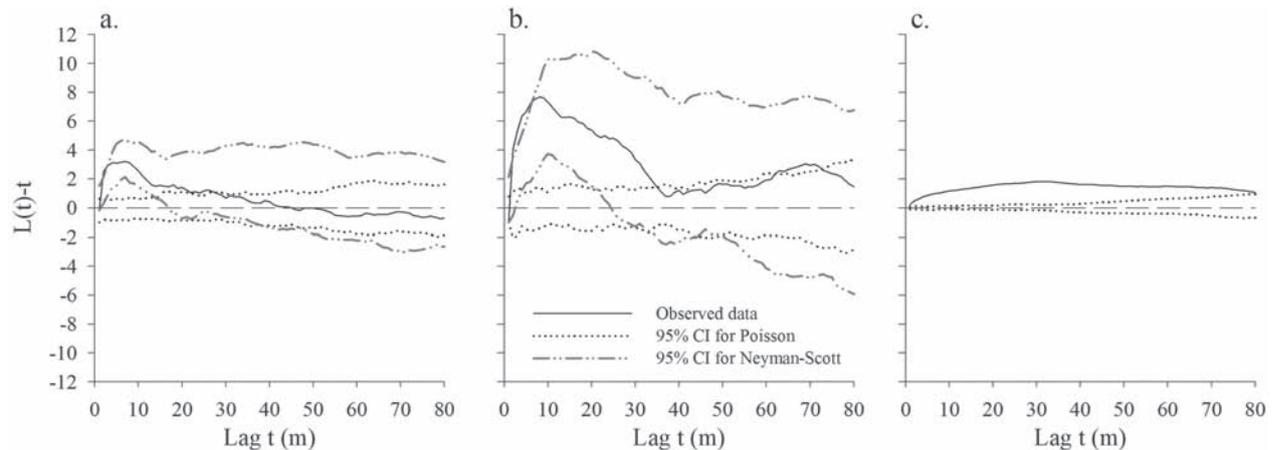


Fig. 2. Ripley's $K(t)$ univariate statistic (transformed as $[L(t) - t]$) as a function of lag distance for three scenarios: **(a)** unharvested (1909, $n = 219$), **(b)** harvested (1909; $n = 134$), and **(c)** contemporary (2002; $n = 1,487$). The horizontal dashed line is the expectation under CSR (random). Calculated values that fall outside of the confidence interval are statistically significant; values > 0 indicate aggregation and values < 0 indicate uniform (regular) spatial distribution.

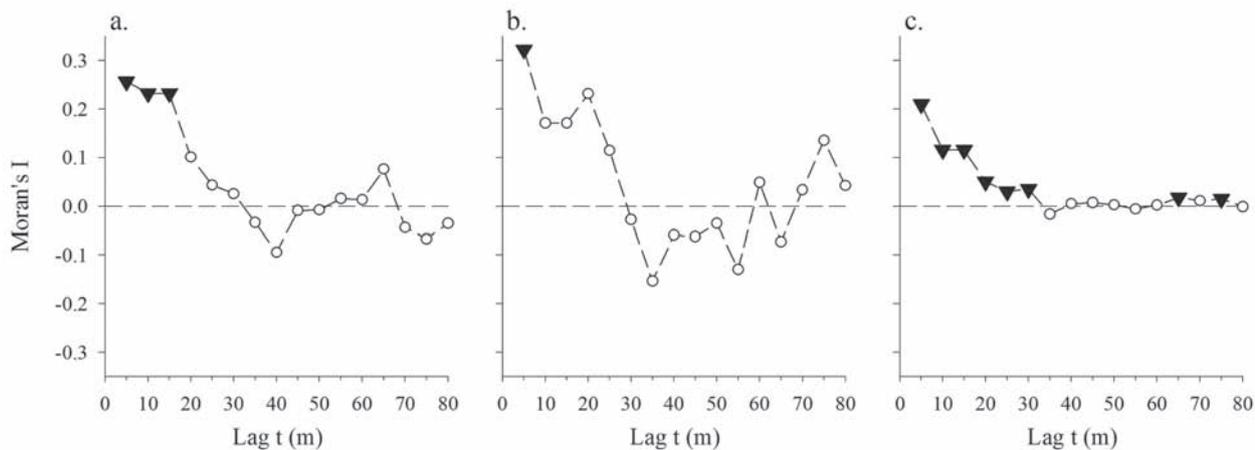


Fig. 3. Correlograms of Moran's I against lag distance for three scenarios: **(a)** unharvested (1909; $n = 219$), **(b)** harvested (1909; $n = 134$), and **(c)** contemporary (2002; $n = 1,487$). The variable analyzed was tree DBH (cm; trees ≥ 9.14 cm DBH). Moran's I can range from +1 (perfect positive spatial correlation) to -1 (perfect negative spatial correlation); 0 indicates no spatial correlation. Black triangles indicate significant autocorrelation ($\alpha = 0.05$, Bonferroni corrected), and white dots indicate no significant autocorrelation.

Tree recruitment patterns

Pine recruitment was aggregated in the early 1900s. Post-harvest seedlings established first in the natural grass openings, and later around stumps and under pre-harvest trees. Subsequent tree recruitment was repulsed from unharvested trees up to 28 m (Fig. 4b) and attracted to cut stumps at distances beyond 8 m. The strength of repulsion with pre-harvest trees peaked at 8 m, which corresponds to the peak in aggregation

observed with Ripley's $K(t)$ for the unharvested and harvested scenarios and the shift from random to positive association with the cut stumps present after the 1894 harvest (Fig. 4c).

The contemporary stand exhibits an uneven-aged distribution, though most trees established within 40 years of the 1894 harvest (Fig. 5a). Tree age was spatially autocorrelated at lag distances up to 22.4 m. The regeneration appears to consist of several cohorts. Following harvest, initial recruitment occurred in the

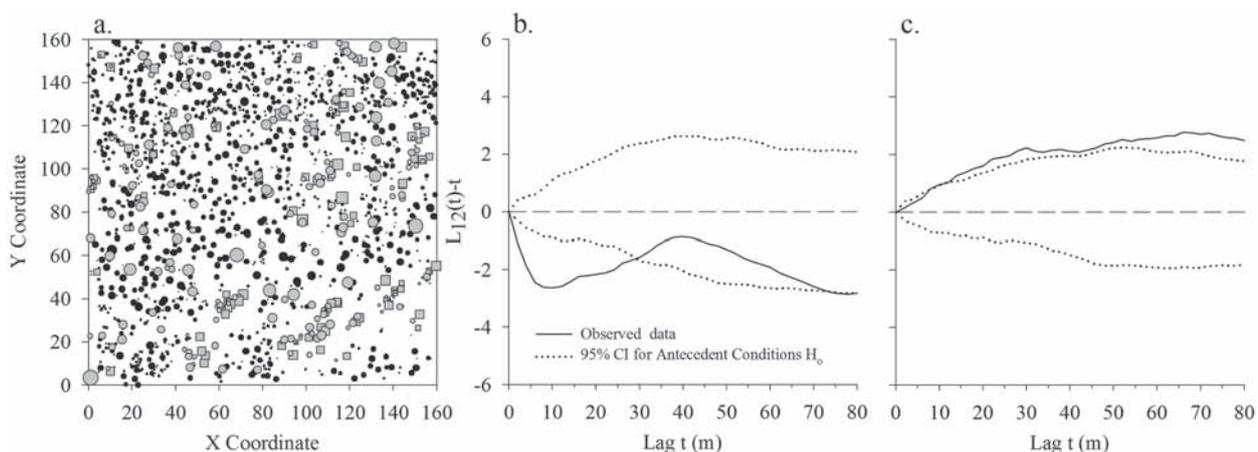


Fig. 4. **(a)** Stem map showing post-harvest trees (grey circles; trees measured in 2002 with a center date ≥ 1894 at 40 cm above ground level; $n = 1405$), unharvested trees (white squares; $n = 134$), and cut stumps (black circles; $n = 85$). The resulting Ripley's $K_{12}(t)$ bivariate statistic (transformed as $[L_{12}(t) - t]$) as a function of lag distance (t) is shown for the comparison of post-harvest recruitment patterns to **(b)** unharvested trees and **(c)** cut stump locations. The horizontal dashed line is the expectation under CSR (random) and the dotted lines are the 95% confidence limits. Calculated values that fall outside of the confidence interval are statistically significant; values > 0 indicate attraction and values < 0 indicate repulsion between the two populations.

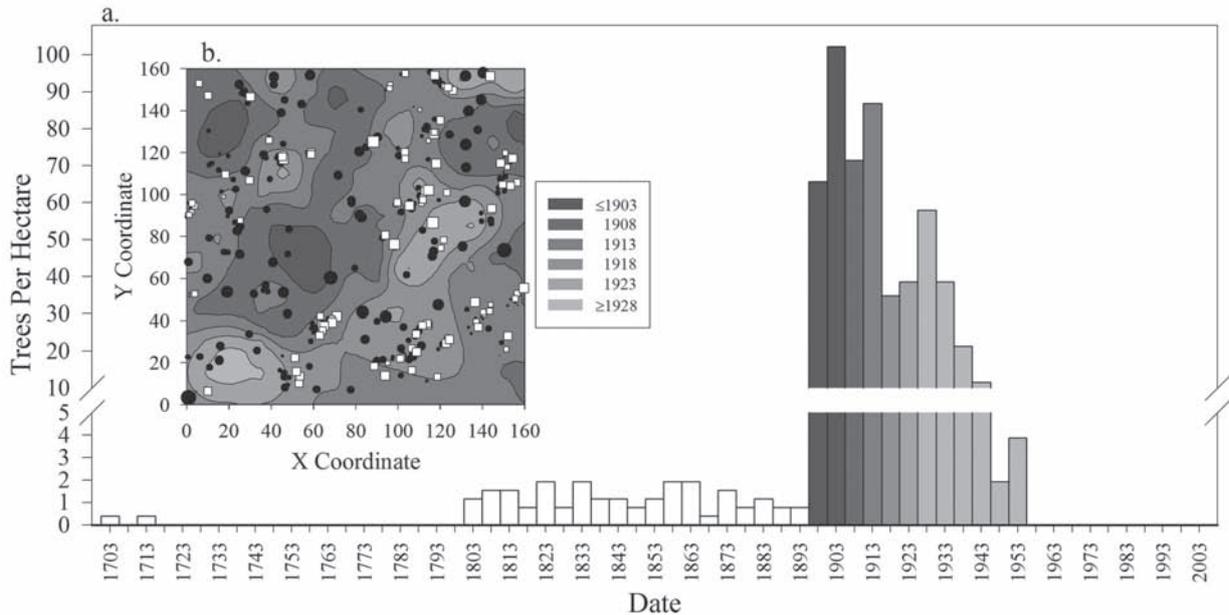


Fig. 5. (a) Age distribution and (b) kriged contour map of post-harvest tree establishment patterns (age on 5 m × 5 m blocks). Note that the same shading pattern is employed in the age distribution and the kriged map. For reference, unharvested trees are shown in white in the age distribution and as white squares on the map (but were not included in the kriging), and stumps are shown as black circles on the map.

middle of the openings between patches of unharvested live trees, which were previously dominated by grasses. Subsequent cohorts (1908-1938) established progressively closer to these trees (Fig. 5a,b), often in the growing spaces created in the 1894 harvest. The last of the recruitment filled in areas not fully occupied by previous cohorts. No recruitment occurred since 1953.

Discussion

One potential issue in our study relates to how representative our study site is compared to other *Pinus ponderosa* stands in northern Arizona. Bell et al. (in press) examined this issue extensively, and considered representativeness with respect to both historical and contemporary data. With respect to historical data, our unharvested tree density in 1909 (85 trees/ha; Table 1) is somewhat higher than historical densities reported for other sites (e.g. 61 trees/ha in 1876 by Mast et al. (1999); 62 trees/ha in 1870 by Waltz et al. (2003); 66 trees/ha in 1883 by Fulé et al. (1997)). Key differences between our study and the studies reported above is that our data are from historical data rather than reconstruction models, and that our data are from three decades after Euro-American settlement of the region while the other studies are from the time of

Euro-American settlement.

Our results show the same trend in tree density and stand basal area as other studies. A comparison of 15 sites in Arizona and New Mexico found an average increase in tree density from 77 to 527 trees/ha (trees ≥ 9.14 cm DBH) and in basal area from 8 to 28.6 m²/ha over a 80+ year period (Moore et al. 2004). Our site was protected from livestock grazing since 1909, and this has been shown to reduce contemporary tree densities (Bakker & Moore 2007). At present, tree density on our site is roughly equal to that on other sites in northern Arizona (e.g., 762 trees/ha (trees ≥ 10.2 cm DBH) on an unharvested site (Covington et al. 1997); 720 trees/ha (trees ≥ 2.54 cm DBH) on a managed site (Fulé et al. 1997).

Tree spatial patterns

In the unharvested scenario, our site was composed of tree patches averaging 0.02 ha in size with sparsely populated zones between patches. The trees were aggregated, but not as strongly as the harvested scenario. Our mean patch size is smaller than that reported by White (1985: 0.1 ha), in part due to the methods by which patches were designated. White (1985) also concluded that old *P. ponderosa* trees were strongly aggregated. In comparison, Cooper (1961) focused on younger stands (< 80 years) and found no evidence

of aggregation; trees in most of his stands were arranged randomly.

It appears that southwestern presettlement stands exhibit similar structural arrangement as stands in other regions. In west-central Washington, Harrod et al. (1999) concluded that *P. ponderosa* was historically aggregated at small scales (≤ 15 m), yet exhibited reduced aggregation and increased density during contemporary times. Boyden et al. (2005) reported a random overstory pattern for *P. ponderosa* in the Colorado Front Range, while Youngblood et al. (2004) observed both aggregated and random spatial patterns in old-growth *P. ponderosa* stands of eastern Oregon and California.

In our study area, the selective harvest in 1894 accentuated the already patchy nature of this forest. The harvest also removed many of the largest diameter trees, leaving smaller more uniform-sized trees. However, the impact on spatial patterns varied with scale. At fine scales (extents ≤ 28 m), tree patch size was largely unaffected. At coarser scales (extents > 28 m), the patchiness of the residual trees was increased because the harvest removed the large trees scattered singly about the plot and also removed entire patches.

The repulsion between regeneration and established trees (Fig. 4b) suggests that recruitment following the harvest established in new patches rather than into existing pre-harvest patches. As later cohorts established, these patches coalesced together such that the contemporary stand is a single large patch. Given the absence of regeneration in the last 50 years, the stand was likely a single patch already by 1950.

Tree recruitment patterns

Our results suggest that pine establishment was highest in interspaces or canopy gap openings, which is consistent with other studies (Pearson 1923; Cooper 1960; White 1985; Mast & Veblen 1999; Boyden et al. 2005). The tree recruitment patterns that we found are consistent with Watt's (1947) 'gap' model, as suggested by Stephens & Fry (2005).

However, a unique finding of our study was that post-harvest recruitment patterns were not spatially random (Fig. 5a). *Pinus* seedlings initially established near the center of natural grass openings and later filled-in the remaining available growing space near the edges of the grass openings and around the stumps created by the 1894 harvest. Many of the trees cored were found to have established between 1894 and 1909 (Fig. 5b) in spite of ongoing livestock grazing.

While canopy gaps are important for tree recruitment in shade intolerant species, regeneration was

more successful in the natural openings than those created by harvesting. These natural openings were originally dominated by grasses and therefore were a focus of livestock, whose overgrazing effectively eliminated competition from herbaceous plants (Pearson 1942; Heidmann et al. 1982). When the site was fenced in 1909, established seedlings were released from trampling and/or browsing (Bakker & Moore 2007). Additional seedlings established after the site was fenced.

Our results indicate that at least two distinct cohorts of pine seedlings established following the initial harvest, with most originating in the highly favorable establishment year of 1919 as reported by Savage et al. (1996). While our results are similar, it should be noted that their study area was only 0.1 ha in size and, since recruitment is not distributed randomly across space, they may not have captured the full range of cohorts.

Ecological and restoration implications

The physical legacy of presettlement tree spatial patterns is still present on many landscapes, though it may be obscured or further altered by past management activities (i.e., harvesting, livestock grazing, fire exclusion) and the natural progression of stand dynamics. At present, land managers are treating thousands of hectares of southwestern *P. ponderosa* forests to reduce wildfire risk through fuel reduction and restoration thinnings, and the occasional commercial harvest. These activities, and their resulting spatial pattern, affect various ecosystem components and processes. For example, the presence of a few large trees in a group has a disproportionately large effect on the location of the future cohorts of pine trees (this study), and a disproportional negative effect on understory production (Laughlin et al. 2006). Wildlife habitat has long been known to be sensitive to spatial pattern (Patton 1977; Graham et al. 1994; Meyer & Sisk 2001; Waltz & Covington 2003).

Our results demonstrate that spatial information can provide new insights into age distribution and other common variables. In addition, spatially-explicit information such as NND, patch density, and patch size should directly inform restoration and management efforts. For example, prescriptions could specify the range of desired NNDs and the number, size, and shape of patches.

Currently, some prescriptions explicitly incorporate presettlement tree evidence while others simply set non-spatial targets (e.g., target stand density or basal area values that are applied to all acres in a stand). Forest thinning activities that do not use presettlement

tree evidence will likely reduce susceptibility to catastrophic fire, but may produce stand structures that are not 'natural' in these forests. For example, fuel reduction treatments often result in random or uniform spatial patterns because these patterns are more easily implemented (J.D. Bakker unpubl. data).

Conclusions

Spatial analysis of structural characteristics and recruitment patterns permits reconstructions of stand development. In this stand, it provided valuable insight into the long-term consequences of the initial selective harvest and subsequent regeneration episodes. By conducting such analyses over time, we increased our understanding of pine establishment patterns, possible driving mechanisms, and the impacts of human disturbance (Foster et al. 2003) within the *P. ponderosa* forests of northern Arizona.

Our findings with respect to within-patch variability and patch size are limited by the area sampled, and should be investigated at larger extents (i.e., larger stands, watershed- or landscape-scale). In addition, this and many other studies that have examined southwestern *P. ponderosa* regeneration patterns were conducted within half a kilometer of one another on a single soil type (Pearson 1923; White 1985; Biondi et al. 1994; Savage et al. 1996; Mast et al. 1999; Kerns et al. 2003). Studies should be conducted on other soil types and parent materials to assess how broadly the patch size and pine seedling recruitment patterns found in these studies can be extrapolated. Doing so will better enable us to make generalizations and explore possible mechanisms and processes behind the spatial patterns.

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