

ENVIRONMENTAL AND ECOLOGICAL EFFECTS ON SIZE CLASS
DISTRIBUTIONS OF FOXTAIL PINE (*PINUS BALFOURIANA*, PINACEAE) IN
THE KLAMATH MOUNTAINS, CALIFORNIA

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ABSTRACT

Variation in size class distributions along elevation gradients can indicate localized spatial expansion by tree populations inhabiting mountaintops. We searched for this pattern in northern foxtail pine (*Pinus balfouriana* Grev. & Balf. ssp. *balfouriana*) stands located in the Klamath Mountains of northern California. Data from 32 belt-transects placed within 16 foxtail pine stands were used to test the hypothesis that this species is expanding downslope locally. Nonmetric multidimensional scaling (NMS) illustrated that size class distributions could be grouped into four types: (1) those at low elevations on north and east aspects; (2) those at low elevations on south and west aspects; (3) those at high elevations on north and east aspects; (4) those at high elevations on south and west aspects. Low elevation transects had greater abundances of small trees, while high elevation transects had greater abundances of large trees. We interpreted this pattern as support for the hypothesis that foxtail pine is locally expanding downslope in the Klamath Mountains. Further analyses showed that NMS dimensions were correlated with estimates of tree density, species diversity, the importance of shade-tolerant conifers, and boulder cover. Moreover, the importance of shade-tolerant conifers was related to aspect, substrate type, boulder cover, and interactions among these variables. The pattern of those correlations suggests that several ecological and environmental factors affect the ability of foxtail pine to expand downslope through alleviation or alteration of competitive interactions. Those results provide an ecological context for climate-mediated range expansions and retractions in northern foxtail pine.

Key Words: foxtail pine, Klamath Mountains, microsites, *Pinus balfouriana*, size class distribution, spatial expansion.

Spatial patterns of dispersion are scale-dependent in forest trees (Szwagrzyk and Czerwczak 1993; Ribbens et al. 1994; Nathan and Muller-Landau 2000; Hubbell 2001). At small spatial scales, dispersion patterns typically differ among size classes, with seedlings and saplings being clumped and adult trees randomly dispersed throughout stands (Platt et al. 1988; Szwagrzyk and Czerwczak 1993; Nathan and Muller-Landau 2000). This pattern is often attributed to dispersal limitations, competition, or the outcome of adaptive life history strategies such as colonization-competition tradeoffs (Ribbens et al. 1994; Clark et al. 2004; McEuen and Curran 2004).

At large spatial scales, adult trees tend to be found on topographically stable landforms, while seedlings and saplings are more common in areas prone to disturbance or resource limitation (Basnet 1992; Desta et al. 2004; Pollmann and Veblen 2004). Patterns such as these have been interpreted in various ways (Fox and Gurevitch 2000). When assemblages are structured along elevation gradients, the typical interpretation of those patterns is one of localized upslope or

downslope expansion (Pollmann and Veblen 2004).

The structure and composition of species assemblages can have large effects on those patterns (Desta et al. 2004). Moreover, moisture availability as a function of aspect is often found to influence the composition and structure of forest tree assemblages (Rundel et al. 1988; Sawyer and Thornburgh 1988; Urban et al. 2000). This is especially true in geographic areas prone to summer drought (Major 1988; Sawyer and Thornburgh 1988). Here, we examine the influence of aspect, elevation, and the distribution of co-occurring conifers on the size class distributions of foxtail pine (*Pinus balfouriana* Grev. & Balf.) stands to test the hypothesis that this species is expanding downslope from mountaintop populations located in the Klamath Mountains.

The Klamath Mountains are a geologically complex system of mountain ranges located in northern California and southern Oregon (Fig. 1). Forest types are diverse and represent mixtures of Cascadian and Sierran elements (Whittaker 1960). These forests likely originated in their modern form no longer than 10,000 to 15,000 yr ago (Sawyer and Thornburgh 1988; Wanket 2002; Sawyer 2006). Regional conifer

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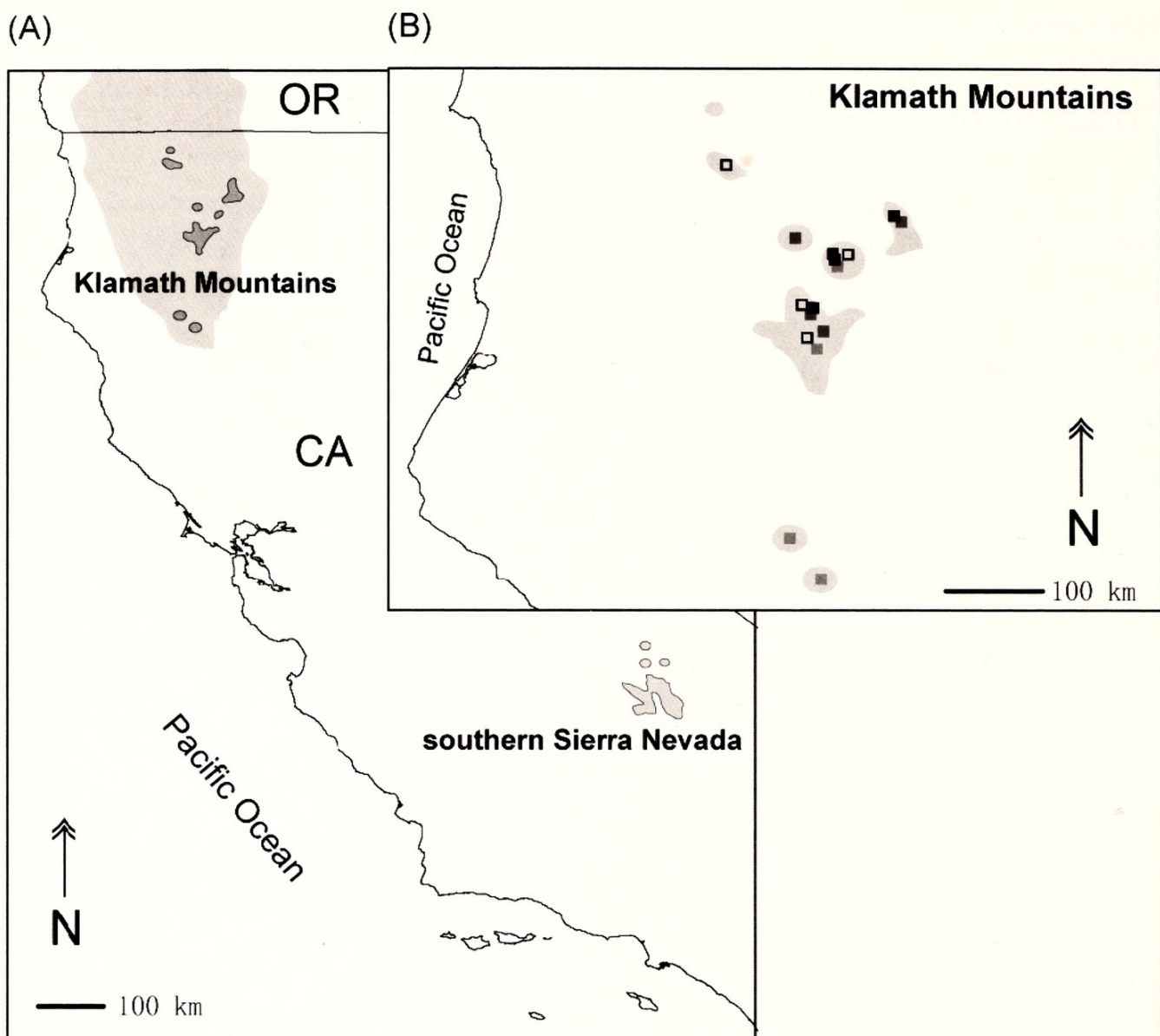


FIG. 1. Distribution of foxtail pine (*Pinus balfouriana* Grev. & Balf.) in California. (A). The distribution of this species in California is disjunct. The extent of the Klamath Mountains is shown in light grey, while the distribution of foxtail pine is shown in dark grey. (B). The distribution of foxtail pine in the Klamath Mountains. Sampled stands are indicated with squares that are color-coded by aspect class (black = north; dark grey = east; light grey = south; white = west).

diversity is high, due in part, to a suite of rare and endemic species.

Northern foxtail pine (*P. balfouriana* ssp. *balfouriana*) is one such conifer. Previous research has shown that this species is largely restricted to localities on ultramafic substrates or those with abundant suitable microsites (Eckert and Sawyer 2002). Foxtail pine stands on ultramafic substrates have reduced densities, basal areas, and frequencies of shade-tolerant competitors such as *Abies magnifica* A. Murr. ssp. *shastensis* Lemmon and *Tsuga mertensiana* (Bong.) Carr., while stands with abundant microsites (i.e., abundant spatially isolated patches of soil amongst inhabitable areas) have increased species diversities (Eckert 2006a). Those patterns of habitat heterogeneity were offered as the primary mechanism of

foxtail pine persistence in the conifer-rich Klamath Mountains through competition avoidance within a variable habitat.

Several ecological and dendrochronological studies of foxtail pine stands in the southern Sierra Nevada indicate that numerous rounds of downslope and upslope expansion have likely occurred in the past as a function of regional climate changes and topographic effects on local climates (Ryerson 1983; Lloyd 1997; Lloyd and Graumlich 1997; Millar et al. 2004; Bunn et al. 2005). Similar studies for the populations of foxtail pine located in the Klamath Mountains are lacking. Patterns of climate-induced tree mortality and population expansions and retractions may differ between the southern Sierra Nevada and the Klamath Mountains, especially given the observed differences in

environmental, climatic, and ecological conditions (Rundel et al. 1988; Sawyer and Thornburgh 1988). Specifically, the ecological context of foxtail pine drastically differs between those regions (Eckert and Sawyer 2002).

In the Klamath Mountains, ecotones are sharp and downslope movement would involve colonization within a dense matrix of shade-tolerant competitors. When coupled with the observations of Eckert (2006a), these patterns suggest that the distribution of competing conifer species, which is in turn a function of habitat heterogeneity (i.e., ultramafic soils and microsites), affects the ability of foxtail pine to expand downslope. Therefore, the influence of aspect, substrate type, and boulder cover on the ability of foxtail pine to expand downslope may be acting through alteration or alleviation of competitive interactions.

The diverse subalpine forests of the Klamath Mountains offer a unique system with which to analyze the effects of topography and species interactions on size class distributions of a locally dominant species. We address this topic for foxtail pine using a four-step approach. First, we use ordination to address the question of whether or not foxtail pine is expanding downslope in the Klamath Mountains as a function of aspect. Second, we investigate the correlation of ecological and environmental variables with observed multidimensional patterns. Third, we test the hypothesis that substrate type, aspect, and microsite availability affect the local dominance of shade-tolerant conifers. Lastly, our results are extended to a generalized hypothesis of how differences in habitat conditions may affect the ability of foxtail pine to expand downslope as a function of the local dominance of shade-tolerant competitors and relate this hypothesis to the further need for climate-based analyses.

MATERIALS AND METHODS

Study Area, Stand Selection, and Sampling

Study Area. In northern California, the Klamath Mountains are a geologically complex mosaic of mountain ranges characterized by diverse substrates, climates, and vegetation types (Major 1988; Sawyer and Thornburgh 1988; Safford et al. 2005). Substrate types range from igneous to ultramafic, with most ultramafic substrates being located in the eastern portion of the region. Climate conforms to a modified Mediterranean type characterized by dry summers and wet winters, with thunderstorms developing during the late summer. Those climate patterns form a sharp wet-to-dry moisture gradient across the west-east axis of the region (Major 1988). Vegetation types range from lowland chaparral to subalpine conifer forests with high levels of plant endemism and diversity.

Stand Selection and Sampling. We identified 16 stands of foxtail pine that were equally distributed among four aspect classes. Selected stands represent a subset of those sampled by Eckert (2006a), who used a stratified random sampling approach for stand selection. Aspect classes were based on the four cardinal directions (north: 315–45°; east: 45–135°; south: 135–225°; west: 225–315°). Within each stand, we established two 200-m long by 50-m wide belt-transects located at the lowest and highest local elevations. The low elevation belt-transects were located at the lowest elevation that still had foxtail pine in densities greater than 50 trees ha⁻¹. At densities less than 50 trees ha⁻¹, foxtail pine is not the dominant tree species (Eckert and Sawyer 2002; Eckert 2006a).

In each belt-transect, the density (trees ha⁻¹) and basal area (m² ha⁻¹) of trees greater than 1.37 m in height were determined using the point-centered-quarter (PCQ) method with 10 randomly spaced points ($n = 40$ trees) and the unbiased estimator of Pollard (1971). Density and basal area were transformed into an index of importance (I) for each species using the following formula:

$$I_i = \left[\frac{D_i}{D} + \frac{BA_i}{BA} \right] / 2$$

where, D_i is the density of species i , BA_i is the basal area for species i , D is the total stand density, and BA is the total stand basal area. Species richness (SR), diversity (Shannon-Wiener information statistic [H']), and equitability (E) were determined from PCQ data using the number of species sampled (species richness) and their relative frequencies (p_i) in the sample (diversity: $H' = -\sum_{i=1}^k p_i \ln p_i$; equitability: $E = H' / \ln SR$).

The diameter at breast height (DBH) was measured for a sample of 75 foxtail pine trees greater than 1.37 m in height. Trees were sampled along a wandering line transect placed within each belt-transect following the protocol outlined by Bonham (1989). The position of each tree was mapped using a GARMIN eTREX Venture GPS receiver (GARMIN International, Olathe, KS), and the mean of their elevation measurements was used as the absolute elevation (m) for each belt-transect. Trees were subsequently classified into one of 10 non-overlapping size classes based on DBH (≤ 25 cm, 25.01–46 cm, 46.01–65 cm, 65.01–84 cm, 84.01–102 cm, 102.01–119 cm, 119.01–136 cm, 136.01–153 cm, 153.01–169 cm, ≥ 169.01 cm), which approximately correspond to 100-year age classes (Eckert and Sawyer 2002). We also estimated boulder cover (%) within each belt-transect using four one-m² plots. The cover of boulders in each of those one-m² plots was visually estimated using a grid with 16 sections. Boulders were defined as rock fragments greater

than 50 cm in diameter. The cover of boulders was equated with microsite availability (see Eckert 2006a).

Statistical Hypothesis Testing

The effects of aspect, elevation, and substrate type on ecological and environmental characteristics of stands were investigated with standard parametric statistical procedures (e.g., two-sample and paired t-tests, analysis of variance [ANOVA], and analysis of covariance [ANCOVA]) using a critical value of $P = 0.05$. All t-tests were two-tailed. All ANOVAs with significant effects were followed by Tukey-Kramer multiple comparison tests to detect differences among treatment means. Data from different transects in the same stand were grouped prior to statistical testing when the hypothesis being tested concerned differences at the stand level. Prior to performing these tests, the assumptions of normality and equal variances were verified using standard procedures (Zar 1999). We log-transformed data when necessary to meet those requirements. All statistical analyses were conducted with NCSS unless otherwise noted (Hintze 2001).

We compared size class distributions among transects using a three-step approach. First, we identified transects with similar size class distributions using ordination. Multivariate distances were constructed among transects ($n = 32$) using unweighted Euclidean dissimilarities based on size class distributions and subjected to nonmetric multidimensional scaling (NMS). This technique is robust to common statistical problems associated with ordination procedures (Kruskal 1964; Fasham 1977; Kenkel and Orlóci 1986; Minchin 1987). The solution from classical multidimensional scaling (CMS) was used as the starting configuration for a maximum of 100 iterative starts in NMS (Torgeson 1965). This was done to minimize the likelihood of identifying local optima. We chose to limit our examination to three dimensions and gauged the fit of the NMS distances to the original dissimilarity matrix with a Shepard plot.

Second, we determined the statistical significance of groups using analysis of similarity (ANOSIM; Clarke 1993). This method constructs a test statistic (R) from the mean ranks of dissimilarity values within versus among categories and tests this statistic by comparison to a null distribution derived from permutations of category labels among samples. Categories correspond to NMS-defined groups, while samples are equated with transects. We performed tests for all groups considered at once and all pairwise two-way comparisons using a Bonferroni correction, so as to approximate standard multiple comparison tests (Zar 1999).

TABLE 1. AVERAGE ENVIRONMENTAL AND ECOLOGICAL CHARACTERISTICS OF 16 FOXTAIL PINE STANDS SAMPLED FROM THE KLAMATH MOUNTAINS GROUPED BY ASPECT CLASS ($N = 4$ STANDS IN EACH CLASS). Standard errors of the mean are located below each average in parentheses. BA = basal area, BC = boulder cover, D = density, E = equitability index, H' = Shannon-Wiener diversity index, $PIBA\ I$ = *Pinus balfouriana* importance index, SR = species richness.

Aspect	Area (ha)	Elevation (m)	Stands on		Slope (%)	BC (%)	D (trees/ha)	BA (m ² /ha)	PIBA I	SR	H'	E
			Serpentine									
North	31.45 (6.84)	2159.00 (80.50)	3		23.64 (6.80)	42.32 (9.11)	220.25 (57.38)	26.76 (4.10)	0.57 (0.14)	5.50 (0.50)	1.11 (0.23)	0.72 (0.06)
East	20.03 (4.64)	2323.75 (67.61)	2		43.30 (3.48)	33.17 (14.05)	188.25 (45.46)	24.65 (5.17)	0.53 (0.13)	5.00 (1.41)	1.11 (0.29)	0.72 (0.09)
South	21.25 (7.14)	2300.75 (27.45)	2		33.22 (2.30)	30.22 (4.67)	176.25 (46.49)	26.89 (7.30)	0.59 (0.04)	4.25 (0.48)	0.97 (0.04)	0.73 (0.07)
West	15.25 (2.71)	2176.25 (39.68)	2		28.58 (7.16)	31.14 (6.55)	137.75 (24.15)	11.40 (3.33)	0.60 (0.09)	4.00 (0.00)	0.99 (0.15)	0.68 (0.08)

TABLE 2. EXPLORATORY ANALYSES (TWO-SAMPLE AND PAIRED T-TESTS AND ANOVAS) FOR THE EFFECTS OF ELEVATION ($DF = 30$), SUBSTRATE TYPE ($DF = 14$), AND ASPECT ($DF_1 = 3$, $DF_2 = 12$) ON ECOLOGICAL CHARACTERISTICS FROM 32 BELT-TRANSECTS LOCATED IN 16 FOXTAIL PINE STANDS DISTRIBUTED THROUGHOUT THE KLAMATH MOUNTAINS OF CALIFORNIA. Significant effects in the ANOVAs were further investigated using Tukey-Kramer multiple comparison tests. Effects refer to the relative magnitudes of the means for samples used in the described statistical tests. BA = stand basal area (m^2/ha), D = stand density (trees/ha), E = east, H' = Shannon-Wiener information statistic, High = high elevation transect, I_{PIBA} = foxtail pine importance, Low = low elevation transect, N = north, nu = non-ultramafic substrate, $SHADE$ = summed importance of shade-tolerant conifers, S = south, SR = species richness, u = ultramafic substrate, W = west.

	Elevation (paired)			Substrate (two-sample)			Aspect		
	<i>t</i>	P	Effect	<i>t</i>	P	Effect	<i>F</i>	P	Effect
<i>SR</i>	2.865	0.008	High < Low	1.000	0.334	$nu = u$	2.465	0.112	$W = S = E = N$
<i>D</i>	0.963	0.343	High = Low	1.334	0.203	$nu = u$	1.010	0.422	$W = S = E = N$
<i>BA</i>	1.269	0.214	High = Low	0.278	0.785	$nu = u$	4.468	0.025	$W < S, E, N$
I_{PIBA}	2.535	0.017	High > Low	2.179	0.047	$nu < u$	0.262	0.851	$W = S = E = N$
<i>SHADE</i>	2.316	0.028	High < Low	2.596	0.021	$nu > u$	0.857	0.489	$W = S = E = N$
H'	3.074	0.004	High < Low	0.875	0.396	$nu = u$	1.733	0.213	$W = S = E = N$

Analyses were performed using the VEGAN package encapsulated in the R environment and 10,000 permutations (Ihaka and Gentleman 1996; Oksanen et al. 2005).

Lastly, simple linear regression models were used to examine the relationships among NMS dimensions, abundances of trees within each size class, and several ecological variables (i.e., H' , species richness, importance index of foxtail pine, summed importance indices of shade-tolerant conifers). Shade-tolerant conifers were defined to be *Abies concolor* (Gordon & Glend.) Lindley, *A. magnifica* ssp. *shastensis*, and *Tsuga mertensiana*. We chose to use separate linear regression models, rather than multiple regression models, to avoid problems associated with multicollinearity (Zar 1999).

RESULTS

Ecological Characteristics of Transects

A total of 32 transects were sampled from 16 stands located throughout the Klamath Mountains (Table 1). Absolute measures of elevation ranged from 1910 m to 2422 m for low elevation transects and from 1956 m to 2527 m for high elevation transects. On average, high and low elevation transects were separated from one another by 95 m (± 47 m) in elevation and were

within one km of each other. Aspect had no effect on elevation (ANOVA: $F_{3,12} = 2.612$, $P = 0.099$) or boulder cover (ANOVA: $F_{3,12} = 1.493$, $P = 0.266$). Substrate type was equally frequent among aspect classes and had no effect on elevation (two-sample t-test: $t = 1.373$, $df = 14$, $P = 0.191$) or boulder cover (two-sample t-test: $t = 1.396$, $df = 14$, $P = 0.184$).

Elevation, substrate type, and aspect differentially affected stand structure and composition (Table 2). The importance of foxtail pine increased with elevation, while species richness, the importance of shade-tolerant conifers, and H' decreased with elevation. Substrate type affected the importance values of foxtail pine and shade-tolerant conifers differently. Foxtail pine importance was greater on ultramafic substrates, while the importance of shade-tolerant conifers was greater on non-ultramafic substrates. Aspect had no effect on most measures of stand structure and composition. However, the basal areas of stands on western aspects were significantly smaller than stands on southern, northern, and eastern aspects.

Substrate type, aspect, and their interaction significantly affected the summed importance indices of shade-tolerant conifers once the effects of elevation and boulder cover were removed (Table 3). Separate ANCOVAs for each shade-tolerant conifer yielded the same result (not shown).

TABLE 3. ANCOVA FOR EFFECTS OF SUBSTRATE TYPE AND ASPECT ON THE SUMMED IMPORTANCE INDICES OF SHADE-TOLERANT CONIFERS WITH ELEVATION (M) AND BOULDER COVER (%) AS COVARIATES.

Factor	df_1	df_2	<i>F</i>	P
Substrate type	1	14	11.09	0.005
Aspect	3	12	5.00	0.015
Substrate type \times Aspect	3	12	6.27	0.008
Elevation (covariate)	1	14	7.65	0.015
Boulder cover (covariate)	1	14	8.24	0.012

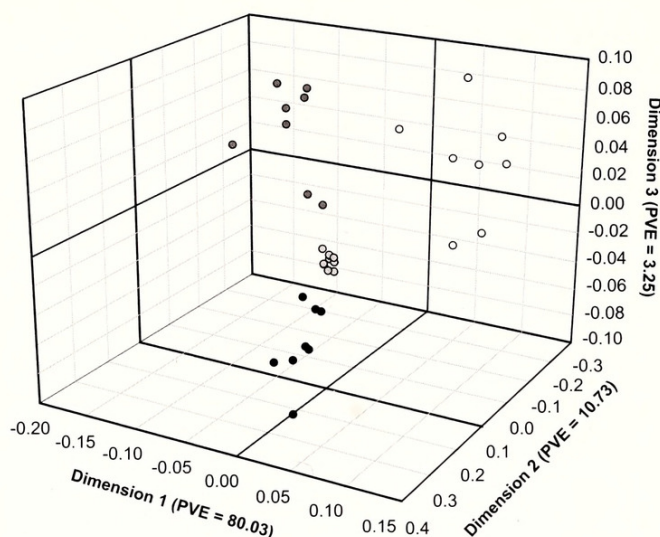


FIG. 2. Results of NMS based on unweighted Euclidean dissimilarities among size class distributions for 16 stands of foxtail pine located in the Klamath Mountains of northern California. The first three dimensions are plotted along with the percent variance explained (PVE) by the dominant eigenvalue for each dimension using the metric solution determined with CMS. Four potential groups are identified based on aspect and elevation — (1) low elevation with north and east aspects (black); (2) low elevation with south and west aspects (light grey); (3) high elevation with north and east aspects (white); (4) high elevation with south and west aspects (dark grey).

NMS Ordination

NMS Results. Ordination using NMS revealed four potential groups of transects defined by aspect and elevation (Fig. 2). Substrate type did not aid with defining these groups. Groups one and three were composed of transects located on north and east aspects at either low or high elevations, respectively. Groups two and four illustrated a similar pattern for transects on south and west transects. Inspection of stress and Shepard plots showed that our three dimensional representation of the original 10 dimensional space resulted in moderate distortion (stress = 0.026) and that transformation of the original dissimilarity matrix did not differentially distort dissimilarities of large magnitude. Adding additional dimensions (i.e., fourth, fifth, etc.) to the NMS analyses did not drastically reduce distortion. Furthermore, the dominant eigenvalues for each of the three dimensions in CMS solution, which was only used as a starting point for NMS, accounted for over 90% of the variation within the data.

Significance of NMS-Defined Groups. Differences among NMS groups were significant (ANOSIM: $R = 0.921$, $P < 0.001$). Alternatively, grouping transects by substrate type was not significant (ANOSIM: $R = 0.052$, $P = 0.365$). All possible pairwise comparisons across the four NMS groups showed that each group was

statistically different from every other group ($n = 6$ pairwise comparisons, ANOSIM: $R > 0.85$, $P < 0.001$). In general, the largest differences were observed between groups differing in elevation. This is apparent in the shape of the average size class distributions for each group (Fig. 3). Transects at lower elevations had reverse J-shaped distributions (Fig. 3A, B), while transects at higher elevations, regardless of aspect, had multimodal distributions skewed towards larger trees (Fig. 3C, D).

Size Class and Ecological Correlates of NMS Dimensions

NMS dimensions were differentially correlated with the abundance of foxtail pine in each size class. Dimension one was positively correlated with size classes one ($r = 0.99$) and two ($r = 0.88$) and negatively correlated with size classes four through 10 ($-0.84 < r < -0.45$). The opposite trend was found for dimensions two and three, which were positively correlated with larger trees ($0.29 < r < 0.77$). These correlations indicated that the differences among NMS-defined groups were largely due to the greater abundances of smaller trees in low elevation transects and greater abundances of larger trees in high elevation transects. The effects of aspect were not as strong, but transects on southern and western exposures had increased abundances of large trees.

Several ecological variables were correlated with NMS dimensions. Dimension one was positively correlated with total density of trees ($r = 0.44$), importance of shade-tolerant conifers ($r = 0.51$), and boulder cover ($r = 0.60$), while it was negatively correlated with foxtail pine importance ($r = -0.47$). Dimensions two and three were not correlated with measured variables, except for the negative correlations of boulder cover ($r = -0.37$) and H' ($r = -0.35$) with dimension three.

DISCUSSION

Size class distributions of foxtail pine in the Klamath Mountains differ by aspect and elevation. At higher elevations, these distributions are skewed towards larger trees, while at lower elevations the skew is towards smaller trees. This trend also characterizes comparisons among aspects, with southern and western exposures having greater abundances of larger trees than northern and eastern exposures. Substrate type had no effect on size class distributions. These patterns were apparent in the NMS and ANOSIM results, which suggested four groups of transects (Fig. 2). Furthermore, the importance of shade-tolerant conifers, species diversity, and boulder cover differed between elevations. Based on these patterns, our hypothesis is that foxtail

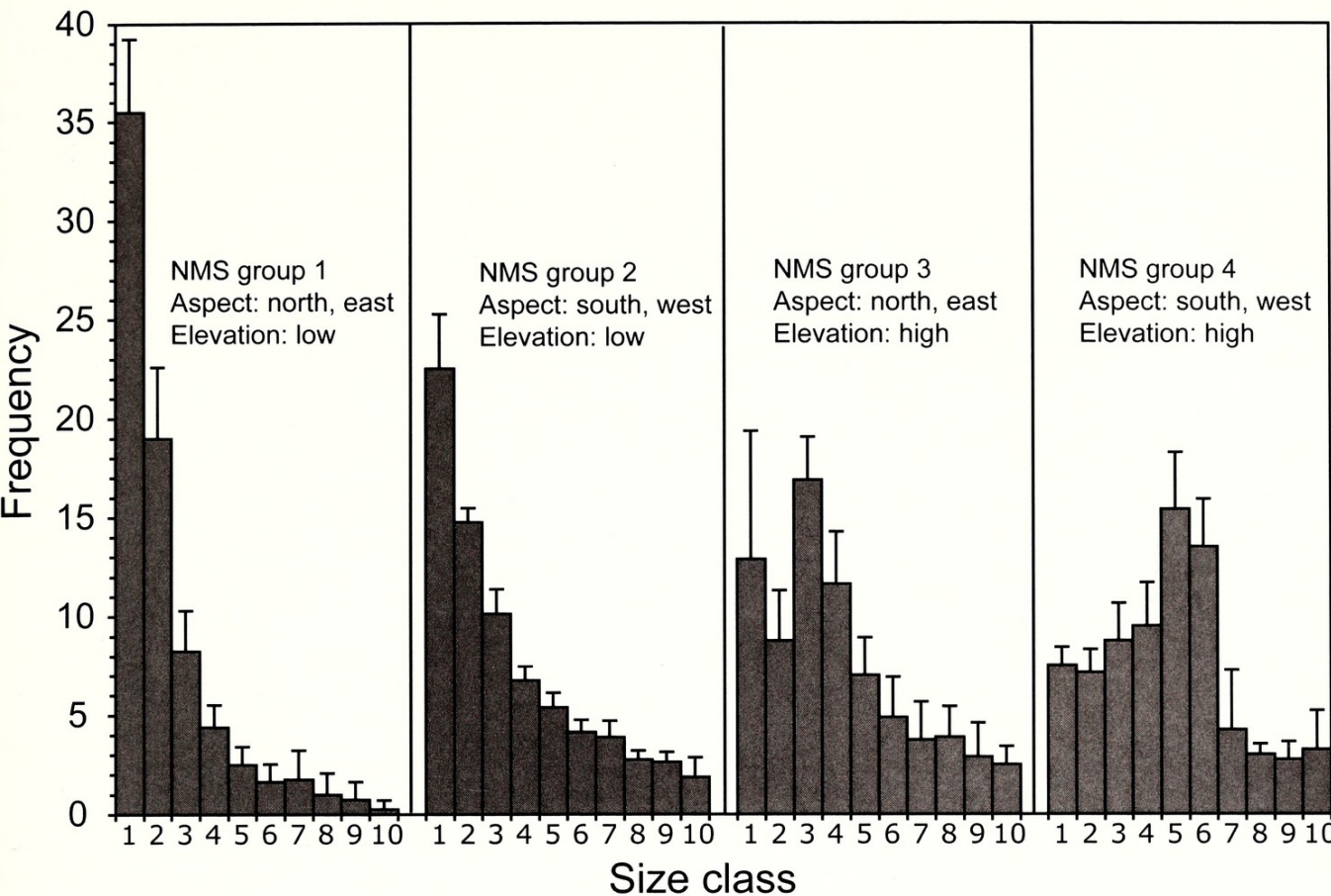


FIG. 3. Average (+ 1 standard deviation) size class distributions of NMS-defined groups.

pine is dispersing into and establishing within downslope stands previously lacking this species as a function of biotic interactions with superior competitors in those stands. We have also related the local distribution of those competitors to two forms of habitat heterogeneity—boulder cover and ultramafic substrates.

The elevation-dependent skew in size class distributions is consistent with the hypothesis that foxtail pine is expanding downslope. The shape of observed size class distributions at low elevations in this study is also consistent with that of growing populations (Harper 1977; Barnes et al. 1998; Silvertown and Charlesworth 2001). The correlation between DBH and tree age bolsters this argument (Eckert and Sawyer 2002). Caution must be used, however, when equating static demographic patterns with trends through time (Clark et al. 1999).

The magnitude of this expansion is localized to downslope areas adjacent to mountaintop foxtail pine stands. The extent of this expansion, therefore, is on the order of a few hectares and has resulted in creating broad ecotones between stands dominated by foxtail pine and downslope stands largely lacking foxtail pine. Furthermore, it appears that this expansion has begun during the past 500 to 1000 yr based on a simple interpretation of the raw demographic data presented in this study (Fig. 3). That interpreta-

tion, however, relies on the assumption that previous rounds of expansion into lower elevations would have left traces in the form of snags or downed trees. The wet climate of the Klamath Mountains makes this unlikely, so those dates need to be interpreted with extreme caution.

Several environmental variables were shown to affect the distribution of shade-tolerant conifers (Table 3). Eckert (2006a) showed that these species out-compete foxtail pine based on an analysis of two morphological indices indicative of competition. Therefore, we hypothesize that it is the distribution of shade-tolerant conifers that constrains the ability of foxtail pine to expand downslope. This is consistent with aspect differentially affecting size class distributions of foxtail pine. Southern and western aspects also had decreased importance values of shade-tolerant conifers, as well as, decreased densities and basal areas of shade-tolerant conifers in downslope stands (data from Eckert [2006a]; ANOVA: $F_{3,12} = 4.111$, $P = 0.032$). Therefore, we conclude that aspect and boulder cover interact to affect the distribution of shade-tolerant competitors, which in turn constrains, or at least affects, the ability of foxtail pine to expand downslope. In other words, foxtail pine is able to expand downslope better on south and west aspects, because shade-tolerant competitors are not as dominant.

Substrate type affected the distribution of shade-tolerant competitors, with ultramafic substrates having stands with decreased importance values of *Abies concolor*, *A. magnifica* ssp. *shastensis*, and *Tsuga mertensiana*. However, substrate had no effect on the size class distributions of foxtail pine. If the hypothesis discussed above is correct, then this result is enigmatic because foxtail pine should also have strong patterns of downslope expansion on ultramafic substrates. That pattern was not observed, which can be explained by the observation that other members of the genus *Pinus* also out-compete foxtail pine for light (Eckert 2006a). This suggests that constraints on downslope expansion may also be tied to the total tree density of downslope stands (i.e., adjacent downslope vegetation where foxtail pine is not the dominant tree). In all cases, the density and basal area of downslope stands were greater than that observed within foxtail pine stands (Eckert 2006a).

Upslope dispersal of shade-tolerant competitors and downslope dispersal of foxtail pine, which would create broad ecotones on sites with high levels of boulder cover, could also explain our results. This interpretation agrees with the observed decrease of shade-tolerant conifers, which dominate most downslope transects, and boulder cover as elevation increases. If this hypothesis is correct, we would expect to observe similar patterns for co-occurring conifers except in reverse (i.e., lower elevations outside of foxtail pine stands should contain the largest individual trees). These patterns, however, are not found in downslope stands, suggesting that it is foxtail pine that is expanding downslope (data from Eckert [2006a]). Moreover, DNA sequence data for foxtail pine obtained from all sampled stands are consistent with the argument of population growth and expansion from severe population bottlenecks (Eckert 2006b).

Our results, however, are also consistent with other explanations, such as spatially localized resource distributions (e.g., soil nutrients), disturbance regimes, or growth patterns of foxtail pine. For example, the basal areas of stands with western aspects were significantly smaller than those on northern, eastern, and southern aspects. This suggests that growth may differ among aspects as a function of moisture availability. The data, however, do not support similar effects on the local distribution of shade-tolerant conifers, suggesting that our inferences concerning their effects on the ability of foxtail pine to expand downslope may be robust to microclimatic differences between aspects.

Most importantly, we have not addressed the role of climate as affecting our results. Climate is likely to jointly confound the downslope expansion of foxtail pine and the distribution of co-occurring conifers. However, this study has

provided the appropriate ecological context for interpreting future climate data. In other words, we have illustrated that there is a strong ecological component to foxtail pine's response to local and regional climate differences and future changes in the Klamath Mountains.

IMPLICATIONS

Size class distributions of foxtail pine in the Klamath Mountains are consistent with the localized expansion of this species into downslope vegetation. Moreover, this expansion is correlated with the distribution of shade-tolerant conifers, which are in turn correlated with habitat heterogeneity (i.e., boulder cover and ultramafic substrates). The implications of such correlations are that the localized expansion by an inferior competitor (e.g., foxtail pine) into habitats dominated by superior competitors (e.g., shade-tolerant conifers) can be facilitated by habitat heterogeneity. Our findings indicate that although historical climate change could be the driving force behind the observed expansions, there exists a strong ecological context to the outcome of downslope expansion by foxtail pine within the Klamath Mountains. Future studies addressing the role of climate in this region, therefore, need to take into account such contexts.

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LITERATURE CITED

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