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Vegetation Change from the Euro-American Settlement Era to the Present in Relation to Environment and Disturbance in Southwest Oregon

Abstract

Faced with landscapes degraded by fire suppression, logging, and grazing, land managers in the interior western US are attempting to restore habitat structure and function. In southwest Oregon, landscape-scale fuels treatments are being implemented with goals including recreating historic vegetation structure, despite poor understanding of the nature of the landscape prior to widespread Euro-American influence, or the patterns and processes of vegetation change over time. We compared a General Land Office-based reconstruction of Euro-American settlement era (1850s) vegetation in southwest Oregon's interior valleys and foothills with modern vegetation interpreted from aerial orthoimages to determine patterns of vegetation distribution in both eras, trajectories of vegetation change, and environmental and disturbance factors related to these themes. We found that this landscape was primarily occupied by closed plant community types in both eras, with a comparatively minor proportion in open types; vegetation was distributed along a dominant environmental gradient that ran from prairies in xeric lowlands to conifer forests in steeper, cooler uplands. Temporal shifts from open to closed vegetation were consistent with expected effects of fire suppression in many cases, but in other cases, the long-term persistence of open vegetation in the absence of recorded fire indicated that other mechanisms were also in operation. Human encroachment into wildlands, particularly in valleys, has also been a major driver of landscape-level change in the past 150 yr. Our results suggest that conservation should focus on lowlands, particularly where uncommon vegetation types such as savanna, shrubland, and prairie still exist.

Key words: vegetation distribution; environmental gradients; General Land Office surveys; southwest Oregon; Klamath-Siskiyou region.

Introduction

Much of the landscape within western North America is thought to be degraded as a result of fire suppression, timber harvest, and overgrazing (e.g., Hessburg et al. 1999). Mitigating degradation and restoring impaired ecosystems requires a thorough understanding of landscape-level processes and trajectories of change. The pre-Euro-American settlement period is often used as a baseline by which to judge the magnitude and direction of landscape change, and to describe reference conditions for restoration planning. The public land survey system, initiated in 1785 and later overseen by the General Land Office (GLO), represents one of the earliest, most reliable and systematic sources of historical landscape data available prior to extensive Euro-American influence (Liu et al. 2011). Although caution in using these records is needed to minimize errors and biases (e.g., Schulte and Mladenoff 2001), surveys in western regions were generally accurate and impartial, permitting detailed and spatially comprehensive vegetation reconstruction (Williams and Baker 2010). Because GLO surveys were implemented in much of the west approximately 150 yr ago (Galatowitsch 1990), assessing vegetation change relative to this baseline has an advantage over studies limited to shorter time periods by capturing a timescale relevant to natural disturbance intervals, forest management cycles, and community succession (Williams and Baker 2010).

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We compared a GLO-based reconstruction of Euro-American settlement era (1850s) vegetation in the Klamath-Siskiyou Mountains region of southwest Oregon with modern vegetation interpreted from aerial orthoimages to determine patterns of vegetation distribution in both eras, trajectories of vegetation change over time, and environmental and disturbance factors related to these themes. The Klamath-Siskiyou Mountain region is an area of tremendous geologic, topographic, and climatic diversity. This region supports an unusually high number of endemic and relic species due to its provision of an east-west dispersal link between the Coastal and Cascade Mountain ranges, and of refugia during glaciations, floods, and volcanic events (Whittaker 1960, Waring 1969). Understanding the nature of pre-settlement landscapes is particularly important in this region, as land managers are implementing landscape-scale vegetation treatments aimed, in part, at recreating historic vegetation structures, as well as at reducing fuels and fire severity (e.g., BLM 2011). While land managers strive for an ecological rationale behind treatments, the understanding of ecological relationships in southwest Oregon is generally poor, particularly for non-coniferous vegetation types (Franklin and Dyrness 1988, Hosten et al. 2006). For example, many land managers, biologists, and members of the public assume that the landscape was formerly much more open than it is at present (Hosten et al. 2007, Johnson and Franklin 2009, BLM 2011). Some contemporary stand structures do provide evidence of increasing woody plant densities (e.g., Hessburg et al. 2005). However, there is also evidence of historically dense vegetation structure (e.g., Detling 1961, Hosten et al. 2007) and of the persistence of some open areas even in the absence of fire (e.g., Hosten et al. 2007, Duren and Muir 2010). Recent calls for a substantial expansion of vegetation thinning projects with purported restoration objectives in this region and throughout the Pacific Northwest (Johnson and Franklin 2009) underscore the need for a better understanding of reference states.

To better understand landscape patterns and trajectories in southwest Oregon, we addressed the following questions: 1) What were the proportions of conifer, hardwood, and mixed conifer-hardwood forests, and savanna, shrubland, and prairie during the Euro-American settlement era? What are the current proportions? 2) What environmental and disturbance factors were associated with vegetation distribution in each era? 3) How has cover and distribution of these vegetation types changed since the settlement era, and what environmental and disturbance factors are related to those changes?

Study Area

Our focus was on an approximately 300,000-ha area in the low to mid-elevation (280 m to 1480 m) inland valleys and foothills of the Applegate, Illinois, and Rogue River watersheds (Figure 1). This area has a Mediterranean climate of cool, wet winters and hot, dry summers, and is the most xeric portion of the hottest, driest region west of the Cascade Mountains (Waring 1969, Franklin and Dyrness 1988). Mean annual precipitation is 820 mm, 7% of which falls in the summer; summer mean maximum temperature is 28.3 °C and winter mean minimum temperature is -0.3 °C (PRISM Climate Group 2006). Topography is steep and rugged with highly diverse soils formed from metasedimentary, metavolcanic, and weathered schist material (NRCS 2006). Generally, upland soils are relatively undeveloped, shallow to moderately deep loams with good drainage; most bottomland and alluvial fan soils are also well-drained but pockets of shrink-swell clays also occur (Franklin and Dyrness 1988).

Vegetation in the interior of southwest Oregon is transitional between the California and Pacific Northwest floristic provinces (Franklin and Dyrness 1988). Dominant conifers include Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and ponderosa pine (*Pinus ponderosa*), with lesser amounts of incense cedar (*Calocedrus decurrens*) and sugar pine (*Pinus lambertiana*), along with Jeffery pine (*Pinus jeffreyi*) on ultramafic soils and white fir (*Abies concolor*) at higher elevations (nomenclature follows Hickman 1993). Common hardwoods are Oregon white oak (*Quercus garryana*), Pacific madrone (*Arbutus menziesii*), California black oak (*Quercus kelloggii*), and bigleaf maple (*Acer macrophyllum*). Chaparral

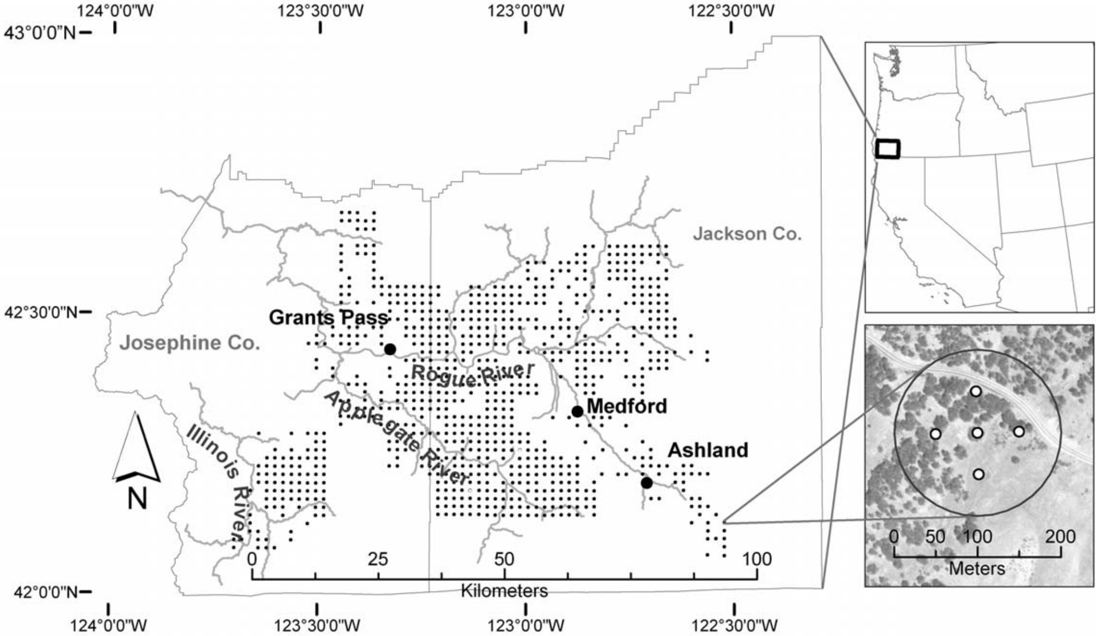

Figure 1. Study area (approximately 300,000 ha) in two counties in southwestern Oregon. Sample points (small dots, *n* = 792) were located at section corners. Current vegetation was interpreted in a circular area (r = 100 m) around each section corner from recent (2005) aerial orthoimages (lower right). Euro-American settlement era vegetation, and values of environmental and disturbance history characteristics, were identified from corresponding layers in a GIS at the section corner and 50 m distant from the corner in each cardinal direction (sampling scheme shown lower right).

shrubland reaches its northernmost extent in southwest Oregon (Detling 1961), and is dominated by buckbrush ceanothus (*Ceanothus cuneatus*) and whiteleaf manzanita (*Arctostaphylos viscida*) at low and mid-elevations, and green leaf manzanita (*Arctostaphylos patula*) at higher elevations. Other common upland shrubs include Pacific poison oak (*Toxicodendron diversilobum*), birchleaf mountain mahogany (*Cercocarpus betuloides*), Klamath plum (*Prunus subcordata*), Saskatoon serviceberry (*Amelanchier alnifolia*), and deer brush (*Ceanothus integerrimus*) (Pfaff 2007). Riparian and floodplain shrublands are composed of willow (*Salix* spp.), alder (*Alnus* spp.), gooseberries and currants (*Ribes* spp.), and salmonberry (*Rubus spectabilis*), among other species. Prairies include both wet and dry types, but xeric upland prairies are most common; these are contemporarily dominated by a mix of native and exotic graminoids and forbs, including Lemmon's needlegrass (*Achnatherum lemmonii*), wild oat (*Avena fatua*), cheatgrass (*Bromus tectorum*) and other exotic *Bromus* spp., hedgehog dogtail (*Cynosurus echinatus*), fescue (*Festuca* spp.), medusahead (*Taeniatherum caput-medusae*), fiddleneck (*Amsinckia* spp.), balsamroot (*Balsamorhiza* spp.), lupine (*Lupinus* spp.), and tarweed (*Madia* spp.) (Pfaff 2007).

Methods

Settlement Era Vegetation Maps

The development of settlement era vegetation maps is described in detail by Hickman and Christy (2009, 2011), but is summarized here for context. In southwest Oregon, the first significant influx of settlers was initiated by the discovery of gold in 1851. The U.S. General Land Office public land survey began in 1854, and although about 75% of field surveys in our study area were completed in the next five years, highly localized areas around mines and camps would have likely experienced minor alterations prior to surveys (Hickman and Christy 2011). Some isolated areas with very rugged terrain and low economic value were not surveyed until after the first decade, but the remoteness of these parcels suggests that they were probably not much changed by settlers before being surveyed (Hickman and Christy 2011). Surveyors established sections, 2.5 km (one mile) on a side, as a regular grid across the landscape; a township comprised a block of 36 sections. At each section corner, GLO surveyors were directed to record data for four bearing trees (when available), one in each compass quadrant, including tree species, diameter, and distance from the corner; information for two trees was recorded at quarter-section corners, halfway between section corners. When walking section lines, surveyors often took notes on vegetation, topography, soils, major disturbances, and locations of change in vegetation type; surveyors also charted a township-level map (see Bourdo 1956 for a detailed description of the grid system and survey methods).

Surveyors' spatially-explicit records formed the basis for maps of reconstructed settlement era vegetation. Consistent plant species groupings and surveyors' original distinctions were used to identify 89 unique vegetation classes, each of which was then assigned to a broad structural group (upland forest, riparian forest, woodland, savanna, shrubland, and prairie) based on distances to bearing trees, supplemented by surveyors' descriptors (e.g., 'dense', 'sparsely timbered') (Christy and Alverson 2011, Hickman and Christy 2011). Estimated mapping precision was highest (± 10 m) along section lines and corners, while vegetation in section interiors was often extrapolated due to limited information (Christy and Alverson 2011). (See Christy and Alverson [2011] and Hickman and Christy [2011] for complete methodology. GLO maps are available for download at http://www.pdx.edu/pnwlamp/glo-historical-vegetation-maps-oregon-0.)

In comparing historical vegetation with current vegetation, we attempted to minimize ambiguities while taking advantage of similarities in the two datasets. We limited comparisons to section corners, where GLO records were most precise and reconstructions were estimated to be most accurate. In an effort to reduce expected sources of error, we reclassified settlement era vegetation into coarse vegetation types defined by physiognomy and estimated tree canopy cover. Coarse vegetation classifications are less sensitive to surveyor bias toward certain species or tree diameters (Manies and Mladenoff 2000, Liu et al. 2011), but species composition information available in the finer vegetation class descriptions was used to guide reclassifications. The upland and riparian forest and woodland GLO structural groups were reclassified into conifer (no hardwoods mentioned in vegetation class descriptions), hardwood (no conifers mentioned), or mixed conifer-hardwood (both conifers and hardwoods mentioned) vegetation types. Savanna, shrubland, and prairie GLO structural groups were retained.

To make comparisons more robust, we estimated the range of canopy covers in each GLO vegetation type from distances to bearing trees (Christy and Alverson 2011), and matched this attribute to canopy cover of contemporary vegetation visible in aerial images. Although surveyors commonly failed to record the required number of trees at section corners, which can have large effects on tree density-based vegetation reconstructions (Williams and Baker 2010), omissions are likely to have had little impact on reconstructions for this project because distances to bearing trees were reported as averages (O. Eugene Hickman, NRCS [retired], personal communication). We used the range in distances to bearing tree to calculate the range in tree density (numbers of trees per ha) in each vegetation type using an alternative point-centered quarter method that requires random distribution around a section corner, rather than random distribution on the landscape (eqn. 4 in Bouldin 2008, derived from Morisita 1957). We estimated ranges in canopy cover by multiplying tree density by canopy widths for dominant, regionally-measured tree species (*Psuedotsuga menziesii* and *Pinus ponderosa*: Hann 1998, Dubrasich et al. 1997, and Gill et al. 2000; *Quercus garryana*: Hann 1998 and Gilligan 2010). The estimated canopy cover ranges in settlement era vegetation were then used, in main part, to define an equivalent set of contemporary vegetation types (Table 1). These methods produced definitions of

TABLE 1. Definitions of current vegetation types used for interpretation of vegetation cover from digital aerial orthoimages.

Canopy cover ≥ 25%	Closed
Canopy cover conifer ≥ 25%, hardwood < 10%	Conifer
Canopy cover conifer < 10%, hardwood ≥ 25%	Hardwood
Canopy cover both conifer and hardwood ≥ 10%	Mixed conifer-hardwood
Canopy cover of neither conifer nor hardwood ≥ 25%; cover of one or the other < 10%	Closed complex [a]
Canopy cover < 25%	Open
Canopy cover 10-24%	Savanna
Canopy cover < 10%, shrub cover > 75%	Shrubland
Canopy cover < 10%, herbaceous cover > 75%	Prairie
Canopy cover < 10%, cover of neither shrubs nor herbaceous > 75%	Mixed shrub-prairie [a]
Human-dominated cover > 25%	Human-dominated [a]

[a] These vegetation types were not represented on GLO maps.

'open' and 'closed' vegetation types that conformed to national vegetation classification standards (Federal Geographic Data Committee 1997).

We identified settlement era vegetation in a GIS at a total of five points around each section corner (at the corner and 50 m distant in each cardinal direction; Figure 1). The section corner was assigned to the vegetation type that occurred at four or more of these points. Site environmental data were not used for classifying the coarse-scale vegetation structural groups used here, but vegetation boundaries were sometimes related to landscape characteristics (e.g., topography and soils; Hickman and Christy 2011). To mitigate the influence of site environment on settlement era vegetation mapped at section corners, we excluded corners with more than one point in a different vegetation type.

Interpretation of Current Vegetation and Comparisons with Settlement Era Vegetation

We interpreted current vegetation from aerial color orthoimages (0.5 m resolution) taken in the summer of 2005 (horizontal accuracy ± 17.75 m; ER Mapper 2007) at 792 section corners where Hickman and Christy (2009) had mapped settlement era vegetation. In a GIS, an interpreter with local field experience (the first author) assigned cover classes (< 10%, 10– 24%, 25– 49%, 50 – 75%, and > 75%) to visible conifer, hardwood, shrub, prairie (forb and graminoid), and 'human-dominated' cover within a circular area around each section corner (r = 100 m). Combinations of these cover values were then used to assign each section corner to a vegetation type (Table 1). Human-dominated cover described areas at which semi-permanent human structures prevailed (e.g., roads, buildings, or agricultural fields). Areas in which human influence was ambiguous (e.g., unirrigated openings near buildings), and areas altered by semi-temporary disturbance (e.g., logged units), were assigned to a vegetation type according to their current cover. Cover classes of combined visible tree cover, and of combined visible prairie and shrub cover, were also recorded. Interpretations were made at 1:2500 without reference to landscape position, aspect, etc., because we later assessed the association of vegetation type to these and other environmental factors. Sample points with > 25% area obscured by shadow were excluded.

We compared settlement era vegetation type to the current vegetation type at each section corner to assess change over time. For insight into trajectories of vegetation change between our two-date sample, we also visually compared the settlement era vegetation map to a georeferenced vegetation map, charted roughly 50 yr after the GLO surveys

(Leiberg 1900), that overlapped roughly half the study area (21 townships).

Partial Assessment of Interpretation Accuracy

We assessed the accuracy of our aerial image interpretations by comparing them to field estimates of vegetation cover made in the same year as the aerial photos (Pfaff 2007). The field data were collected as part of a separate project, however, and so were not entirely congruous: vegetation cover was visually estimated using a relevé approach (Minnesota Department of Natural Resources 2007) rather than measured, and estimates were for patches that were not always the same size or coverage as our interpretation points. Nonetheless, this was the best comparison dataset available. In a GIS, we interpreted and classified vegetation from digital aerial images, as described above, within a circular area (r = 100 m) randomly positioned in patches where vegetation cover had been field-estimated ($n = 102$). To make field cover estimates and aerial interpretation more comparable, we adjusted the field cover estimates based on the assumption that conifer species overtopped hardwood species, and that hardwood species overtopped shrub and herbaceous species. We then assigned each field site to a vegetation type according to the same scheme as aerial interpretation sites. To reduce uncertainties introduced by the relevé-style approximations of field cover, we excluded from the comparison field sites near the cutoff between closed and open vegetation type definitions (25% ± 5% tree cover). A sufficient number of field sites were available for assessing aerial photo interpretation accuracy of only the closed hardwood and open (combined savanna, shrubland, and prairie) vegetation types.

The Relationship of Environment and Disturbance to Settlement Era Vegetation, Current Vegetation, and Patterns of Vegetation Change

Values of environmental characteristics likely to influence settlement era vegetation, and of environmental and disturbance characteristics potentially important to contemporary vegetation and vegetation change (Table 2), were sampled in a GIS at section corners and 50 m distant from the corner in each cardinal direction (Figure 1). We calculated the value for quantitative variables as the average of the five points, and the value for categorical variables as the value at site center. Environmental variables included climate, terrain, and geology and soils characteristics. Disturbance variables included: recorded fire history; distance to the nearest public highway, road, or trail as an indicator of potential anthropogenic disturbance; and percent of sections around the corner in federal ownership as an indicator of certain anthropogenic disturbances such as agriculture or forestry.

To identify major gradients in environment and disturbance, and vegetation associations with those gradients, we mapped each site in the space defined by its environmental and disturbance attributes using nonmetric multidimensional scaling (NMS) ordination, implemented in PC-ORD version 6.255 (McCune and Mefford 2011). Separate ordinations were carried out for each era. We assumed that abiotic environmental conditions were reasonably stable from the settlement era to the present; therefore, strategies for ordination of historical and current sites differed only in the inclusion of disturbance and land ownership variables for the latter. Variations in climate are likely to influence expansions and contractions of vegetation communities (e.g., Bachelet et al. 2011), but tracking these trends was beyond the scope of this paper. Categorical attributes (e.g., parent material type) were first converted into sets of binary membership/non-membership variables. Quantitative variables with skew > 1 were log-transformed to improve homogeneity of variance, and all variables were relativized by their standard deviates so that each contributed equally to the ordination (McCune and Grace 2002). Twenty-nine outlier sites were detected and removed from datasets for both eras, and analysis proceeded with $n = 763$. NMS was run using Euclidean distance with a random starting configuration and 250 runs with real data; the final solutions were produced by rerunning NMS with the best ordination as the starting configuration. We overlaid vegetation type identity on the ordinations and inspected correlation coefficients (Pearson's r) between

TABLE 2. Site environmental and disturbance characteristics analyzed in relation to Euro-American settlement-era vegetation, contemporary vegetation, and vegetation change.

	Measures	Source
Climate	Precipitation (spring, summer, fall, winter, and annual); min. temperature in each season and avg. annual min. temperature; and max. temperature in each season and avg. annual max. temperature (all based on monthly averages, 1971–2000)	PRISM Climate Group 2006
Terrain	Elevation, % slope, and aspect folded to reflect potential moisture (= |180−|aspect−225||; McCune 2007)	Calculated from a digital elevation model (BLM n. d. a)
	Potential direct incident radiation and heat load (indices of solar interception)	Calculated in HyperNiche (McCune and Mefford 2008); see McCune 2007
	Sixth field watershed membership	NRCS 2008
	Subecoregion membership	EPA 2011
Geology and soils	Parent material; % clay, silt, and sand; cation exchange capacity; pH; linear extensibility; depth to restrictive layer; drainage class	NRCS 2006
Recorded fire disturbance (1905-2005)	Number of fires, number yr since last fire, max. interval between fires, min. interval between fires	BLM 2006
Potential human access and disturbance	Distance to nearest highway, road, or trail	Calculated from a transportation layer (BLM n. d. b)
	Percent of site in federal ownership	BLM 2009

ordination axes and quantitative environmental and disturbance variables to detect variables most strongly associated with vegetation distribution in each era.

We also identified environmental and disturbance characteristics predictive of historical and contemporary vegetation distributions, and of transitions in vegetation over time (e.g., change from historical prairie to contemporary savanna), using nonparametric multiplicative regression (NPMR). Models for the full data set (n = 792) were explored for each vegetation type in each era, and for all transitions between vegetation types. Variables available for model selection included: slope, aspect, elevation, minimum winter and maximum summer temperature, annual precipitation, parent material, soil % sand and clay, soil pH, drainage, depth to restrictive layer, distance to nearest highway, road, or trail, and fire history. Predictors with skew > 1 were log-tranformed. We implemented this analysis in HYPERNICHE version 2.13 (McCune and Mefford 2008) using local mean, Gaussian weights, and minimum average N^* = 38; minimum N^* = 42 was required to produce an estimate. Model statistical significance was evaluated with 20 randomizations, moderate controls on overfitting, and the same N^* as model building.

Differences in environment and disturbance characteristics among vegetation types or between time periods were tested with multi-response permutation procedure (MRPP; Mielke and Berry 2001) with relative Euclidean distance, in PC-ORD. With large sample sizes, statistical significance ($P \leq 0.05$) may result even when the size of the difference, A (range 0-1), is small (McCune and

Grace 2002). Therefore, we considered results with $A < 0.2$ to lack ecological significance, and these were not interpreted.

Results

Landscape-scale Vegetation in the Settlement and Contemporary Eras

Overall accuracy of aerial image interpretation of current closed hardwood and open vegetation types, relative to field-approximated cover, was 76.5%. Because the distinction between these vegetation types, particularly between short hardwoods and tall shrubs, was more difficult than the distinction between other vegetation types, we consider this to be minimum accuracy for the study as a whole.

The interior valleys and foothills of southwest Oregon in both the Euro-American settlement era and in the present were primarily covered in closed forests, with a comparatively minor proportion in open vegetation types (Table 3). In the settlement era, most forested areas were mixed conifer-hardwood, with the balance distributed more or less equally between conifer and hardwood. Most of the open areas were dominated by prairie, with only minor shrubland and savanna components. This overall pattern is still generally true today, except that among closed types, mixed conifer-hardwood appears to have diminished while conifer and hardwood have each increased; among open types, savanna cover has increased and prairie cover has decreased such that the cover of these types is now similar. Human-dominated areas have usurped a substantial proportion of the modern landscape.

Vegetation Associations with Environment and Disturbance

The environmental associations of vegetation, as depicted by ordinations (Figure 2), were nearly identical in both eras, as would be expected if abiotic environmental conditions and their influences on vegetation were fairly stable across time. Therefore, we present results from the ordination of current vegetation (Table 4) as representative of both time periods. Ordinations were high quality for both eras, with ≥ 85.1% cumulative R^2 over three axes when varimax rotated (ordination of current vegetation: stress = 18.98, 38 iterations, instability < 0.00001; ordination of historical vegetation: stress = 15.30, 122 iterations, instability < 0.00001). All three axes provided more reduction in stress than expected by chance ($P \leq 0.01$, Monte Carlo test with 250 randomized runs).

Patterns in vegetation distribution were mostly described by Axis 1, which represented a gradient

TABLE 3. Proportions (%) of section corners (n = 792) in each vegetation type in historic (Euro-American settlement era) and contemporary landscapes. See Table 1 for vegetation type definitions.

	Sum closed types	Conifer	Hardwood	Mixed-conifer-hardwood	Closed complex
Historic	**82.4**	4.9[a]	1.0	76.5	–[b]
Current	**78.2**	21.1	18.2	38.4	0.5
Change	***-4.2***	*+16.2*[a]	*+17.2*	*-38.1*	*+0.5*[b]

	Sum open types	Savanna	Shrubland	Prairie	Mixed shrub-prairie
Historic	**17.6**	1.5	1.1	14.9	–[b]
Current	**12.4**	5.9	1.1	4.3	1.0
Change	***-5.2***	*+4.4*	*0*	*-10.6*	*+1.0*[b]

	Human dominated
Historic	**–**[b]
Current	**9.5**
Change	***+9.5***[b]

[a] GLO vegetation descriptions were sometimes ambiguous and suggest that about one third of these sites may be alternatively classified as mixed conifer-hardwood.

[b] These vegetation types were not represented on GLO maps.

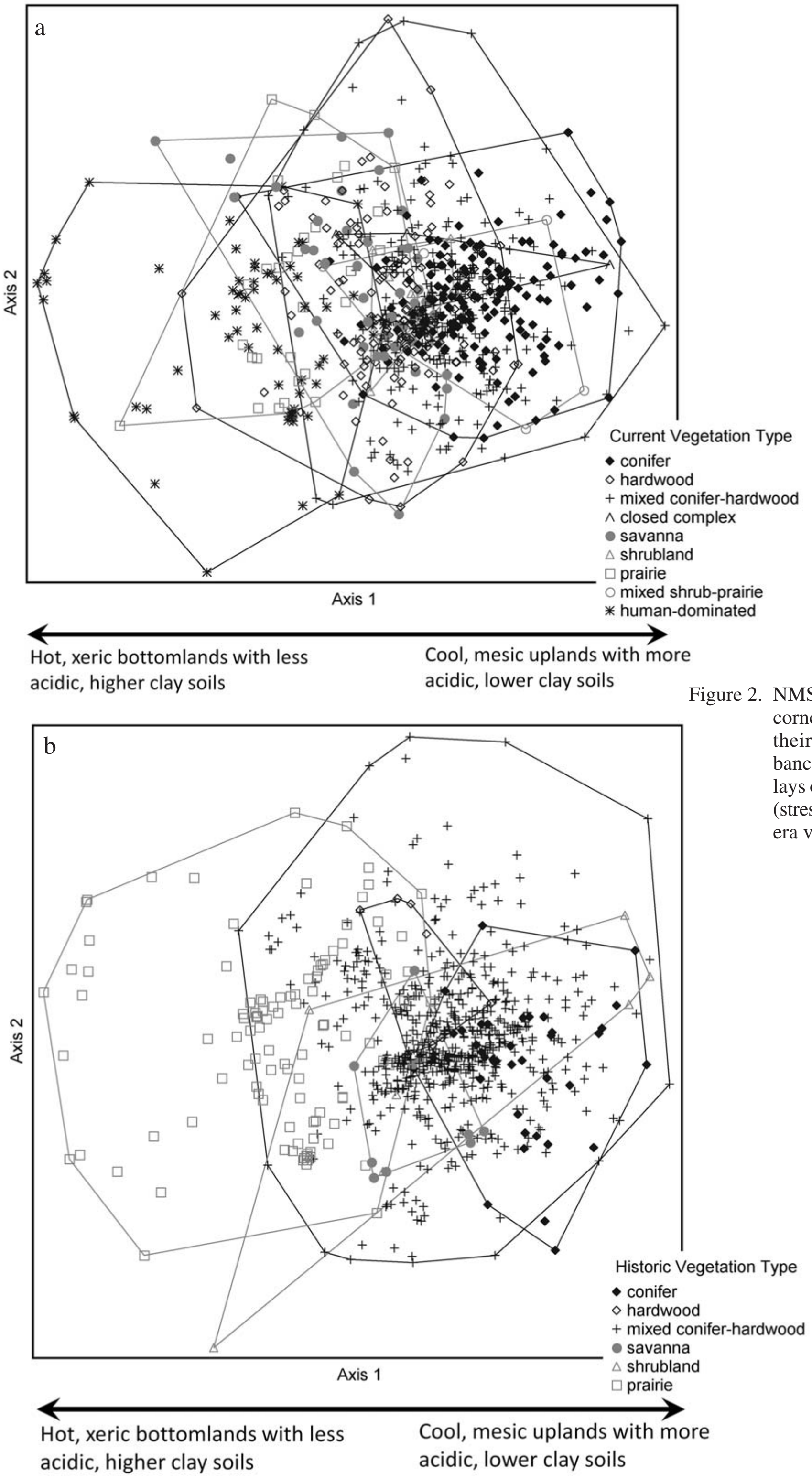

Figure 2. NMS ordination of sites (section corners) in the space defined by their environmental and disturbance characteristics, with overlays of their (a) current vegetation (stress = 18.98), and (b) settlement era vegetation (stress = 15.30).

TABLE 4. Correlations (Pearson's r) of quantitative environmental and disturbance variables with NMS ordination axes for the ordination of current vegetation. Patterns in vegetation distribution were mostly described by Axis 1. This ordination was nearly identical to the ordination of settlement era vegetation, which included the same environmental characteristics but excluded disturbance variables. Only correlations with $r > |0.500|$ are shown.

Axis:	1	2	3
% Variation represented (R^2)	43.2	22.8	19.1
Max. temp., avg. (°C)	-0.701	-	-
Max. temp., summer (°C)	-0.737	-	-
Max. temp., spring (°C)	-0.717	-	-
Max. temp., winter (°C)	-0.615	-	-
Max. temp., fall (°C)	-0.579	-	-
Min. temp., avg. (°C)	-	-0.637	-
Min. temp., spring (°C)	-	-0.699	-
Min. temp., winter (°C)	-	-0.672	-
Precipitation, annual (mm)	0.532	-	-0.583
Precipitation, summer (mm)	0.530	0.527	-
Precipitation, winter (mm)	0.523	-	-0.599
Precipitation, fall (mm)	0.505	-	-0.602
Slope (%)	0.687	-	-
Elevation (ft)	0.666	-	-
Soil pH	-0.559	-	-
Soil linear extensibility (%)	-0.535	-	-
Soil clay (%)	-0.521	0.505	-
Soil sand (%)	-	-0.530	-
Soil cation exchange capacity (mEq per 100 g)	-0.561	-	-

from hotter, drier, flatter, lower elevation sites with less acidic soils higher in clay and linear extensibility to colder, moister, steeper, higher elevation sites with more acidic soils lower in clay and linear extensibility (Table 4). Sites supporting prairie tended to aggregate toward the lower elevation, more xeric end of the gradient. Savannas, hardwood, and mixed conifer-hardwood had more mesic affinities, and conifer sites were associated with the highest, coolest, and wettest end of the gradient. Shrubland sites lacked a unified association with environment: shrubland sites in colder, steeper, higher elevation areas of the ordination were identified on GLO maps as high-elevation type chaparral, while shrub sites in warmer, flatter, lower elevation areas were described as creek brush. Open areas with mixed shrub-prairie vegetation (a type not identifiable in settlement era vegetation) shared environmental space with closed vegetation types; half of these points had been burned or treated with fuels management in the last 25 yr. Areas now dominated by human activities were mainly in the lowest, hottest, flattest, driest parts of the landscape. Associations of settlement era vegetation with environment were very similar to those of current vegetation, except that savannas appear to have been historically less associated with the lower elevation, hotter, flatter end of the environmental gradient.

Environmental characteristics selected by regression models as most predictive of vegetation distribution in the settlement era and in the present reflected similar relationships as those described by ordinations (data not shown). Models underscored the importance of moisture and temperature to vegetation distribution. For example, some lower elevation, flat areas supported conifer-dominated vegetation, as long as precipitation was high or summer temperatures were cool.

Little relationship of current vegetation to indicators of known or potential disturbance history was identifiable from ordinations ($r \leq |0.166|$). Similarly, regression models did not identify any disturbance variables as strongly associated with current vegetation.

Changes in Vegetation from the Settlement Era to the Present

Most section corners with conifer vegetation in the settlement era still support that type in the contemporary landscape (Table 5, Figure 3). Much of the historical mixed conifer-hardwood is still in this vegetation type, but substantial portions appear to have transitioned to either conifer or hardwood. Most former hardwood vegetation is now savanna, while the majority of settlement era savanna is now hardwood or mixed conifer-hardwood. Most historical shrublands are now conifer. About a third of the section corners supporting prairie in the settlement era are still in this vegetation type, but half are now human-dominated, with the remainder in either savanna or closed vegetation types.

TABLE 5. Vegetation transitions or stabilities from the Euro-American settlement era (1850s) to the present (2005) as the proportion of total sites (section corners) within each historic vegetation type. Entries indicating vegetation stability are *italicized*; dominant pathways are **bolded**. The number of sites in a given vegetation type is indicated by n. Column or row summations that differ from totals are the result of rounding.

	Historical cover type									
Current cover type	Prairie ($n = 118$)	Mixed shrub-prairie ($n = 0$)[a]	Shrubland ($n = 9$)	Savanna ($n = 12$)	Closed complex ($n = 0$)[a]	Hardwood ($n = 8$)	Mixed conifer-hardwood ($n = 606$)	Conifer ($n = 39$)	Human-dominated ($n = 0$)[a]	Current proportion of total sites in landscape ($n = 792$)
Prairie ($n = 34$)	*0.280*	0	0	0	0	0	0.002	0	0	0.043
Mixed shrub-prairie ($n = 8$)	0.008	*0*	0	0	0	0	0.012	0	0	0.010
Shrubland ($n = 9$)	0	0	*0*	0.083	0	0	0.013	0	0	0.011
Savanna ($n = 47$)	0.102	0	0	*0.083*	0	**0.625**	0.046	0.026	0	0.059
Closed complex ($n = 4$)	0	0	0	0	*0*	0	0.007	0	0	0.005
Hardwood ($n = 144$)	0.059	0	0.111	0.167	0	*0.250*	0.218	0	0	0.182
Mixed conifer-hardwood ($n = 304$)	0.017	0	0	**0.583**	0	0	***0.469***	0.282[b]	0	0.384
Conifer ($n = 167$)	0.017	0	**0.556**	0.083	0	0.125	0.216	***0.692***	0	0.211
Human-dominated ($n = 75$)	**0.517**	0	0.333	0	0	0	0.018	0	*0*	0.095
Historical proportion of total sites in landscape ($n = 792$)	0.149	0	0.011	0.015	0	0.010	0.765	0.049	0	1.000

[a] These vegetation types were not represented on GLO maps.

[b] GLO vegetation descriptions were sometimes ambiguous and suggest that about one third of these sites may be alternatively classified as mixed conifer-hardwood.

Both the 1850s GLO map and Leiberg's (1900) later vegetation map showed woodlands and forests above generally open valleys, with strips of gallery forest lining larger rivers. Leiberg's map, however, depicted the replacement of many wooded areas on lower slopes with what he classified as "non-forested [such] as marshes, meadows, or agricultural lands", probably reflecting the expanding land modifications of Euro-American settlers.

Although many observed transition pathways were not represented by enough cases to produce interpretable models, some relationships between environment and vegetation transitions or stabilities were identified in NPMR (Table 6). We interpreted only those models with reasonable explanatory power ($\text{ave}B \geq 1.06$; see table caption). All models presented were statistically significant ($P < 0.05$).

Areas with apparently stable closed vegetation tended to be on steeper slopes, but were also in flatter areas with cooler summer temperatures. Areas supporting open vegetation in both eras tended to be on flatter slopes, and were somewhat more likely on Holocene and Pleistocene-age parent material of terraces, pediments, and lag gravels, a geology type often found in valley bottoms near rivers. Sites supporting apparently stable prairie were at lower elevations, and were also associated with terrace, pediment, and lag gravel parent material. Areas that had historically supported open vegetation in general, or prairie in particular, but that were currently human-dominated, were associated with the driest, hottest parts of the landscape. Human-dominated areas occupied the same environments as settlement era and current

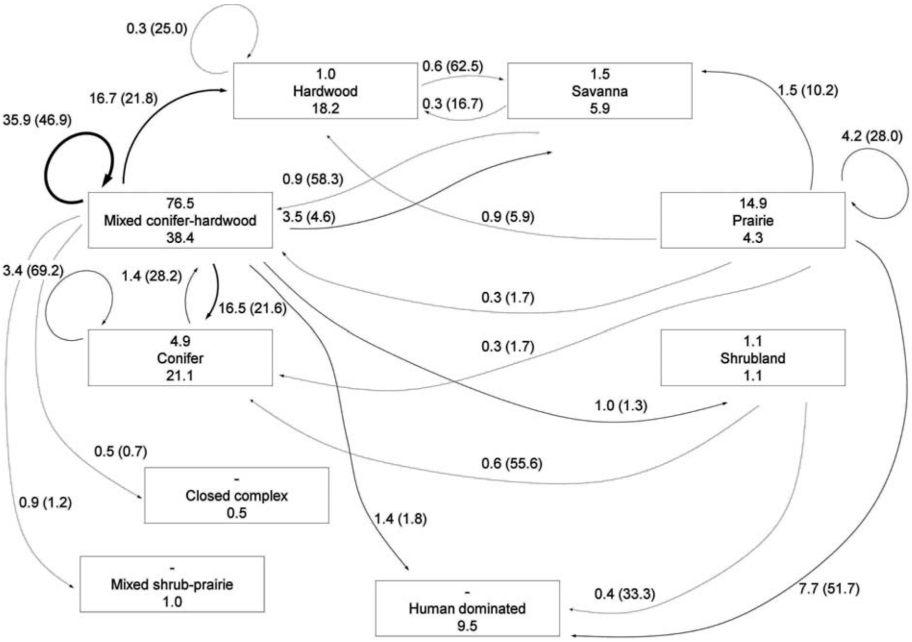

Figure 3. Major vegetation states and rates of transition over 150 yr from the Euro-American settlement era to the present. All pathways with > 0.2% of sampled sites (section corners) are shown (*n* = 784; 99% of all sites). Arrow thickness is proportional to the relative dominance of the transition pathway; numbers with arrows are the percent of all sites that followed that pathway and, in parentheses, the percent of sites in that historic vegetation type that followed that pathway. Numbers above and below vegetation types in boxes are, respectively, historic (early 1850s) and current (2005) percentages of the landscape in that vegetation type. Closed complex, mixed shrub-prairie and human-dominated types had no historic analog. (Figure style adapted from Kennedy and Spies 2004.)

TABLE 6. NPMR models describing environmental and disturbance characteristics predictive of transitions between settlement era and current vegetation. "Stable" indicates no change between eras. Model fit, ave*B*, describes how much more likely the selected model is than the null model. A minimum ave*B* of 1.06 (each sample improves the likelihood of the selected model over the null model by 6%) was required to consider the model interpretable. The cross-validated pseudo-R-squared, xR^2, also describes model fit; this statistic is included for illustrative purposes, though it is less relevant to the type of model building used here. Relative predictor importance (sensitivity) is listed in parentheses; a value of 1.0 means that nudging the predictor by a given amount results in a change in the response of equal magnitude, and a value of 0.0 means that nudging the predictor has no effect on the response (McCune and Mefford 2008). Sensitivities for parent material, a categorical variable, are not interpretable, as indicated by (-).

Response	ave*B*	xR^2	Selected predictors	
Stable closed vegetation types (*n* = 592)	1.30	0.517	Max. summer temp.(0.1733)	Slope (0.1613)
Stable open vegetation types (*n* = 48)	1.12	0.365	Slope (0.2201)	Parent material Qt (-)[a]
Stable prairie (*n* = 33)	1.08	0.276	Elevation (0.1305)	Parent material Qt (-)[a]
Former open vegetation now human-dominated (*n* = 64)	1.22	0.603	Max. summer temp. (0.1946)	Ann. precipitation (0.1318)
Former prairie now human-dominated (*n* =61)	1.20	0.571	Max. summer temp. (0.1904)	Ann. precipitation (0.1407)

[a] Qt is a geological unit of terraces, pediments, and lag gravels of Holocene and Pleistocene age; these are generally found in valley bottoms near rivers.

prairie vegetation (i.e., differences in environment were ecologically insignificant, $A < 0.2$, MRPP).

Regressions describing transitions from closed to open vegetation were weak (ave$B < 1.06$), but a closer look at the 50 section corners where such transitions occurred showed that about half had been disturbed within the last 25 yr (fuels treated, $n = 10$; burned, $n = 13$) or were bisected by roads ($n = 3$); the remainder, however, had no recorded or visible (from aerial images) history of disturbance. Of the historically open areas, recorded fire history was not different between those that were still open and those now closed ($P = 0.302$, MRPP); most had not had a recorded fire in ≥ 69 yr. Section corners with historically open vegetation that was now closed were more likely to be at least partially federally-owned than were those that remained open ($A = 0.255$, $P < 0.0001$, MRPP).

Discussion

Vegetation in the Settlement Era

Our results, along with the notes of early surveyors and settlers (Leiberg 1900; Pullen 1996; Hickman and Christy 2009, 2011), provide a snapshot of the varied Euro-American settlement era landscape in the interior valleys and foothills of southwest Oregon. Foothills were mostly covered in mixed conifer-hardwood forests that included a variety of hardwoods with moist mixed-species conifer or dry, relatively open pine. Foothills also supported more limited conifer forests of true fir or mixed Douglas-fir and ponderosa pine, and hardwood forests of Oregon white oak or madrone. Open vegetation types covered just under a fifth of the landscape. On foothills were found occasional grass balds and chaparral patches of ceanothus, manzanita, and mountain mahogany, or mid-elevation brushfields of serviceberry, cherry, plum, and scrub oak, but most open vegetation was in the valleys. Bottomlands were dominated by prairie, including xeric upland types or vernal pool and marshy wet meadow, but some mixed conifer-hardwood stands and minor amounts of pine or oak savanna, riparian hardwood forests, willow swamps, and brushy floodplains were also found in valleys. Chaparral patches grew in valley ravines or were scattered across savannas and prairies (Pullen 1996, Hickman and Christy 2009). Although these and other shrublands occupied only a fragment of the landscape (~1 %), shrubs were important components of many other vegetation types: many forest understories were shrubby (Leiberg 1900, Pullen 1996, Hickman and Christy 2009) and settlers and surveyors often complained that dense brush impeded travel or concealed enemies (Pullen 1996). All vegetation types were also present as inclusions within other vegetation but were often too small to be mapped (Hickman and Christy 2011).

Vegetation and the Environment

A predominant environmental gradient in both the settlement and contemporary eras ran from (1) the lowest, flattest, most xeric conditions supporting prairie, through (2) increasingly mesic areas associated with savanna, hardwood, mixed conifer-hardwood, and some shrubland types, to (3) higher elevation, steeper, wetter locations supporting conifer as well as other shrubland types. Foothill upper slopes and ridges also sustain grass balds, but often above the elevations sampled in this study (Pfaff 2007). Although ours is the first *a priori* attempt of which we are aware to quantitatively identify factors important to the landscape-scale distribution of all major valley and foothill vegetation types, our results reaffirm previous studies that similarly describe the importance of these characteristics to regional vegetation (Waring 1969, Riegel et al. 1992, Ohmann and Spies 1998, Taylor and Skinner 1998, Pfaff 2007).

Topographic and moisture gradients tend to be more influential on species distribution in drier climatic regions (Ohmann and Spies 1998), and have long been thought to be primary drivers of the complex vegetation mosaics of southwest Oregon (Leiberg 1900, Whittaker 1960, Pullen 1996) and similar regions of California (Barbour 1987, Gudmunds and Barbour 1987). For example, mesic sites are able to support conifer and mixed conifer-hardwood vegetation that often exclude slower-growing, shade-intolerant hardwoods such as Oregon white oak (Stein 1990). Hotter aspects and lower elevation areas, on the other hand, have higher moisture stress and soil temperatures that limit conifer seed germination and seedling survival (Herman and Lavender 1990, Oliver and Ryker 1990), favoring Oregon white oak (Whittaker 1960, Ohmann and Spies 1998). Topography also influences soil characteristics we identified as important to vegetation distribution. For example, dissolved salts move downslope and accumulate in lower-lying areas (Brady and Weil 2002), increasing the pH of lowland soils on which open vegetation types tended to occur. Soil clay content and linear extensibility tended to be greater at lower elevations; these soil characteristics may be more suitable to oak savanna and other open vegetation types (Hosten et al. 2007), as Douglas-fir and ponderosa pine are less tolerant of poor wet-season drainage, limited dry-season water availability, and high soil strength of high-clay soils than is Oregon white oak (Herman and Lavender 1990, Oliver and Ryker 1990, Stein 1990).

Environmental associations of uncommon vegetation types were unclear. Relationships can be obscured by within-type heterogeneity (e.g., the different shrubland types in our study area have unique associations with elevation, moisture, and soils conditions; Pfaff 2007). The association of a vegetation type with one environmental gradient can also be modified by another (e.g., whiteleaf manzanita occurred on xeric sites on 'normal' soils, but on mesic sites on ultramafic soils; Whittaker 1960). Future studies may benefit from finer distinctions within vegetation types, but this would require a much larger sample size than we had to work with, and would also require species-level vegetation data.

Long-term Vegetation Change

Although change from one vegetation type to another occurred at most (56.2%) section corners, transitions tended to balance out such that the overall character of the landscape was similar between the settlement era and the present. In both eras, the landscape was mostly covered by closed forests and woodlands, with a comparatively minor proportion in open vegetation types. When sites from one historical vegetation type changed into multiple contemporary vegetation types, we usually lacked sufficient sample sizes to explore statistically factors related to different transition pathways. Successful models generally described sites where vegetation had not transitioned; we interpreted these models as simply reflecting the environmental or disturbance conditions with which a particular vegetation type was associated. Despite these limitations, several interesting transition patterns emerged.

Our results, in some cases, substantiate the conventional wisdom that altered fire dynamics have been instrumental in landscape change: 21.7% of the transitions were consistent with the expected effects of fire suppression policy, which, in our study area, resulted in the exclusion of most fires after the first half of the 1900s (Atzet 1996). Observed conversions of former mixed conifer-hardwood to conifer vegetation are consistent with the loss of less shade-tolerant hardwoods that is associated with fire exclusion, as are recorded encroachments of trees into former prairies, shrublands, and savannas. The loss of open area was not substantial in our study area (17.6% historically vs. 12.4% in the present), but is consistent with a trend documented by other regional comparisons of historical and current conditions (Thilenius 1968, LaLande 1995, Skinner 1995, Kennedy and Spies 2004, Hosten et al. 2007). Federal ownership was greater for sites that transitioned from open to closed vegetation, as has been observed in other parts of western Oregon (Ohmann and Spies 1998, Kennedy and Spies 2004), which may suggest that federal management strategies have more effectively excluded disturbance than has private management at many sites.

Of course, landscape-level dynamics also shifted much earlier than the effective implementation of fire exclusion policy. The mass arrival of Euro-Americans in the 1850s substantially altered fire and grazing regimes (Leiberg 1900, Whittaker 1960, LaLande 1995, Pullen 1996, Borman 2005), which coincided with climatic periods favorable to tree establishment (Borman 2005). Nearby dendroecological studies have recorded shifts in tree recruitment dynamics and species composition corresponding to both the settlement period and the later implementation of effective fire suppression (Gilligan and Muir

2011, Messier et al. 2012). We did not detect an explicit association of known fire history with vegetation distribution or with changes over time, but our ability to do so may have been hampered by changes in the fire regime prior to the earliest available records (ca. 1910), as well as the less robust quality of the early records.

Although transitions from open to closed vegetation were common, we also recorded the long-term persistence of many prairie sites, even in the absence of recorded fire, as has been documented in other grasslands, savannas, and shrublands in the region (Detling 1961, Hosten et al. 2007, Duren and Muir 2010). This apparent stability suggests that patterns of vegetation change cannot be explained simply by shifts in fire regimes, but that other factors are also important. Xeric conditions and edaphic factors such as heavy clay soils can limit tree encroachment, as discussed above. Human activities such as historical Native American burning (Pullen 1996) and modern mowing or light grazing may maintain some lowland prairie sites that would otherwise be favorable to closed vegetation. (These uses would not necessarily have been identified as the 'human-dominated' cover type if the result appeared similar to unmanaged areas in aerial images.) Alternatively, the conversion from open to closed vegetation may be occurring on some sites on a timescale longer than that of this study (> 150 yr).

Among closed vegetation types, transitions were primarily to other closed types. The transition from mixed conifer-hardwood to conifer may be a result of fire exclusion, as discussed above. The factors underlying the redistribution of former mixed conifer-hardwood into hardwood are less clear, although a transition of similar magnitude was observed in the central Oregon coast range and attributed to logging disturbance (Kennedy and Spies 2004). This pattern may also, to some extent, be an artifact of differences and ambiguities in settlement era and modern era datasets.

Human encroachment into wildlands has also been a considerable force for landscape-level change in the past 150 yr in southwest Oregon, particularly in the relatively flat lowland areas. Most areas now in semi-permanent human use were once prairies, which were presumably easiest to clear for development, though some former mixed conifer-hardwood and shrubland sites have also been converted. Comparison of the 1850s GLO map to a 1899 vegetation map reflected human encroachment into valleys and lower slopes only ~50 yr after settlement. Contemporaneous government surveyors noted widespread timber cutting, burning, and cultivation during this time (Leiberg 1900, Gannett 1902, Harvey 1909, Hosten et al. 2007), resulting in a much greater proportion of the landscape in open area (Gannett 1902) compared to the settlement era. Today, the two counties that encompass the study area (Jackson and Josephine counties) are ranked first and second in the western region in area of development near wildlands (Gude et al. 2008). Nearly all (99.7%) of our sample sites were within 1 km of a road; this figure includes only public roads, and suggest that human impacts extend far beyond those areas where human infrastructures dominate land cover. The increasing imprint of roads, agriculture, and urban lands is a common pattern throughout the west (Hessburg et al. 1999, Kennedy and Spies 2004).

Our results should be considered within the limits of our data sources and methodology. Because our sampling scheme was designed to reflect vegetation occurrence on a landscape scale, we had lower inferential power for relatively uncommon vegetation types. Further, our analyses relied mainly on one timestep spanning 150 yr, and were designed to detect only wholesale conversions from one broad vegetation type to another. Vegetation changes on much shorter or longer timescales would be invisible to our methods, as were other types of long-term changes that have been documented in the region, such as declines in Oregon white oak establishment (Gilligan and Muir 2011), or disturbance and climate-related shifts in structure and composition within vegetation types (Taylor and Skinner 1998, Kennedy and Spies 2004, Harrison et al. 2010, Messier et al. 2012).

Despite these limitations, we can draw several conclusions: 1) At individual section corners, a high level of vegetation change from the settlement era to the present was the major tendency, but complimentary increases and decreases within vegetation types maintained the overall character of the landscape; 2) results are consistent with the expected effects of fire exclusion in many cases, but the long-term persistence of some prairies in the absence of recorded fire suggests that vegetation stability or transition cannot be explained simply by shifts in fire regimes; and 3) human encroachment into wildlands, particularly in valleys, has also been a major driver of landscape-level change in the past 150 yr.

Management Implications

Most conversions of vegetation to human uses were in the relatively flat lowlands, suggesting that remnant vegetation in these landscape positions, particularly native prairies, should be a high priority for conservation. Grazed or mowed areas may have been included in our estimation of prairie area, suggesting that native prairies and the functions they provide for dependent species are even more rare on the current landscape than our estimates indicate. Uncommon vegetation types such as savanna and shrubland are also important conservation targets (Clinton 2000, BLM 2008) as they contribute to landscape-level diversity, provide habitat for specialized sensitive species, and contribute to other ecological functions not necessarily served by other vegetation types. Non-coniferous vegetation in southwest Oregon is not well understood, and should be targeted for further research (but see Hosten et al. 2006, Pfaff 2007, Perchemlides et al. 2008, Duren and Muir 2010, Gilligan and Muir 2011). Different sub-types, particularly of shrublands, appear to have different environmental associations and may have different ecological functions; lumping them together for management purposes may not be justified.

The belief that woody species have encroached into formerly open areas motivates many fuels management projects (e.g., BLM 1998, 2008, 2011), but was only partially validated by our study. Although there was a small decline in the proportion of the landscape in open vegetation types since the settlement era, results do not justify the conviction that the landscape was historically much more open. Settlement era surveyors recorded much more closed canopy forest and woodland than open savannas and prairies in valleys and foothills, a condition confirmed by settler descriptions and early photos. Shrubs, too, are claimed to have encroached into open areas (e.g. BLM 1998, 2008). Observations suggest that density may have increased in some areas (LaLande 1995, Hosten et al. 2007), but the historical presence of high-density, high-cover shrublands in pure stands, as patches in savanna or grasslands, or in the understories of forest and woodland has also been widely documented by early settlers, surveyors, and photographers (Leiberg 1900, Pullen 1996, Hosten et al. 2007, Hickman and Christy 2009). Evidence of widespread transition from prairie to shrublands was lacking in our results.

Settlement era vegetation maps provide an excellent starting point for describing reference conditions and planning appropriate fuels management and other treatments where restoration is an objective. However, the complexity of southwest Oregon vegetation and its relationships to environment and disturbance underscore the necessity for management prescriptions to be tailored to unique site types, rather than applying uniform approaches across this diverse landscape.

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