

Spatial patch patterns and altered forest structure in middle elevation versus upper ecotonal mixed-conifer forests, Grand Canyon National Park, Arizona, USA

Joy Nystrom Mast^{a,*}, Joy J. Wolf^b

^a Department of Geography, Carthage College, Kenosha, WI 53140, USA

^b Department of Geography, University of Wisconsin-Parkside, Kenosha, WI 53141, USA

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Abstract

In the American Southwest, mixed-conifer forest experienced altered disturbance regimes with the exclusion of fire since the early 1900s. This research analyzes patch development and tree spatial patterns in the middle versus upper mixed-conifer forests at Grand Canyon National Park in Arizona (USA). The methods used include: (1) size–structure analyses, to compare species patch development; (2) dendrochronological dating of tree establishment and fire history; (3) tree ring master chronology, to determine periods of suppressed growth, compared to a palmer drought severity index; (4) spatial analyses by size and age, with univariate and bivariate analyses of spatial association as well as spatial autocorrelation. Results show that unlike the lower ecotone of the mixed-conifer zone, both the middle elevation and upper ecotone were mixed-conifer forests before Euro-American settlement. At the upper ecotone, two decades (1870s and 1880s) had no successful conifer establishment but instead aspen cohorts, corresponding to the fire history of synchronized fires. Overall, the upper ecotone has shifted in composition in the absence of surface fires from mixed conifer to encroachment of subalpine species, particularly Engelmann spruce. Spatial patterns of tree sizes and tree ages imply development of a size hierarchy in an aging patch. In addition, shifts in species composition from ponderosa pine and white fir overstory to Engelmann spruce and Douglas-fir understory affected within-patch spatial patterns. These results provide quantitative evidence of past and present forest conditions for the development of restoration strategies for Southwestern mixed-conifer forests.

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1. Introduction

In order to guide forest managers, knowledge of historic range of natural variability and current ecological conditions is required. In the arid American Southwest, there has been limited research on mixed-conifer forests. Many of these mixed-conifer forests are visibly altered due to fire suppression practices over the last 80+ years. In the present study, patch development and tree spatial patterns are compared between the mixed-conifer forest at the middle of its elevational gradient and its upper ecotone with subalpine forests on the North Rim of Grand Canyon National Park in Arizona (USA) (Fig. 1). This research continues our previous studies of mixed-conifer forest dynamics along the lower ecotone in Grand Canyon National

Park (Mast and Wolf, 2004) and fire history dating of three elevations of mixed-conifer forests in Grand Canyon National Park (Wolf and Mast, 1998).

Situated at higher elevations (ca. 2100–2900 m) than ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests, the mixed-conifer forest consists of ponderosa pine, white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) and aspen (*Populus tremuloides* Michx.) in the overstory (nomenclature follows USDA NRCS, 2006). At the upper ecotone of mixed-conifer zone, forests also include Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco). Blue spruce (*Picea pungens* Engelm.) was combined with Engelmann spruce category for this study due to difficulties in differentiating the two species in young trees (Fulé et al., 2003).

In the semi-arid American Southwest, landscape community assemblages are shifting in response to fluctuations in disturbance regimes (Savage and Mast, 2005). We theorize

* Corresponding author. Tel.: +1 262 551 5387; fax: +1 262 551 6208.

E-mail address: jmast@carthage.edu (J.N. Mast).

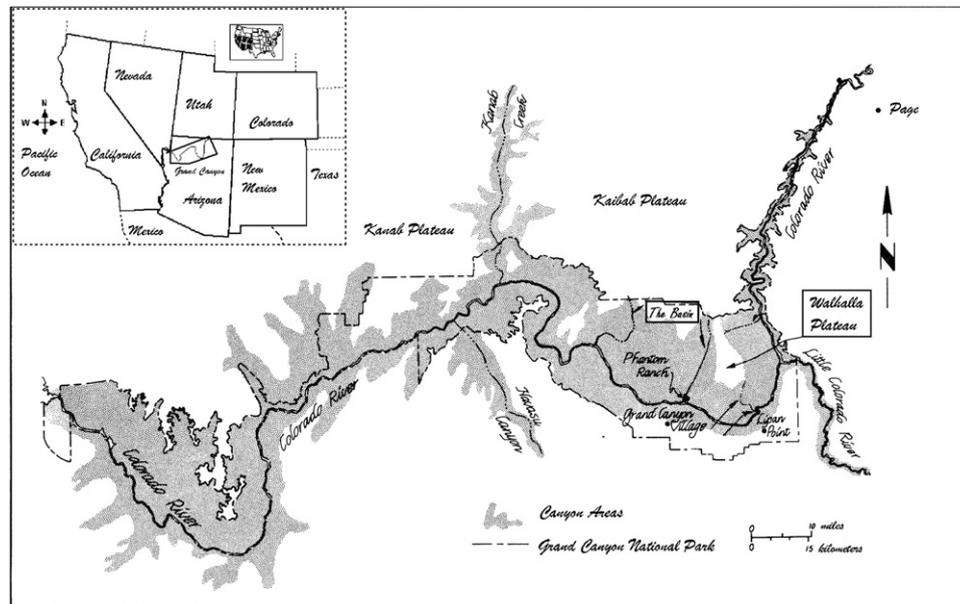


Fig. 1. Map of study area, North Rim of Grand Canyon National Park, Arizona, USA.

that ponderosa pine regeneration is decreasing in both mixed-conifer forests and at the mixed-conifer/subalpine forest ecotone due to altered disturbance regime increasing competition with other conifer species. Ponderosa pine regeneration requires a combination of several factors, such as a good seed year, adequate seedbed conditions, sunlight (seedlings are shade-intolerant), and absence of drought or fire. Historically, mixed-conifer forests of the southwest are transition zones for fire regimes, from surface to stand-replacing fire patterns. Significant differences in fire regime can occur over a short distance, such as the mean fire interval of 6.2 years in a southern Arizona mixed-conifer forest located adjacent to a spruce-fir forest that had not burned in >300 years (Grissino-Mayer et al., 1995). In this heterogeneous landscape, areas with frequent surface fires were maintained in open conditions, favoring moderately shade-intolerant ponderosa pine while reducing more shade-tolerant conifer species (Dieterich, 1983; Savage, 1991; Harrington and Sackett, 1990; Wolf and Mast, 1998; Fulé et al., 2000). In contrast, higher severity fires created patches for fire-adapted aspen. Subsequent cessation of the mixed-severity fires on most of the North Rim resulted in increased density and distribution of shade-tolerant conifer species (White and Vankat, 1993; Fulé et al., 2002, 2003). In addition, overgrazing by domestic livestock until 1938 decreased fire frequency and fire spread, altering the natural evolution of a forest (Leopold, 1943; Savage and Swetnam, 1990; Covington and Moore, 1994). The resulting increase in fuel accumulation favors future high intensity stand-replacing fires over lower intensity surface fires. The National Park Service mandate is to support forests in their natural condition. As a result, changes in structure, species composition and spatial patterns arising from management practices are considered unnatural (Bonnicksen and Stone, 1985; Parsons et al., 1986; Covington et al., 1994). Hence, restoration would be needed for the Park Service to fulfill its mandate.

Quantitative analyses of tree spatial patterns and age structures can be helpful in interpreting patterns of forest development. Initially spatial patterns are often determined by regeneration mechanisms, although subsequent spatial distributions may result from the ability of individual trees to survive competition and dominate the patch (Oliver and Larson, 1990; Deutschman et al., 1993). Tree distributions within a patch as forests age may shift from a clumped distribution to a random (or regular) distribution due to self-thinning and/or succession to shade-tolerant species (Laessle, 1965; Whipple, 1980; Good and Whipple, 1982; Peet and Christensen, 1987; Mast and Veblen, 1999). In other words, from a patch of small even-aged trees, only a smaller number of trees can attain dominance and large size within the patch. In the lower mixed-conifer forest ecotone at the North Rim of Grand Canyon National Park, our previous research found patches with mixed-sized but not mixed-aged ponderosa pine trees (Mast and Wolf, 2004). Hence, from the initial even-aged patches, a size hierarchy developed with one or a few trees reaching size dominance in a patch.

Our research hypotheses are two-fold. First, in our previous study we found the lower ecotone of the mixed-conifer forest on the north rim was a ponderosa pine forest before Euro-American settlement (Mast and Wolf, 2004). In this paper, regarding both the middle zone and upper limits of its current elevational range, we hypothesize that mixed-conifer forests predate changes to the fire regimes and were mixed-conifer forests before Euro-American settlement. In addition, we hypothesize that the current upper ecotonal mixed-conifer forests had little or no Engelmann spruce prior to the 1870s and that this subalpine species established continuously since fire suppression began in the 1920s.

Second, from the spatial pattern analyses and following the cohort aging theory (Kenkel, 1988; Szwagrzyk, 1992), we hypothesize that internal patch structure should become less

clumped as cohort patches age, with only a few trees attaining size dominance in a small patch. Specifically, internal patch structure in these current upper ecotonal mixed-conifer forests should be comprised of Engelmann spruce and Douglas-fir poles (>2.5 cm, but <15 cm dbh) with a scattered remnant large ponderosa pine and white fir in the overstory. Based on this hypothesis, the spatial analysis questions addressed are: Are there differences in the spatial patterns of tree ages and tree sizes that imply development of a size hierarchy in an aging patch? In addition, how does the hypothesized shift in species composition from ponderosa pine and white fir overstory to Engelmann spruce and Douglas-fir understory affect within-patch spatial patterns?

2. Area descriptions

The areas sampled are in the middle elevation and the upper ecotone of the mixed-conifer forests of the North Rim of Grand Canyon National Park, part of the Kaibab Plateau located at 36°00' to 36°21'N and 111°46' to 112°30'W in north-central Arizona (Fig. 1). The study sites for the middle elevational mixed-conifer forests are on the upper elevations of the Walhalla Plateau, a subunit of the larger Kaibab Plateau, with plots from 2480 to 2690 m (Moir and Ludwig, 1979). The upper ecotone sites are located in the Basin area, ranging from 2600 to 2830 m, with a moister, cooler climate. The Basin is the “catch basin” for surface runoff, so these trees experience less drought stress than drier regions on the Walhalla Plateau. Underlying the conifer forests in the North Rim, the uppermost layer of rock is the highly porous Kaibab limestone (100 m thick), which explains the lack of surface water (Maurer, 1990). Mean annual precipitation in the study area is 642 mm (White and Vankat, 1993). May and June are drought months, while July and August have monsoon precipitation. Temperature averages January minimum of -2°C and an average July maximum of 26°C (White and Vankat, 1993).

Tree species present are ponderosa pine, white fir, Douglas-fir, Engelmann spruce and aspen. Understory species include Sweet William (*Verbena ciliata* Benth.), yarrow (*Achillea millefolium* L.), lupine (*Lupinus argenteus* Pursh), serviceberry (*Amelanchier utahensis* Koehne), strawberry (*Fragaria ovalis* [Lehm.] Rydb.), locust (*Robinia neomexicana* Gray), geranium (*Geranium richardsonii* Fisch. & Trautv.), creeping barberry (*Berberis repens* [Lindl.] G. Don), buckwheat species (*Eriogonum* Michx.) and brome grass (*Bromus ciliatus* L.). All of the stands contained ponderosa pine established prior to 1860 (i.e., the stands are >140 years old) and no cut stumps were found in the study areas.

For thousands of years prior to European settlement, Paiute and Navajo Indians lived on the North Rim in the summers and contributed to frequent fire occurrence (Hughes, 1978; White and Vankat, 1993; Allen, 2002). Euro-Americans did not settle in northern Arizona until the late 1800s (Altschul and Fairley, 1989; Moore et al., 1999). These homesteaders, primarily Mormon settlers and ranchers, impacted the North Rim forests through logging and livestock grazing. The North Rim became part of Kaibab National Forest in 1883, and then was included

in Grand Canyon National Preserve in 1906. As early as 1890, the estimated head of cattle on the North Rim was >100,000 with an additional 250,000+ head of sheep grazing the land (Hughes, 1978). Cessation of livestock grazing and the formal policy of fire suppression began in 1919 when the North Rim joined Grand Canyon National Park (Hughes, 1978), although de facto fire exclusion began with the introduction of livestock decades earlier.

3. Methods

Plot size (0.1 ha plots, 20 m × 50 m) and sampling plot design followed the National Park Service criteria for fire-monitoring permanent plots (Western Region Fire Monitoring Handbook, 1992), with adjustments to allow for more extensive sampling for dendroecological information. These plots serve as assessment on pre-prescribed fire conditions, and later to monitor both immediate postfire effects and long-term change. Plots were located randomly on the upper elevations of the Walhalla Plateau (five plots) and the Basin area (five plots) by using an overlay grid system of topographic maps. Plots were rejected if they were located within 0.5 km of a road or did not fit the criteria of the dominant vegetation characteristics (two or more conifer tree species present in the overstory). Diameter at breast height (dbh) was recorded for all live and dead trees within each plot. In addition, tree cores were taken near the base (ca. 10 cm) of every live and dead tree >2.5 cm in each plot for age analyses and master chronology development. For the spatial analysis, locations of trees were measured and mapped to the nearest 0.5 m using nine 50 m tapes (four at outer edges, one at 10 m short axis, and four at 10 m marks on long axis) in order to record X and Y coordinates in a grid system. Understory non-tree species were also surveyed along two 50 m line transects that delineate the outside long axis of each forest plot using the point–line–intercept method (Veirs and Goforth, 1988) to measure the frequency of species occurrence and relative cover by species.

Tree age data consisted of ring counts from increment cores that were mounted and fine-sanded with successively finer grades of sand paper to reveal annual rings (following technique in Stokes and Smiley, 1968). Rings were counted using a binocular microscope to determine marker years which are annual rings with very narrow ring widths or signatures (Visser, 1995). Samples were cored near the ground to reasonably determine establishment period (no estimate of stem age at coring height was added), with age structure subsequently analyzed in 10-year age classes. Ring counts were corrected for false and missing rings by use of marker years. Although there are shortcomings of using static age distributions to interpret population dynamics (which include both recruitment and mortality), given the dry climate, longevity of the three tree species, and lack of local disturbance by fire, logging, or firewood collection within our sampled stands, we believe that the record of tree mortality during the last century is adequately preserved in dead snags and logs. Fire histories were determined from a total of 60 crossdated fire-scars (Wolf and Mast, 1998).

In addition to visually cross-dating the cores and fire-scar wedges, the tree-ring program MeasureJ2X was used to determine ring widths to the nearest 0.01 mm from a subset of ponderosa pine using a binocular microscope with an incremental measuring machine. From these measurements, master chronologies were each created from 40 fire-scarred wedges found within a 300-m radius of the plots. The tree-ring program COFECHA (Holmes, 1983; Grissino-Mayer and Holmes, 1993) helped to detect dating problems, such as false or missing rings, by shifting series in time (Dieterich and Swetnam, 1984; Fritts and Swetnam, 1989). Once dating problems were eliminated, master chronologies were created using the tree-ring computer program ARSTAN (Cook and Holmes, 1984) and skeleton plot strips. ARSTAN creates master chronologies by standardizing (60-year spline) and reducing variances by assigning a dimensionless index to each ring width. To better detect disturbances, a horizontal line detrending option was chosen to avoid masking the growth trend of each tree, i.e. the narrowing of rings due to the tree's geometry (Fritts and Swetnam, 1989; Visser, 1995). In order to obtain the longest possible record, 76% of the samples for the master chronology came from dead trees, with the master series length dating back to 1800 for the middle elevation and 1762 for the upper ecotone (Table 1). In addition, we obtained palmer drought severity index (PDSI) data that began in 1895 to determine any relationships between climate and our master tree-ring chronology (National Climatic Data Center, 1994).

3.1. Spatial statistics techniques

Spatial patterns from mapped tree and pole (live and dead) locations were analyzed by computing spatial statistics. Ripley's $K(t)$ was used to determine pattern with clumped distributions indicated by high values of $K(t)$, random pattern indicated by values within the confidence intervals, and dispersed (or uniform) distributions indicated by low values (Ripley, 1977, 1981; Diggle, 1983). For the $K(t)$ analyses, spatial analyses were performed for two size classes, trees and poles. Ripley's $K_{12}(t)$ was used to determine spatial association

Table 1
Master chronology characteristics for middle elevation mixed-conifer forest vs. upper ecotonal mixed-conifer forests

Characteristic	Middle elevation	Upper ecotone
Total dated rings checked	2116	1823
Series intercorrelation	0.597	0.458
Average mean sensitivity	0.263	0.233
Variance due to autoregression	68.0%	84.5%
Mean correlation	0.476	0.515
Average standard deviation of index means	0.417	0.337
Correlation between indices and standard deviations	0.137	0.641
Signal-to-noise ratio	11.809	12.770
Variance in first eigenvector	54.20%	56.49%
Common interval mean	0.772	0.749
Common interval standard deviation	0.359	0.297

between groups, with high values of $K_{12}(t)$ indicating attraction between the two groups, values within the confidence interval indicating no spatial relation (independence), and low values indicating negative spatial association between the two groups (Lotwick and Silverman, 1982; Diggle, 1983; Upton and Fingleton, 1985). Moran's I , a measure of spatial autocorrelation, was computed for age and tree diameter sizes (Moran, 1950; Cliff and Ord, 1973, 1981; Odland, 1988; Legendre and Fortin, 1989). Significant positive spatial autocorrelations indicated patches of similar trees (same age or same dbh), whereas negative spatial autocorrelation indicated patches of dissimilar trees (uneven aged or mixed dbh) (Legendre, 1993; Haase, 1995; Mast and Veblen, 1999; Mast and Wolf, 2004).

Duncan's (1990) spatial statistics program was used for these spatial statistics computations. Statistical significance for each test was determined by computing 95% confidence intervals using 99 simulations (Besag and Diggle, 1977; Marriott, 1979). All analyzes were based on a distance step size of 0.5 m and calculated up to 10 m (one half the distance of the shortest plot) since edge effects become a concern at greater distances. The edge effects were accounted for by using Ripley's (1977) toroidal correction. After testing the sites for directional orientation of trees (anisotropy), all were found to meet the assumption of isotropy (no directional orientation in the point pattern) necessary for K -analysis.

4. Results

4.1. Climate and fire

In the middle-elevation zone of the mixed-conifer forest, our master tree-ring chronology since 1800 shows drought years in 1819, 1837, 1843, 1846, 1860, 1864, 1880, and 1886 (series intercorrelation = 0.597). Fires occurred in the middle-elevation mixed-conifer type every 8.41 years (S.D. = 4.73, cv. = 0.562, skewness = 0.936) until 1870, when the area was settled by Euro-Americans (Wolf and Mast, 1998). Three larger fires corresponded with regionally lower precipitation in 1819, 1845, and 1863 (Table 2). A widespread fire occurred in 1879. After the PDSI data began in 1895, negative PDSI values are correlated with our tree-ring master chronology showing drier years in 1896, 1899, 1904, 1934, 1951, 1963 and 1977 (Fig. 2). In the span of the PDSI data, fires occurred in the middle elevation mixed-conifer forest in 1904, 1908 and 1937. Although the PDSI values indicate a drier year in 1904 than in 1908, the 1908 fire had more recording trees, indicating a wider extent of fire.

In the upper ecotone of the mixed-conifer forest, our master tree-ring chronology since 1762 shows drought years in were 1807, 1818, 1828, 1845, 1847, 1880, and 1883 (series intercorrelation = 0.458). From 1895 on, negative PDSI values are correlated with our master tree-ring chronology indicating drought years in 1896, 1899, 1934, 1936, 1963, 1973, and 1989–1990 (Fig. 3). Fire frequency was lower in the upper ecotone compared to the middle elevation mixed-conifer forest. Before settlement of 1870, the MFI (mean fire interval) was

Table 2
Fire interval summary showing temporal and spatial variation by elevation (middle elevation/upper ecotone elevation)

	Eras		
	Pre-Euro-American era 1805–1869 (middle/upper)	Settlement era 1870–1919 (middle/upper)	Suppression era 1920–1995 (middle/upper)
All scarred samples			
Mean fire interval	8.41/10.33	4.75/6.40	75/18.75
Median fire interval	7.00/9.00	4.5/7.00	n/a
Weibull mean probability index (years)	7.94/8.68	4.56/6.39	n/a
>10% scarred samples			
Mean fire interval	8.94/11.92	7.60/6.25	n/a
Median fire interval	8.00/10.00	5.00/6.00	n/a
Weibull mean probability index (years)	8.30/10.83	n/a/6.19	n/a
>25% scarred samples			
Mean fire interval	9.53/19.00	n/a	n/a
Median fire interval	10.00/19.50	n/a	n/a
Weibull mean probability index (years)	8.89/17.79	n/a	n/a

10.33 years (S.D. = 9.13, cv. = 0.884, skewness = 1.84) (Wolf and Mast, 1998). Prominent fires at this elevation were recorded for 1748, 1785, 1806, 1841, and 1873 (Table 2). At this elevation, where the species composition should represent a less fire-adapted community, the prominent fires created larger burn patches than in the other years. Specifically, the 1873 fire was documented on over 75% of the recorded trees.

When the middle elevation zone was tested against the upper ecotone for fire synchronicity, the null hypothesis was rejected ($p < 0.005$) indicating fire dates are not statistically independent between these sites (Wolf and Mast, 1998). These fires occurred either in the middle or late summer seasons, which is consistent with seasonality of recorded fires from the National Park since 1926 (Bennett, 1973). In the pre-Euro-American era before 1880, the mesic conditions of the upper ecotone warranted longer fire intervals although still within the range of the frequent fire regime. According to the Park fire management officer (personal comm.), in recent years approximately 50% of the mixed-conifer forests have burned due to large fires (Outlet fire in 2000 and Poplar fire in 2003 which burned over 11,000 acres alone).

4.2. Size analyses

In the middle elevation of the mixed-conifer zone, ponderosa pine occurs evenly at all size distributions up to 100 cm dbh, except only 2% in the 0–9 cm dbh class (Fig. 4a). In contrast, the 54% of live white fir occurs in the 0–19 cm dbh classes. Yet more large white fir are found in the middle elevation than the lower ecotone of the mixed-conifer forest (Mast and Wolf, 2004). Aspen are primarily distributed in the 20–29 cm dbh size class for live trees and 10–20 cm dbh for dead aspen.

In the upper ecotone of the mixed-conifer forest, ponderosa pine occurs evenly again in all size distribution up to 110 cm dbh (Fig. 4b), with 14% in the 0–9 cm dbh size class. Dead ponderosa pines occur primarily in the 10–29 cm size classes. White fir are predominantly (84%) found in the 0–29 cm dbh size classes, with 43% occurring in the 0–9 cm dbh class. There are more large aspen (up to 69 cm dbh) compared to the middle elevation sites. As for subalpine species, Engelmann spruce are as common as white fir in the upper ecotone sites, mostly (77%) in the 0–29 cm dbh classes.

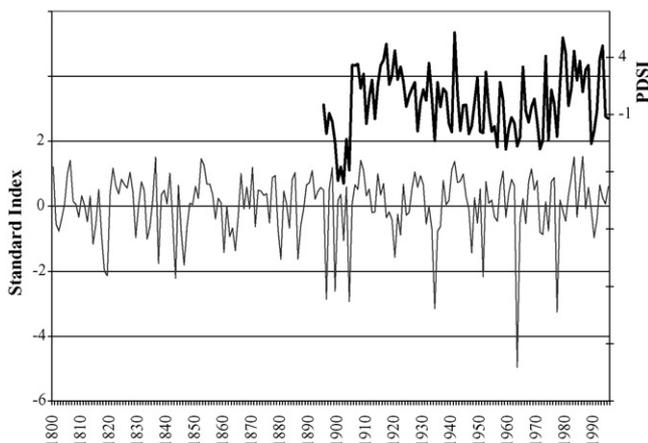


Fig. 2. Middle elevation mixed-conifer forest tree ring chronology and palmer drought severity index by decade.

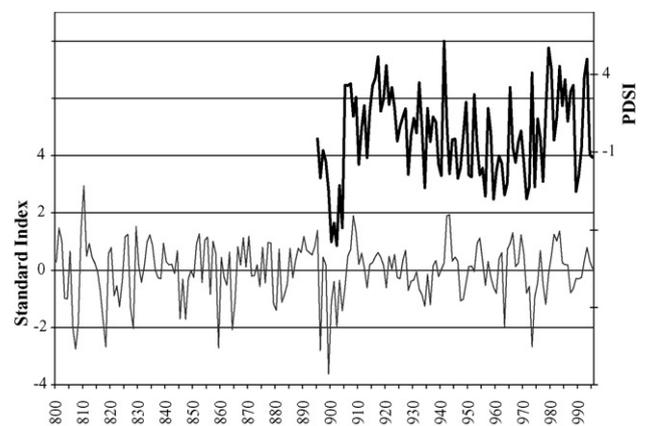


Fig. 3. Upper ecotone mixed-conifer forest tree ring chronology and palmer drought severity index by decade.

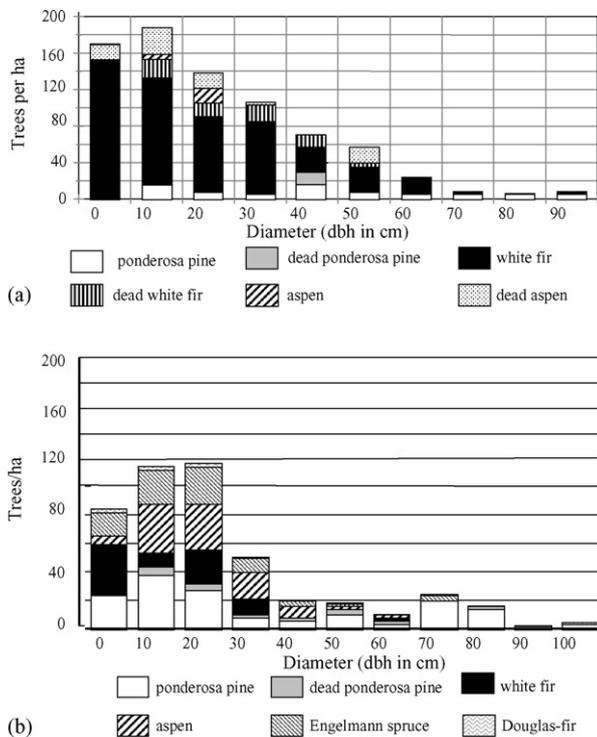


Fig. 4. Size structure for (a) middle elevation vs. (b) upper elevation mixed-conifer forest.

Douglas-fir are also present at this upper ecotone, although all are in the smaller 0–29 cm dbh size classes.

4.3. Spatial analyses for size

For the overall spatial pattern analyzed using the univariate spatial statistic Ripley’s $K(t)$, middle elevation sites showed trees with clumped distributions from 1.5 to 3.5 m patch radius, and random distributions at other patch sizes up to 10.0 m radius (Table 3 composite, example stem map Fig. 5a). In comparison, poles at middle elevation sites display clumped distributions at all distances from 0.5 to 10.0 m. Unlike the middle elevation site, trees were significant clumped in the upper ecotone at greater patch radius distances (4.5, 5.0, 6.5–10.0 m) (Table 3, example stem map Fig. 5b). Pole size class at the upper ecotone sites were less clumped than middle elevation sites, with clumped distributions at 2.5, 3.0, and 5.0 m, but random distributions at all other distances up to 10.0 m radius.

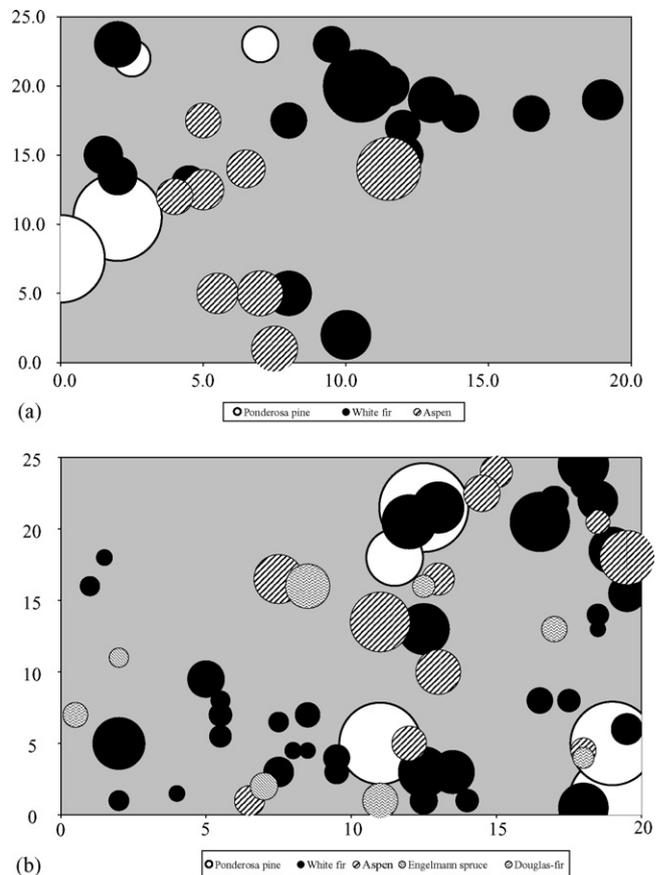


Fig. 5. Stem plot map partial plot examples in meters by species for (a) middle elevation vs. (b) upper elevation mixed-conifer forest, with circle size representing diameter at breast height.

In the bivariate Ripley’s $K_{12}(t)$ test, trees and poles were positively spatially associated (attracted) at shorter distances for both the middle elevation sites (at 1.0, 1.5, and 3.0 m patch radius) and for the upper elevation sites (2.5 m) (Table 3). At greater distances, trees and poles were positively associated (attracted) at middle elevation sites (6.5 and 7.0 m), but negatively spatially associated (repulsed) for upper ecotone sites (7.5 m).

For testing spatial autocorrelation based on size, Moran’s I test was run for both trees and poles combined and for trees alone in order to distinguish between patches of mixed-sized trees versus patches of trees mixed with poles. When analyzing

Table 3
Composite spatial univariate and bivariate summary statistical results, middle elevation mixed-conifer forests and upper ecotonal mixed-conifer forest

Area	Test	Class	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0
Middle	$K(t)$	Trees			+	+	+	+	+													
Middle	$K(t)$	Poles	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Upper	$K(t)$	Trees				+						+	+		+	+	+	+	+	+	+	+
Upper	$K(t)$	Poles					+	+				+										
Middle	$K_{12}(t)$	Trees vs. poles		+	+			+							+	+						
Upper	$K_{12}(t)$	Trees vs. poles					+															

Note: For $K(t)$, a plus sign indicates clumped distribution and an empty cell indicates a random distribution for at least three of the five sites; for $K_{12}(t)$, a plus sign indicates a positive spatial association, a minus sign indicates a negative spatial association, and an empty cell indicates a spatial independence for at least three of the five sites.

Table 4
Spatial autocorrelation summary results, middle elevation mixed-conifer forests and upper ecotonal mixed-conifer forest

Area	Test	Class	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	
Middle	Moran's I	Size: trees and poles			+	+			+	+	+	-								-	-		-
Middle	Moran's I	Size: trees				+									-								
Middle	Moran's I	Age: trees									+						+				+		+
Upper	Moran's I	Size: trees and poles				+	+	+					-		+			-					-
Upper	Moran's I	Size: trees				+					+				+								
Upper	Moran's I	Age: trees					+			-		+				+							

Note: A plus sign indicates positive spatial autocorrelation, a minus sign indicates a negative spatial autocorrelation, and an empty cell indicates no spatial autocorrelation for at least three of the five sites.

the tree and poles together, positive spatial autocorrelation (patches with similarly sized stems) was found for smaller patch radius sizes at both middle elevation sites (1.5, 2.0, 3.5, 4.0, and 4.5 m) and at upper ecotone sites (2.0, 2.5, and 3.0 m) (Table 4 composite). In contrast, negative spatial autocorrelation occurred for larger patches at the middle elevation sites (5.0, 8.5, 9.0, and 10.0 m) and the upper elevation sites (8.0 and 9.0 m), representing differences in sizes within larger patches. When analyzing the tree size class only, middle elevation sites has positive spatial autocorrelation (similarly sized trees in patch) at 2.0 m radius, but negative spatial autocorrelation (mixed-sized trees in patch) at 6.5 m radius. At the upper ecotonal sites, trees of similar sizes (positive spatial autocorrelation) were in patches of 2.0, 4.5 and 6.5 m.

4.4. Age analyses

The middle elevation of the mixed-conifer zone sites have been mixed-conifer forests (ponderosa pine and white fir) since at least the 1830s (Fig. 6a). From dating live and dead trees,

episodic ponderosa pine establishment occurred with older cohorts in 1790–1809 and in 1840–1859. Peak ponderosa pine establishment in the middle elevation sites occurred in the Euro-American settlement periods (62%), dating to 1880–1919. The dead ponderosa pines dated from 1900 to 1909. Almost no ponderosa pine have established since the 1930s. White fir establishment was more continuous from 1830 to 1970, but similarly peaked from 1880 to 1930s. The dead ponderosa pines dated from 1850 to 1889. Unlike ponderosa pine, white fir continued to establish (38%) after fire suppression began (1920s onward). With regards to aspen, the oldest cohort established in the 1890s with ca. 50% still alive today. Another aspen cohort was established in the 1920s, dated entirely from snags with no surviving trees. A final episode of aspen establishment occurred in the 1980s.

Ponderosa pines in the upper ecotone mixed-conifer zone dated to the late 1500s. Based on live and dead trees, episodic ponderosa pine establishment occurred with oldest cohorts in 1590–1619 and 1720–1759. Peak ponderosa pine establishment occurred during the 1830–1860s and again during the settlement period from 1890 to 1919 (Fig. 6b). Almost no ponderosa pine have established since the 1940s. White fir establishment is again traced back to the 1830s, with increases during the 1890–1919 settlement period and in the 1940s. After an 1873 fire, aspen regeneration occurred and no new conifer establishment was found at the upper ecotone sites for two decades (1870s and 1880s). No aspen survived from the 1930s, possibly due to mortality by heavy deer browsing (Rasmussen, 1941; Merkle, 1954; Fulé et al., 2002, 2003). Unlike the middle elevation, the upper ecotone mixed-conifer forests experienced a shift to higher amounts of subalpine tree species since fire suppression. Engelmann spruce established particularly from 1920 present, while lesser amounts of Douglas-fir established since the 1930s.

4.5. Spatial analyses for age

When analyzed by age, significant positive spatial autocorrelation occurred at middle elevation sites at both smaller distances (4.5 m) and at larger distances (7.5, 9.0 and 10.0 m), indicating even-aged patches (Table 4). For upper ecotone sites, positive spatial autocorrelation again occurred at smaller patch distances (2.0 m), representing small even-aged patches, and at larger distances (5.0 and 7.0 m), indicating larger even-aged patches. Negative spatial autocorrelation existed only at the

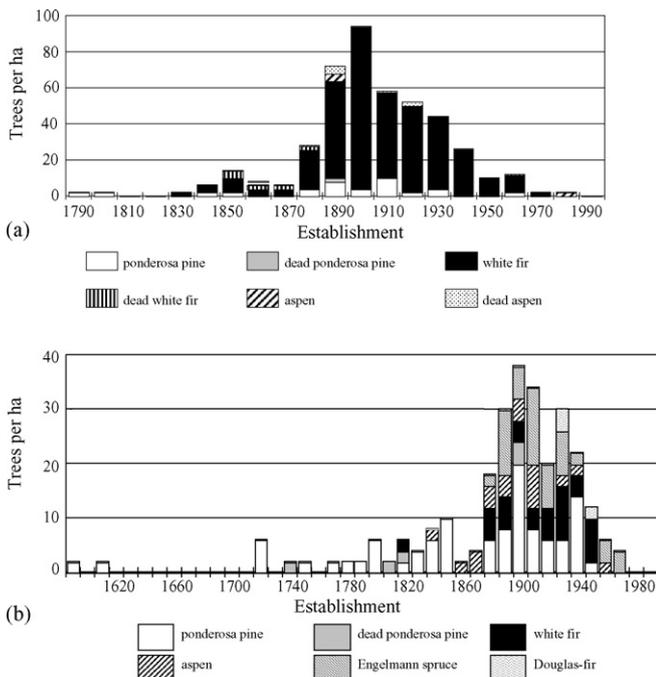


Fig. 6. Age structure for (a) middle elevation vs. (b) upper elevation mixed-conifer forest.

upper ecotone at 4.0 m, indicating mixed-aged patches of an older trees mixing with younger poles.

5. Discussion

In our previous study, we found the lower ecotone of the mixed-conifer forest on the north rim was a ponderosa pine forest before Euro-American settlement (Mast and Wolf, 2004). In this paper, we provide evidence that mixed-conifer forests at the middle zone and upper ecotone predate changes to the fire regimes and Euro-American settlement. Similar to other studies (Fulé et al., 2003), the mixed-conifer forest experienced regeneration for several decades prior to 1880. Pine and white fir establishment is episodic at the stand scale, with peak ponderosa pine and white fir establishment from 1880 to 1919. But unlike ponderosa pine, white fir has continued establishment since fire suppression began (1920s onward).

At the upper ecotone, we found subalpine tree species in the upper ecotone since the 1870s. Unlike the middle elevation mixed-conifer forests, the upper ecotone experienced a shift to higher amounts of Engelmann spruce from 1920 present and Douglas-fir since the 1940s. These subalpine species have expanded down into the historic (pre-Euro-American settlement) mixed-conifer forest. As a result, tree density became significantly higher for smaller-sized shade tolerant subalpine trees species in the upper-ecotonal mixed-conifer forest. One likely mechanism for encroachment of subalpine tree species is fire suppression, since Engelmann spruce are relatively fire-intolerant. Yet spruce expansion may also be a result of a complex interaction of mechanisms, including cessation of cattle grazing as well as a drought that immediately preceded peak Engelmann spruce establishment. In addition, the upper ecotone provides evidence for a larger scale fire that created aspen regeneration cohorts while prohibiting new conifer establishment for 20 years (1870s–1890). These aspen trees survived and subsequently shade-tolerant Engelmann spruce filled the understory. Other aspen regeneration may be tied to past by fires creating openings where aspen suckers would thrive. We speculate that in turn the complex forest mosaic indicated by our data was in part maintained in the reestablishment rates and growth characteristics of these tree species.

We hypothesized that internal patch structure should become less clumped as single cohort patches age, with only a few trees attaining size dominance in a small patch. Based on this hypothesis, the spatial analysis questions addressed whether there are differences in the spatial patterns of tree ages versus tree sizes that imply development of a size hierarchy in an aging patch. At the middle elevation, spatial analyses at smaller patch sizes revealed clumps of poles and trees, representing small radius patches of shade-tolerant white fir poles growing under a canopy ponderosa pine and white fir trees. Patch structure at larger distances at the middle elevation sites show two types of patches. First, patches occurred with different sized but similar aged trees, representing a size hierarchy but not an age hierarchy for trees. Second, other

patches occurred that were made of larger overstory trees mixed with smaller poles.

In contrast to middle elevation zone, we hypothesized that internal patch structure in these current upper ecotonal mixed-conifer forests should be comprised of Engelmann spruce and Douglas-fir poles with a scattered remnant large ponderosa pine and white fir plus aspen in the overstory. Based on this hypothesis, the spatial analysis questioned how the hypothesized shift in species composition would affect within-patch spatial patterns. In contrast to middle elevation site, the upper ecotone has patches of trees at all the larger patches sizes but not clumps of poles, with relatively little clumped patterns at smaller distances. When analyzing the tree and poles together, large patches with mixed sizes occurred at the upper elevation sites. Yet when analyzing trees only, there is no mixed-sized patch at larger distances. When analyzed based on tree age, neither mixed-age nor similar-aged patches occurred at these larger distances. Hence, the large patches of mixed sizes represent patches of large trees mixed with smaller poles, not a size-hierarchy of canopy trees at the upper elevation sites.

By understanding the range of natural variability in the mixed-conifer forest, it becomes clearer to delineate the transition zones between the forest communities (Fulé et al., 2002). In this light, we emphasize that management is especially critical in the mixed-conifer forest of the American Southwest. Information on altered stand structures due to human influences, modified species compositions, and shifted successional patterns can all assist in developing forest plans for restoration of southwestern mixed-conifer forests. These adaptive management efforts should include landscape spatial patterns, natural patch mosaics, and within-patch patterns including smaller groups of clumps. Overall, mixed-conifer forest need to be viewed not as one entity, but instead management efforts should incorporate awareness of spatial patterns, transition zones, and the influence of changes in disturbance regimes.

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