



Quantifying habitat loss: Assessing tree encroachment into a serpentine savanna using dendroecology and remote sensing



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ABSTRACT

For over a century, increases in the abundance of woody plants in savannas have been occurring worldwide in a process known as encroachment. Encroachment into savannas is a significant management concern because it affects the unique values associated with savanna systems, including high levels of both taxonomic and landscape diversity. Improving methods for reconstructing encroachment patterns should aid savanna management, especially if the methods provide a baseline from which to assess and project ecological change. We reconstructed the encroachment history of a small serpentine Jeffrey pine savanna and forecasted future landscape change using two distinct approaches. First, we used dendroecology to determine encroachment rates, establish historical site reference conditions, and project tree-growth trends. Second, we used historical aerial photographs to construct a spatial model of past tree encroachment and to predict near future encroachment. We found encroachment began ~1850 and was not related to differences in topography across the landscape. Trees greater than 30 cm in diameter have increased from a mean stem density of ~1.6 trees per ha in 1890 to a mean stem density of ~13.8 trees per ha in 2009. Concomitant with the increase in tree density and average tree size was the contraction of the grass-dominated areas of the savanna, which represented ~50% of Little Bald Hills in 1942, but less than 10% in 2009. If current encroachment rates continue, our models suggest that less than 5% of Little Bald Hills will be grassland in 50 years. This is not the first study to utilize both historical photo analysis and dendroecology, but it is the first to use these tools to identify explicit locations where encroachment is likely to occur in the near future.

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1. Introduction

Savanna ecosystems worldwide have been noted for their significant contribution to global biodiversity, and savannas are often associated with rare species and higher levels of taxonomic diversity than surrounding forested habitat (e.g.; Latham et al., 1996; Krannitz, 2007; Bond and Parr, 2010; Burley and Lundholm, 2010; Ratajczak et al., 2012). Savanna systems are referred to variously as wooded grasslands, rangelands, shrublands, barrens, and woodlands, but the unifying characteristic among these ecosystems is an herbaceous understory dominated by grasses and a sparse or open woody plant overstory (Cole, 1986; House et al.,

2003). It has long been observed that many savannas are experiencing afforestation by woody plants in a process known as encroachment (e.g.; Miller, 1921; Bragg and Hulbert, 1976; Scholes and Archer, 1997; Franco and Morgan, 2007; Van Auken, 2009; Buitenwerf et al., 2012). The ecological consequences of woody plant encroachment into savannas are wide-ranging and include alterations in species richness, landscape habitat heterogeneity, carbon storage, soil chemistry, and the abundance and distribution of animals (Franklin et al., 1971; Skinner, 1995; Jackson et al., 2002; Griffiths et al., 2005; Krannitz, 2007; Halpern et al., 2010; Ratajczak et al., 2012).

A growing body of research has illustrated the importance of disturbance regimes and unique edaphic conditions, singly, or in combination, as predictors of savanna occurrence (e.g., Bond, 2008; Staver et al., 2011; Favier et al., 2012; Murphy and Bowman, 2012). Edaphic savannas are generally small, insular areas that stand out as distinct from the surrounding vegetation because their underlying parent material is different from the surrounding areas. In northwestern United States, one unique type of edaphic savanna

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is restricted to serpentine outcrops of the Klamath Mountains. Serpentine, a common name for soils derived from ultramafic parent material, often harbors uniquely-adapted vegetation (Kruckeberg, 1954; Whittaker, 1954). While several studies have focused on tree encroachment into mid- and high-elevation non-serpentine meadows of the Cascade Mountains (Franklin et al., 1971; Miller and Halpern, 1998; Griffiths et al., 2005; Haugo and Halpern, 2007; Zald, 2008; Halpern et al., 2010), to our knowledge no studies of tree encroachment into the serpentine-derived edaphic savannas of western North America have been published. One such serpentine savanna, Little Bald Hills of northern California, has very unique vegetation and has been experiencing rapid conifer encroachment. In areas such as Little Bald Hills, appropriate management of encroached savannas requires an understanding of historical reference conditions and likely trajectories. Retrospective studies can establish a baseline ecosystem condition that can help in the development of criteria for evaluating management strategies (Landres et al., 1999; Swetnam et al., 1999; Kipfmüller and Swetnam, 2001). In addition, management efforts will likely be informed by data-driven predictions of future encroachment; such forecasts about ecosystem trajectories enable managers to target areas for encroachment prevention based on where encroachment is most likely to occur next.

Both the establishment rates of encroaching vegetation and the geographic extent of encroachment have been shown to be mediated by topographic conditions such as elevation and aspect (Mast et al., 1997; Carmel and Kadmon, 1999; Bai et al., 2004; Coop and Givnish, 2007). In some regions of the northern hemisphere, for example, south-facing aspects have experienced lower rates of tree and shrub encroachment than more northerly-facing aspects, likely due to their higher rates of insolation that increase water stress for seedlings and juveniles (Mast et al., 1997; Carmel and Kadmon, 1999; Bai et al., 2004). Additionally, more precipitation tends to fall on the windward side of hills and mountains, increasing the amount of water available to plants on windward aspects and slopes, thereby enhancing successful seedling establishment (Arazi et al., 1997). Encroachment has also been found to occur in some localities more rapidly at higher elevations, with a strong interaction between the effects of elevation and slope leading to increased encroachment on mountain slopes compared with valley bottoms (Coop and Givnish, 2007).

By using multiple lines of evidence, such as tree-ring reconstruction coupled with repeat aerial photographic analysis, the extent of ecological change can be examined over larger areas of varying topographic features and can produce more accurate reconstructions of reference conditions (Swetnam et al., 1999). Aerial photographic records are available in many areas of the United States beginning in the 1930s or 1940s, and are ideal for studies of ecosystems and fine-scale features like trees because of their high level of spatial and radiometric detail (Lillesand et al., 2008; Morgan et al., 2010). Several studies have combined dendrochronology and historical photo analysis to quantify the extent of past encroachment into a variety of ecosystems and for a variety of purposes (e.g., Fulé et al., 2003; Pellerin and Lavoie, 2003; Bergeron et al., 2004; Coop and Givnish, 2007; Franco and Morgan, 2007), but to our knowledge none have modeled past and future tree encroachment using these complementary techniques.

To document and predict tree encroachment in Little Bald Hills, we first used tree ages and sizes inferred from tree-ring data to reconstruct historical stand conditions. We then used changes in historical basal area reconstructed from tree rings to create a model of future basal area increase. Next, we evaluated encroachment rates for the past ~150 years and their relation to slope, aspect, and elevation. Subsequent analyses utilized a series of historical vertical aerial photographs spanning the years 1942–2009. We produced a GIS model that captured the spatial extent and pat-

tern of encroachment at given time intervals, and we used that model to predict future encroachment trends. Our study goals were to use these dendroecology and remote sensing/GIS techniques to (1) explore historical patterns of encroachment in Little Bald Hills, (2) relate encroachment rates to topographic variables, (3) reconstruct historic savanna conditions to be used as reference criteria for ecological restoration, and (4) develop predictive models of tree encroachment to inform management decisions for Little Bald Hills. More generally, our aim was to provide a suite of techniques that can be applied to similar systems.

2. Materials and methods

2.1. Study area

The Little Bald Hills study area, centered roughly at 41°45'N, 124°2'W, is located ~25 km south of the Oregon–California border, ~5 km east of the Pacific Ocean and falls almost entirely within the boundaries of Redwood National Park in Del Norte County, California (Fig. 1). The small, roughly 175 ha Jeffrey pine savanna from which Little Bald Hills derives its name ranges in elevation from 450 to 620 m above mean sea level and is characterized by an overstory of scattered Jeffrey pine (*Pinus jeffreyi*) and a more or less continuous herbaceous understory dominated by Idaho fescue (*Festuca idahoensis* ssp. *roemerii*). Shrub cover is limited and the savanna is surrounded by a forested matrix composed predominantly of coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*; Appendix A). The site's climate is heavily influenced by its proximity to the coast; mean temperatures vary only 5 °C between the hottest month, August, and the coldest month, December (14 °C and 9 °C, respectively). The nearest weather station is located outside of Gasquet, CA, ~10 km north-northeast of Little Bald Hills at an elevation of 150 m (NCDC COOP station number 043357), which in 2011 reported a 55-year mean annual precipitation of 2350 mm, 77% of which fell between November and March. The distinct savanna vegetation of Little Bald Hills is attributed to a narrow, approximately 1 km-wide band of serpentine soil (serpentinized peridotite in this case) that runs roughly north–south through the western Klamath Mountains (Fig. 1). Little Bald Hills is the only area of serpentine soil within Redwood National Park and represents a regionally infrequent habitat (Goforth and Veirs, 1989; Skinner, 1995).

In addition to the underlying edaphic conditions, disturbance is believed to have been a primary factor contributing to the vegetation structure in Little Bald Hills; like most terrestrial ecosystems of western North America, fire is presumed to have shaped many of the characteristics of this area (Goforth and Veirs, 1989; Jimerson et al., 1995; Taylor and Skinner, 1998). Other past disturbances in Little Bald Hills include settlements, roads, and ranching. For the purposes of this study, we defined Little Bald Hills using a vegetation alliance GIS layer created by Redwood National and State Parks. The Jeffrey pine savanna polygon was buffered by 70 m to include what might previously have been savanna before the vegetation alliances were mapped in the 1980s. We chose a buffer distance of 70 m because that distance effectively encompassed islands of mixed-conifer vegetation types within the savanna, and also captured a reasonable area of possible pre-1980s savanna outside the Jeffrey pine savanna polygon. An approximately 6-ha area not covered by a 1-m digital elevation model (DEM) was excluded from the northern section of the study area.

2.2. Reconstruction of conifer age structure, size, and establishment

We set up 29 plots during summer and fall of 2009. Each 0.05 ha circular plot location was generated randomly using ArcGIS 9.3.1.

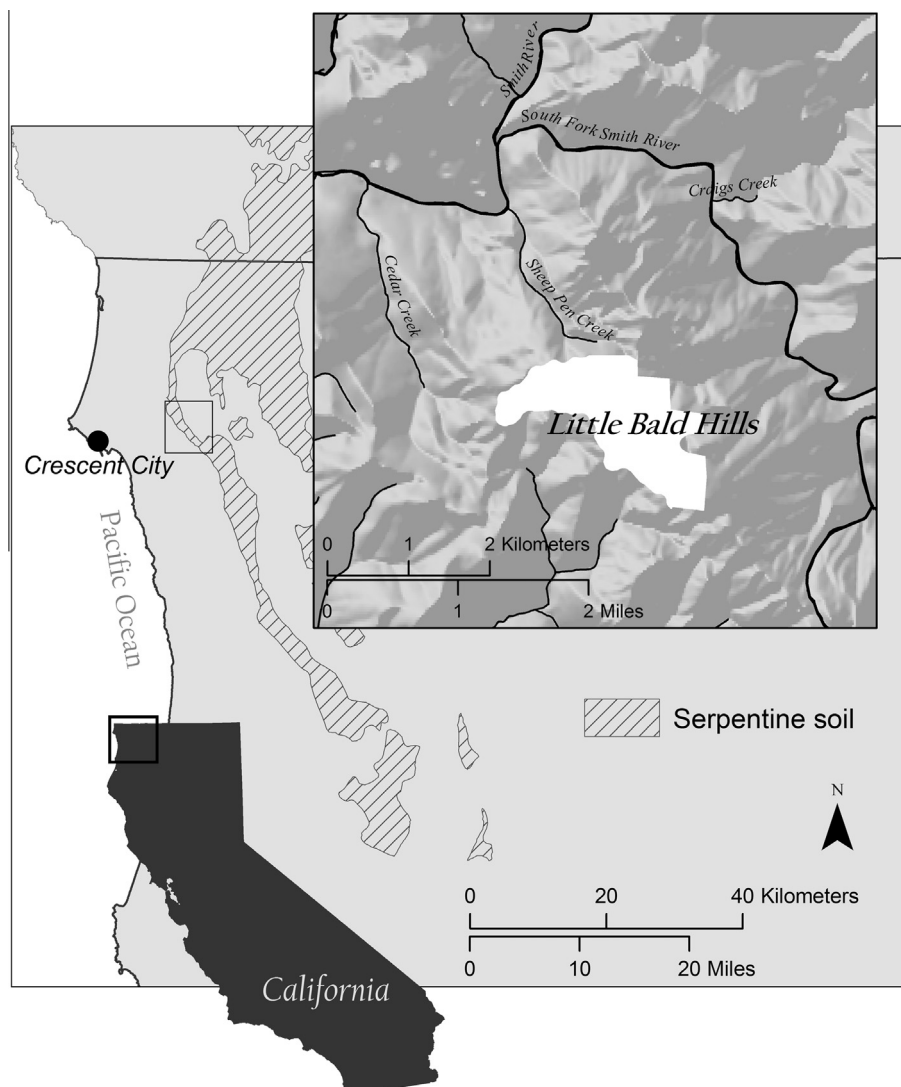


Fig. 1. Location of the study area in Redwood National Park, Del Norte County, California, USA. Little Bald Hills is shown in white in the topmost inset. Serpentine rock and soil running through this area, shown in the middle inset, have given rise to a low-elevation pine savanna within predominantly redwood and Douglas-fir forest types. Map sources: Cal-Atlas Geospatial Clearinghouse, USDA Geospatial Data Gateway.

At the center of each plot, we recorded values of canopy cover (using a spherical densiometer), slope inclination degrees, and slope aspect. Slope aspect was transformed for statistical analysis as described by Beers et al. (1966). We defined A_{\max} to be 45° , so that northeast-facing aspects have the highest transformed value of 2 and southwest-facing aspects have the lowest value of zero. Higher transformed aspect values therefore correspond to lower insolation. Diameter at breast height (DBH) was recorded for all trees greater than 7 cm DBH, including snags. Trees < 7 cm DBH, including seedlings, were tallied by species in all plots. A maximum of ten trees < 7 cm DBH, hereafter juveniles, of each tree species present were cut no more than 3 cm above ground level and tree cross-sections were collected to determine juvenile establishment year. In 27 plots, trees > 7 cm was sampled using an increment borer as close to the base of the tree as possible, heights of 15 cm or 30 cm were used, depending on the size of the increment borer. Of the remaining two plots, one plot contained > 200 trees so trees within this plot were subdivided into 10 cm diameter size classes and ten trees per size class were haphazardly selected for coring. Another plot included 12 cut tree stumps that could not be aged due to bark growth over the cut surface and stump heights too low to core, so this plot was subsequently excluded from all

analyses. Although a few other stumps were found throughout the study area, this was the only plot that contained any stumps; the study site did not have any evidence of commercial timber harvesting, presumably because of the low density of trees.

Tree core and cross-section samples were sanded using progressively finer sandpaper, from 120 to 1500 grit, until each ring's structure was clearly visible under a dissecting microscope. All samples were visually cross-dated and the program COFECHA was used as a cross-dating quality control check (Holmes, 1983). Annual growth rings were measured to 0.001 mm using a Velmex measuring stage (TA 4030H1-S6 Unislide, Bloomfield, New York, USA). For cores that did not intersect the pith, ring-pattern templates of variously sized concentric circles were used to estimate the number of missing rings. To derive accurate establishment dates, we corrected for sampling height by selecting saplings of Douglas-fir ($n = 10$), Jeffrey pine ($n = 11$), and Port Orford-cedar ($n = 9$) growing in open canopy conditions. We removed these 30 saplings from the ground with root material intact and subsequently sanded the main root until the root-shoot interface was visible. Rings were then counted at 10 cm intervals along the stem from the root-shoot interface to determine the mean number of rings present at coring height, and this number was added to the

earliest visible ring year of a given tree core (Appendix B). No correction was applied to juveniles collected near ground height (sampling height < 3 cm above the ground surface). For the plot with > 200 trees, we assigned an establishment decade to trees tallied by size class based on the proportion of establishment dates of trees in a given size class for all sampled trees ($n = 701$). A similar method was used to assign an establishment date to tallied juveniles ($n = 393$).

We used cross-dated raw ring-width radial measurements to calculate past basal area. In order to derive the most accurate measurements for basal area, the slope derived from a linear regression of the ring-width derived diameter and measured DBH in 2009 ($\beta = 0.270$, $n = 641$, adjusted $R^2 = 0.62$) was used as a bark correction factor. This bark correction factor was added to past diameters to account for bark not directly measured, since only ring widths were used to calculate diameter. We excluded the plot with >200 trees from all past-basal area analyses because not all trees were cored. The historical reconstruction of tree basal area was used to create an annual time series of basal area for each plot. We evaluated tree basal area as a proxy for encroachment because basal area is generally a more ecologically meaningful parameter than the density of stems in a given plot. While encroachment implies the influx of many individual trees, a few large trees can affect nutrient and light availability, as well as available establishment area, more than many small stems.

In order to estimate encroachment rates from the basal area time series, we fit autoregressive moving average (ARIMA) models of the form

$$Y_i(t + \Delta t) = Y_i(t) + r_i \Delta t + \varepsilon_i(t) \quad (1)$$

where $Y_i(t)$ is the basal area in plot i at time t , r_i is the linear rate of encroachment in plot i , and $\varepsilon_i(t)$ is temporally independent process error, which has a normal distribution with variance σ_i^2 . These were fit as ARIMA (0,1,0) models with year as an external regressor, using function `arima` in R, which fits time series models by maximizing the state-space likelihood (R Development Core Team, 2011). Some plots exhibited an exponential increase in basal area (Appendix C), so we also fit the ARIMA models to log-transformed basal area so that we could determine whether we should use growth rates derived from linear or exponential growth models. We used Akaike's Information Criterion values adjusted for small sample size (AICc) to compare the log-transformed basal area models (exponential growth) to the untransformed basal area (linear growth) models. Since the likelihoods for the exponential growth models were expressed as the normal likelihood of the logarithm of basal area, we adjusted these likelihoods to represent the lognormal likelihood of basal area so that the linear and exponential models could be compared using AICc (Burnham and Anderson, 2002). Linear growth models had lower AICc values in 15 of the 26 plots, so we chose to use the parameter estimates from the linear growth models as the best rates of basal area growth in all plots, and consequently the best estimates of tree encroachment over the entire study area.

To determine whether encroachment was dependent on slope inclination, slope aspect, elevation, and/or the interaction between slope inclination and elevation, we used an AICc-based model selection approach with the encroachment rates fit from the ARIMA models as response variables in linear regression using function `lm` in R (R Development Core Team, 2011). We chose to limit the potential interactions between explanatory variables to slope and elevation and not include aspect because upper slopes and ridgetops were thought to be dominated by Jeffrey pine (Alexander et al., 2007) and field reconnaissance supported the impression that ridgetops are being encroached last in Little Bald Hills. To include all possible interaction terms would have increased the number of potential models from ten to greater than 20, an unreasonable number of models for 26 observations.

In order to predict future basal area over the entire study area, we used the 26 different estimates of encroachment rate obtained by fitting Eq. (1) to develop a single time series model

$$Y(t + 1) = Y(t) + r \Delta t + \varepsilon(t) \quad (2)$$

where $Y(t)$ is total basal area at time t and r is the mean encroachment rate over the study area. We estimated r as the mean of the 26 plot-level estimates \hat{r}_i (i.e., $\hat{r} = \frac{1}{26} \sum_{i=1}^{26} \hat{r}_i$), and we took the variance of the area-wide process error $\varepsilon(t)$ to be the maximum value of $\hat{\sigma}_i^2$ observed across the 26 plots. This leads to the following equation used to calculate future basal area at a given time t :

$$Y(t) = Y_0 + \hat{r}t + \sum_{j=1}^t \varepsilon_j(t) \quad (3)$$

where $Y_0 + \hat{r}t$ is equal to the predicted basal area at time t years beyond 2009, and Y_0 is equal to the mean basal area for Little Bald Hills in 2009. The variance associated with the predicted basal area values was calculated as

$$\text{Var}(Y(t)) = t^2 \text{Var}(\hat{r}) + t \text{Var}(\varepsilon_t) \quad (4)$$

where $\text{Var}(\hat{r}) = \frac{1}{26} \sum_{i=1}^{26} \text{Var}(\hat{r}_i) + \frac{1}{26} \sum_{i=1}^{26} (\hat{r}_i - \hat{r})^2$. All calculations were done in R; the package `dplR` was used to import raw ring width files (Bunn, 2008; R Development Core Team, 2011).

2.3. Historical image analysis

We collected existing vertical aerial photographs and digital photographic images whose coverage included the study area so we could evaluate tree encroachment into the Jeffrey pine savanna of Little Bald Hills using digital imagery. We acquired 16 images total, spanning the years 1942 to 2009 (Appendices D and E). We digitally scanned hardcopy black-and-white photographs maintained by Six Rivers National Forest at 600 dpi for five image years, and digital images for 11 years were downloaded through USGS Earth Explorer, USDA Geospatial Data Gateway, and Cal-Atlas. The downloaded images included black-and-white, color-infrared, and true-color photographs. We selected images for analysis based on scale and area covered; all images needed to have a resolution of at least 1 m or smaller and to encompass the study area so no mosaicking would be necessary. Based on these qualities, nine of the 16 acquired image years were selected as suitable for analysis. One image (2005) was later removed from the analyses due to a classification accuracy of less than 80% (Appendix F). The final collection of eight images included the years 1942, 1960, 1975, 1980, 1988, 1993, 1998, and 2009 (Appendices D and E).

Images from 1942, 1960, 1975, and 1980 were assigned a projected spatial reference to UTM zone 10 north, North American Datum 1983, using ERDAS Imagine 2010 software. These images were orthorectified to a 10-m National Elevation Dataset DEM and referenced to a 1988 color-infrared digital orthophoto quadrangle. A minimum of ten ground control points (GCPs) were used for reference in each image; the low number of GCPs used was due to the rural setting of Little Bald Hills and the paucity of consistently recognizable landmarks in each image (Appendix D). Total root-mean-square (RMS) error for each non-orthorectified image was less than 5 m for all images. A hybrid classification approach was then used to spectrally classify every image using ERDAS Imagine. An 8–12 class unsupervised classification was first performed and classes were subsequently merged into three classes: shadow, grass-dominated areas, and woody vegetation. A supervised classification was then performed on the images and additional class signatures were digitized if the initial classification was deemed inaccurate. Since the earliest photos were black-and-white panchromatic, all classifications were run on single-band images. For consistency in analysis, the green band was

selected for classification in three and four-band images, which is comparable to a single-band black and white image. Classification accuracy assessment used the original photographic image for reference and took into account color, pattern, and texture. Eighty-five accuracy points were assigned to each class, for a total of 255 accuracy assessment points per image. Only images with classification accuracies greater than 80% for every category were used for analysis. Kappa statistics (Cohen, 1960) and error matrices were used to assess classification accuracy (Appendix F). Pixels classified as shadow were eliminated; i.e., coded as No Data, in ArcGIS using the reclassify tool for subsequent analyses, leaving two types of classified pixels: grass and woody vegetation (hereafter grass pixel and tree pixel, respectively).

We derived a predictive model of future tree encroachment by assigning 500 random points to each classified image year, for a total of 4000 sampling points. Each sampling point was associated with a value of zero for classified grass pixels and one for tree pixels, which were used as binary response variables in generalized linear models (function `glm`) with a binomial probability distribution and a logit link function (logistic regression) in R (R Development Core Team, 2011). A 1-m, LIDAR-derived DEM was used to generate the explanatory variables slope inclination and aspect. Sampling points were then associated using Hawth's Tools in ArcGIS (Beyer, 2004) with the following topographic variables: elevation, slope inclination in degrees, and transformed aspect. In addition to the topographic variables, we used the distances to the nearest tree in each image year as predictors by calculating the Euclidean distance to the nearest tree pixel in ArcGIS for each classified image. We excluded distances for the image years 1988 and 2009 because the original classification accuracies for those years fell below 90% for grass-dominated areas. The Euclidean distance for any sampling point located within a tree pixel was zero.

We used an AIC-based model selection approach to evaluate 511 models with different combinations of the explanatory variables fit to the data. All models evaluated contained the year a photo was taken as a predictor, and year was used as a continuous variable in order to create a predictive model. Parameter estimates were derived by model-averaging all models with an AIC weight greater than zero (Burnham and Anderson, 2002); i.e., eight models contained explanatory information and were used to derive accurate coefficients. All analyses were conducted using the program R (R Development Core Team, 2011).

To create a spatial model of tree encroachment, we used the model-averaged parameter estimates to create raster layers of probabilities for given years using the map algebra tool in ArcGIS. Each pixel was assigned to the grass or tree class based on the model-derived probabilities, with probabilities greater than 0.5 being assigned a tree classification. Model accuracy was evaluated by comparing 200 randomly-assigned points in the model-derived probability raster and comparing it to the original image for each of the eight image years, similar to accuracy assessment for the original classifications, for a total of 1600 accuracy points. To assess how well the model predicted grass and tree presence, we used error matrices and calculated an overall kappa statistic (Cohen, 1960).

3. Results

3.1. Reconstruction of conifer age structure, size, and establishment

A total of 825 tree cores and basal cross sections were processed from 755 live trees and five snags. Cores and cross sections from 681 trees representing three species; Douglas-fir, Jeffrey pine, and Port Orford-cedar (*Chamaecyparis lawsoniana*) were used to build species-specific chronologies spanning 143 years that served

as quality controls for visual cross-dating. All snags were Jeffrey pine. Of the 760 trees sampled, one Douglas-fir and one Jeffrey pine could not be aged due to irregular ring formation. One Pacific madrone (*Arbutus menziesii*) with an establishment date of 1945 was excluded from the chronology and subsequent establishment analyses because of the low frequency of the species across the landscape ($n = 3$, all < 10 cm DBH). Jeffrey pine was the most frequently encountered tree ($n = 1123$), followed by Douglas-fir ($n = 457$), Port Orford-cedar ($n = 80$), and tan oak (*Notholithocarpus densiflorus*; $n = 3$, all < 10 cm DBH). The density of Douglas-fir, Jeffrey pine, and Port Orford-cedar trees present per plot differed significantly (Kruskal Wallis rank sum test, $\chi^2 = 41.45$, d.f. = 2, $P < 0.001$; Fig. 2). Port Orford-cedars were found in only five (18%) plots; four plots had 6 or fewer while one plot had 65 trees and juveniles present. Since Port Orford-cedar establishment is limited to specific high moisture availability areas in Little Bald Hills, we focused subsequent analyses on Jeffrey pine and Douglas-fir as the major species of encroachment.

The oldest live trees encountered in this study were single Douglas-fir and Jeffrey pine trees, both of which established in 1855. After low levels of early establishment, Douglas-fir and Jeffrey pine exhibited two periods of increased establishment, the first beginning ~ 1940 and continuing through 1890, the second from ~ 1980 through 1990 (Fig. 2a). Tree establishment in the 2000 decade was comparable to that of the pre-1950s decades (Fig. 2a), although we suspect that was due to sampling bias – trees that established during the 2000 decade were generally smaller than 20 cm in height and were easily overlooked amongst the grasses. The majority of trees establishing in Little Bald Hills have been Jeffrey pine. Our sampling did not detect any Port Orford-cedars until 1916 and very few Port Orford-cedars established until the 1990s; establishment frequency was less than 5 trees per ha per decade until the 1990s when $54 (\pm 38 \text{ SE})$ trees per ha established (Fig. 2a). Concomitant with the increase in tree establishment is a steady increase in stem density (Fig. 2b). The density of both Douglas-fir and Jeffrey pine exhibit an exponential increase from the 1940s through the 2000s (Fig. 2b). While Jeffrey pines have dominated the landscape since the middle of the 19th century, the establishment frequency and density of Douglas-fir and Jeffrey pine did not significantly differ until the 1950s, when the increase in Jeffrey pines greatly outpaced that of Douglas-fir. The mean density of Douglas-fir and Jeffrey pine trees present in 2000 were significantly different (Kruskal Wallis rank sum test, $\chi^2 = 8.36$, d.f. = 1, $P = 0.0004$).

The size structure of trees in Little Bald Hills has changed dramatically in the past 150 years. In 1890 our sampling detected no trees greater than 40 cm in diameter, and there were approximately equal numbers of Jeffrey pines in the < 10 cm, 10–19.9 cm, and 20–29.9 cm classes (Fig. 3a–c), although a few large-diameter cut stumps were present on the landscape that could not be aged, indicating larger trees were present at earlier time periods. The greatest number of Douglas-fir present in 1890 was in the juvenile class, a trend that continues through the 2000s (Fig. 3). Until the mid-20th century, a more varied Jeffrey pine size structure was evident (Fig. 3), but by 1960 the < 10 cm size class contained over five times as many individuals as any other size class, and by 2000 the density of trees < 10 cm in diameter in all three taxa were an order of magnitude greater than any other size class (Fig. 3a). While the number of small trees has increased dramatically in the past 150 years, the density of trees in all size classes has also increased, and there is a clear positive trend in the numbers of trees present in larger size classes (Fig. 3). Interestingly, Douglas-fir has consistently dominated the largest diameter size classes (Fig. 3).

The number of trees in larger size classes over time is also reflected in the increasing tree basal area values in all plots,

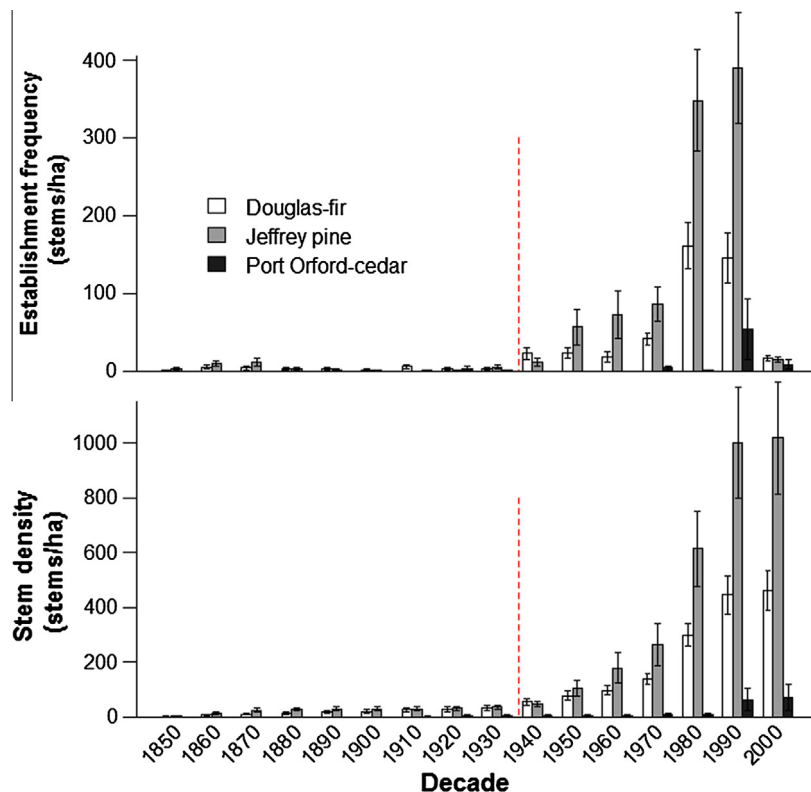


Fig. 2. Establishment (a) and stem density (b) of the three most frequently encountered tree species in Little Bald Hills. In panel a, each decade represents the mean number of trees establishing per hectare in the decade from year 0 to 9; i.e. the plotted value in 2000 is the mean number of trees that established during the years 2000–2009. In panel b, the density of stems plotted is the number of stems present in year 9 of the decade; i.e. mean stem density in decade 2000 is the density of stems present in 2009. Error bars represent ± 1 SE. The dashed line marks 1940, the date of the last known fire in Little Bald Hills.

although the rate of basal area increase was highly variable across the landscape (Appendix C). Several plots exhibited small increases in basal area since 1867, while others began to increase almost immediately, and others still did not see an increase until the 1940s (Appendix C). Four plots did not see any tree establishment until post-1940, but there was no relationship between the age of the oldest tree in a plot and its rate of basal area increase. Basal area in Little Bald Hills has increased from 0.01 m²/ha in 1870, to 20 m²/ha in 2009 at a rate of approximately 0.14 ± 0.013 SE m²/ha/year. If this growth trend continues, total basal area in Little Bald Hills will approach 35 m²/ha in 100 years (Fig. 4). The mean basal areas of Douglas-fir and Jeffrey pine were statistically comparable.

There was little evidence that basal area changes were significantly influenced by slope inclination, slope aspect, or elevation, nor of an interaction between slope inclination and elevation (Appendix G). Slope inclination in plots ranged from 0° to 30° with a mean value of 11° ($\pm 0.35^\circ$ SE); aspect ranged from 0 (SW) to 1.99 (NW) per plot and had a mean value of 0.70 (± 0.02 SE), and elevation ranged from 470 to 599 m with a mean value of 548 (± 2 m SE). When examined separately, encroachment values for Douglas-fir and Jeffrey pine were not substantively different than those of all trees together. The null model was 1.3 times more likely to be the best of the candidate models than the next best model in the set, which suggests that the prediction of encroachment in a given plot could not be improved upon by the addition of any combination of topographic variables. The likelihood of the model that included only slope aspect as a predictor was the same as the null model (Appendix G), suggesting the addition of slope aspect added no new predictive ability to the model. Although several additional models in the set had some model weight, the 95% confidence intervals around the estimated coefficients for all topographic site

variables included zero, another indication that topography had no influence on encroachment rates (Table 1).

3.2. Historical image analysis

Image classification accuracies for assigning pixels as tree, grass, and shadow were high (Appendix F) and the total area classified after shadow pixels were removed for each image year ranged between 70% and 87%, with a mean of 82%. Out of the 511 models in the logistic regression candidate set, eight had model weight greater than zero (Appendix H). The eight top models each included year and distance from nearest tree pixel for every image year as predictors. The respective coefficient estimates and confidence intervals for year and tree distances were almost identical in all eight models, further evidence of the importance of year and location of the nearest tree in governing whether a given pixel is tree or grass.

The logistic regression model used in ArcGIS to assign a probability of being a tree pixel was moderately accurate when assessed using randomly assigned points for reference (overall accuracy = 0.81, kappa = 0.56; Table 2). Most of the model classification errors were incorrect assignment of grass pixels to woody vegetation; i.e., fewer grass pixels were predicted by the model than were present. Visual assessment of the model indicates good spatial fit of the model to the reference images, although the model underpredicts grass-dominated areas, as indicated by the accuracy assessment (Table 2 and Fig. 5). The percent of Little Bald Hills represented by grass-dominated areas in the logistic regression model was 52% in 1942 and 9% in 2009 (Table 3). Predictions of grass-dominated areas projected out 10, 25, 50, and 100 years after the field study in 2009 indicate the percent of grass in Little Bald Hills to be 7%, 6%, 4%, and 2%, respectively (Table 3 and Fig. 6).

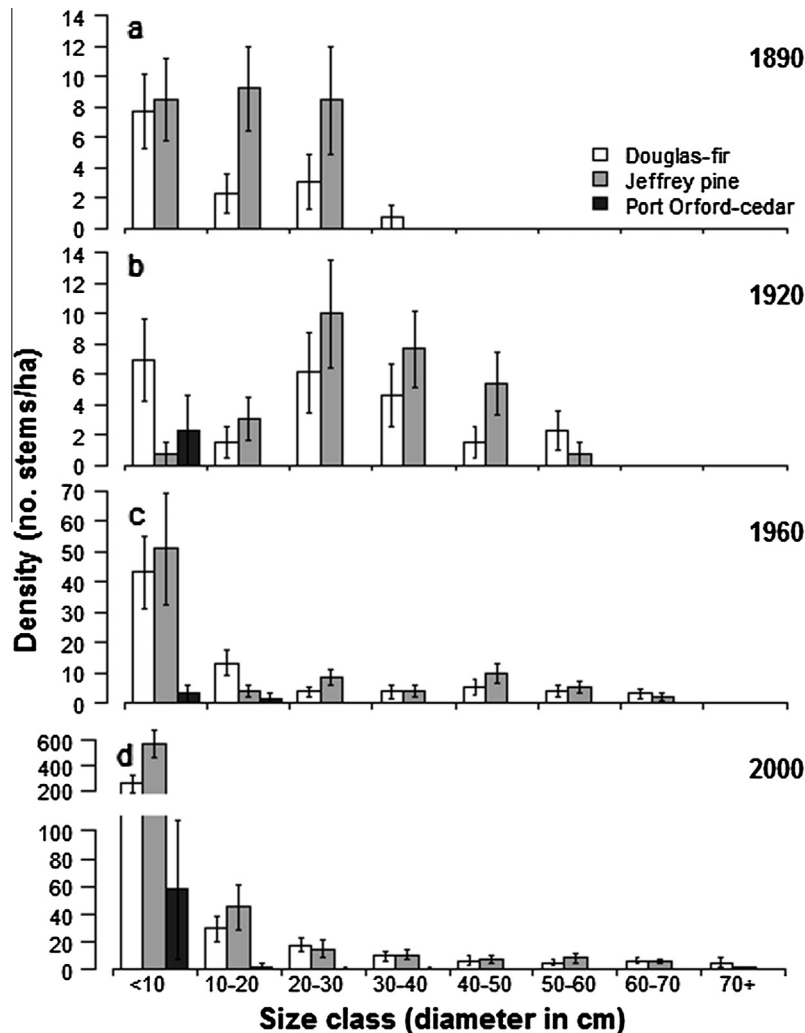


Fig. 3. Size structure of trees present in Little Bald Hills for four different years: 1890, 1920, 1960, and 2000. Error bars are ± 1.0 SE. Note the different y-axes in panels c and d, and the broken axis in panel d.

4. Discussion

Little Bald Hills has been experiencing rapid changes in community structure over the last 150 years. Tree densities have increased exponentially since ~ 1850 (Fig. 2) and grass-dominated areas have declined substantially since the 1940s, thereby reducing the amount of area capable of supporting shade-intolerant herbaceous plant communities distinct from the surrounding forest. Between the years 1890 and 2000 there was a 50-fold increase in tree density in the smallest size class and a steady proliferation in the number of trees in the larger size classes for all species (Fig. 3). Our most conservative estimates of change in grass-dominated areas were built on linear rate of increase averaged over the entire time series, which we chose based on the best fit to growth in the majority of plots over the longest period of time. These estimates show a decrease from 75 ha in 1942 to 21 ha in 2009. The predictive model of basal area growth indicated average basal area values will approach 35 m²/ha in 100 years (Fig. 4), which is near the value reported by Spies and Franklin (1991) for young Douglas-fir stands on productive, non-serpentine sites in the Cascade and Coast Ranges of the Pacific Northwest USA. Our work demonstrates a rapid progression away from a grass-dominated savanna toward a forested state common in the region, and provides explicit predictions about where on the landscape the highest rates of future encroachment are.

Past trends indicate that future tree composition could shift notably from a Jeffrey pine-dominated system to one dominated by Douglas-fir. While Jeffrey pines can establish in harsh environments and xeric sites (Burns and Honkala, 1990; Stuart and Sawyer, 2001), Douglas-fir is known to be limited by water availability (Littell et al., 2008). Douglas-firs regularly establish near other trees, and facilitative interactions during seedling establishment have been shown to influence encroachment rates and patterns (Kennedy and Sousa, 2006). It is probable that Jeffrey pine is the primary colonizer of more xeric, open sites in Little Bald Hills, creating a more favorable micro-site environment for Douglas-fir to establish secondarily. Interestingly, our sampling indicated that Douglas-fir has been present within the savanna for the same length of time as Jeffrey pine; however, tree ages pre-1940 were significantly different between Douglas-fir and Jeffrey pine, with Jeffrey pines the older of the two species (Welch two-sample *t*-test, $t = 3.06$, d.f. = 41, $P = 0.003$). Post-1940 mean ages of Douglas-fir and Jeffrey pine were not different (Welch two-sample *t*-test, $t = -0.37$, d.f. = 238, $P = 0.713$), and both establishment and density of Douglas-fir and Jeffrey pine were not significantly different until after 1950, when Jeffrey pine began to dominate both categories (Fig. 2). Although Jeffrey pine can live 500–600 years under optimal growing conditions, it is highly shade intolerant and does not grow as tall as Douglas-fir (Burns and Honkala, 1990; Stuart and Sawyer, 2001). Jeffrey pine is likely to

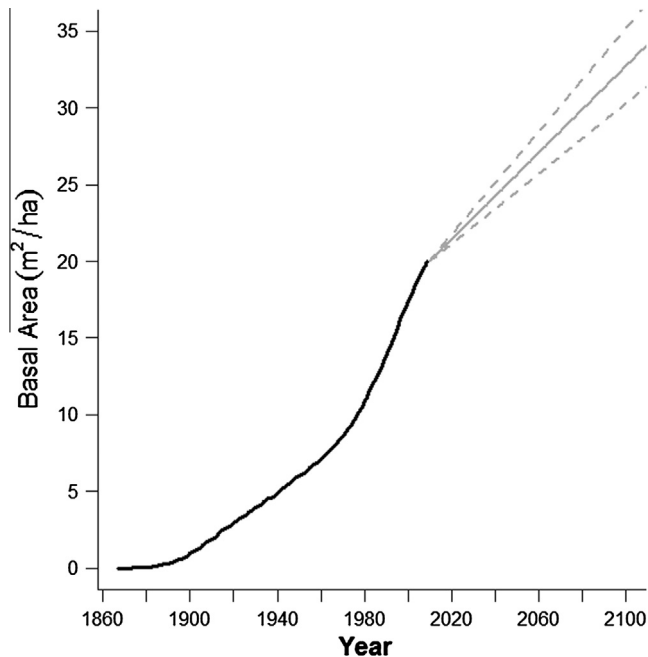


Fig. 4. Mean tree basal area in Little Bald Hills over time. The thick line represents the observed increase in tree basal area, while the thinner gray line represents predicted values of basal area through 2109. Dashed gray lines are 95% prediction intervals. Estimated average basal area in 2059 is 26.92 ± 1.36 m²/ha, and 33.13 ± 1.94 m²/ha in 2109. Data for basal area begins in 1867.

be eventually outcompeted by Douglas-fir for light. The patchy distribution and low frequency of occurrence of Port Orford-cedar is likely due to its growth requirements; we found Port Orford-cedar only in mesic areas such as drainages and concave slopes, which is consistent with their known habitat preferences (Burns and Honkala, 1990; Stuart and Sawyer, 2001).

The rapid increase in the number of individual trees we observed in Little Bald Hills contrasts with other studies of plant community change on serpentine soils in the Pacific Northwest. Although they did not study encroachment *per se*, Damschen et al. (2010) found reduced numbers of conifers in serpentine areas in southern Oregon in 2007 compared with 1950. Briles et al. (2011) found only small changes in the relative composition of woody taxa on serpentine in the Klamath Mountains, including Jeffrey pine, throughout the long-term climate fluctuations of the Holocene epoch. Indeed, the comparative stability of serpentine communities has been proposed as fundamental to the evolution and retention of rare and disjunct plant populations. In contrast, our Little Bald Hills sites had a mean density of $14.2 (\pm 1.1 \text{ SE})$ trees per ha during the years 1850 and 1939, which increased to $236.4 (\pm 21.0 \text{ SE})$ for the years 1940–2009. The cool, wet climate of Little Bald Hills stands in sharp contrast to the more continental climates that the Damschen et al. (2010) and Briles et al. (2011) studies focused on. It is likely the coastal influence moderates the long and short-term changes in temperature and precipitation that more continental climes are subject to, allowing for greater rates of tree establishment at Little Bald Hills. Niche-partitioning models suggest that the differing abilities of grasses and woody vegetation to access soil water are what maintain the coexistence of herbaceous grassland and trees in savannas (Beckage et al., 2009), but this is likely not as important a factor in mesic savannas (Cole, 1986). While there may be some degree of seasonal water stress during summer months in Little Bald Hills, it likely has far less influence there than it would on hotter, drier inland sites, because the coastal savanna receives year-round fog or cloud cover, in addition to large amounts of winter rain. Ratajczak et al. (2012) report

Table 1
Coefficient estimates and their confidence intervals for the set of linear models relating rate of basal area growth to slope, elevation, and aspect for 26 plots. Bracketed numbers represent the 95% confidence interval around the coefficient estimates. The model with the lowest AICc value (Appendix G) was the null model.

Model	α	Slope	Elevation	Aspect	Slope x Elev.
Null (mean only)	0.1412 [0.1006, 0.1818]	*	*	*	*
Slope	0.1073 [0.0432, 0.1715]	0.0031 [−0.0015, 0.0076]	*	*	*
Elevation	0.2125 [−0.3458, 0.7707]	*	−0.0001 [−0.0011, 0.0009]	*	*
Aspect	0.1400 [0.0783, 0.2018]	*	*	0.0017 [−0.0640, 0.0674]	*
Slope + Elevation	0.0402 [−0.5692, 0.6496]	0.0033 [−0.0017, 0.0082]	0.0001 [−0.0010, 0.0012]	*	*
Slope + Aspect	0.1044 [0.0232, 0.1856]	0.0031 [−0.0016, 0.0077]	*	0.0040 [−0.0608, 0.0688]	*
Aspect + Elevation	0.2130 [−0.3587, 0.7846]	*	−0.0001 [−0.0012, 0.0009]	0.0026 [−0.0649, 0.0702]	*
Slope + Aspect + Elevation	0.0406 [−0.5839, 0.6652]	0.0033 [−0.0018, 0.0083]	0.0001 [−0.0010, 0.0012]	0.0034 [−0.0633, 0.0610]	*
Slope + Elevation + Slope × Elevation	0.0416 [−0.5840, 0.6672]	0.0033 [−0.0018, 0.0083]	0.0001 [−0.0010, 0.0012]	*	$4.769e-06$ [−0.0010, 0.0010]
Slope + Elevation + Aspect + Slope × Elevation	0.5081 [−0.5301, 1.5463]	−0.0249 [−0.0055, 0.0673]	−0.0007 [−0.0026, 0.0011]	0.0009 [−0.0655, 0.0673]	0.00005 [−0.00004, 0.0001]

Table 2

Classification error matrix for the logistic regression spatial model of encroachment. Numbers in bold are from the logistic regression model with model-averaged topographic parameter estimates, while non-bolded numbers are from the model with no topographic variables included.

	Reference condition		Producer's accuracy	User's accuracy
	Grass	Tree		
<i>Model classification</i>				
Grass	353/ 361	101/ 75	0.61/ 0.62	0.78/ 0.83
Tree	230/ 222	916/ 942	0.90/ 0.93	0.80/ 0.81
	Overall accuracy	0.79/ 0.81		
	Kappa	0.53/ 0.56		

Producer's accuracy is a measure of what percentage given reference data was correctly classified. User's accuracy is a measure of what percentage of the modeled class was correctly classified. Overall accuracy is a measure of the number of correctly classified pixels. The kappa statistic is a measure of the difference between actual and chance agreement in correct classifications; a kappa value of 0 indicates agreement is no better than by chance.

both the spatial extent and the impact of encroachment on species richness is related to precipitation, where higher precipitation corresponds to increased encroachment and decreased species richness.

While the maritime climate is likely key to the greater establishment and encroachment of conifers in Little Bald Hills when compared with inland serpentine sites, it does not account for the initiation of encroachment or the pulses in establishment occurring in the 1940s and 1980s. Lack of fire coupled with changes in land use since 1850 are likely the most important factors promoting conifer encroachment in Little Bald Hills. A fire history study for the Mill Creek watershed, which is directly adjacent to the study area and dominated by coast redwood, reports a composite mean fire return interval for a site ~1 km south of Little Bald Hills as 15.4 years \pm 7.3 SD for the years 1700–1849, and 21 years \pm 8.9 SD for the years 1850–1920 (Norman, 2007, see also Brown and Swetnam, 1994). The last fire known to directly impact Little Bald Hills occurred ~1940, 70 years before our encroachment study. Many fire ignitions in this area pre-1850 were likely of human origin (Norman, 2007; Lorimer et al., 2009) as the pre-European inhabitants of this area were known to seasonally burn hill-sides near their settlements (Drucker, 1937; Gould, 1975), although it is unknown how frequently. After the decline and expulsion of the indigenous inhabitants in the mid-19th century, ranching was the most common land use in Little Bald Hills through at least the 1950s, and both establishment rates and density of conifers during this time were low and steady (Fig. 2). The

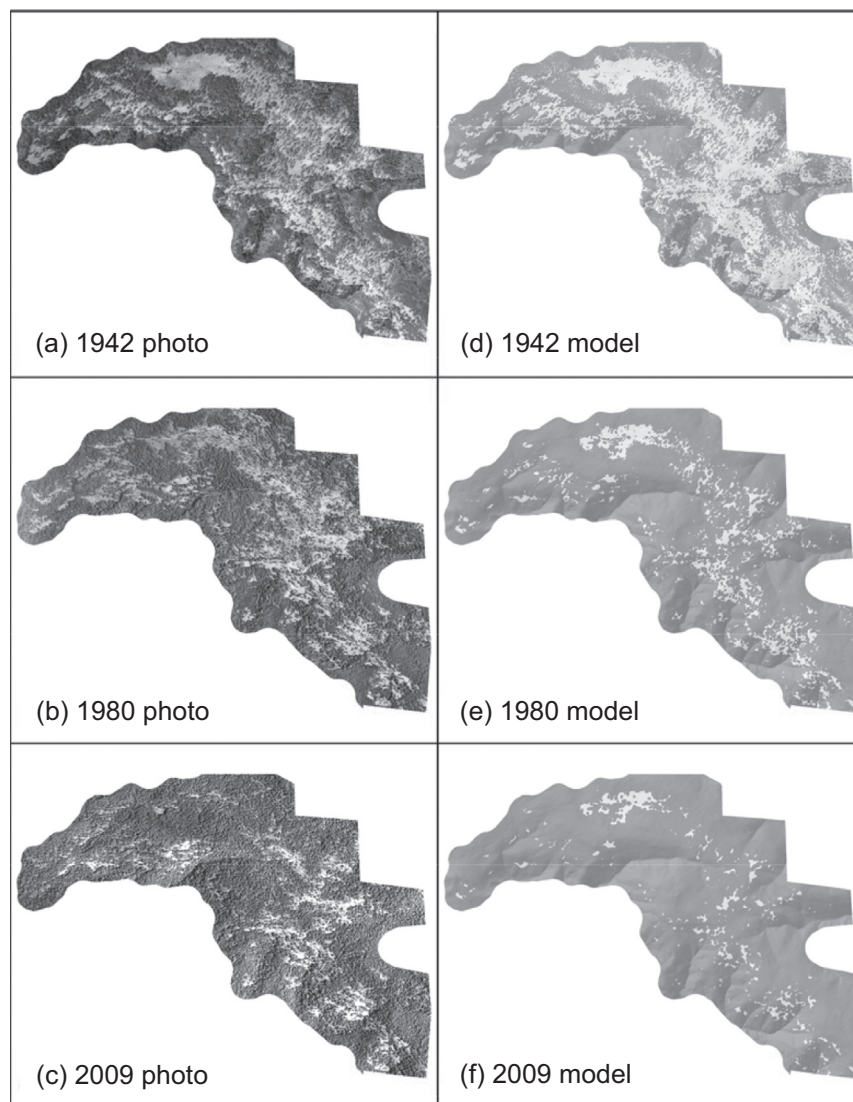


Fig. 5. Images of the Little Bald Hills study area for three given years with a resolution of 1-m or less (a, b, c) and their corresponding logistic regression model representations (d, e, f). In each of the model panels the raster resolution is 1-m, tree pixels are dark gray, and grassland pixels are light gray.

Table 3
Image classification and logistic regression model results of the historical aerial images analyzed and the proportion of each image predicted to be tree or grass. The logistic regression model results include four future predictions of grassland proportion. Numbers in bold are from the logistic regression model with model-averaged topographic parameter estimates, while non-bolded numbers are from the model with no topographic variables included.

Image year	Image classification proportion shadow	Image classification proportion grass	Logistic regression model proportion grass	
1942	0.1855	0.3286	0.5102	0.5208
1960	0.1329	0.3331	0.2766	0.2811
1975	0.1252	0.2686	0.1830	0.1861
1980	0.1393	0.2456	0.1622	0.1649
1988	0.2519	0.4017	0.1353	0.1375
1993	0.1442	0.2248	0.1216	0.1235
1998	0.2469	0.1128	0.1097	0.1114
2009	0.1812	0.0951	0.0887	0.0901
2019	–	–	0.0740	0.0751
2034	–	–	0.0569	0.0577
2059	–	–	0.0370	0.0376
2109	–	–	0.0165	0.0169

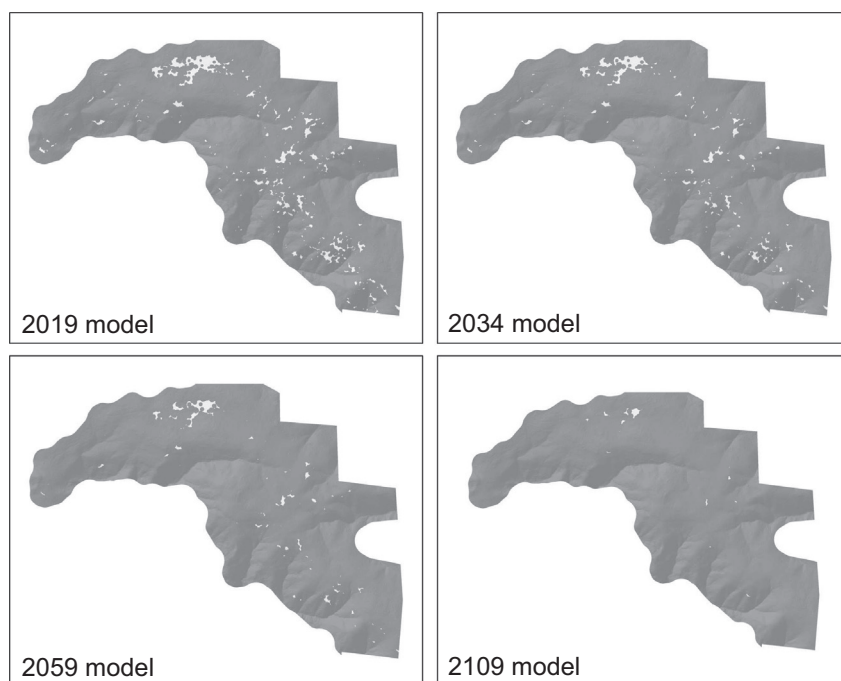


Fig. 6. Logistic regression model predictions of grassland (light gray) and tree (dark gray) coverage in Little Bald Hills for the years 2019, 2034, 2059 and 2109.

reported effects of grazing on tree establishment and encroachment are mixed, with grazing shown to both increase and reduce tree establishment (Madany and West, 1983; Miller and Halpern, 1998; Carmel and Kadmon, 1999; Silva et al., 2001; Sankey et al., 2006) and we were unable to test directly whether grazing reduced tree establishment in Little Bald Hills. But lower rates of tree establishment were evident through the 1940s, when earlier fire return intervals were likely much shorter than in the latter part of the 20th century and grazing was common in the area. The pulse of establishment beginning in the 1980s could be related to the closure of Little Bald Hills to off-road vehicle use in 1987 by Redwood National Park, or it could be a density-dependent demographic shift. As the first pulse of trees that established in the 1940s became reproductive individuals, a large increase in seed output could have resulted in the 1980 pulse, a trend that could continue as increasing numbers of trees reach reproductive maturity. Tree density was the most influential parameter in determining future locations of encroachment in the spatial logistic regression model.

That spatial model of tree encroachment is very useful for predicting areas where encroachment is likely to occur in the future across the landscape. General knowledge of system trajectories

and landscape-scale changes are often enough to provide land managers with the tools necessary for worthwhile ecological management. In Little Bald Hills, the predictive spatial logistic regression model is a good landscape-scale representation of encroachment (Table 2, Figs. 5 and 6) and has enabled park officials to develop an effective plan that will mitigate the effects of encroachment by targeting specific areas that meet restoration criteria and obtain funding through grant resources (S. Samuels, *personal communication*). A further management application is to utilize the reference conditions documented and assign restoration objectives a specific stand tree age, size, and density structure reflected by a specific time period. It is then possible to evaluate the effectiveness of restoration in meeting those criteria. Additionally, the spatial model created can be updated or modified as land use changes. National Agriculture Imagery Program (NAIP) projects are contracted annually and are currently on a three-year acquisition cycle, making free, highly accurate (within one meter), and geospatially rectified photos regularly available. As more imagery becomes available, a spatial model could be created that contains data from periods of specific land use, so that encroachment rates under varying land use histories can be determined. In other sav-

annas where topography might play a greater role in encroachment, the spatial logistic regression model could also be used to identify more specific microenvironments to target restoration efforts.

We expected to find a relationship between encroachment rates and elevation and slope since the serpentine vegetation community in this area is generally thought to be composed of scattered individuals of Jeffrey pine on xeric upper slopes and ridgetop sites (Alexander et al., 2007). Surprisingly, we found no relationship between encroachment and elevation or any other topographic site variable in the linear regression analysis (Appendix G, Table 1) and concluded that areas with Douglas-fir are just as likely to be encroached as those without.

In apparent contradiction to the results from the linear regression relating the rate of change in basal area to topography, seven of the top eight logistic regression models included topographic variables as predictors. However, the coefficient estimates for each topographic variable were all nearly zero, and the 95% confidence intervals for the three model-averaged topographic parameters all included zero, meaning the true parameter estimates of the variables were probably no different from zero (Appendix I). The inclusion of these variables in the top models is likely a result of the very large sample size of 4000. The maximum log-likelihood estimates for a model are the sums of the log-likelihoods for individual observations, and so even though the estimated parameters derived from the maximum likelihood estimates are small, when summed over 4000 observations the log-likelihoods were large enough to give a lower AIC value to models containing the topographic parameters than to the model that included only year and tree distance in 1942 as predictors. The estimated parameter coefficients for the topographic variables were so small that including the parameter estimates in the final model used to predict tree pixels changed less than 0.3% of the pixel assignments. It is therefore doubtful that the logistic regression analysis revealed a relationship between slope, aspect, and elevation that was not evident in the linear regression of encroachment rates by plot. However, model accuracy was slightly better using the model-averaged topographic parameters (Table 3) and including the topographic predictors created a cohesive model that could be applied to similar savanna systems where the influence of topography could play a larger role in encroachment rates and patterns.

There is some question as to whether the effects of encroachment are reversible. Rapid shifts in soil chemistry from grassland to forest characteristics that have been reported from tree invasion and encroachment studies are significant obstacles to overcome in restoring encroached areas (Hibbard et al., 2001; Suding et al., 2004; Griffiths et al., 2005; Browning et al., 2008). In addition to modifications of the soil, encroachment patterns that alter the composition of dominant plant species can make ecosystems resistant to the efforts of restoration (Suding et al., 2004). However, a recent study evaluating the success of restoration efforts, including prescribed fire and mechanical removal of stems, in an encroached meadow in the Cascade Mountains of Oregon indicated that the long-term presence of trees did not prevent recovery of herbaceous meadow species, and that restoration efforts of encroached areas can be successful (Halpern et al., 2012). Because none of the conifer species we studied resprout, removal of seedlings through prescribed fire or mechanical means are likely to be at least temporarily effective. Restoration plans for Little Bald Hills initiated by Redwood National Park in 2012 include the removal of trees in specific areas, opening up several avenues for future encroachment and restoration work.

Little Bald Hills is home to a large number of endemic, rare, and uncommon species and is also an important part of a larger pattern of landscape heterogeneity in the Klamath Mountains

(Duebendorfer, 1987; Jimerson et al., 1995; McGee-Houghton, 1995). While there is evidence that climate change is negatively affecting the herbaceous serpentine communities of the Klamath Mountains (Damschen et al., 2010), the mild, maritime climate of Little Bald Hills might temper the effects of climate change on herbaceous plants. However, the mild climate also appears to be allowing for encroachment of trees. The increase in cover and abundance of conifer species will likely lead directly to declines in species richness, as many of the species are associated with the grass-dominated vegetation in the area. In fact, one rare and endangered butterfly species whose southernmost habitat is Little Bald Hills, the Mardon skipper (*Polites mardon*), is dependent upon open grassy areas in the Pacific Northwest and loss of habitat is directly threatening its existence (United States Department of the Interior Fish and Wildlife Service, 2009).

The results of this study provide a quantitative basis for management and restoration plans in Little Bald Hills, providing suitable goals and appropriate evaluation measures. Moreover, the methods we used should be readily applicable for evaluating historical reference conditions, rates of change, and projected outcomes in other savanna areas that are suspected to be undergoing tree encroachment. It is unique in providing a cohesive approach to using both historical photo analysis and dendroecology to make predictions about future conditions. Our study is not the first to document changes in vegetation over time (e.g., Fulé et al., 2003; Coop and Givnish, 2007; Franco and Morgan, 2007), but in the case of Little Bald Hills, the loss of this rare serpentine savanna is predicted to be dramatic and our results broaden the argument for restoration efforts in a case where managers have, until now, relied on scant information about ecosystem changes (Goforth and Veirs, 1989; Redwood National and State Parks, 2010).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.12.019>.

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