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RESEARCH ARTICLE

Pre-EuroAmerican settlement forests in Redwood National Park, California, USA: a reconstruction using line summaries in historic land surveys

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Abstract Extensive logging in the twentieth century destroyed much of the coniferous forests in the lower Redwood Creek basin of Redwood National Park. Restoration of cutover lands requires the identification of historical, pre-logging reference conditions. Field notes from the original Public Land Surveys were used to reconstruct the pre-EuroAmerican settlement forests. Most reconstructive studies based on historic surveys rely on bearing tree evidence over large areas to determine vegetation patterns over several hundreds to thousands of square kilometers. Due to the small size of the study area (approximately 200 km^2), bearing tree evidence could not accurately reconstruct the vegetation at this scale. Instead, lists of the overstory and understory vegetation for each surveyed mile (line summaries) were employed. Analysis of line summaries evidence identified the historical importance, geographical range, and environmental influences on woody species and vegetation communities. Topography, especially elevation, and soil texture were significantly correlated with plot-scale ordination scores derived from non-metric multidimensional scaling. The influence of topography and distance to ocean coast on the historical distribution of dominant woody species concurs with findings from present-day field studies of local and regional old-growth forest. A comparison with present-day vegetation maps revealed that coast redwood (*Sequoia sempervirens*), Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and red alder (*Alnus rubra*) experienced the most substantive changes in the vegetation as a result of twentieth century land use activities.

Keywords Vegetation reconstruction · Public Land Survey · *Sequoia sempervirens* · Reference ecosystems · Topography

Introduction

Ecological restoration of degraded or destroyed ecosystems depends, in part, on identification of reference ecosystems (SER 2004; Egan and Howell 2005). Present-day analogues of the damaged ecosystem and historical reconstructions prior to degradation serve as references to guide ecosystem recovery (SER 2004). The response of degraded ecosystems to global climate change involves a great deal of uncertainty, thus reference ecosystems more appropriately serve as guides rather than prescriptions for restoration of ecological processes (Harris et al. 2006).

Knowledge of historical changes in ecosystem states may become increasingly relevant in development of ecosystem-response models to global climate

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change (Harris et al. 2006). Restoration of more resilient ecosystems is particularly important for California's coast redwood forests as some models have predicted significant declines in this forest type with changing climate (Lenihan et al. 2008). Restored ecosystems are more likely to withstand the stresses wrought by global climate change, and can help mitigate those changes through increased carbon sequestration and storage (Biringer and Hansen 2005).

Over the last 150 years, logging has destroyed approximately 96% of old-growth coast redwood (*Sequoia sempervirens*) forests (U.S. Fish and Wildlife Service 1997). The largest remaining contiguous section of old-growth redwood forest—which represents approximately 45% of all remaining old-growth redwood forest—is found in the cooperatively managed Redwood National and State Parks in northwestern California, a United Nations World Heritage Site and International Biosphere Reserve (RNSP 2000, 2008). Due to extensive logging that occurred prior to the establishment of the national park, the lower Redwood Creek basin (41°N, 124°W) represents the focal point of the only national park devoted to both protection and restoration of coast redwood forests (Fig. 1). The original Public Land Surveys (PLS) comprise the most extensive classification and mapping of the basin prior to logging, and thus represent a highly relevant line of evidence in reconstructing the historic forest.

Thus, this study addresses the following questions. What were the distributions of major tree species, as suggested by the PLS records? How do the species distributions organize into communities? What relationships exist between species, communities, and environmental factors such as topography?

The original PLS records capture a snapshot of the early Euro-American settlement forest in much of the western and mid-western U.S. For forests of the Pacific Northwest—where tree ages mean that relatively few generations have existed over Holocene times—the PLS records provide a particularly strong reconstruction of historic vegetation. Indeed, in the Pacific Northwest, this nineteenth century snapshot of the forest can contribute to understanding landscapes hundreds to thousands of years prior to the survey (Collins et al. 2003). Many of the species that dominate the overstory are those that live up to or

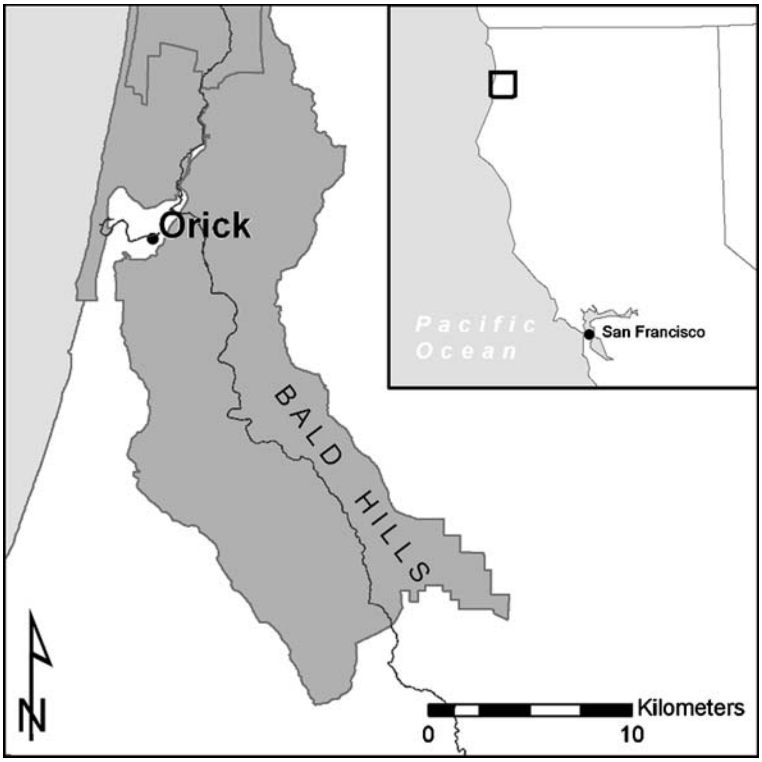

Fig. 1 Lower Redwood Creek basin in Redwood National Park, California, USA

exceeding 500–1000 years, e.g., Western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Western redcedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*, although individuals older than 500 years are rare in California), and coast redwood (*Sequoia sempervirens*; Burns and Honkala 1990).

Thus, the PLS record—in conjunction with pollen and dendroecological evidence—can significantly contribute to reconstructing the *pre-Columbian* forest overstory throughout the Pacific Northwest. In the northern coast redwood forests, such as the lower Redwood Creek basin in Redwood National Park, an old-growth stand typically has trees averaging 600 years old with a few individuals exceeding 1500 years old (Veirs 1982). Since many of the overstory trees present in today's old-growth redwood forests were established during the medieval warming period (Sawyer et al. 2000a), the PLS records can aid in reconstructing overstory forest composition as far back as 600–900 years. This time period is particularly relevant because the species composition and structure of today's old-growth redwood forests are believed to represent environmental changes of the last 2000–4000 years (Sawyer et al. 2000a, b).

Field notes from the PLS record include bearing trees, locations where surveyors entered different ecosystems, vegetation composition summaries in order of abundance at the end of every section mile, and indications of recent disturbances to the environment such as fires and landslides. Numerous studies have relied on bearing tree data for broad-scale reconstructions of vegetation communities spanning landscapes several hundreds to thousands of square kilometers in area (e.g., Grimm 1984; Almendinger 1997; Cogbill et al. 2002; Bollinger et al. 2004). Researchers have suggested that bearing tree data are most appropriate for reconstructions at the county or regional scale due to the limited number of trees sampled per corner and decreased variability of differences between surveyors (Abrams 2001; Manies et al. 2001; Schulte and Mladenoff 2001). The lower Redwood Creek basin covers approximately 200 km^2, thus bearing tree evidence could not accurately reconstruct the vegetation at this scale.

The following analysis relied primarily on line summaries: lists of overstory and understory species, in order of abundance, compiled for each section mile. Despite the potentially useful nature of this data, few researchers have relied upon line summaries in their reconstructions of community composition. Wang (2005) suggests this may be due to the ease of using quantitative bearing tree data. Researchers may also be uncomfortable with the assumption required in the analysis of line summaries, that surveyors truly did list the species in order of abundance. However, surveyors were repeatedly instructed to list the timber and undergrowth vegetation "in the order in which they predominate" (White 1984: 473). Thus, line summary data can be quantified and analyzed in reconstructing historic vegetation communities (e.g., Seischab 1990, 1992; Fritschle 2007; Scull and Richardson 2007).

Study area and data

The original PLS were conducted in the eight townships encompassing the lower Redwood Creek basin from 1875 to 1886. Survey methods followed the standardized instructions in the 1855 General Land Office *Manual of Instructions*, annual updates and instructions issued to the regional Surveyor Generals, and region-specific instructions (Stewart 1935). Although fraudulent surveys were a growing problem in California during this time period (Uzes 1977), only one township's original survey in the study area was rejected and then re-surveyed 4 years later in 1886. Subsequent partial township resurveys conducted in the 1920, 1930, 1950, 1970, and 1980s confirm the veracity of the original surveys (Fritschle 2007). From 1850 until the time of the surveys, limited Euro-American settlement was predominately restricted to the oak woodlands and prairies found in the eastern end of the lower basin, and to a lesser extent in the Orick valley on the coast (Greene 1980; Fritschle 2008).

Methods

Species nomenclatures change through time, and surveyors did not employ scientific names in their descriptions of the vegetation. Ambiguities in nomenclature necessitated an investigation of the taxonomic historical context using nineteenth century forestry papers and the modern identifications of the same trees provided by the resurveys (Fritschle 2007). Thus, species nomenclatures follow Chase (1874), Little (1994), RNP (1996), and Calflora (2006).

The line summaries of vegetation recorded for each section mile were developed from surveyors' visual assessments along one-mile transects. Surveyors listed the types of plants in order of abundance (Stewart 1935; White 1984), usually including separate entries for the overstory or "timber" and the understory. A typical entry for a section mile in Redwood Creek might be recorded as: "Timber Redwood, Fir, Oak; Brush Same." When the surveyor did not list separate entries for the overstory and understory, only those species obviously belonging to the understory (e.g., hazel) were assigned as understory plants. Each line summary was treated as a sampling plot and only species occurring in more than 2% of line summaries were included in the analysis (e.g., Manies and Mladenoff 2000).

To reconstruct the vegetation communities represented in the original PLS, hierarchical, polythetic, agglomerative cluster analysis using Jaccards distances and the within-groups linkage method was performed using the presence/absence of species in overstory line summaries. An agglomerative approach has been found to be the best solution for small areas and results in an empirical, *a posteriori* classification of the vegetation (Tart et al. 2005). Similar line summaries were grouped into classes based on their floristic composition (presence/absence) in a plot.

Based on cluster membership, vegetation community types were assigned to each cluster. Community types reflect the order in which surveyors listed species in the majority of cases within the cluster. If two or more conifers, or two or more hardwoods, were listed, then the designation "mixed conifer" or "mixed hardwood" was included in the community name. If the majority of understory line summaries within a cluster included a particular vegetation type, such as chaparral, this was added onto the end of the community name. This resulted in a final classification of vegetation communities. Results were exported into a GIS to map section lines according to community type. The resultant maps illustrate mid-nineteenth century vegetation communities in the lower Redwood Creek basin based on the Public Land Surveys.

To ascertain the abundance of various species in a community, importance values are typically calculated from measures of relative density, cover, and frequency (Kent and Coker 1992). Since basal area data were unavailable to calculate relative cover for the line summaries analysis, other methods were required to compare the abundance of different species. Seischab (1990) transformed qualitative line summaries of species listed in order of abundance to quantitative frequency and relative weight measures that can be used to gauge importance. Each line summary was treated as a sampling plot. Frequency was calculated for the number of plots in which a species was present compared to the total number of line summaries (240 surveyed miles). Species were assigned a relative weight (RW) based on their order and relativized to the number of species listed so that each plot's species RW values added up to 100.

For example, a list of three species would be assigned values of 50, 33.3, and 16.7, while a list of four species would be assigned values of 40, 30, 20, and 10, in order from first to last. Seischab (1990) provides a table of RW values ranging from single-species entries to entries including as many as twelve different species. If a surveyor included different listings for the overstory and understory, or divided the listing according to the first and second half-miles, RW values were halved and then added together so the total weight of every plot would still equal 100. An overstory entry of "fir, redwood, and oak," relative weights would be assigned as 25.0, 16.65, and 8.35, respectively, and an understory entry of "fir, redwood, oak, and hazel" equaled 20, 15, 10, and 5. The overstory and understory RW values were then added together resulting in a total relative weight of fir = 45.0, redwood = 31.65, oak = 18.35, and hazel = 5. The results were mapped in *ArcMap 9.1* (ESRI 2005).

Ratios of species with the greatest abundance (highest frequencies and relative weights) in the study area were calculated for understory and overstory average relative weights in a community. For example, when a ratio for overstory fir versus overstory redwood was calculated for a community, a value of greater than 1.0 indicated that fir had a higher average overstory relative weight in the community compared to redwood, a value less than 1.0 indicated a higher average overstory relative weight for redwood, and a value equal to 1.0 indicated that fir and redwood had the same average overstory relative weight in the community. A paired two-tailed Student's *t*-test then tested for significant difference between the overstory versus understory ratios for each community in which both species were present. For example, the *t*-test determined whether the overstory fir:redwood ratio was significantly different from the understory fir:redwood ratio.

Non-metric multidimensional scaling (NMDS) was performed on both relative weights of species and presence/absence of species to compare composition among plots. NMDS is a nonparametric indirect gradient analysis method that orders plots along multiple axes or dimensions based on species associations (McCune and Grace 2002). Multiple solutions of NMDS were run to test for consistency of interpretation in PC-ORD v. 5.0 using Sørenson's distance measure (McCune and Mefford 1999). To test the real data results, NMDS was performed with 250 iterations of the real data and 250 randomized Monte Carlo simulation runs. Sørenson's coefficient is recommended for NMDS analyses using community data (McCune and Grace 2002).

Topographically-influenced water availability and fire regime primarily influence the distribution of plant communities in the basin (EPA 1998). To explore the influence of these environmental factors on the vegetation, correlation coefficients were calculated—using the nonparametric Kendall tau method—to compare axis scores from the NMDS ordination with soil, topographic, and climatic variables (data sources: NRCS 2007; Daly and Taylor 1998; CERES 1997). Only variables that varied spatially within the study area were included in the analysis. Soil data was derived from SSURGO (soil erodibility, indicated by the *T* factor estimate of annual soil erosion in tons/acre/year; soil texture, or the percent of sand, silt, and clay; and soil moisture, measured as available water capacity, available water supply to a depth of 100 and 150 cm, and organic matter content). Soil polygon variables were overlaid with the mile-long PLS section lines. Values for a variable along a section line (e.g., available water capacity) were averaged and weighted according to line segment length. For example, a section line that intersected two available water capacity polygons would be divided into two segments. The longer segment would contribute more to the total section line's average water capacity value.

Climatic variables and topographic variables derived from 30-meter digital elevation models (DEMs) were averaged across each 1-mile section line (elevation, slope, aspect, heat load, annual precipitation). Annual precipitation amounts in the study area are strongly influenced by the orographic effect (Davey et al. 2007), therefore this variable was grouped with other topographically-influenced variables. Slope aspect was rescaled to range from 0 to 180°, such that southwest slopes (folded aspect = 180°) receive the most solar radiation while northeast slopes (folded aspect = 0°) receive the least (McCune and Keon 2002). Folded aspect, slope steepness, and latitude were converted to radians and used to calculate an index of heat load ranging from 0, the coolest slope, to 1, the warmest slope (McCune and Keon 2002).

Results

Fir (*Pseudotsuga menziesii/Abies grandis*) had the highest frequency and relative weight in the lower Redwood Creek basin, followed by redwood (*Sequoia sempervirens*) and oak (*Lithocarpus densiflorus/Quercus garryana/Q. chrysolepis/Q. kelloggii/*; Table 1). Of those species found exclusively in the understory, chaparral (*Baccharis pilularis*) had frequency and relative weight values more than double the next most important understory species, salal (*Gaultheria shallon*). Fir had relative weights greater than 25% throughout most of the basin, with the highest values in the easternmost Bald Hills and the lowest values in the Orick valley (Fig. 2). Redwood was concentrated in the northern two-thirds of the basin with the highest values along the west-facing slopes in the northeast. Oak was most prominent in the southern half with the highest value in the easternmost Bald Hills. Pine (*Pinus jeffreyi/P. attenuate*) was found primarily along the east-facing ridges in the southern half of the basin. Madrone (*Arbutus menziesii*) was most associated with the Bald Hills. Spruce (*Picea sitchensis*), alder (*Alnus rubra*), and chaparral were found almost exclusively in the northern half of the basin.

For the numerical classification of the overstory line summaries, 234 overstory cases divided into 13 clusters. The final grouping of clusters resulted in six community types (Fig. 3; Table 2). Fir-dominated communities comprised the highest percentage (46%) of communities in the basin, followed by oak- (33%) and redwood-dominated communities (21%). Redwood- and oak-dominated communities were

Table 1 Frequency (F) and relative weight (RW) of line summary species (%)

PLS name	Species equivalent in Redwood Creek	Frequency	Rank (*F*)	Relative weight	Rank (RW)
Fir	*Pseudotsuga menziesii* *Abies grandis*	96.3	1	29.4	1
Redwood	*Sequoia sempervirens*	80.8	2	23.0	2
Oak	*Lithocarpus densiflorus* *Quercus garryana* *Quercus chrysolepis* *Quercus kelloggii*	68.8	3	18.3	3
Spruce	*Picea sitchensis*	35.4	4	5.5	6
Chaparral	*Baccharis pilularis*, or general brush vegetation	30.4	5	6.5	4
Madrone	*Arbutus menziesii*	29.6	6	4.1	7
Pine[a]	*Pinus jeffreyi* *Pinus attenuate*	27.9	7	6.5	5
Alder	*Alnus rubra*	15.8	8	1.5	9
Salal	*Gaultheria shallon*	10.0	9	3.0	8
Hazel	*Corylus cornuta californica*	9.6	10	0.4	11
Huckleberry	*Vaccinium ovatum* *Vaccinium parviflorum*	5.0	11	1.4	10
Buckeye	*Aesculus californica*	2.5	12	0.2	13
Maple	*Acer macrophyllum* *Acer circinatum*	2.1	13	0.3	12

[a] Although Douglas fir (*Pseudotsuga menziesii*) was also known as Oregon or Humboldt pine, there are only three out of 75 listings (4%) in the overstory and understory line summaries in which "pine" is not listed with "fir." Therefore it is likely that in at least 96% of cases when surveyors listed pine in the line summaries they are referring to either Jeffrey pine (*Pinus jeffreyi*) or knobcone pine (*Pinus attenuate*)

spatially grouped while fir-dominated communities ranged across the basin (Fig. 4). Oak-dominated communities were primarily found in the south half of the basin, while redwood-dominated communities were grouped together in the north. The majority of heavy redwood-fir forest was found in the Lost Man Creek sub-basin located in the northwestern end of the study area, although redwood may have been overrepresented in this sub-basin due to surveyor bias.

The most abundant species throughout the basin—fir, redwood, and oak—were compared with one another in the overstory and understory of each community. In comparing fir with redwood, fir had higher overstory RW ratios in three of five communities (Table 3a). In both redwood-dominated communities, the abundance of redwood over fir increased significantly in the understory compared to the overstory. Redwood had the greatest abundance over fir in the heavy redwood-fir understory community. In contrast to the fir-redwood ratios, fir was less dominant than oak in the majority of overstory communities (Table 3b). Average RW ratios for fir-redwood and fir-oak decreased from the overstory to the understory in every community (Table 3a, b). This indicates that fir lost some of its abundance in the understory. This difference was strongly statistically significant when compared to redwood in the redwood-dominated communities ($P = 0.0000$), and when compared to oak in the fir-dominated communities ($P = 0.0009$ and 0.0001). Redwood had higher RW ratio values than oak in the fir-dominated communities (Table 3c). Redwood-oak RW ratios declined significantly from the overstory to the understory in these communities, indicating a decline in redwood abundance over oak. In comparing spruce–alder RW ratios, spruce dominated over alder in both the overstory and understory of the fir-mixed conifer-mixed hardwood/chaparral community (Table 3d). The increased ratio of spruce to alder

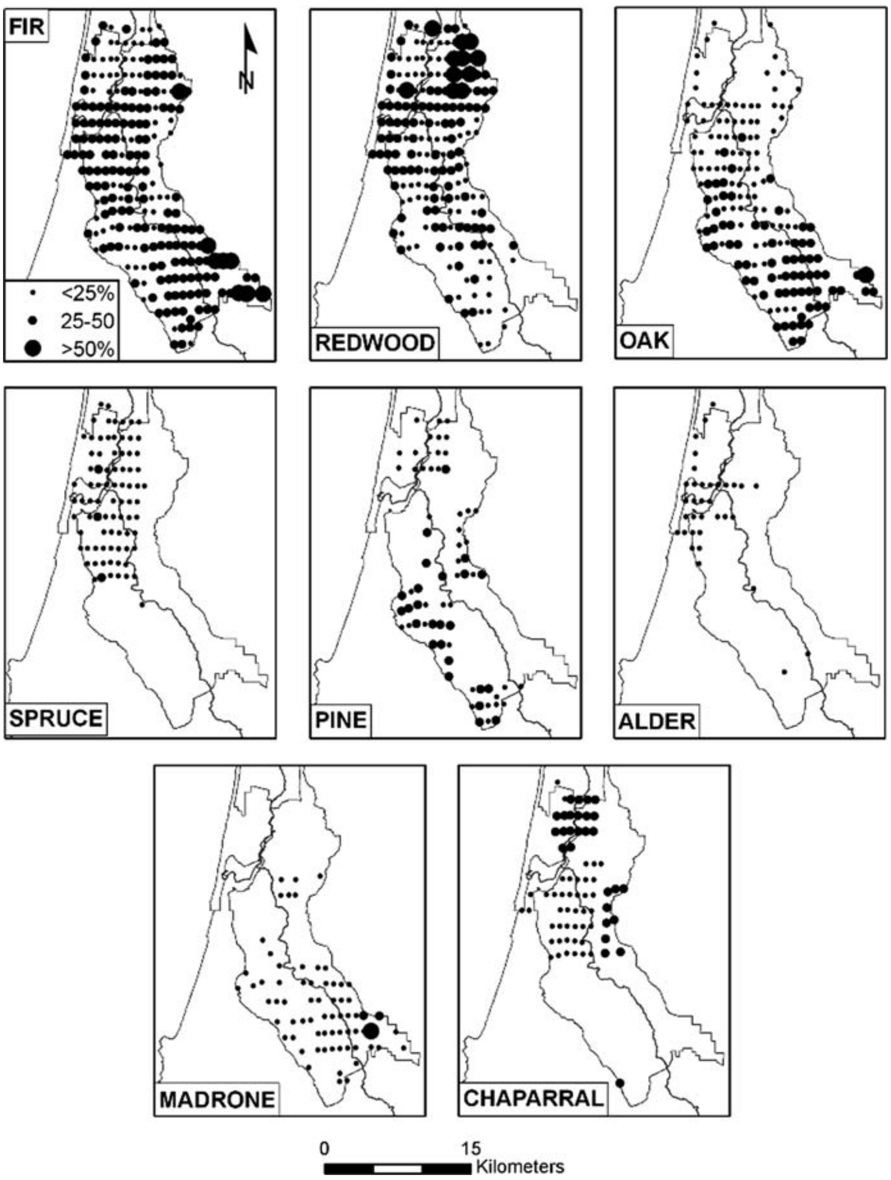

Fig. 2 Relative weight (*RW*) maps of line summary taxa. Species were assigned a relative weight based on their order and relativized to the number of species listed so that each plot's species RW values added up to 100 (after Seischab 1990). *Points* represent the location along section lines in which the surveyor provided the line summary data

in the understory was statistically significant ($P = 0.0438$), indicating even greater importance of spruce over alder in the community.

Non-metric multidimensional scaling (NMDS) of 13 taxa relative weights at the plot-scale resulted in a two-dimensional ordination (randomization test $P = 0.004$, final stress = 22) that cumulatively represented 80.1% of the variance in species data based on Sørenson's distance measure (first axis $r^2 = 44.4\%$, second axis $r^2 = 36.8\%$). The variance is indicated by the coefficient of determination (r^2), a coefficient that denotes the distances in the original data space and ordination space. The coefficient of determination varies according to the number of variables in the dataset; an acceptable r^2 may be as low as 30–50% per axis for a more heterogeneous dataset (McCune and Grace 2002). Orthogonality of the two axes was close to 100% (95.3%), thus the two axes were essentially statistically independent (McCune and Mefford 1999).

A multidimensional mapping of species ordinations indicated that redwood was most closely associated with spruce and alder, while fir was associated with oak and hazel (*Corylus cornuta californica*; Fig. 5).

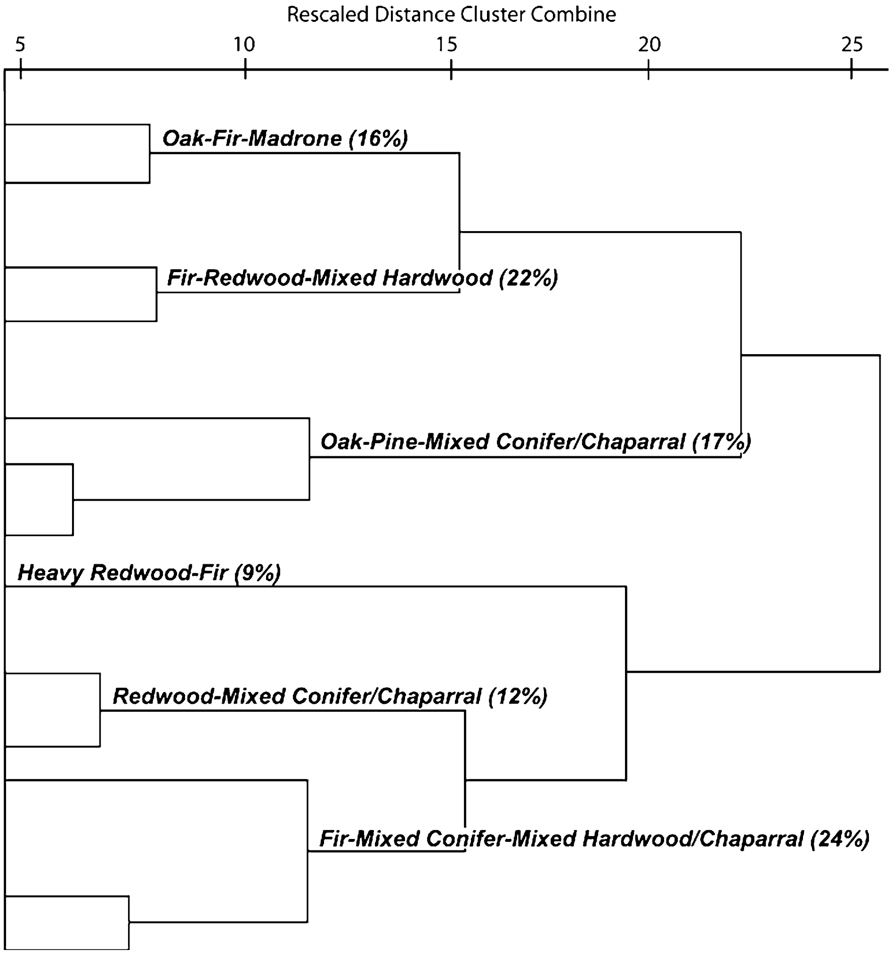

Fig. 3 Dendrogram of vegetation communities and percent of section line miles in study area included in each community resulting from hierarchical, polythetic, agglomerative cluster analysis using Jaccards distances and the within-groups linkage method performed on the presence/absence of species in overstory line summaries

The location of species in ordination space generally indicated a moisture and west–east geographic gradient along the first axis, and a range in shade tolerance along the second axis. Species with the lowest scores on the first axis were associated with mesic habitat types, while species with the highest scores were either found on more xeric habitats (e.g., buckeye, *Aesculus californica*, pine, madrone) or tolerate a range from mesic to xeric (e.g., fir, oak, maple). Species on the left side of axis 1 typically have the highest abundance closest to the coast: spruce, chaparral, alder, and redwood. Species that tend to have more importance in drier, inland sites were found on the right side of axis 1: fir, oak, and madrone. With the exception of alder and buckeye, species occupying the lower one-third of the second axis were intermediate to very shade tolerant.

The grouping of plots in ordination space reflected the communities derived from cluster analysis (Fig. 6). Correlation of plot-scale ordination scores with environmental variables indicated an ordering of plots along the first axis that reflected the influence of certain topographic and soil properties on vegetation abundance and community composition (Table 4). With the exception of slope aspect, all topographic and soil texture factors were correlated with the distribution of species and communities along the first axis. Elevation, clay content, and silt content were moderately significantly correlated, while slope steepness, annual precipitation, sand content, and heatload were weakly correlated. Thus, the ordination of vegetation communities revealed a west to east pattern, mesic to xeric gradient, and fining of soil texture along axis 1, transitioning from redwood- to fir- to oak-dominated communities. The ordination of communities along the second axis did not illustrate an obvious environmental gradient; no environmental factors were significantly correlated with the second axis.

Table 2 Average relative weight of species by community (%)

Community	Fir	Redwood	Oak	Spruce	Pine
Fir-mixed conifer-mixed hardwood/chaparral	30.5	26.8	17.5	15.3	0.4
Fir-redwood-mixed hardwood	30.8	28.0	20.4	0.0	0.6
Fir-dominated communities	*30.7*	*27.4*	*19.0*	*7.7*	*0.5*
Heavy redwood-fir	32.0	49.8	0	0	0
Redwood-mixed conifer/chaparral	15.1	24.3	2.6	12.7	9.0
Redwood-dominated communities	*23.5*	*37.1*	*1.3*	*6.3*	*4.5*
Oak-fir-madrone	41.8	0	36.2	0	5.2
Oak-pine-mixed conifer/chaparral	20.6	15.1	20.0	0.5	25.0
Oak-dominated communities	*31.2*	*7.6*	*28.1*	*0.2*	*15.1*

	Alder	Madrone	Maple	Buckeye	Hazel
Fir-mixed conifer-mixed hardwood/chaparral	4.0	0.8	0.6	0	1.4
Fir-redwood-mixed hardwood	0.0	5.5	0.6	1.0	0.0
Fir-dominated communities	*2.0*	*3.2*	*0.6*	*0.5*	*0.7*
Heavy redwood-fir	2.7	0	0	0	0
Redwood-mixed conifer/chaparral	0	0	0	0	0.4
Redwood-dominated communities	*1.3*	*0*	*0*	*0*	*0.2*
Oak-fir-madrone	0.5	16.2	0	0	0
Oak-pine-mixed conifer/chaparral	0	1.1	0	0	0
Oak-dominated communities	*0.3*	*8.6*	*0*	*0*	*0*

	Chaparral	Salal	Huckleberry
Fir-mixed conifer-mixed hardwood/chaparral	1.6	0.9	0.1
Fir-redwood-mixed hardwood	0.1	2.9	2.2
Fir-dominated communities	*0.9*	*1.9*	*1.2*
Heavy redwood-fir	0.5	6.7	8.3
Redwood-mixed conifer/chaparral	29.4	5.4	1.2
Redwood-dominated communities	*17.3*	*6.1*	*4.8*
Oak-fir-madrone	0	0	0
Oak-pine-mixed conifer/chaparral	14.6	3.1	0
Oak-dominated communities	*7.3*	*1.5*	*0*

Italicized values represent the average relative weight of species within communities grouped according to dominant species (e.g., the average relative weight of fir in communities dominated by fir)

Discussion

Mixed evergreen forest historically covered much of the lower Redwood Creek basin, and continues to predominate today. However, more than two-thirds of the coniferous forest in the lower Redwood Creek basin was logged (Best 1995). As a result, the dominant forest structure in the basin has shifted from uneven-aged stands containing large old-growth trees to very dense stands of small trees (Muldavin et al. 1981; Veirs and Lennox 1981; Veirs 1986; RNSP 2000; Remote Sensing Lab 2004, 2005). Several notable shifts in species composition have occurred, including changes in the abundance of fir, redwood, spruce, and alder.

Fir was noted in nearly all section line summaries and possessed the highest average relative weight (see Table 2). It was most dominant in the eastern Bald Hills and at mid- to higher elevations, however throughout most of the lower basin fir possessed high relative weight values. When compared with the overstory relative weight ratios between dominant species, fir decreased in understory importance relative to either redwood or oak in every community (see Table 4). This suggests that at the time of the survey,

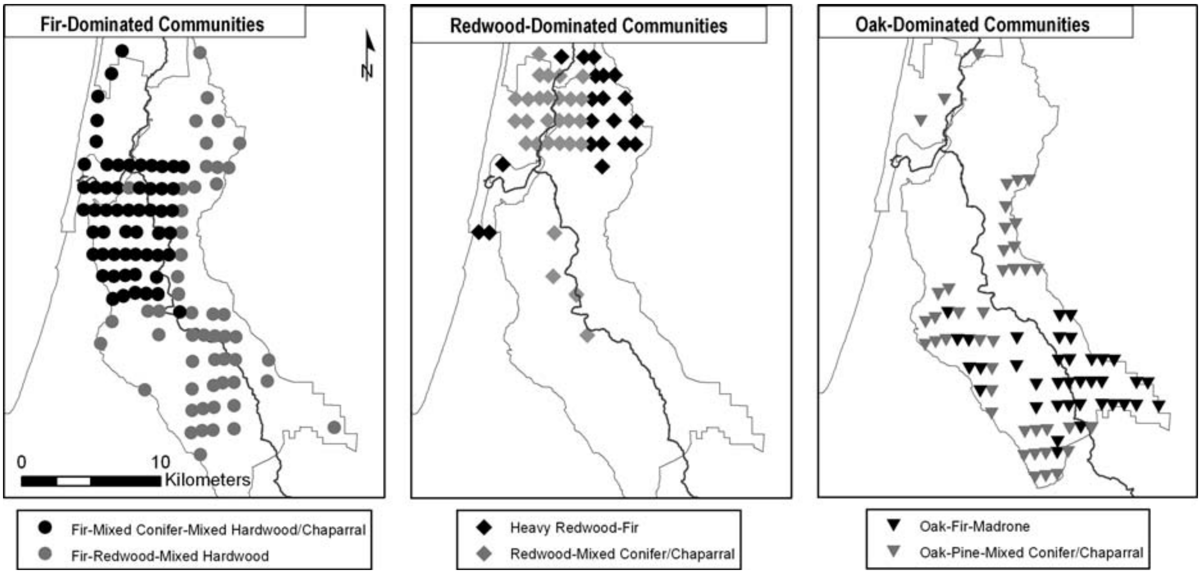

Fig. 4 Map of historic vegetation communities, 1875–1886. *Points* represent the location along section lines in which the surveyor provided the line summary data

Table 3 Overstory and understory species average relative weight (RW) ratios

Community	Overstory	Understory	*P* value
(a) Fir vs. redwood			
Fir-mixed conifer-mixed hardwood/chaparral	1.23	1.17	0.0583
Fir-redwood-mixed hardwood	1.12	1.03	0.3854
Heavy redwood-fir	0.64	0.21	0.0000**
Redwood-mixed conifer/chaparral	0.71	0.24	0.0000**
Oak-pine-mixed conifer/chaparral	1.17	0.88	0.0990
(b) Fir vs. oak			
Fir-mixed conifer-mixed hardwood/chaparral	1.83	1.56	0.0009**
Fir-redwood-mixed hardwood	1.48	0.76	0.0001**
Redwood-mixed conifer/chaparral	0.34	0.20	0.1745
Oak-fir-madrone	0.78	0.65	0.1124
Oak-pine-mixed conifer/chaparral	0.70	0.46	0.0310*
(c) Redwood vs. oak			
Fir-mixed conifer-mixed hardwood/chaparral	1.60	1.37	0.0001**
Fir-redwood-mixed hardwood	1.45	0.89	0.0025*
Redwood-mixed conifer/chaparral	0.21	0.15	0.2599
Oak-pine-mixed conifer/chaparral	0.45	0.14	0.0791
(d) Alder vs. spruce			
Fir-mixed conifer-mixed hardwood/chaparral	0.17	0.19	0.0438*

Ratio values >1.0 indicate higher average relative weights of the species listed first; values <1.0 indicate higher average relative weights of the species listed second; a value of 1.0 indicates the same average relative weight for both species

* Significant at the 0.05 level

** Significant at the 0.001 level

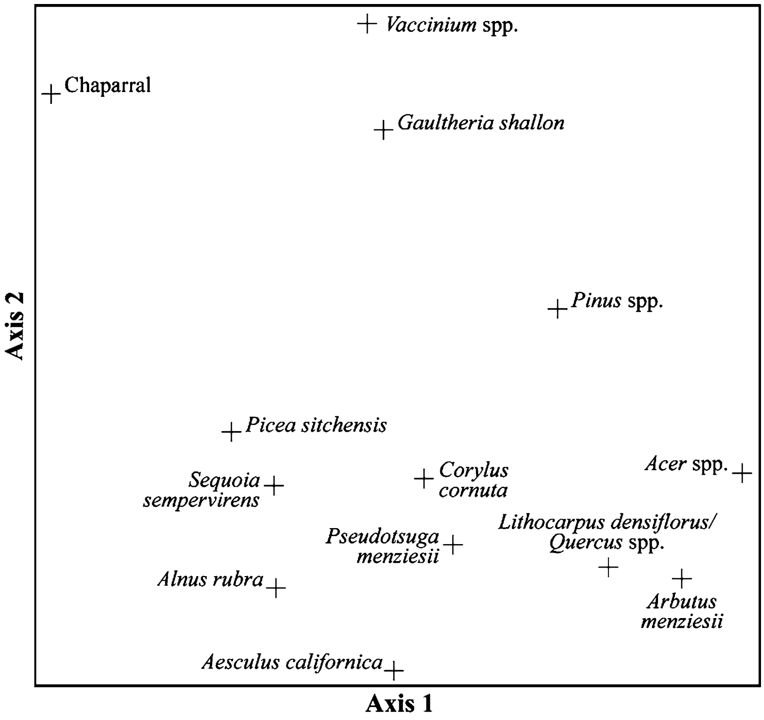

Fig. 5 Ordination of species resulting from non-metric multidimensional scaling (*NMDS*) performed on the relative weights of species in PC-ORD v. 5.0 using Sørenson's distance measure (McCune and Mefford 1999). *Points* represent taxa in two-dimensional ordination space

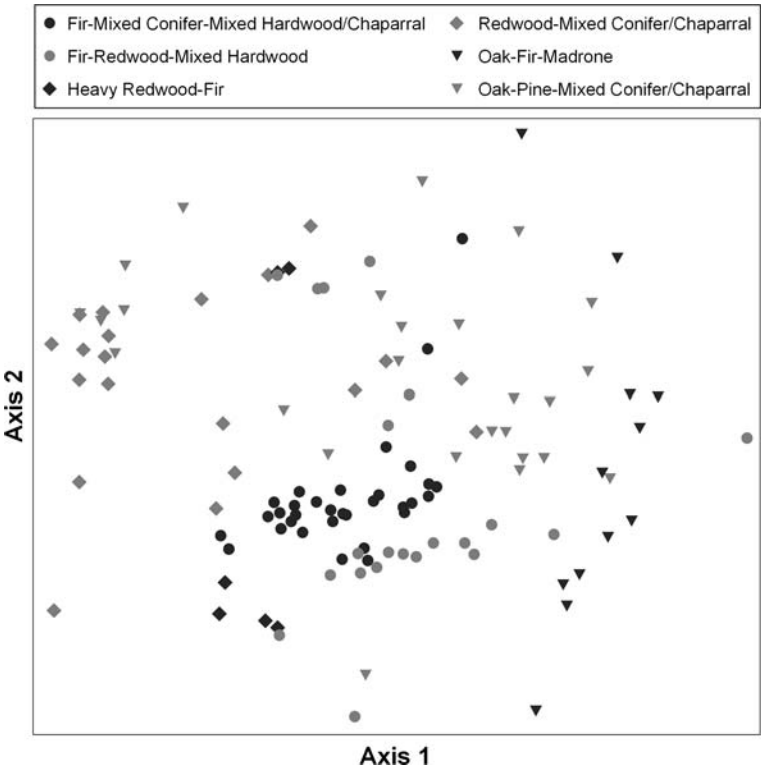

Fig. 6 Ordination of communities and sampling plots resulting from non-metric multidimensional scaling (NMDS) performed on the relative weights of species in PC-ORD v. 5.0 using Sørenson's distance measure (McCune and Mefford 1999). *Points* represent sampling plots (section line summaries) in two-dimensional ordination space

Table 4 Kendall's Tau ranked correlation coefficients between NMDS ordination scores of plots along the first and second axis ($n = 234$) and environmental factors

Environmental factors	Axis 1 (τ)	Axis 2 (τ)
Topography/climate		
Elevation	0.380**	−0.078
Slope steepness	0.152**	−0.031
Slope aspect, folded	−0.079	0.010
Heatload index	−0.090*	−0.005
Annual precipitation	0.133**	0.001
Soil moisture		
Available water supply (100 cm)	−0.054	0.061
Available water supply (150 cm)	−0.053	0.062
Available water capacity	0.060	0.010
Organic matter content	0.047	0.032
Soil texture		
Proportion of clay	0.212**	−0.048
Proportion of sand	−0.100*	0.073
Proportion of silt	0.232**	−0.030
Soil erodibility		
T factor	−0.020	0.046

* Significant at the 0.05 level

** Significant at the 0.001 level

fir recruitment in the understory was less prevalent relative to its two most important cohorts in the basin.

Redwood was also found extensively in the study area however, it was much more prevalent in the northern half of the lower Redwood Creek basin, at lower elevations along rivers and streams, and on slightly sandier soils. The greatest concentration of very large trees, with diameters in excess of 3 m, was primarily found in stream valleys north of Orick. One tree measured 7.6 m in diameter. Small redwood trees, 25–50 cm diameter, comprise the present-day forest structure and composition in most of these areas (Remote Sensing Lab 2004, 2005).

In the overstory of redwood-dominated communities, redwood was strongly dominant over fir and oak, and significantly increased in abundance in the understory (see Table 3). This finding suggests a nineteenth century compositional equilibrium in redwood; in other words, the redwood-dominated overstory was likely replacing itself in the understory at the time of the survey. This dramatically changed in the wake of twentieth century logging activities. Timber companies planted and aerially seeded fir on logged-over lands (RNSP 2000). Thus, fir greatly outnumbers redwood by as much as 10:2 on many of the post-logging forest stands (Muldavin et al. 1981; Veirs and Lennox 1981; Veirs 1986; RNSP 2000). In the PLS record, the greatest ratio of fir to redwood relative weights was 4:1.

Historically, oak ranked third in both frequency and average relative weight in the lower Redwood Creek basin, after fir and redwood. It was present throughout the basin, however it increased in importance further upstream and inland, and ranged in elevation from stream valleys to ridge tops. Its closest associates were pine, fir, and madrone. In the fir-redwood-mixed hardwood community, oak significantly increased in understory importance relative to fir and redwood, suggesting understory recruitment at the time of the survey. Post-logging mixed conifer-hardwood forest composed primarily of redwood and fir now dominates these areas with small oak or alder trees (Remote Sensing Lab 2004, 2005).

At the time of the original surveys, alder was associated primarily with low elevations in the Orick valley. A comparison of the historic record with present-day classifications of the vegetation reveals an increase in both the importance and geographic extent of alder in the lower Redwood Creek basin. Much of the spruce forest in the Orick valley has been replaced by agricultural fields and alder woodland. Alder comprises 60–100% of the vegetation cover in these single-storied canopy woodlands (Remote Sensing Lab 2004, 2005). Further inland and west of Redwood Creek in cutover coniferous forest lands, alder woodlands have established in areas that in the original surveys were dominated by oak, fir, pine, and redwood. These woodlands are found almost exclusively on logged-over lands. Oak, and to lesser extents pine, fir, and madrone, dominated what is now alder woodlands in the upper reaches of Redwood Creek within the lower basin. Downstream alder woodlands along Redwood Creek were dominated by fir and redwood. Shade intolerant alder typically colonizes gaps created from disturbance in mesic coniferous forest and riparian habitats, and may eventually be overtaken by shade tolerant species in the absence of disturbance (Burns and Honkala 1990).

No single source of evidence in the survey notes, including the line summaries, is completely free from surveyor bias. Furthermore, the purpose of the surveys was an economic rather than scientific assessment of the land (Stewart 1935). Nonetheless, the reconstruction of nineteenth century vegetation communities and dominant woody species distributions based on the original PLS line summaries is consistent with field-based studies of modern old-growth forests conducted in and adjacent to the lower Redwood Creek basin. Indeed, this northern redwood ecoregion has been extensively studied and classified (Mahony and Stuart 2007), and the findings of a number of these studies correlate with the PLS reconstruction. Fir has been found to increase with increasing elevation and slope position (i.e., mid- to upper slopes and ridge tops), and distance from the ocean coast (Waring and Major 1964; Lenihan 1990; Mahoney and Stuart 2000). These represent more xeric sites, with lower incidences of summer fog, subject to higher fire frequency and intensity, which favors fir over redwood.

Redwood attains its greatest dominance at moist, low elevation sites on stream alluvium, and gradually declines upslope as fir becomes codominant (Waring and Major 1964; Lenihan 1990; Mahony and Stuart 2000; Busing and Fujimori 2002). In the Little Lost Man Creek subbasin (in the northwest lower Redwood Creek basin), Lenihan (1990) found oak in redwood forests ranging from mesic mid-slope sites to more xeric upper slopes and ridges. Madrone is found in fir-redwood forests, and increases in importance at higher elevations and further inland (Waring and Major 1964; Lenihan 1990). Similarity in findings based on the PLS reconstruction and these old-growth field studies increases confidence in the nineteenth century vegetation patterns identified by this study.

Conclusion

Restoration of logged-over forests requires the identification of multiple reference ecosystems (SER 2002; Egan and Howell 2005). This study provided a historical reference of the lower Redwood Creek basin prior to extensive logging. Specifically, it identified fine-scale environmental influences, historical distribution of dominant woody species and vegetation communities, and subsequent changes in the vegetation as a result of twentieth century land use activities. Line summaries in the PLS record may also prove useful as a data source for similar studies at broader scales. Finer-scale field studies, particularly of remaining old-growth forest in lower Redwood Creek (e.g., Lenihan 1990; Russell and Jones 2001) are also critical to ecological restoration because they contribute to an understanding of community-level structure, composition, and heterogeneity. Additional research is needed to ascertain if these old-growth patches can serve as modern analogues of the former forest, or if they represent unique ecosystems that occupied a narrow niche within the larger landscape. Further study of the former forest described in the PLS record may be useful in identifying modern old-growth analogues for restoration of second-growth forests in lower Redwood Creek.

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References

Abrams MD (2001) Eastern white pine versatility in the presettlement forest. Bioscience 51(11):967–979. doi:10.1641/0006-3568(2001)051[0967:EWPVIT]2.0.CO;2

Almendinger JC (1997) Minnesota's bearing tree database. Natural heritage information system. Section of Ecological Services, Division of Fish and Wildlife, Minnesota Department of Natural Resources, Minnesota

Best DW (1995) History of timber harvest in the Redwood Creek basin, northwestern California. U.S. geological survey professional paper 1454-C. In: Nolan KM, Kelsey HM, Marron DC (eds) Geomorphic processes and aquatic habitat in the Redwood Creek basin, northwestern California. U.S. Government Printing Office, Washington, DC, pp C1–C7

Biringer J, Hansen LJ (2005) Restoring forest landscapes in the face of climate change. In: Mansourian S, Vallauri D, Dudley N (eds) Forest restoration in landscapes: beyond planting trees. Springer, New York, pp 31–37

Bollinger J, Schulte LA, Burrows SN, Sickley TA, Mladenoff DJ (2004) Assessing ecological restoration potentials of Wisconsin (U.S.A.) using historical landscapes reconstruction. Restor Ecol 12(1):124–142. doi:10.1111/j.1526-100X.2004.00285.x

Burns RM, Honkala BH (tech coords) (1990) Silvics of North America, vol 1: conifers, vol 2: Hardwoods, Agriculture Handbook 654, Forest Service, U.S. Department of Agriculture, Washington, DC. http://www.na.fs.fed.us/pubs/silvics_manual/table_of_contents.shtm. Accessed 09 Mar 2009

Busing RT, Fujimori T (2002) Dynamics of composition and structure in an old *Sequoia sempervirens* forest. J Veg Sci 13(6):785–792

Calflora: Information on California Plants for Education, Research and Conservation (2006) Pseudotsuga menziesii (Mirbel) Franco var. menziesii, Taxon report 6907. The Calflora Database, Berkeley, California. http://www.calflora.org/. Accessed 18 Mar 2009

California Environmental Resources Evaluation System (CERES) (1997) Digital elevation model (30 m). Teale GIS Solutions Group, California Environmental Resources Evaluation System, California. http://gis.ca.gov/casil/gis.ca.gov/dem/. Accessed 18 Mar 2009

Chase AW (1874) Timber belts of the Pacific coast. Overl Mon Out W Mag 13(3):242–249

Cogbill CV, Burk J, Motzkin G (2002) The forests of presettlement New England, U.S.A.: spatial and compositional patterns based on town proprietor surveys. J Biogeogr 29:1279–1304. doi:10.1046/j.1365-2699.2002.00757.x

Collins BD, Montgomery DR, Sheikh AJ (2003) Reconstructing the historical riverine landscape of the Puget Sound Lowland. In: Montgomery DR, Bolton S, Booth DB, Wall L (eds) Restoration of Puget sound rivers. University of Washington Press, Seattle, pp 79–128

Daly C, Taylor G (1998) Klamath network average annual precipitation, 1961-90. Water and climate center of the natural resources conservation service, Portland, Oregon. http://science.nature.nps.gov/nrdata/datastore.cfm?ID=37483. Accessed 24 Feb 2007

Davey CA, Redmond KT, Simeral DB (2007) Weather and climate inventory, National Park Service Klamath Network. Natural Resource Technical Report NPS/KLMN/NRTR—2007/035, WRCC Report 2007-10. Natural Resource Program Center, National Park Service, U.S. Department of Interior, Fort Collins, Colorado

Egan D, Howell EA (2005) Introduction. In: Egan D, Howell EA (eds) The historical ecology handbook: a restorationist guide to reference ecosystem. Island Press, Washington, DC, pp 1–23

Environmental Protection Agency (EPA) (1998) Redwood creek sediment total maximum daily load. Water Division, Region 9, U.S. Environmental Protection Agency

ESRI (2005) ArcMap 9.1. Environmental Systems Research Institute, Redlands

Fritschle JA (2007) An intermediate-scale reconstruction of historic vegetation in Redwood National Park using the Public Land Survey. Dissertation, University of Wisconsin-Madison

Fritschle JA (2008) Reconstructing historic ecotones using the Public Land Survey: the lost prairies of Redwood National Park. Ann Assoc Am Geogr 98(1):24–39. doi:10.1080/00045600701734018

Greene LW (1980) Historical overview of the Redwood Creek Basin and Bald Hills regions of Redwood National Park, California. National Park Service, U.S. Department of the Interior, Denver

Grimm EC (1984) Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. Ecol Monogr 54(3):291–311. doi:10.2307/1942499

Harris JA, Hobbs RJ, Higgs E, Aronson J (2006) Ecological restoration and global climate change. Restor Ecol 14(2):170–176. doi:10.1111/j.1526-100X.2006.00136.x

Kent M, Coker P (1992) Vegetation description and analysis: a practical approach. CRC Press, Ann Arbor

Lenihan JM (1990) Forest associations of Little Lost Man Creek, Humboldt County, California: reference-level in the hierarchical structure of old-growth coastal redwood vegetation. Madrono 37(2):69–87

Lenihan JM, Bachelet D, Neilson RP, Drapek R (2008) Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. Clim Change 87(suppl 1):S215–S230. doi:10.1007/s10584-007-9362-0

Little EL (1994) National Audubon society field guide to North American trees, western region. Alfred A. Knopf, New York

Mahony TM, Stuart JD (2000) Old-growth forest associations in the northern range of coastal redwood. Madrono 47(1):53–60

Mahony TM, Stuart JD (2007) Status of vegetation classification in redwood ecosystems. In: Standiford RB, Giusti GA, Valachovic Y, Zielinski WJ, Furniss MJ (eds) Proceedings of the redwood region forest science symposium: what does the future hold? General technical report PSW-GTR-194. Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Albany, pp 207–214

Manies KL, Mladenoff DJ (2000) Testing methods to produce landscape-scale presettlement vegetation maps from the U.S. Public Land Survey records. Landscape Ecol 15:741–754. doi:10.1023/A:1008115200471

Manies KL, Mladenoff DJ, Nordheim EV (2001) Assessing large-scale surveyor variability in the historic forest data of the original U.S. Public Land Survey. Can J For Res 31:1719–1730. doi:10.1139/cjfr-31-10-1719

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon

McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. J Veg Sci 13:603–606

McCune B, Mefford MJ (1999) PC-ORD, Multivariate analysis of ecological data, version 5.0. MjM Software, Gleneden Beach, Oregon

Muldavin EH, Lenihan JM, Lennox WS, Veirs SD (1981) Vegetation succession in the first 10 years following logging of the coast redwood forests. Redwood National Park technical report no. 6. National Park Service, U.S. Department of the Interior, Arcata, California

Natural Resources Conservation Service (NRCS) (2007) Partial soil survey geographic (SSURGO) database for Humboldt and Del Norte Area, California. U.S. Department of Agriculture, Fort Worth, Texas. http://SoilDataMart.nrcs.usda.gov/. Accessed 18 Mar 2009

Redwood National Park (RNP) (1996) Checklist of the vascular plants of Redwood National Park. Species in parks, flora and fauna database, online query system. Information Center for the Environment, University of California, Davis, and National Park Service, Davis, California. http://ice.ucdavis.edu/nps/sbypark.html. Accessed 12 July 2006

Redwood National and State Parks (RNSP) (2000) General management plan, Redwood National and State Parks, Humboldt and Del Norte Counties, California. National Park Service, U.S. Department of the Interior, California Department of Parks and Recreation, Denver Service Center, Colorado

Redwood National and State Parks (RNSP) (2008) Fact sheet. Redwood Park Association, National Park Service, U.S. Department of the Interior, California Department of Parks and Recreation, Redwood National and State Parks, California. http://www.nps.gov/redw/planyourvisit/brochures.htm#CP_JUMP_134687. Accessed 18 Mar 2009

Remote Sensing Lab (2004) Vegetation Classification, Vegetation Descriptions, North Coast and Montane Ecological Province—CALVEG Zone 1. Pacific Southwest Region, Forest Service, U.S. Department of Agriculture. http://www.fs.fed.us/r5/rsl/projects/classification/ncoast-veg-descript.shtml. Accessed 18 Mar 2009

Remote Sensing Lab (2005) FSSDE.EvegTile01A/B (vector digital data), 1:100,000. Pacific Southwest Region, Forest Service, U.S. Department of Agriculture, McClellan, California. http://www.fs.fed.us/r5/rsl/clearinghouse/aa-ref-sec263a.shtml. Accessed 18 Mar 2009

Russell WH, Jones C (2001) The effects of timber harvesting on the structure and composition of adjacent old-growth coast redwood forest, California, USA. Landscape Ecol 16:731–741. doi:10.1023/A:1014486030462

Sawyer JO, Gray J, West GJ, Thornburgh DA, Noss RF, Engbeck JH Jr, Marcot BG, Raymond R (2000a) History of redwood and redwood forests. In: Noss RF (ed) The redwood forest: history, ecology and conservation of the coast redwoods. Island Press, Washington, DC, pp 7–38

Sawyer JO, Sillett SC, Popenoe JH, LaBanca A, Scholars T, Largent DL, Euphrat F, Noss RF, Van Pelt R (2000b) Characteristics of redwood forests. In: Noss RF (ed) The redwood forest: history, ecology and conservation of the coast redwoods. Island Press, Washington, DC, pp 39–80

Schulte LA, Mladenoff DJ (2001) The original US Public Land Survey Records: their use and limitations in reconstructing presettlement vegetation. J For 99:5–10

Scull P, Richardson JL (2007) A method to use ranked timber observations to perform forest composition reconstructions from land survey data. Am Midl Nat 158:446–460. doi:10.1674/0003-0031(2007)158[446:AMTURT]2.0.CO;2

Seischab FK (1990) Presettlement forests of the Phelps and Gorham Purchase in western New York. Bull Torrey Bot Club 117:27–38. doi:10.2307/2997126

Seischab FK (1992) Forests of the Holland Land company in western New York, circa 1798. In: Marks PL, Gardescu S, Seischab FK (eds) Late eighteenth century vegetation of central and western New York State on the basis of original land survey records, New York State Museum Bulletin, New York State Museum. University of the State of New York, Albany, pp 36–53

Society for Ecological Restoration Science & Policy Working Group (SER) (2004) The SER International primer on ecological restoration, version 2. http://www.ser.org/content/ecological_restoration_primer.asp. Accessed 18 Mar 2009

Stewart LO (1935) Public land surveys: history, instructions, methods. Arno Press Inc, New York

Tart D, Williams C, DiBenedetto J, Crowe E, Girard M, Gordon H, Sleavin K, Manning M, Haglund J, Short B, Wheeler D (2005) Sect. 2: existing vegetation classification protocol. In: Brohman R and Bryant L (eds) Existing vegetation classification and mapping technical guide, Gen. Tech. Rep. WO–67, Ecosystem Management Coordination Staff, Forest Service, U.S. Department of Agriculture, Washington, D.C., pp. 2.1–2.34

U.S. Fish and Wildlife Service (1997) Recovery plan for the marbled murrelet (Brachyramphus marmoratus) in Washington, Oregon and California. U.S. Fish and Wildlife Service, Portland

Uzes FD (1977) Chaining the land: a history of surveying in California. Landmark Enterprises, Sacramento

Veirs SD (1982) Coast redwood forest: stand dynamics, successional status, and the role of fire. In: Means JE (ed) Forest succession and stand development research in the northwest. Forest Research Laboratory, Oregon State University, Corvallis, pp 119–141

Veirs SD (1986) Redwood second-growth forest stand rehabilitation study, Redwood National Park: evaluation of 1978–79 thinning experiments. Redwood National Park, Orick, California

Veirs SD, Lennox WS (1981) Rehabilitation and long-term management of cutover redwood forests: problems of natural succession. Symposium of Watershed Rehabilitation in Redwood National Park and Other Pacific Coastal Areas, Redwood National Park Archives, Arcata, California

Wang Y (2005) Presettlement land survey records of vegetation: geographic characteristics, quality and modes of analysis. Prog Phys Geogr 29(4):568–598. doi:10.1191/0309133305pp463ra

Waring RH, Major J (1964) Vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light, and temperature. Ecol Monogr 34(2):167–215. doi:10.2307/1948452

White CA (1984) A history of the rectangular survey system. Bureau of Land Management, Government Printing Office, Washington, DC