RESEARCH ARTICLE

FIRE-EXCLUDED RELICT FORESTS IN THE SOUTHEASTERN KLAMATH MOUNTAINS, CALIFORNIA, USA

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ABSTRACT

The rare relict ponderosa pine (*Pinus ponderosa* C. Lawson) mixed-conifer forests of northern California's Whiskeytown National Recreation Area (WNRA), USA, present a classic example of fire exclusion. Altered fire regimes in this biologically unique area have been documented, but the resulting changes in forest composition and structure have not previously been described. A fully randomized, park-wide sampling of relict forest structure at WNRA reveals a high degree of topographic variability in tree species composition, but strikingly similar changes in recent structural development. A distinct cohort of encroachment trees initiated approximately 64 yr to 67 yr ago with little age variation (2 yr SE), with distinct strata now distinguishing the relict and encroachment cohorts. Over the past five decades, the average periodic annual basal area growth of relict trees has remained at a virtual constant of 24 cm^2 to 27 cm^2 per tree. In contrast, the annual basal area increment of encroachment trees has been steadily increasing, from 3 cm^2 per tree in 1955 to 16 cm^2 per tree in 2005. Whereas relict trees are comprised primarily of pine species (76 %), they represent just 17 % of encroachment trees. In contrast, white fir, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco.), and tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehder) are rare among relicts (16 %) but are the most predominant species among encroachment trees (64 %). This study's findings should inform the planning of restoration activities to reduce threats to relict forests at the WNRA as well as similar forests in the southeastern Klamath Mountains.

Keywords: California, ecological restoration, fire exclusion, fire suppression, fire regimes, forest stand dynamics, Klamath Ecoregion, old-growth forest, ponderosa pine, stand structure

Citation: Leonzo, C.M., and C.R. Keyes. 2010. Fire-excluded relict forests in the southeastern Klamath Mountains, California, USA. Fire Ecology 6(3): 62-76. doi: 10.4996/fireecology.0603062

INTRODUCTION

Alteration of historical fire regimes during the twentieth century has transformed the structure of many ponderosa pine (*Pinus ponderosa* C. Lawson) and mixed-conifer forests (McKelvey *et al.* 1996, Covington *et al.* 1997, Veblen *et al.* 2000, Allen *et al.* 2002). As a result, older forests of the interior West commonly exhibit declining tree health and stand productivity, heightened vulnerability to disease and insect attacks, and increased susceptibility to stand replacing fires (Cooper 1960, Covington and Moore 1994, Fulé *et al.* 1997). The emerging consensus is that unless affected ecosystems are restored to a condition within their natural range of variability, critical elements of ecological importance in older forests will likely be further degraded and perhaps lost (Covington 2000, Kloor 2000, Allen *et al.* 2002, Spies *et al.* 2006). Relict ponderosa pine forests can serve as critically useful benchmarks for such restoration management (Stephens and Fulé 2005).

Relict forests are rarely occurring ecosystem remnants, often believed to be representative of forests that once dominated historic landscapes (e.g., Cornelius *et al.* 2000, Reinhardt and Smith 2008). Where they exist, these fragments often figure prominently in biological conservation planning (e.g., Vargas-Rodriguez *et al.* 2010), and study of their structure and function can guide the management of younger regrowth forests or older forests that have been heavily impacted by human activities (e.g., Stephens 2004, Linares and Carreira 2009). Relict forests represent an imperfect target for managing forests under the specter of changing climate (Millar and Wolfenden 1999), but they do serve in this role for many agencies. For fire-evolved forests impacted by fire suppression, using historic conditions as a strategic reference inevitably leads to restoration strategies that reduce stand densities and fuel loads and presumably enhance their resilience in the face of future threats and stressors.

The relict ponderosa pine mixed-conifer forests of northern California's Whiskeytown National Recreation Area (WNRA) are a classic example of fire exclusion and post-settlement practices (Figure 1) (USDI 2003, Fry and Stephens 2006). The WNRA is at the southeastern extent of the Klamath Mountains, a region noted for its rich floristic diversity (Whittaker 1961, Sawyer and Thornburgh 1977) and for its many ecological systems, of which fire historically contributed strongly (Skinner 2003*a*, 2003*b*; Taylor and Skinner 2003). The WNRA forests are truly fire-adapted: natural ignitions are common, and Native American burning (particularly by the Wintu tribe) was widespread prior to Euro-American settlement in the Whiskeytown area during the mid nineteenth century (Fry and Stephens 2006).

Similar to other ponderosa pine forest relicts (Stephens and Fulé 2005), the inaccessibil-

Figure 1. A relict mixed-conifer forest on the slopes of Shasta Bally at Whiskeytown National Recreation Area, California, USA. (Photo credit: Amy Roberts)

ity of WNRA's relict forests (high elevations and steep slopes) helped spare them from many of the impacts of industrial society—logging, mining, and grazing—that resulted in the degradation of adjacent areas throughout Klamath Mountain forests and woodlands during the twentieth century. Their acquisition by the National Park Service ensured their protected status by 1972, but they are far from being unimpacted by human activity, having been subjected to decades of active fire exclusion. For managers of the WNRA, the irreplaceable ecological, scientific, and recreational values of these relict forests, combined with the imminent risk of losing them to catastrophic fire events and vigor decline, lends urgency to the implementation of restoration treatments (USDI 2003).

Fire history study has confirmed the change in fire regimes at WNRA (Fry and Stephens 2006), but the ability of managers to develop appropriate restoration strategies has been hampered by lack of information about the resulting forest condition. This study was conducted to address that problem by analyzing the structure and composition of fire-excluded relict forests at the WNRA. Because the study was designed to complement and extend the local fire history study by Fry and Stephens (2006), its findings are expected to inform and aid the restoration of similar relict forests throughout the southeastern Klamath Mountains.

METHODS

Study Area

Whiskeytown National Recreation Area is a 17 200-hectare park located in the southeastern Klamath Mountains 13 km west of Redding, California, USA. Its purpose is to provide recreational opportunities for present and future generations, and to safeguard natural, scientific, and cultural resources (Public-Law 89-336). The park's recreational opportunity spectrum is all-encompassing, providing both land-based recreation throughout the unit and aquatic activities at Whiskeytown Lake.

The Whiskeytown ecosystems exhibit striking biological richness that is typical of the Klamath Ecoregion (Whittaker 1961, Skinner *et al.* 2006). The ecosystems are influenced by the park's proximity to the Sacramento Valley and the Cascade and Coast ranges, and by its wide altitudinal gradient: 190 m at Lower Clear Creek, 1892 m at Shasta Bally summit. The park's topography is typified by steep terrain. The area has a Mediterranean climate of wet-cool winters and dry-hot summers, with temperatures ranging from subfreezing in winter months to over 38 °C during the summer (USDI 2003). Mean annual precipitation is 152 cm and mostly comes as rainfall from November through April (USDI 2003); the upper elevation snowpack often remains into June. The WNRA soil types consist of entisols, inceptisols, spodosols, alfisols, and a few mollisols (USDI 2003). While upper elevation steep hillsides are composed of poorly developed entisols and inceptisols, the lower elevation areas are mainly composed of well developed alfisols and spodosols (USDI 2003, Fry and Stephens 2006). Mollisols are found in grasslands and broadleaf forests (USDI 2003).

The relict forests of the WNRA are dispersed throughout the park in different size patches occupying a combined area of approximately 2225 ha. Although older trees occur throughout the park, the sections with lesser impacted forests were easily identified as they appeared on photographs with highly distinct boundaries that distinguished them from more heavily impacted sections. Ground reconnaissance with pilot data collection confirmed their relict status and confirmed the need for and usefulness of this study. The majority of sites are located in the park's western half and mainly at its upper elevations (Figure 2, top). Crystal Creek Road, Shasta Bally Road, Mill Creek Road, and many hiking trails provide access to this region.

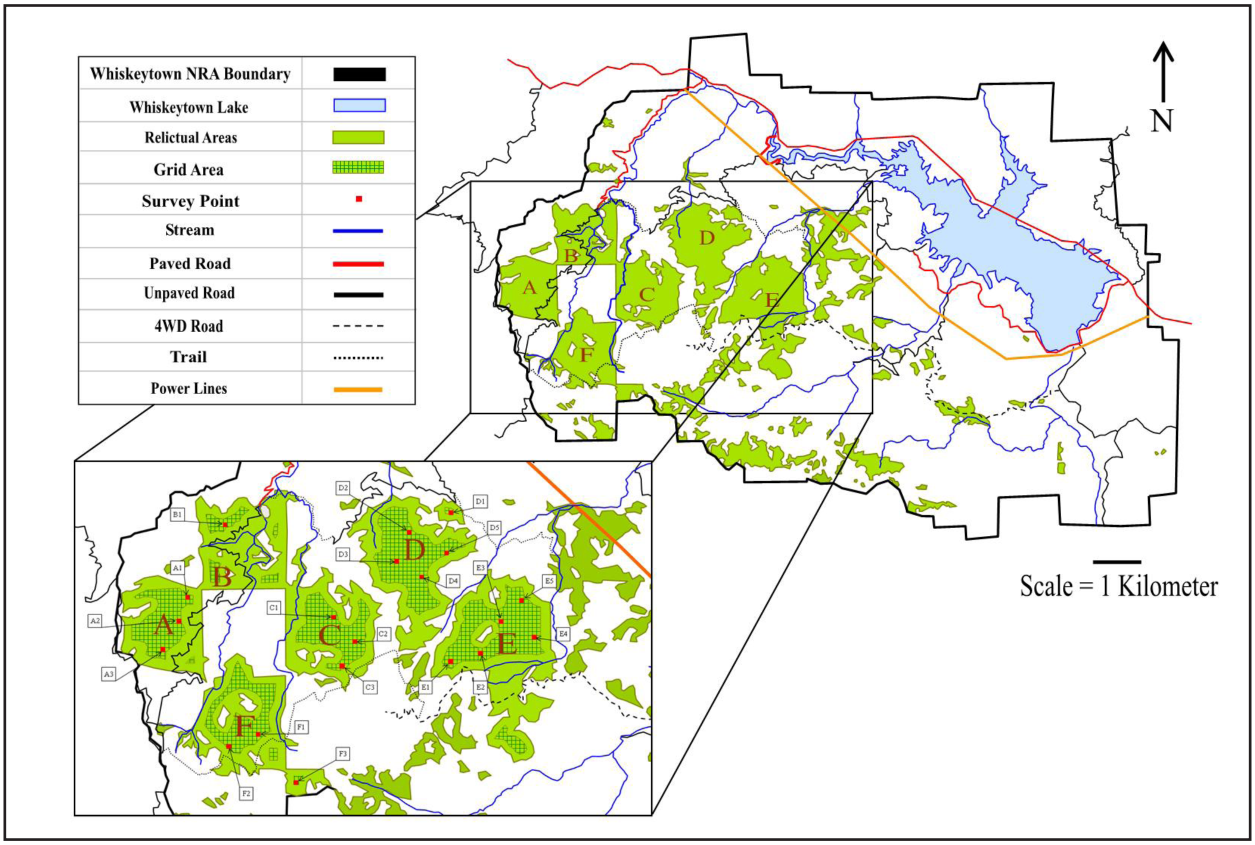

Figure 2. Whiskeytown National Recreation Area relict forest locations (A-F), with potential sampling areas (0.534-hectare grids) and randomly determined sample points (red) denoted.

Data Collection and Analysis

Aerial photographs and a historical timber type map, combined with discussions with park managers, were used to locate the relict zones and to choose the most intact areas to conduct the study. Six large tracts encompassing 70 % of the remaining relict forest were selected for sampling (Figure 2, bottom). A numbered grid simulating 0.534 ha squares was placed over these areas to randomly select 20 measure point locations. Constraining rules on sample locations included a minimum distance of 512 m between sites, and no-placement buffer strips of 146 m along perennial streams, roads, and forest condition edges. Measure points were distributed following a proportional allocation system so that larger areas would receive more points than smaller ones; the area size used for allocation was the available area left after the no-placement strips were in place. Random numbers were electronically generated to position the measure points. The UTM coordinates for the randomly determined survey sites were acquired with the TOPO! Explorer map software (National Geographic, Evergreen, Colorado, USA). A GPS unit (Garmin GPS Map 76; Garmin International, Olathe Kansas, USA), a compass, and a topographic map were used to navigate and locate the coordinates in the field.

To conduct the inventory, a variable-radius point sample strategy was implemented using a cruise angle tool with a metric basal area factor (BAF) of 1.148 (m^2 ha^{-1}) (Avery and Burkhart 2002). The wide spacing of the relict trees and the need to capture species diversity by having more sample trees made the use of a small BAF essential. For each measure point, four count points were taken to adjust the final stand tables according to sampling procedures described by Bell (1988) and Marshall and Iles (1999). Count point placement was in a cluster pattern around the measure point; count points were 40 m from the measure point and 90° apart from one another. To determine the location of the first count point, a random azimuth direction was obtained by looking at the second hand of a wristwatch and multiplying the observed value by six.

Elevation, aspect, slope, and canopy layer observations were documented for measure and count points. Elevation was determined with a wrist-top computer altimeter (Suunto Vector; Suunto, Vantaa, Finland), and aspect and slope with a compass and clinometer. For measure point sample trees ("in" trees), species and live crown ratio were recorded, and diameter at breast height (dbh), tree height, and live crown base height were measured with a metal tape and clinometer; for count point sample trees, species was recorded. The minimum tree size to be included was 3 cm dbh. Diameters were categorized in 5 cm dbh classes. A snag inventory was performed at each surveyed site, applying similar methodology as for live trees. To account for any past logging practices, the occurrence of stumps was noted.

Six to ten tree cores were collected from each measure point to evaluate stand age distributions and growth rates, and to help parse the encroachment trees and relict trees during subsequent data analysis. Encroachment trees were cored to pith to find their age of establishment and growth rate; relict trees were cored to a depth of approximately 14 cm to assess their growth patterns immediately preceding and following the emergence of an encroachment cohort. Cores were removed from the most vigorous (as indicated by crown ratio, crown form, and foliar density) trees using an increment borer, and were typically taken at breast height (1.4 m), with exceptions as necessary as low as approximately 0.4 m, as dictated by site and tree conditions. The fittest trees were selected to reduce noise in the data and to focus on what we considered the most relevant subsets of both relict and encroachment elements. In the case of relict trees, vigorous specimens were assumed to be the most likely to persist, possibly the oldest, and hence arguably the most important individuals, as well as the most likely to benefit from and respond to restoration treatment. In the case of encroachment trees, vigorous specimens were assumed to be at the vanguard of the encroachment cohort, and representing the fittest, presumably oldest, most likely to persist, and most competitive individuals that would challenge relict trees for scarce site resources into the foreseeable future. Core sampling was proportionally allocated among species present at each plot, taking care to collect samples from each species captured by the angle gauge at the measure point.

Where possible, core sampling was divided evenly between apparent relict and encroachment trees, with 35 cm dbh used as a guide. The 35 cm dbh break was used to assist field workers in data collection with clear protocols that would ensure adequate core collection for each cohort at each plot, but it was not used as the criterion for sorting trees into relict and encroachment cohorts. That determination was made using visible tree cues as selection criteria, including bark thickness and coloration, branch and twig thickness, foliage density, and crown form. Morphological differences (which are often the manifestation of recent past stand development) were usually accompanied by differences in tree species. These development inferences and cohort assignments were visually cross checked with neighbor tree spatial patterns. Sampling of largest trees suspected to be of the encroachment cohort was helpful in validating the visual cues. Although not a foolproof or quantitative method to distinguish between relict and encroachment cohorts, we did not encounter trees that could not be resolved with satisfaction, and therefore infer that technique's potential error is low.

Ring measurements were conducted in the laboratory with the aid of a digital caliper and an illuminated magnifier. Cores of relict and encroachment trees were used to determine periodic annual radial increment in 10 yr intervals from the inception of the encroachment cohort. For relict tree cores, an additional 10 yr period was measured to capture the growth rate prior to the appearance of the encroachment cohort. Robust, species-specific, and size-appropriate models of bark thickness from southern Oregon (Larsen and Hann 1985) were employed in the calculation of annual basal area increment from the measures of radial growth. Because cores were taken from bole locations between approximately 0.4 m to 1.4 m, subsequent calculations of radial and basal area increment derived from the cores are best interpreted as broadly representing the segment of tree boles within those height bounds, rather than at a specific height (e.g., tree base or breast height). In circumstances where cores did not permit accurate readings (e.g., heavy tannin accumulation and indistinguishable rings), they were discarded from the analysis. Different sample sizes were employed to estimate periodic annual increment due to variation in total number of annual rings per core.

RESULTS

The sample rendered a total of 3775 live trees and 281 snags in 20 measure points and 80 count points. Of those, metrics were recorded in the measure points for 432 trees and 54 snags, and 123 cores were analyzed. Measure point slopes averaged 27° (range 12° to 37°). Eighteen of twenty measure points possessed two obvious canopy layers; the remainders possessed only one. From the analysis of encroachment tree cores (n = 37), it was determined that most of the encroachment trees emerged within the past 60 yr, with little age variation. Ages of cored trees averaged 51 yr (median of 50 yr) with a 2 yr standard error. The oldest of the cored trees was 67 yr, and the ninetieth percentile of ages was 64 yr, thus we generalize that encroachment commenced during the late 1930s to early 1940s.

Five conifer and six hardwood tree species comprised the sample: Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), white fir (*Abies concolor* [Gord. & Glend.] Lindl. Ex Hildebr.), ponderosa pine, sugar pine (*Pinus lambertiana* Douglas), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), black oak (*Quercus kelloggii* Newberry), canyon live oak (*Quercus chrysolepis* Liebm.), tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehder), Pacific dogwood (*Cornus nuttallii* Audubon ex Torr. & A. Gray), bigleaf maple (*Acer macrophyllum* Pursh), and white alder (*Alnus rhombifolia* Nutt.). Primary among the observed shrubs were shrub tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehder var. *echinoides* [R. Br.] Abrams), manzanita (*Arctostaphylos* spp. Adans.), chinquapin (*Chrysolepis* spp. Hjelmquist), prostrate ceanothus (*Ceanothus prostratus* Benth.), and Pacific poison oak (*Toxicodendron diversilobum* [Torr. & A. Gray] Greene). Much of the variation in tree species composition was explained by elevation (Figure 3). Lower elevation areas had higher occurrences of Douglas-fir, oaks, and tanoak, while upper elevation sites had higher occurrences of pines and white fir. Pines, incense-cedar, and Douglas-fir were the only species found throughout the entire elevation range. Oaks and tanoak were not documented above 1310 m. Dogwood, maple, and alder were mostly found at lower elevations.

The average stem density (inclusive of all trees 5 cm dbh and larger) was 467 trees ha^{-1} (Table 1). The vast majority of trees were encroachment trees. Only nine percent were relict with stand densities ranging from 2 to 291 trees ha^{-1}, with a mean of 42 trees ha^{-1}. In contrast, average stem densities for encroachment trees were 10 times higher than relict trees—425 trees ha^{-1} (range 0 to 1571 trees ha^{-1}). The data indicate a successional change in tree species composition. The fire-adapted pines ac-

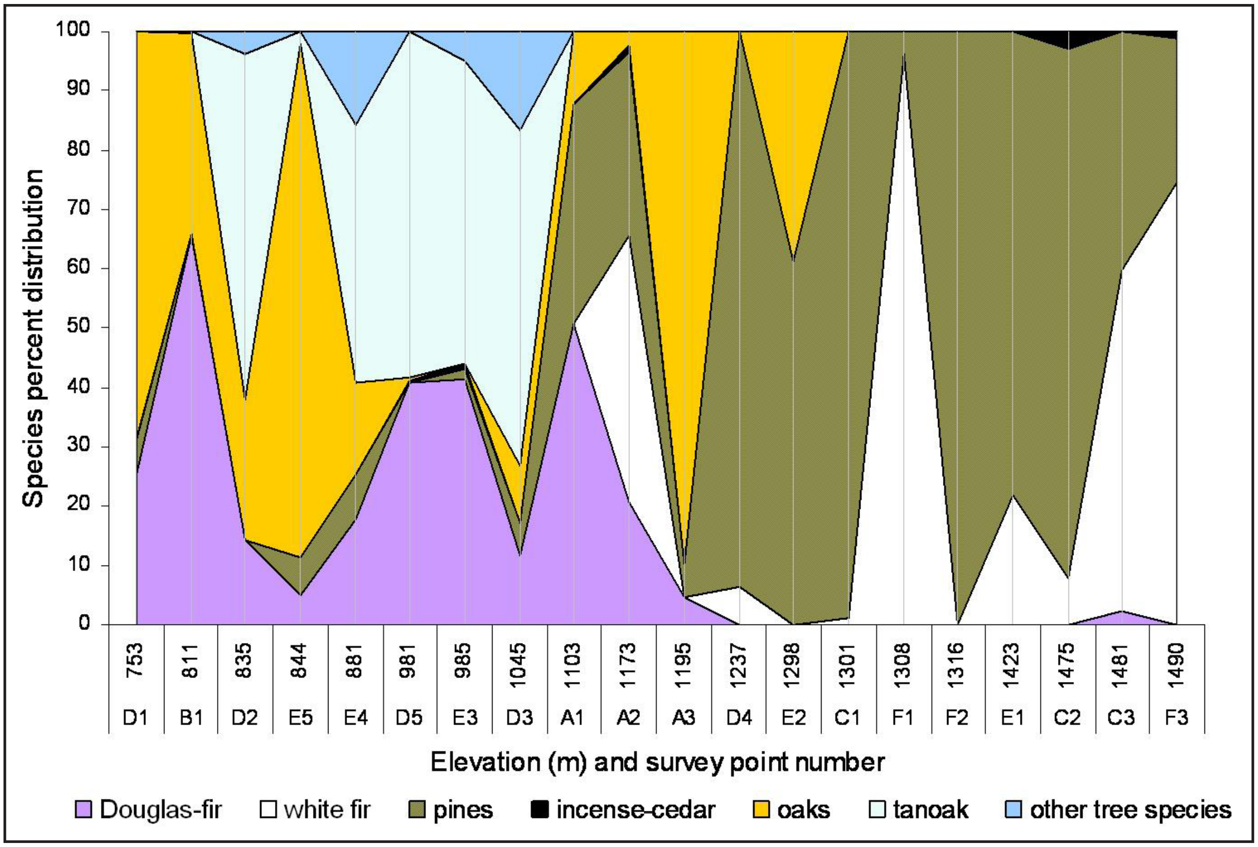

Figure 3. Proportional composition of tree species, sorted by elevation. Survey point number reflects tract (A-F) and plot.

counted for 76% of the relict component, followed by white fir (9%) and Douglas-fir (7%). In contrast, pines accounted for just 17% of encroachment trees. Species of lesser fire tolerance, which together accounted for just 19% of the relict element, comprised 64% of the encroachment cohort. The most ubiquitous of the encroachment cohort was white fir (approximately one of every three trees). Encroachment Douglas-fir, pines, oaks, and tanoak were evenly represented by a 17% occurrence rate. No encroachment incense-cedars were captured by measure points.

Diameters ranged from 5 cm to 208 cm, with a 15 cm median and 23 cm quadratic mean diameter (QMD). Ninety-two percent of all trees were less than 38 cm dbh (Figure 4). Pines were the principal contributors to basal area, providing 37% of the total. Basal areas for all species ranged from 10.3 m^2 ha^{-1} to 31.9 m^2 ha^{-1}, with a mean of 21.1 m^2 ha^{-1}. Basal area composition was almost evenly distributed between the two elements: 54% relict and 46% encroachment. Encroachment tree basal area was particularly pronounced at lower elevations; as elevation increased, the proportion of basal area in relict components was proportionally greater, signifying that the greatest changes are occurring at elevations below 1000 m (Figure 5).

Snags consisted primarily of pines (45%) and Douglas-firs (41%) (Table 1). Snag densities ranged from 0 snags ha^{-1} to 713 snags ha^{-1}, averaging 35 ha^{-1}. Diameters were 5 cm to 66 cm, with a median of 10 cm. Although snags over 38 cm dbh accounted for just 10% of the total number of snags, they comprised 73% of total snag basal area.

Stands were typically characterized by a dual-layered canopy, with distinct strata distin-

Table 1. Elements of live tree and snag structure and composition in relict forests at Whiskeytown National Recreation Area, California, USA. Pines consist of ponderosa pine and sugar pine; oaks consist of black oak and canyon live oak.

			Douglas-fir	**White fir**	**Pines**	**Incense-cedar**	**Oaks**	**Tanoak**	**Other**	**Total**
Live trees	Number (n)	Total	1534	2513	2097	20	1527	1472	164	9327
		Relicts	61	75	628	20	44	2	0	831
		Encroachment	1473	2438	1469	0	1483	1469	164	8496
	Density (trees ha^{-1})	Mean	77.0	126.0	105.0	1.0	76 .0	74.0	8.0	466.0
		SE	32.4	82.6	41.6	0.5	28.8	33.8	4.6	96.7
		Percentage	16.0	28.0	22.0	0.0	16.0	16.0	2.0	100.0
		Median	23.0	0.0	31.0	0.0	5.0	0.0	0.0	314.0
	dbh (cm)	QMD	26.3	16.7	30.6	79.3	21.6	22.0	23.1	24.0
		Median	15.2	5.1	5.1	30.5	15.2	15.2	10.2	15.2
	Basal area (m^2 ha^{-1})	Mean	4.2	2.8	7.7	0.5	2.8	2.8	0.3	21.1
		SE	1.0	1.1	1.2	0.2	0.9	1.1	0.2	1.4
		Percentage	20.0	13.0	37.0	2.0	13.0	13.0	2.0	100.0
		Median	3.4	0.0	6.9	0.0	1.0	0.0	0.0	21.1
Relicts	Density (trees ha^{-1})	Mean	3.0	4.0	31.0	1.0	2.0	0.0	0.0	42.0
		SE	1.2	2.3	13.5	0.5	1.0	0.1	0.0	13.8
		Percentage	7.0	9.0	76.0	3.0	5.0	0.0	0.0	100.0
		Median	0.0	0.0	18.0	0.0	0.0	0.0	0.0	26.0
Encroach-ment	Density (trees ha^{-1})	Mean	74.0	122.0	73.0	0.0	74.0	73.0	8.0	425.0
		SE	32.2	82.8	40.6	0.0	28.9	33.9	4.6	101.6
		Percentage	17.0	29.0	17.0	0.0	17.0	18.0	2.0	100.0
		Median	16.0	0.0	0.0	0.0	0.0	0.0	0.0	279.0
Snags	Density (trees ha^{-1})	Mean	14.0	1.0	16 .0	0.0	0.0	3.0	0 .0	35.0
		SE	10.0	0.9	8.6	0.0	0.2	2.1	0.1	12.1
		Percentage	41.0	4.0	45.0	0.0	1.0	9.0	0.0	100.0
		Median	0.0	0.0	2.0	0.0	0.0	0.0	0.0	10.0
	dbh (cm)	QMD	8.5	55.1	28.7	81.3	53.2	20.3	58.5	24.4
		Median	5.1	45.7	10.2	81.3	45.7	15.2	50.8	10.2
	Basal area (m^2 ha^{-1})	Mean	0.1	0.3	1.0	0.0	0.1	0.1	0.0	1.6
		SE	0.05	0.27	0.27	0.02	0.04	0.06	0.02	0.34
		Percentage	5.0	19.0	62.0	1.0	5.0	6.0	1.0	100.0
		Median	0.0	0.0	0.5	0.0	0.0	0.0	0.0	1.1

guishing the relict and encroachment components (Table 2, Figure 6). The mean height of relict trees was 32.3 m. Douglas-fir and pines dominated the upper canopy strata with mean heights of 41.5 m and 32.3 m, respectively. Average relict live crown base height (LCBH) was 11.3 m; Douglas-fir (15.8 m) had the highest and white fir (5.8 m) the lowest mean LCBH. Mean height of encroachment trees was 15.8 m, with a 2.7 m to 37.5 m range. Douglas-fir and tanoak were the tallest species of the encroachment cohort. Live crown base height for encroachment trees was 6.7 m on average, and ranged from 0.3 m to 18.0 m. White fir and oaks had the lowest LCBH with an average height of 5.5 m.

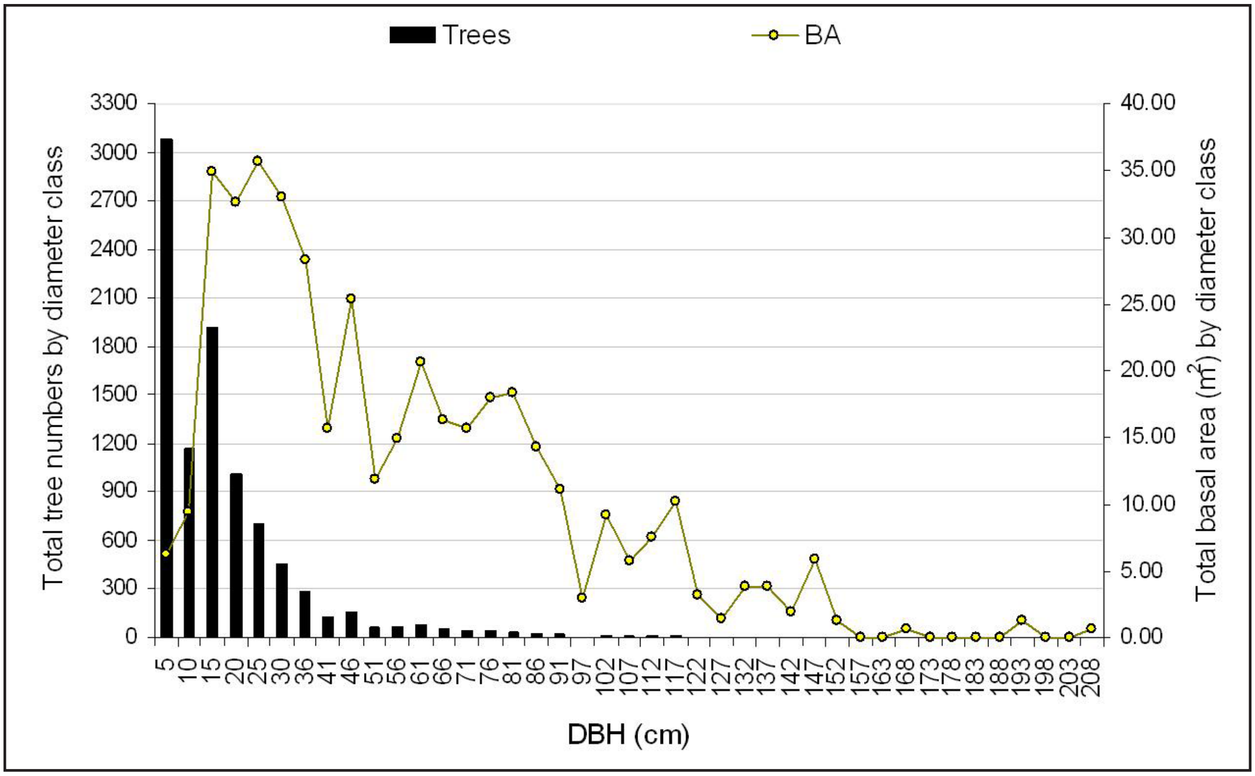

Figure 4. Frequency distribution of tree numbers and basal area by diameter class.

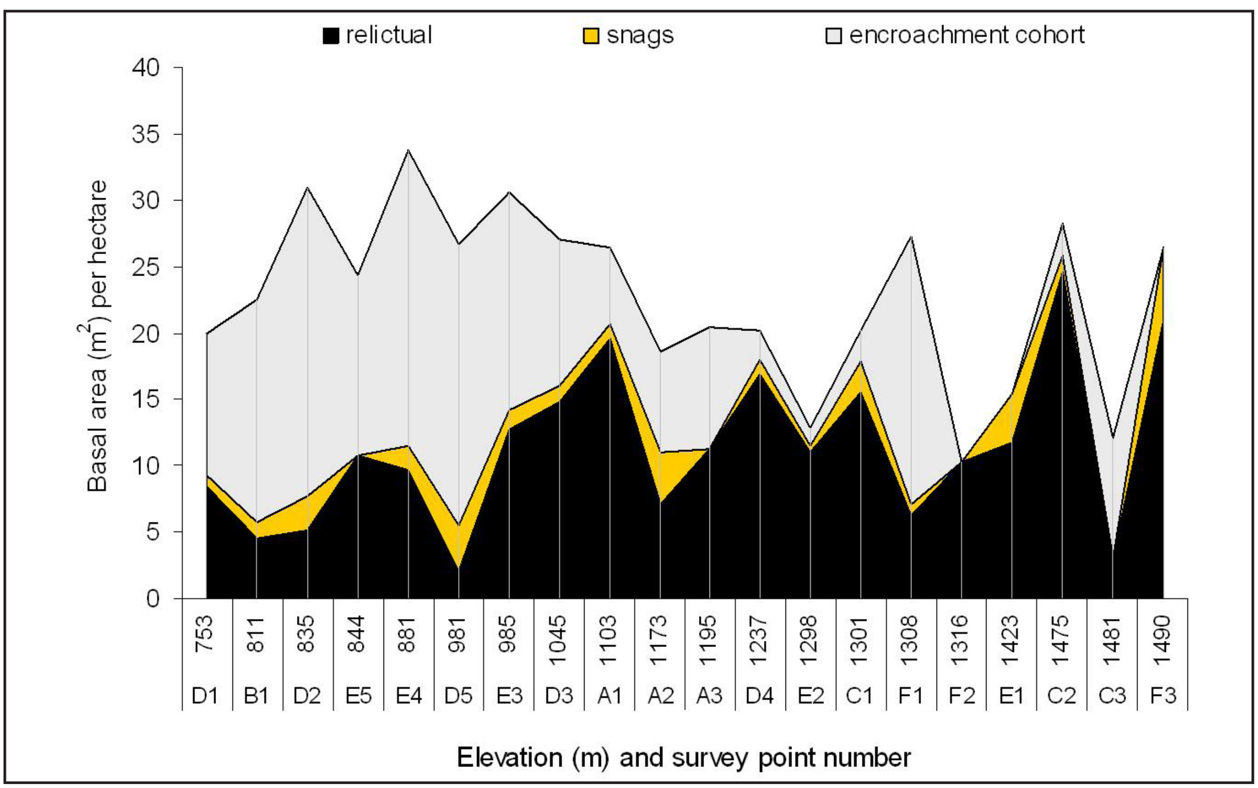

Figure 5. Proportional composition of relict tree, encroachment tree, and snag basal area, sorted by elevation. Survey point number reflects tract (A-F) and plot.

Table 2. Elements of vertical structure (heights, live crown base heights (LCBH)) in relict forests at Whiskeytown National Recreation Area, California, USA. Pines consist of ponderosa pine and sugar pine; oaks consist of black oak and canyon live oak.

			Douglas-Fir	White fir	Pines	Incense-cedar	Oaks	Tanoak	Other	Total
Relict trees		Number (n)	24	18	145	12	9	2	0	210
	Height (m)	Mean	41.5	29.0	32.3	29.3	19.2	27.4	0.0	32.3
		SE	2.4	1.8	0.6	3.0	1.2	2.7	0.0	0.6
		Median	40.2	30.8	32.9	29.9	19.2	27.4	0.0	32.9
	LCBH (m)	Mean	15.8	5.8	11.6	11.6	7.3	6.4	0.0	11.3
		SE	1.2	0.6	0.3	1.5	1.2	0.6	0.0	0.3
		Median	14.3	5.8	11.0	12.2	7.6	6.4	0.0	10.4
Encroachment trees		Number (n)	36	30	17	0	42	88	5	218
	Height (m)	Mean	18.3	14.6	16.2	0.0	12.5	17.1	12.5	15.8
		SE	0.9	1.5	2.1	0.0	0.6	0.6	3.0	0.3
	LCBH (m)	Median	18.0	13.7	14.9	0.0	12.2	16.2	9.1	15.2
		Mean	7.3	5.5	7.9	0.0	5.5	7.6	7.0	6.7
		SE	0.9	0.6	0.9	0.0	0.3	0.3	1.2	0.3

Table 3. Periodic annual basal area (cm^2) increment of trees in relict forests at Whiskeytown National Recreation Area, California, USA. Number (n) refers to number of cores with rings extending to column date.

		1945	1955	1965	1975	1985	1995	2005
Relict trees	Number (n)	66	78	84	86	86	86	86
	Mean	23	26	27	24	26	25	26
	SE	2	2	2	1	2	2	2
	Median	19	23	25	22	23	24	24
Encroachment trees	Number (n)	0	8	17	30	37	37	37
	Mean	0	3	5	7	9	13	16
	SE	0	1	1	1	1	2	3
	Median	0	2	4	3	7	11	10

Over the past five decades, the average periodic annual basal area growth of relict trees has remained at a virtual constant of 24 cm^2 to 27 cm^2 per tree (Table 3). In contrast, the annual basal area increment of encroachment trees has been steadily increasing at a linear rate, from 3 cm^2 per tree in 1955 to its most recent rate of annual growth of 16 cm^2 per tree in 2005. If these trends are held constant, the growth rate of encroachment trees could surpass that of relict trees within two decades.

DISCUSSION

Although compositionally diverse, structures and recent development of WNRA relict forests were consistently similar. Studies in regions of northern Mexico, where fire regimes have remained intact, determined that forest structures (i.e., live tree and snag attributes) in that region were characterized by substantial variation (Stephens and Fulé 2005, Stephens and Gill 2005). Fire regimes have been dramatically altered at the WNRA, and have ap-

Figure 6. Representative images of Block F at its three sample points. Photos indicate the range of structural differences and commonalities. Pines and incense-cedar dominate the overstory, dense shrub tanoak dominates the shrub layer, and an understory cohort (primarily of white fir) occurs at variable densities.

parently promoted the opposite: a ubiquitous forest condition of distinguishable relict and encroachment components.

Shift in species composition due to differences in fire tolerance is one major consequence of fire exclusion. Fire-adapted ponderosa pine mixed-conifer forests across the western United States are transitioning into ecosystems dominated by white fir, Douglas-fir, and other species that are fire-intolerant when occurring at small sizes (Taylor 2000, Allen *et al.* 2002, Graham and Jain 2005). At the WNRA, comparison of species composition among relict and encroachment components provides strong evidence that such a transition is well underway. The most dramatic transition was observed at one survey site (D5), where a complete shift in species composition had occurred: the relict pine forest, all snags, was engulfed by a dense encroachment cohort of tanoak and Douglas-fir. The replacement most likely had been completed within the last five years, given the presence of some relict pine snags with needles still attached (interpretation based on Raphael and Morrison 1987). The cause of pine mortality was not apparently external (e.g., bark beetles); competition-induced stress was theorized to be the likely mortality agent.

Among the most immediate threats to the WNRA's relict forests appears to be a high susceptibility to stand-replacing wildland fire that the presence of the encroachment cohort has introduced in the form of ladder fuel continuity. Crown fires were historically rare in ponderosa pine dominated forests, primarily due to the scarcity of ladder fuels (Skinner and Chang 1996). As is common for ponderosa pine forests, the forests of the WNRA are believed to have evolved under a regime of frequent fire occurrence that kept those ladder fuels at bay (USDI 2003). The incidence of fires that would have kept those ladder fuels at bay diminished substantially around 1925 (Fry and Stephens 2006). The current arrangement of understory and mid-story strata has resulted in greater vertical connectivity of fuel complexes in WNRA relict forests; in many cases, there is no spatial segregation of surface and aerial fuel complexes. Given the park's inherently high risk of fire occurrence (presence of a major highway through the park; close proximity to the city of Redding), this hazard presents an acute condition that chronically threatens the WRNA's relict forests.

Relict areas that were not embedded in encroachment trees were either open, partially open, or had a dense shrub-tanoak understory. Shrub-tanoak densities were, for the most part, extremely high in areas where this species was present. The extent to which fire exclusion has modified historical shrub presence cannot be answered with the results from this study, but since it is known that tanoak is a fire sensitive species (Tappeiner *et al.* 1990, Jensen *et al.* 1995), it is reasonable to infer that current shrub-tanoak densities are also beyond their natural range of variability. Past distributions and densities were most likely irregular, much unlike the continuous shrub matrix that was commonly observed.

Increasing densities of shrub-tanoak may also be promulgating further tree recruitment and ladder fuel development. Evidences of positive seedling-shrub relationships in the natural recruitment of ponderosa pine suggest that the net effect of shrubs on tree seedling recruitment is positive (Keyes and Maguire 2005), as they shelter seedlings from moisture stress and reduce the high seedling mortality rates that typically occur during summer months (Keyes *et al.* 2007, 2009). In the WNRA, this dynamic was visually suggested by the many seedling and sapling clusters that were observed throughout dense shrub-tanoak areas. Subsequent study of this issue, where a shrub layer exists but an understory tree cohort is not apparent, would help identify ecosystem changes that are underway but not yet readily evident.

This study's results are presented as a reference sample of relict forest landscape conditions and the patterns occurring within them. The information will be helpful in guiding vegetation management objectives and restoration strategies at the planning level. For the purpose of applying these findings in site-specific ecological restoration prescriptions, project scale data collection and analysis will still be necessary. A comprehensive restoration of historical conditions to relict forests at WNRA is not a realistic goal given current climatic changes, levels of ecological disruption, physiographic and economic challenges to treatments, and social constraints on management actions. Nevertheless, a general promotion and protection of those historical, diminishing, and threatened ecological elements occurring in the WNRA's relict forests is an attainable goal. It is hoped that this study's findings will help inform the future planning and management of restoration activities in pursuit of that goal.

ACKNOWLEDGEMENTS

This study was performed with funding from the National Park Service (Task Agreement Number J8485 05 0065 of Cooperative Agreement Number H8480 01 0009 between the Department of the Interior, National Park Service, Redwood National Park, and Humboldt State University Foundation), and with the support of J. Gibson (Ecologist, Whiskeytown National Recreation Area), and L. Arguello (Supervisory Botanist, Redwood National Park). The study was made possible in part by the Applied Forest Management Program at the University of Montana, a research and demonstration unit of the Montana Forest and Conservation Experiment Station. We recognize the valuable assistance of A. Roberts, J. Plummer (Fremont-Winema National Forests) and J. Teraoka (Redwood National Park).

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