Structure and Dynamics of an Upland Old-Growth Forest at Redwood National Park, California

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Abstract

Many current redwood forest management targets are based on old-growth conditions, so it is critical that we understand the variability and range of conditions that constitute these forests. Here we present information on the structure and dynamics from six one-hectare forest monitoring plots in an upland old-growth forest at Redwood National Park, California. We surveyed all stems ≥20 cm DBH in 1995 and 2010, allowing us to estimate any systematic changes in these stands. Stem size distributions for all species and for redwood (*Sequoia sempervirens* (D. Don) Endl.) alone did not appreciably change over the 15 year observation interval. Recruitment and mortality rates were roughly balanced, as were basal area dynamics (gains from recruitment and growth versus losses from mortality). Similar patterns were found for *Sequoia* alone. The spatial structure of stems at the plots suggested a random distribution of trees, though the pattern for *Sequoia* alone was found to be significantly clumped at small scales (< 5 m) at three of the six plots. These results suggest that these forests, including populations of *Sequoia*, have been generally stable over the past 15 years at this site, though it is possible that fire exclusion may be affecting recruitment of smaller *Sequoia* (< 20 cm DBH). The non-uniform spatial arrangement of stems also suggests that restoration prescriptions for second-growth redwood forests that encourage uniform spatial arrangements do not appear to mimic current upland old-growth conditions.

Key words: forest dynamics, forest structure, old-growth, spatial pattern

Introduction

Remnant old-growth stands represent only a small fraction of current redwood forest area (Sawyer et al. 2000a), but play crucial roles in conservation and restoration of these ecosystems. As our best analogue to redwood forest conditions prior to the arrival of industrialized human settlement, remnant old-growth redwood stands are used as reference conditions for managers seeking to accelerate the development of second-growth forests (e.g., NPS 2008). In spite of their importance, relatively little is known about the basic structure and function of old-growth redwood forests (Busing and Fujimori 2002, Lorimer et al. 2009). Part of the difficulty is that old-growth conditions are relatively difficult to describe; by definition old-growth forests contain trees from a wide range of ages and sizes, with areas of closed canopy and open gaps (i.e., high spatial complexity) (Franklin et al. 2002). This structural complexity is magnified in old-growth redwood forests, which contain some of the oldest and largest trees known (Sillett et al. 2010).

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Further complications arise from the fact that old-growth redwood forest conditions vary across topographic gradients, from alluvial terraces to steep hillsides and ridgetops. Redwood forests on alluvial flats are comprised of almost pure stands of redwood *Sequoia sempervirens* (hereafter *Sequoia*) while upland stands are composed of a mix of species including *Sequoia*, Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), tanoak (*Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*) and other species (Sawyer et al. 2000b). Redwood stands on alluvial terraces and upland stands experience contrasting disturbance regimes, with stands found on alluvial areas subject to periodic inundation and deposition following floods, while upland stands are more prone to fire (and to a lesser extent landslides and windthrow) (Lorimer et al. 2009). There is some concern that *Sequoia* may not be able to maintain dominance in the absence of fire, although Busing and Fujimori (2002) show that at an alluvial habitat *Sequoia* populations have been stable. It is unclear how well this finding may hold in upland habitats where historically fires were more common (Lorimer et al. 2009).

The spatial structure of stands is another important, but undocumented, potential difference between alluvial and upland habitats. The spatial arrangement of stems (the degree to which the distribution of trees in a stand can be considered clumped, random or uniform) is a defining structural element of stands, determining local competitive environments (Biging and Dobbertin 1992, Das et al. 2008). Recently, Dagley (2008) described old-growth alluvial redwood forest spatial structure as clumped to random for overstory forest trees. Establishing if non-random spatial structure is also common in upland stands is highly relevant for redwood forest restoration; many thinning prescriptions for second-growth forest restoration may create uniform conditions (NPS 2008), which may persist for decades, but may or may not mimic old-growth forest spatial patterns.

Here we present information on forest structure and dynamics from six upland forest stands in Redwood National Park. We analyze differences in forest structure among our sites in terms of species composition, stem size distributions and the spatial arrangement of stems. Our information is derived from repeated surveys of these sites, so we also are able to directly calculate key demographic rates, including recruitment, growth and mortality. Our results largely confirm earlier findings from alluvial forests (Busing and Fujimori 2002, Dagley 2008), in that redwood forest populations appear to be generally stable and forest spatial patterns are not uniform.

Methods

Study sites

The region around Redwood National Park features a Mediterranean climate, with mild, rainy winters and cool, dry summers (Sawyer et al. 2000b). Annual mean temperatures are approximately 15 °C, with annual precipitation of about 170 cm, mostly occurring as winter rain. Summer fog is common near the coast, moderating the dry summer conditions. Soils are primarily derived from sandstone, mudstone and schist. Historically, fire has shaped coastal redwood forests, but has been largely excluded in the region of our study sites over the past 100 years (Ramage et al. 2010).

We surveyed six 1 ha plots to determine forest structure in an upland redwood forest (*fig. 1*). The sites have never been logged. Frequent fires characterized the forests prior to Euro-American settlement, but there is no recent record of fire in the areas containing the study plots. The plots were established in 1995 to compare forest structure in these old-growth areas to an adjacent second-growth stand known as the Whiskey Forty (Teraoka and Keyes 2011). Surveys mapped all stems ≥20 cm diameter at breast height (DBH, 1.37 m), measured tree diameters, and assessed tree status (live vs. dead) (*table 1*). In 2010 we surveyed these stands again for trees ≥20 cm DBH, recording current DBH, mortality (of trees extant in 1995), and recruitment (trees now ≥20 cm DBH but not recorded in 1995). Radial growth was determined from repeated stem diameter measurements. There were 13 instances of negative growth and 21 instances of unrealistically large radial growth (>15 mm year^{-1}), which probably arose from measurement error. We wished to remove outliers with exceptionally large negative and positive growth rates, but did not wish to bias our results in a positive direction by removing all negative growth rates. For this reason we removed from analysis stems that had radial growth rates < -2 mm year^{-1} or >15 mm year^{-1}, roughly 1 percent of our observations.

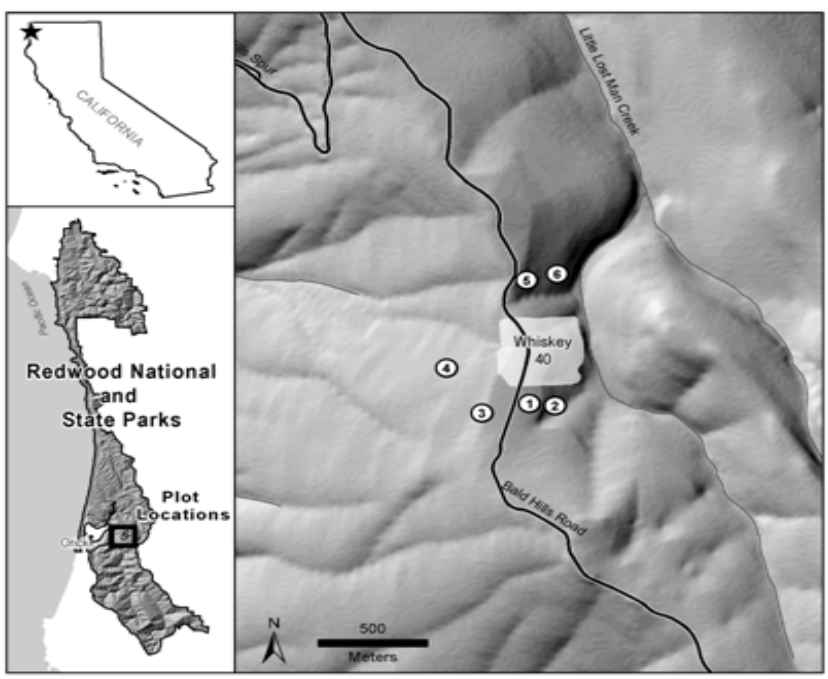

Figure 1—Location of the six upland old-growth redwood forest plots. The plots are located near an area of second-growth forest (locally known as the "Whiskey 40"), but are in a large, otherwise undisturbed old-growth forest.

Data analysis

We determined forest structure in terms of stand density (stems ha^{-1}), basal area (m^2 ha^{-1}), and size class distributions. We measured patterns of stem size distributions at each plot using a departure index, M, that is similar to the Gini coefficient, but can distinguish both the magnitude and direction of change (Menning et al. 2007). The departure index M was calculated for 1995 versus the 2010 censuses, and compared against a null model that assumed no

Table 1—*Characteristics of forest monitoring plots at the time of establishment in 1995 (stems >= 20 cm DBH).*

Plot identifier	UTM* Easting	UTM Northing	Elevation (m)	Stem count (ha) 1995	Stem count (ha) 2010	Basal area (m^2 ha^{-1}) 1995	Basal area (m^2 ha^{-1}) 2010
Plot 1	415657	4570743	472	230	244	174	165
Plot 2	415776	4570731	446	185	175	163	176
Plot 3	415440	4570690	460	134	131	205	231
Plot 4	415276	4570941	403	153	163	133	136
Plot 5	415645	4571428	461	185	193	138	146
Plot 6	415786	4571464	412	212	183	198	195

Table 1 (continued)

Plot identifier	Species comprising > 1% of stem counts**
Plot 1	TSHE 42%; SESE 27%; PSME 22%; LIDE 8%
Plot 2	TSHE 42%; SESE 29%; PSME 25%; LIDE 3%; ABGR 1%
Plot 3	SESE 46%; ABGR 21%; TSHE 16%; PSME 10%; LIDE 8%
Plot 4	SESE 38%; LIDE 27%; ABGR 17%; TSHE 13%; PSME 5%
Plot 5	LIDE 30%; SESE 29%; PSME 25%; TSHE 16%
Plot 6	SESE 37%; TSHE 37%; PSME 23%; LIDE 3%

* UTM coordinates in NAD 1983, zone 10.
** At time of plot establishment. ABGR = *Abies grandis* (Dougl. ex D. Don) Lindl.; LIDE = *Notholithocarpus densiflorus* syn. *Lithocarpus densiflorus*; PSME = *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco; SESE = *Sequoia sempervirens* (D. Don) Endl.; TSHE = *Tsuga heterophylla* (Raf.) Sarg. Percentages may not add to 100 due to rounding.

differences between these measurement intervals. Differences in M between the observed values and null model were compared using a Wilcoxon signed rank test. We compared demographic rates (recruitment and mortality) as well as basal area dynamics (basal area gains from recruitment and growth versus basal area losses from mortality) using paired randomization tests to account for small sample sizes and non-normal distributions (Manly 2001).

We described tree spatial distributions within each plot by considering individual trees as points, and examined nearest neighbor patterns at multiple scales using the inhomogeneous K-function, a second-moment measure that accounts for variability in the average density (also called intensity) of trees across each plot (Baddeley 2008). Intensity is the expected number of points per unit area, and may be constant (homogenous) or vary across locations (inhomogeneous). Plots of kernel estimates of intensity suggested high variations in intensity, suggesting that inhomogeneous models were more appropriate for our data. For each plot we considered spatial patterns within a search radius of up to 25 percent the side of the plots, 25 m. We determined the significance of the departure from complete spatial randomness (CSR) by comparing observed values to the 95 percent simultaneous critical envelope (Baddeley 2008) [avoiding inflation of type I errors (Loosmore and Ford 2006)], calculated from 999 simulations of random point fields, with intensity patterns estimated using a kernel smoothing function. Results are presented in terms of the normalized K statistic, L(h) (where h represents the search radius), which is centered on zero. L(h) values within the 95 percent critical envelope are consistent with a

random distribution of stems, while values below the critical envelope are considered significantly uniform, and values above the critical envelope are considered significantly clumped.

We used a marked point process model to directly test if *Sequoia* has a different spatial structure compared to other co-occurring species, using the inhomogeneous K-function normalized at zero [i.e., $L_{Sequoia,\ \mathrm{Other}}(h)$]. We created a 95 percent simultaneous critical envelope from 999 simulations using random toroidal shifts of the pattern for each taxonomic group, where observed values within the envelope indicate similar distributions, values below the envelope indicate the species groups "repulse" each other in space, values above the envelope indicate "attraction" in the groups' spatial pattern.

Results

At the time of plot establishment in 1995 stem density for trees ≥20 cm DBH ranged from 134 to 230 trees ha^{-1} and averaged 183 trees ha^{-1} (±2 SE = 29) and basal area ranged from 133 to 205 m^2 ha^{-1} and averaged 169 m^2 ha^{-1} (±2 SE = 24) (*table 1*). Although *Sequoia* comprised on average only a small proportion of stems at each plot (mean ± 2 SE = 61 ± 8 trees ha^{-1}, 33 percent of stems), this species comprised the majority of average basal area (mean ± 2 SE = 100 ± 30 m^2 ha^{-1}, 59 percent of total average basal area). There was little change in density or basal area for trees ≥20 cm DBH from 1995 to 2010 (*table 2*).

At the time of plot establishment in 1995 stems >20 cm DBH generally followed a negative exponential ("inverse-j") size class distribution (*fig. 2A*). Stem size classes were similar in 2010, so that the negative exponential distributions were maintained (*fig. 2B*). The departure index M was relatively unchanged over this time period (average M = + 0.002, average range of M = -0.388 to 1.612), and was not significantly different compared against a null model of no change (Wilcoxon signed rank test, $P = 1$). For *Sequoia*, there was a suggestion that stems size distributions were becoming more skewed in favor of large stems from 1995 to 2010 (average M = + 0.044, average range of M = -0.611 to 1.389, Wilcoxon signed rank test, $P = 0.049$), but changes were small (*fig. 2*).

The relative lack of change in stand structure from 1995 to 2010 was also supported by demographic measurements. Plot-level average recruitment and mortality rates were balanced (annualized recruitment rate = 0.700 percent, annualized mortality rate = 0.698 percent, paired randomization test, 9999 iterations, $P = 0.46$) (*table 2*). The demographic rates for *Sequoia* also were essentially equivalent (annualized recruitment rate = 0.229 percent, annualized mortality rate = 0.325 percent, paired randomization test, 9999 iterations, $P = 0.77$). The dynamics of basal area from 1995 to 2010 did not suggest substantial changes; annualized basal area gain from recruitment and growth (average = 0.98 m^2 ha^{-1} $year^{-1}$) was roughly balanced by losses from mortality (average = 0.80m^2 ha^{-1} $year^{-1}$) (paired randomization test, 9999 iterations, $P = 0.26$) (*table 2*). Similar patterns in basal area dynamics also were found for *Sequoia* (average basal area gain from recruitment and growth = 0.50 m^2 ha^{-1} $year^{-1}$; average basal area loss from mortality = 0.38 m^2 ha^{-1} $year^{-1}$; paired randomization test, 9999 iterations, $P = 0.35$) (*table 2*).

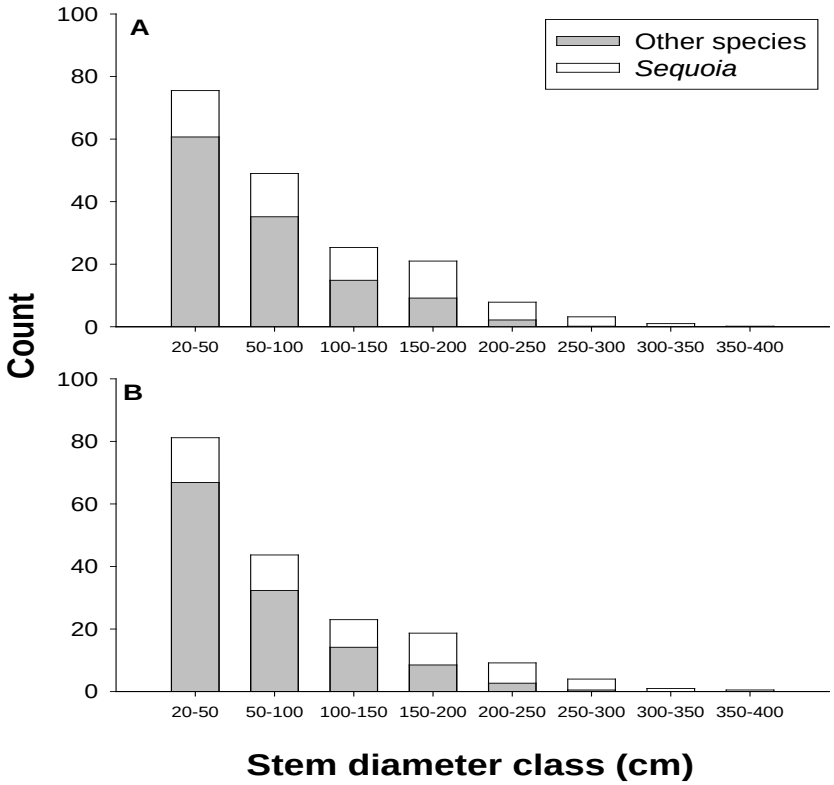

Figure 2—Stem size class distributions averaged across six 1-ha plots for trees ≥20 cm DBH in 1995 (A), and in 2010 (B).

Contour plots of the spatial intensity showed that the density of stems was highly variable across each plot (not shown), indicating the need to use the inhomogeneous measures of spatial pattern. The inhomogeneous L(*h*) statistic showed a random arrangement of stems at most spatial scales across all plots (although a single plot showed a minor degree of clumping at small scales) (*fig. 3A*). Estimates of the spatial pattern of *Sequoia* alone suggest significant clumping at small scales for three of the six plots (*fig. 3B*). Direct comparison of *Sequoia* versus other co-occurring species suggests that these groups are strongly segregated at spatial scales greater than approximately 10 m (*fig. 3C*).

Table 2—*Annualized demographic rates and basal area dynamics (gains from recruitment and growth and losses from mortality) from 1955 to 2010 for trees >20 cm DBH. Demographic rates were roughly balanced (P = 0.46), as were losses and gains in basal area (P = 0.26) (paired randomization tests). Similar patterns were found for Sequoia. Confidence intervals were determined from 1000 bias corrected bootstrapped samples.*

	Plot identifier	**Recruitment rate (%)**	**Mortality rate (%)**	**Basal area gain (m^2 ha^{-1} $year^{-1}$)**	**Basal area loss (m^2 ha^{-1} $year^{-1}$)**
All species	Plot 1	1.02	0.73	1.02	1.57
	Plot 2	0.35	0.64	1.04	0.36
	Plot 3	0.53	0.46	1.23	0.17
	Plot 4	1.01	0.59	1.02	0.82
	Plot 5	0.98	0.60	0.75	0.48
	Plot 6	0.31	1.16	0.78	1.41
	average	***0.70***	***0.70***	***0.98***	***0.80***
	95% CI	*0.46 to 0.94*	*0.58 to 0.99*	*0.85 to 1.1*	*0.41 to 1.28*
Sequoia only	Plot 1	0.11	0.67	0.42	0.40
	Plot 2	0.00	0.26	0.44	0.20
	Plot 3	0.11	0.11	0.92	0.02
	Plot 4	0.66	0.35	0.64	0.66
	Plot 5	0.25	0.13	0.21	0.26
	Plot 6	0.25	0.44	0.36	0.77
	average	***0.23***	***0.33***	***0.50***	***0.38***
	95% CI	*0.1 to 0.43*	*0.19 to 0.5*	*0.35 to 0.71*	*0.19 to 0.61*

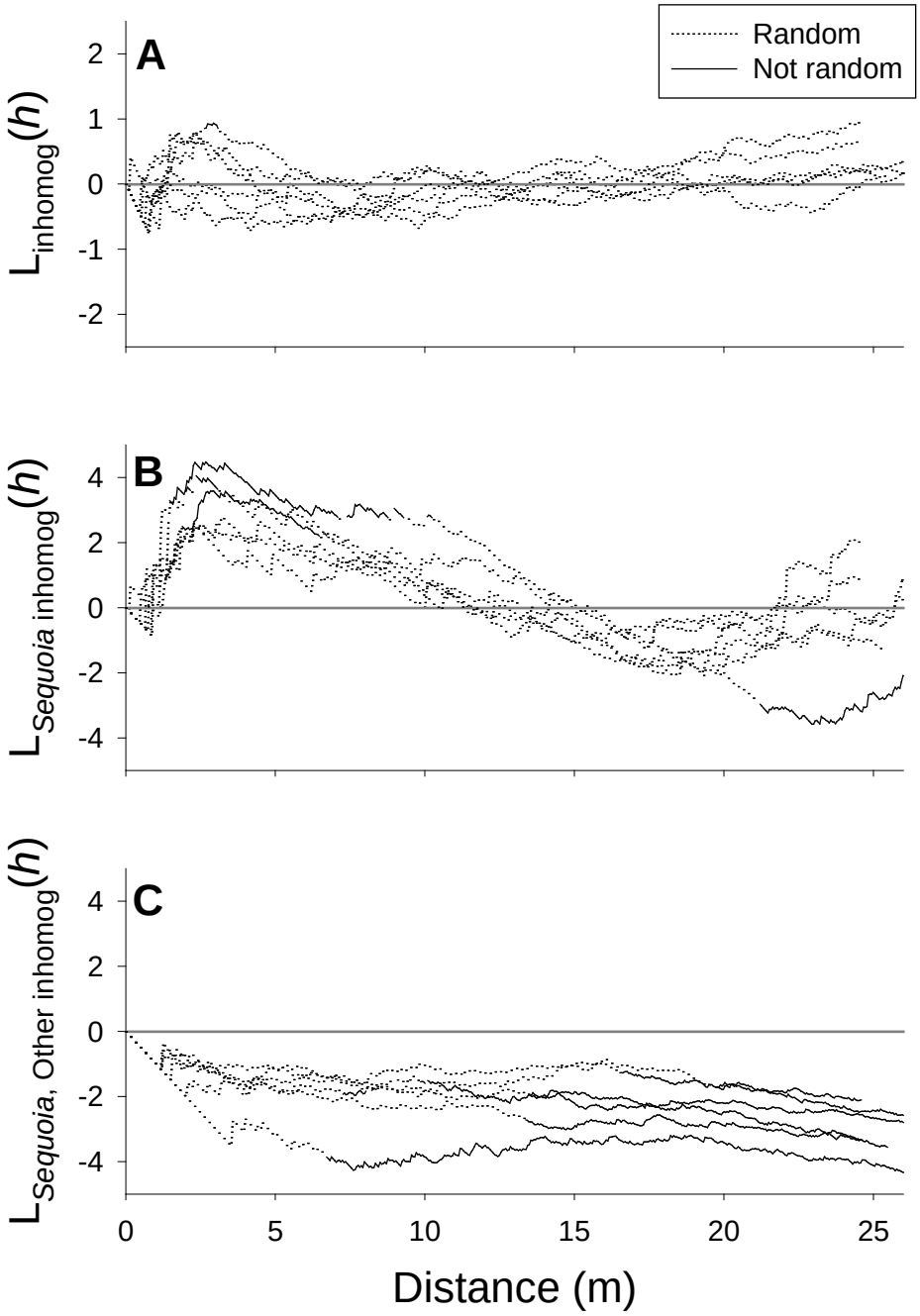

Figure 3—Tree spatial pattern for all species at six upland old-growth redwood stands (A), the pattern for *Sequoia* alone (B), and *Sequoia* versus all other species (C). Lines are the observed normalized K-function [L(*h*)] for individual plots. Dashed intervals represent random distributions and solid intervals above and below the zero control line indicate statistically significant (α = 0.05) clumping or repulsion, respectively. Significance was determined by departures from 95 percent simultaneous critical envelopes (Baddeley 2008).

Discussion

Our old-growth redwood stands appeared to be generally stable from 1995 to 2010, a finding in agreement with earlier observations from an alluvial terrace (Busing and Fujimori 2002). Stem size class distributions generally followed an "inverse-j" distribution, which suggests stable populations in old-growth stands (Avery and Burkhart 2002). Stable stem size distributions and direct measurements of forest dynamics suggest that these stands did not experience large changes over the 15 year observation interval.

There has been speculation that in the absence of moderate disturbance from fire *Sequoia* might fail to maintain its dominant status in these communities (Lorimer et al. 2009), but our observations failed to provide clear support for this idea. We found some evidence that *Sequoia* stem size distributions may have become less dominated by small trees over time, but recruitment and mortality rates for *Sequoia* were roughly balanced, as were gains and losses in basal area. However, our measurements of recruitment include only stems that were ≥ 20 cm DBH, so it is possible that we are missing early signals of reproductive failure in the absence of fire (Ramage et al. 2010). More detailed observations of small tree dynamics are needed to fully document the reproductive output of *Sequoia* (whether by seed or sprouting) in upland old-growth forests under current conditions. Moreover, the 15 year length of observations presented here is short in comparison to ages of dominant trees in our study site. It may be that large changes in stand and population dynamics occur infrequently or will only be detectable over longer time scales.

In terms of spatial structure, with very little exception we found a random arrangement of stems across all spatial scales at all six upland stands. This finding was promoted by the use of the inhomogeneous formulation of the K-statistic and a more statistically defensible method of determining statistical significance, resulting in tests that were more conservative and less likely to show significant clumping or uniformity. In spite of this, we still identified strong evidence of clumping at small spatial scales (from approximately 1 to 5 m) for *Sequoia* at half of the plots, an unsurprising finding given the sprouting habit of this species. Moreover, there appeared to be segregation between *Sequoia* and other species at large (approximately > 10 m) spatial scales. Thus, the general conclusions of Dagley (2008) concerning the restoration targets for alluvial stands appear to hold for upland stands: thinning prescriptions that encourage uniform spatial arrangements of stems do not appear to mimic current old-growth structure.

How well current old-growth conditions reflect stand structure prior to European settlement is difficult to determine precisely (Stephenson 1999). The disruption of historic disturbance regimes, exotic species (including pathogens), and other changes have likely altered these forests. But until a better model for restoration targets is identified, these stands provide our best understanding of reference conditions. Continued measurement and monitoring of old-growth upland stands is needed to insure we are able detect any subtle, pervasive trends that may be occurring (van Mantgem et al. 2009).

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