Regeneration and Recruitment Correlate with Stand Density and Composition in Long-Unburned Aspen Stands Undergoing Succession to Conifer in the Sierra Nevada, USA

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Abstract

Succession of aspen stands to conifer in the Sierra Nevada Mountains of California and Nevada, USA, is being interrupted by forest managers thinning conifers to sustain aspen stands *in situ*. However, patterns of stand density, species composition, and regeneration prior to management intervention have scarcely been described. We established a grid of sample plots throughout nine aspen stands encircling Lake Tahoe in the central Sierra Nevada. The degree of succession to conifer throughout each aspen stand was spatially heterogeneous. Patches of pure aspen were rare. Stand density index (SDI) reached an upper limit of 1700 in pure aspen. As composition shifted in favor of conifer, SDI approached or attained a maximum of 2500 in some plots. Stand density and species composition data were tested as predictors of conifer and aspen regeneration densities in each plot. Conifer seedlings had an average density of 3261 ha^{-1}; they were most abundant in aspen-dominated areas of any density, and in conifer-dominated areas of higher density. Aspen regeneration had an average density of 3211 ha^{-1} and was one order of magnitude less frequent in areas of pure conifer versus areas of pure aspen, but remained relatively abundant in most areas. Aspen saplings were rare (average density of 42 ha^{-1} for saplings 10-15 cm DBH), especially at high stand densities or in areas where conifers dominated. Our findings suggest that forest managers interested in sustaining aspen stands *in situ* will need to control stand density to promote recruitment of younger aspen to the overstory.

Introduction

Succession from quaking aspen (*Populus tremuloides*) to coniferous species is occurring throughout many forests of North America [1-7]. Aspen is a pioneer species adapted to disturbance [8,9]. Some aspen form pure stands and appear to remain stable in that state, but in many cases succession to conifer is expected in the absence of disturbances such as fire that kills young conifers establishing within aspen stands [8]. Longer fire return intervals under active wildfire suppression throughout much of the 20th Century have given conifers time to establish and develop thicker fire-resistant bark with advancing size and age [10]. Conifers may eventually overtop aspen and suppress aspen regeneration and the herbaceous vegetation layer where much of the biodiversity is concentrated.

At the western edge of aspen's natural range, in the Sierra Nevada Mountains of California and Nevada, aspen stands ranked higher in biodiversity than meadows and conifer stands [11]. Pure aspen stands support a diverse herbaceous understory and a greater abundance of bird species than mixed stands where aspen is intermingled with conifers [12]. In the vicinity of Lake Tahoe, in the central Sierra Nevada, aspen are mostly restricted to riparian areas where their vegetation community stabilizes the banks of streams flowing into Lake Tahoe [13].

Forest managers want to maintain an aspen component within the conifer-dominated forests surrounding Lake Tahoe, but have limited options for intervention. Options not widely publicly supported include clearcutting or allowing fire to kill patches of mature trees and create openings for pioneering aspen to invade and occupy. Managers are constrained and must be cautious in their use of prescribed fire as a tool for restoration and management. Concerns over smoke, high fuel loads, and risk of escape and damage to dwellings throughout the wildland-urban interface have prompted forest managers to favor mechanical or manual conifer removal in aspen stands undergoing succession to conifer. Removal of smaller conifers from aspen stands is being undertaken throughout the Lake Tahoe Basin, with the objective of regenerating aspen *in situ* or thinning to relieve crowding.

Basal area (BA) and stand density index (SDI) are measures of stand density that consider tree size and number of trees per unit area. They are useful predictors of aspen tree growth and vigor [14]. Forest managers who are aware of an upper limit to stand density can evaluate stands and prescribe treatments that control stand density (i.e., occupied growing space) to achieve objectives such as enhancing tree growth or promoting regeneration; these 'stand density management regimes' are based on growing space occupancy relative to the maximum for any combination of age classes of trees [15]. Unlike the upper limit of BA which we expect to be higher in stands with older/larger trees, the upper limit of SDI offers the convenience of remaining fairly constant for a range of tree sizes/ages and site qualities for any single species. Less is known about how the upper limit of SDI may vary according to species composition in mixed stands [16].

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We sought to describe patterns of stand density, species composition, and regeneration in aspen stands undergoing succession to conifer throughout the Lake Tahoe Basin. This was a unique opportunity to sample an array of long-unburned stands prior to management intervention in the succession process (i.e., conifer removal). Specifically, we aimed to define an upper limit to SDI according to the degree of succession to conifer, and describe patterns of conifer and aspen regeneration and test for correlations with stand density and species composition. We hypothesized that: (i) the upper limit of SDI was significantly higher in areas of aspen stands that had succeeded to conifer; (ii) conifer regeneration was more frequent, and aspen regeneration less frequent, in areas of higher stand density and conifer dominance, and; (iii) aspen saplings whose presence we assumed indicated a higher probability of successful recruitment of aspen regeneration to the overstory were less common in areas of the aspen stands with higher stand densities dominated by conifer.

Methods

Study region

The Lake Tahoe Basin is a 1,310 km^2 watershed located in the central Sierra Nevada Mountains of California and Nevada, USA. Climate in the Lake Tahoe Basin (39°05'N latitude, 120°02'W longitude) is classified as Mediterranean continental with cold winters and summers with cool nights and warm days. Near lake level, at the Lake Tahoe Airport (elevation 1,906 m), August is usually the warmest month with an average maximum of 25.9°C and average minimum of 4.3°C. January is the coolest month with an average maximum of 5.0°C and average minimum of -9.4°C. Minimum temperatures of 0°C or lower occur on an average of 231.8 days annually. Mean annual precipitation varies between years, on average ranging from 660 mm near lake level on the east side of the basin to over 1440 mm on the west side of the basin. Most precipitation falls as snow between November and April (http://www.wrcc.dri.edu).

Field data collection

We selected nine aspen stands undergoing succession to conifer for sampling. These stands encircled Lake Tahoe, ranging in elevation from 1,900-2,260 m above sea level, with three located on the eastern shore of the Lake Tahoe Basin, three in the south, and three in the west [15]. There was no visible evidence of past wildfire in any stand. We established a systematic grid of sample points throughout a one-hectare study area in each stand, with sample points (i.e., plot centers) spaced 10 m apart along transect lines spaced 25 m apart, for a total of 28-30 sample points per study area. The one-hectare study areas were made square (100 × 100 m) or rectangular to fit inside each aspen stand. A square area had three long transects and rectangular study areas had 5-7 shorter transects.

Aspen and conifer regeneration <10 cm diameter at breast height 1.37 m (DBH) were counted in circular 0.004 ha plots (3.57 m radius) at each sample point. Aspen root suckers were tallied if their stem was not joined with adjacent suckers at/above ground level. Conifer tallies excluded seedlings in their first growing season since we expected that many of these seedlings would not survive and become established [17]. We recorded the proportion of area within each regeneration sample plot covered by large rocks (preventing regeneration), allowing for calculation of regeneration counts per unit of unobstructed ground area. Within each one-hectare study area, we mapped tree locations using a tripod-mounted flux gate compass to obtain azimuth and sonar hypsometer for distance from a series of survey points to each tree. Species and DBH were recorded for each aspen >10 cm DBH and conifer >20 cm DBH. Conifer saplings 10-20 cm DBH were so numerous that we counted them within the 0.004 ha regeneration plots instead of mapping and measuring them throughout each study area.

Analysis

Species composition and the upper limit of stand density

Tree data were summarized to describe the relative abundance of each species throughout the nine study areas. Each study area was spatially heterogeneous in terms of species composition and stand density. Therefore, we sought to quantify stand density at localized areas throughout each study area, and examine its relationship with species composition at each of these localized areas. We created a stem location map for each one-hectare study area by converting tree location data from distance and azimuth to an easting (x) and northing (y) for each stem. We used ArcGIS to query each stem location map and derive stand density and species composition in the vicinity of each systematic sample grid point. This was achieved by creating a buffer of 7.98 m radius around each sample point and clipping tree data in each buffer, giving tree data for a series of 0.02 ha circular plots throughout each study area. Tree data from each 0.02 ha plot were summarized, giving BA per hectare and SDI for the aspen and conifer stand components, and other hardwoods when present. SDI was calculated by summing individual tree SDI because the DBH data were not normally distributed: $SDI=\sum(0.04DBH_i)^a$ where DBH_i=DBH in cm of the ith tree in the plot, and a=1.605 [17,18]. Species composition in each plot was calculated as the proportion of aspen and proportion of conifer in terms of BA.

We sought to define an upper limit to SDI [19] according to species composition. A scatterplot of total SDI in each 0.02 ha plot versus species composition (ranging from pure conifer to pure aspen) revealed a paucity of data for aspen-dominated areas of higher SDI. Therefore, we established a second series of 0.02 ha sample plots at each study area, systematically sampling in between the first series of sample points, along parallel transects offset 12.5 m from the original transect lines. We also selected six pure aspen stands for sampling at different locations around Lake Tahoe, and established a 0.02 ha circular plot in what appeared to be a fully stocked area within each stand. These six stands covered a wide range of elevations, from 1920m (near lake level) at Burke Creek, Burton Creek, Spring Creek, and Tallac Creek and 1950 m at Fallen Leaf Lake, up to 2415 m at Marlette Lake. The supplemental SDI and composition data were added to the dataset and scatterplot. To define an approximate upper limit of SDI - exclusive of extreme 'outlier' data the SDI data were binned according to species composition, and the 99th percentile of SDI calculated for each bin. We regressed the 99th percentile of SDI against the mean species composition for each bin using PROC REG in SAS [20], defining the approximate upper limit of SDI for any composition. Cook's distance revealed low SDI in the 60-80% aspen bin, supporting collection of additional data. This prompted installation of plots in dense, aspen-dominated mixtures at South Lake Tahoe (1920 m elevation), Spooner Lake (2150 m), Upper North Canyon (2300 m), and 2 km south of Incline Lake at 2440 m elevation.

Regeneration patterns

Count data for regeneration in each 0.004 ha plot were regressed against estimates of stand density and species composition from the 0.02 ha plots centered on the same sample points. The regeneration frequency data had numerous 'zero' counts and a few very high counts (i.e., 'reverse-J' distribution), prompting fitting and testing of four

candidate regeneration models: Poisson, negative binomial, zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB) using PROC COUNTREG in SAS [20]. Models were fitted to frequency data for conifer seedlings (DBH <10 cm) and two size classes of aspen: regeneration (DBH <10 cm) and saplings (DBH 10-15 cm). Aspen sapling counts were extracted from the stem map data for trees in each 0.02 ha plot used to estimate stand density and species composition around each systematic sample point.

Finally, we constructed generalized linear mixed-effects models and specified a negative binomial distribution to describe relationships between frequency of regeneration, the dependent variable, and candidate explanatory variables: stand density (SDI or BA) and species composition (aspen BA % or conifer BA %). Models were fitted using PROC GLIMMIX in SAS [21]. The nesting of sample plots within different stands was accounted for by specifying 'stand' as a random effect in the mixed-effects model. Selection of variables for inclusion in the final model was based on likelihood ratio tests comparing the full model against reduced models in terms of model chi-square. The full model included quadratic terms for stand density and species composition (e.g., $SDI + SDI^2$) and an interaction between stand density and composition. To depict the influence of stand density and species composition and their interactions on conifer and aspen regeneration, and recruitment of aspen to the sapling stage, we used the best generalized linear mixed-effects models to generate average (expected) values of regeneration density (stems ha⁻¹) for a range of stand densities in pure aspen stands, and aspen-conifer mixtures with either 75%, 50%, 25% or 1% aspen BA.

Results and Discussion

Species composition and the upper limit of stand density

Different combinations of hardwood and conifer species were present in each sample stand (Table 1). Pines were much less common than the true firs: red fir (*Abies magnifica*) and white fir (*Abies concolor*). Conifers accounted for between 52% and 95% of stand BA in the nine stands. Six of these stands comprised >75% conifer BA. Hardwoods other than aspen were only found adjacent to stream channels, and rarely exceeded 20 cm DBH.

The scatterplot of SDI and species composition (in terms of percent aspen BA) revealed that within the aspen-conifer stands we selected for sampling, conifers were frequently found in pure patches (at the scale of ~200 m² patch size; i.e., 0.02 ha plot size) (Figure 1). Within the nine one-hectare study areas, pure aspen patches were a minority with only 6% of the plots being pure aspen. The majority (70%) of the plots contained a mixture of conifer and aspen. Among mixed plots, almost

3/4 (i.e., 72% of mixed plots) were dominated by conifer in terms of BA.

The upper limit of SDI was higher in conifer-dominated areas. The 99th percentile of SDI in 0.02 ha plots was 2499 in areas of pure conifer and 1716 in pure aspen. The linear regression fitted to binned SDI-composition data defined an approximate upper limit of SDI for any composition. The t-test for the regression slope coefficient (P<0.0001) indicated that the upper limit of SDI correlated with species composition in terms of percent aspen. Woodall et al. [22] reported approximately 30% higher maximum SDI for pure aspen and aspen-dominated stands (composition 80-100% aspen) from a nationwide study. Being based on the 99th percentile of data, their estimate could be a reflection of high SDI in a few special areas where aspen were well adapted and had formed pure stands. Alternatively, our upper limit of SDI for central Sierra Nevada stands may be underestimated and should be validated with independent data. Conversely, our maximum SDI values for Sierra Nevada aspen-conifer mixtures (composition 20-80% aspen) were 15-25% higher than those presented by Woodall et al. [22]. This suggests that Sierra Nevada aspen-conifer mixtures are atypical, possibly because they are often restricted to wetter, more productive areas with deeper soils, such as lower slopes and alluvial flats [13]. In our nine sample stands, the most common conifer associates were red fir and white fir that are shade tolerant and support very high stand densities [19]. In other regions, aspen are widespread and may be more negatively affected by a different suite of competitors or found in forests that do not attain such high SDI [23].

Beneath the maximum SDI line, we also present a dashed line at 60% of maximum SDI, considered to represent the lower limit of a zone – or 'threshold' – of imminent competition-mortality above approximately 55-60% SDI [24-26] (Figure 1). Given that a relationship between SDI and competition-induced aspen mortality has not been defined for the Sierra Nevada, it would be prudent for forest managers interested in averting excessive crowding, mortality of aspen, and succession to conifer to maintain stand density below 1000 SDI (i.e., <60% of maximum SDI for pure aspen). Our findings also suggest that in conifer-dominated areas with SDI >1500 (i.e., >60% of maximum SDI for pure conifer), competition-induced mortality would only be "imminent" for conifer whereas aspen in a stand at 1500 SDI would be experiencing intense competition and may soon be extirpated while conifer tree growth proceeded and SDI attained and exceeded the upper limit of approximately 1700 SDI for aspen.

Aspen regeneration and recruitment to the overstory

Conifer seedling densities rivaled aspen regeneration densities, on average, throughout the nine sample stands surrounding Lake

Stand	POTR		PIJE		PICO		ABCO		ABMA	
BC20	44	(4.8)	24	(8.5)	6	(0.6)	326	(86.1)	-	-
BP2	185	(43.2)	22	(9.8)	28	(7.0)	218	(40.0)	-	-
CV05	119	(48.2)	3	(1.0)	52	(17.6)	103	(26.5)	38	(6.7)
CV06	54	(13.6)	-	-	68	(22.0)	69	(30.6)	80	(32.3)
NC03	73	(21.4)	48	(24.7)	-	-	54	(15.0)	110	(38.9)
SHC01	165	(22.2)	17	(24.1)	6	(4.4)	107	(48.4)	-	-
SSP24	122	(22.2)	8	(3.8)	28	(7.1)	371	(62.8)	3	(4.2)
TC01	192	(29.4)	7	(3.6)	-	-	134	(37.7)	58	(25.6)
WA38	58	(12.8)	-	-	63	(28.7)	117	(33.5)	93	(24.9)

Species included: *Populus tremuloides* (POTR), *Pinus jeffreyi* (PIJE), *P. contorta* (PICO), *Abies concolor* (ABCO), and *A. magnifica* (ABMA). Species not included: *Alnus incana* ssp. *tenuifolia* (2 trees ha⁻¹ at SHC01), *P. monticola* (1 tree ha⁻¹ at CV06) and *Salix spp.* (3 trees ha⁻¹ at SHC01 and 26 trees ha⁻¹ at TC01).

Table 1: Density (trees ha⁻¹) and species composition (percent of stand basal area; in parentheses) of aspen and conifer trees >20 cm DBH within nine aspen-conifer stands surrounding Lake Tahoe, California.
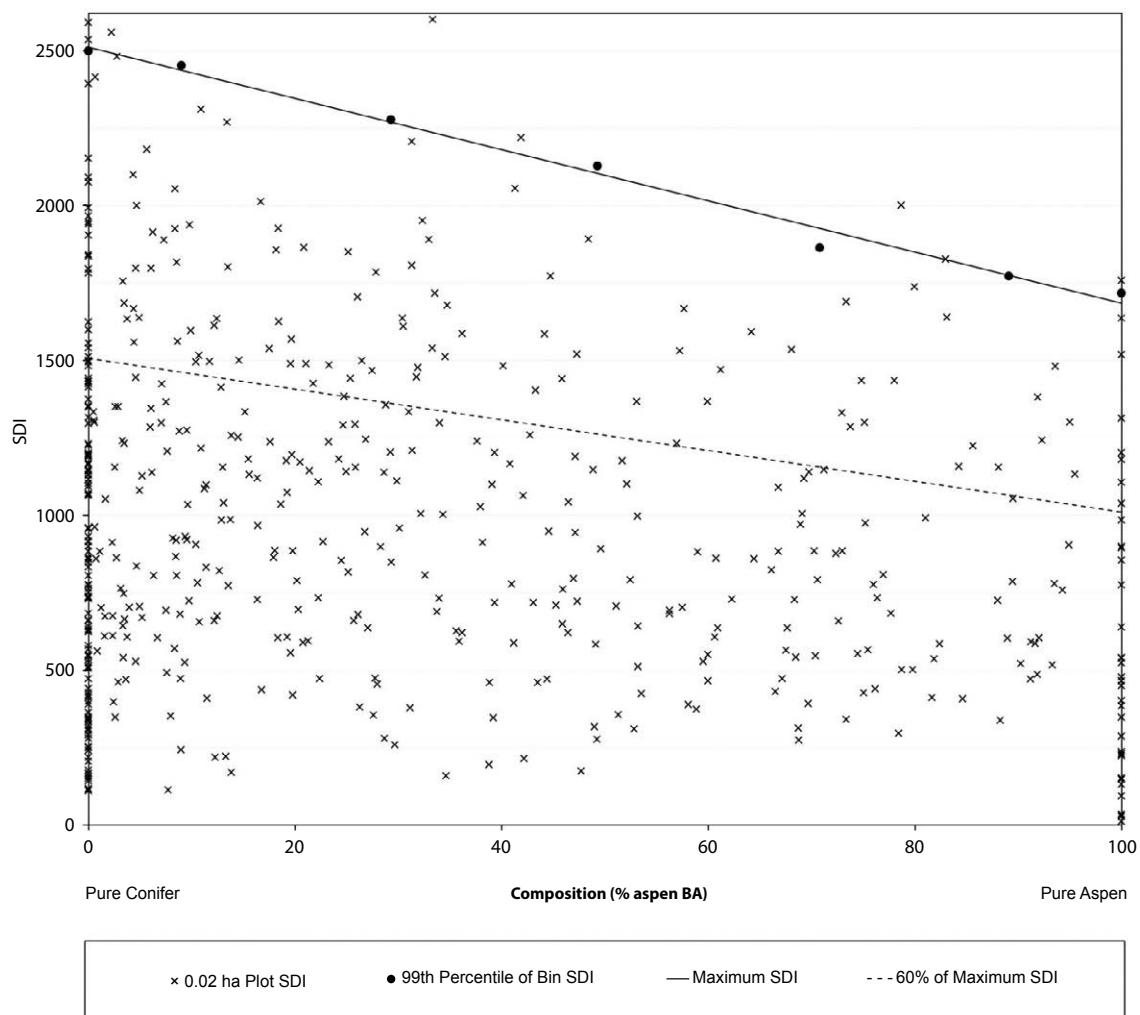
Figure 1: Stand density index (SDI) and species composition in terms of percent aspen basal area (% aspen BA) in 0.02 ha circular fixed-radius plots at 19 locations throughout the Lake Tahoe Basin, California. Maximum SDI for any composition defined by relationship between 99th percentile of SDI and the mean composition (% aspen BA) in each bin (0%, 0.01-20%, 20-40%, 40-60%, 60-80%, 80-99.99%, 100% aspen BA) where SDI_{max} = 2511.2 – 8.264 *%aspenBA* (R^2=0.99).

Tahoe. In the 10-20 cm DBH size class, aspen were outnumbered by conifers of which 5% were pines and 95% true firs. High variability in counts of conifer seedlings (DBH <10 cm) and conifer saplings/poles (10-20 cm DBH) within 0.004-ha plots located throughout the sample stands indicated that conifer regeneration patterns were spatially heterogeneous. Counts of aspen regeneration (DBH <10 cm), saplings (DBH 10-15 cm), and pole-sized aspen (DBH 15-20 cm) also varied between plots. The sharp decrease in densities of aspen saplings vis-à-vis aspen regeneration suggested that few regenerating aspen were advancing to the sapling and pole size classes (Table 2).

On average, aspen saplings numbered only approximately 1.3% of aspen regeneration. Aspen poles numbered <1% of aspen regeneration. Regression analysis of factors correlated with density of regeneration and small trees revealed that models specifying a negative binomial distribution fit the reverse-J frequency distributions better than Poisson-distributed models, ZIP, or ZINB models. Significant over dispersion was detected in all cases. Generalized linear mixed-effects models specifying a negative binomial distribution accounted for the over dispersion (many zero counts, few high counts), and revealed that frequency of aspen and conifer regeneration, and frequency of aspen

saplings, correlated with stand density and species composition (Table 3).

Stand BA consistently outperformed SDI as a predictor of conifer regeneration. This could mean that conifer seedlings were more frequent near larger conifers, but we did not explicitly test for the effect of tree size or reproductive maturity of trees in 0.02 ha plots centered on 0.004 ha plots where conifer seedlings were counted. Conifer seedling counts were highest in conifer-dominated areas with higher stand densities (in terms of stand BA) (Figure 2a). At higher stand densities, the expected frequency of conifer seedlings was similar in areas with composition ranging from 0-60% conifer BA (40-100% aspen); however, conifer seedling frequencies were exponentially higher in areas where conifer composition exceeded 60%. Conifer seedlings were least frequent in open areas (low stand BA), especially open areas with proportionally more conifer than aspen (in terms of percent BA). Areas of low stand density in association with widely-spaced aspen often had a layer of organic matter accumulated beneath a diverse herbaceous vegetation layer. These factors may deter or provide a physical barrier to conifer regeneration. Exposed soils or woody shrubs were characteristic of the more xeric areas where conifers were found at low stand densities. In

Species and size class	Plot size (ha)	No. of plots	Density (stems ha⁻¹)			
			Mean	s.d.	min.	max.
Conifer seedlings <10 cm DBH	0.004	249	3261	6589	0	79250
Conifers 10-20 cm DBH	0.004	249	248	387	0	2750
Aspen regeneration <10 cm DBH	0.004	249	3211	4353	0	26250
Aspen saplings 10-15 cm DBH	0.02	449	42	76	0	550
Aspen poles 15-20 cm DBH	0.02	449	26	64	0	450

Note: aspen sapling and pole data from only 8 stands (BC20 stand with zero saplings/poles excluded).

Table 2: Summary data for density (trees ha⁻¹) of young conifer and aspen in plots systematically located throughout nine aspen-conifer stands surrounding Lake Tahoe, California.

Species and size class	Effect	Estimate	Std. Error	Pr > |t|
Conifer seedling <10 cm	Intercept	-0.9832	0.83	0.2695
n = 249 plots in 9 stands	AScomp$^{0.5}$	2.2885	0.82	0.0057
-2LL = 826.5	(BA+1)$^{0.5}$	0.8157	0.21	0.0001
	BA+1	-0.0384	0.01	0.0023
	Ln(BA+1) x AScomp$^{0.33}$	-0.7254	0.21	0.0006
	Random intercept (by stand)	0.3139	0.18	--
	Scale (dispersion)	1.3461	0.13	--
Aspen regen. <10 cm	Intercept	1.9401	0.41	0.0014
n = 249 plots in 9 stands	AScomp$^{0.5}$	1.7246	0.26	<.0001
-2LL = 817.5	Ln(MSDI+1)	-0.8170	0.31	0.0084
	Random intercept (by stand)	0.8955	0.48	--
	Scale (dispersion)	1.2097	0.13	--
Aspen sapling 10-15 cm	Intercept	-3.4500	1.02	0.0118
n = 449 plots in 8 stands	AScomp$^{0.5}$	5.6906	1.33	<.0001
-2LL = 1783.1	(MSDI+1)$^{0.5}$	-2.3267	0.98	0.0181
	(MSDI+1)$^{0.5}$ x ((1-AScomp)+1)^{2}	0.8532	0.29	0.0039
	Random intercept (by stand)	0.2066	0.15	--
	Scale (dispersion)	1.3639	0.18	--

Note: AScomp = aspen BA as proportion of total BA in plot (range: 0-1); MSDI = SDI/1000; -2LL = Model goodness of fit in terms of -2 Residual Log Pseudo-Likelihood. Aspen sapling data from only 8 stands (BC20 stand with zero saplings excluded from analysis).

Table 3: Coefficients for generalized linear mixed-effects negative binomial log-link models of conifer and aspen regeneration (DBH <10 cm) count density in 0.004 ha plots, and aspen sapling (DBH 10-15 cm) count density in 0.02 ha plots systematically located throughout nine aspen-conifer stands surrounding Lake Tahoe, California. Log-link models give expected values for natural logarithm of mean count per plot assuming negative binomial distribution.

these drier areas, desiccation of ephemeral conifer seedlings likely kept seedling densities low [27].
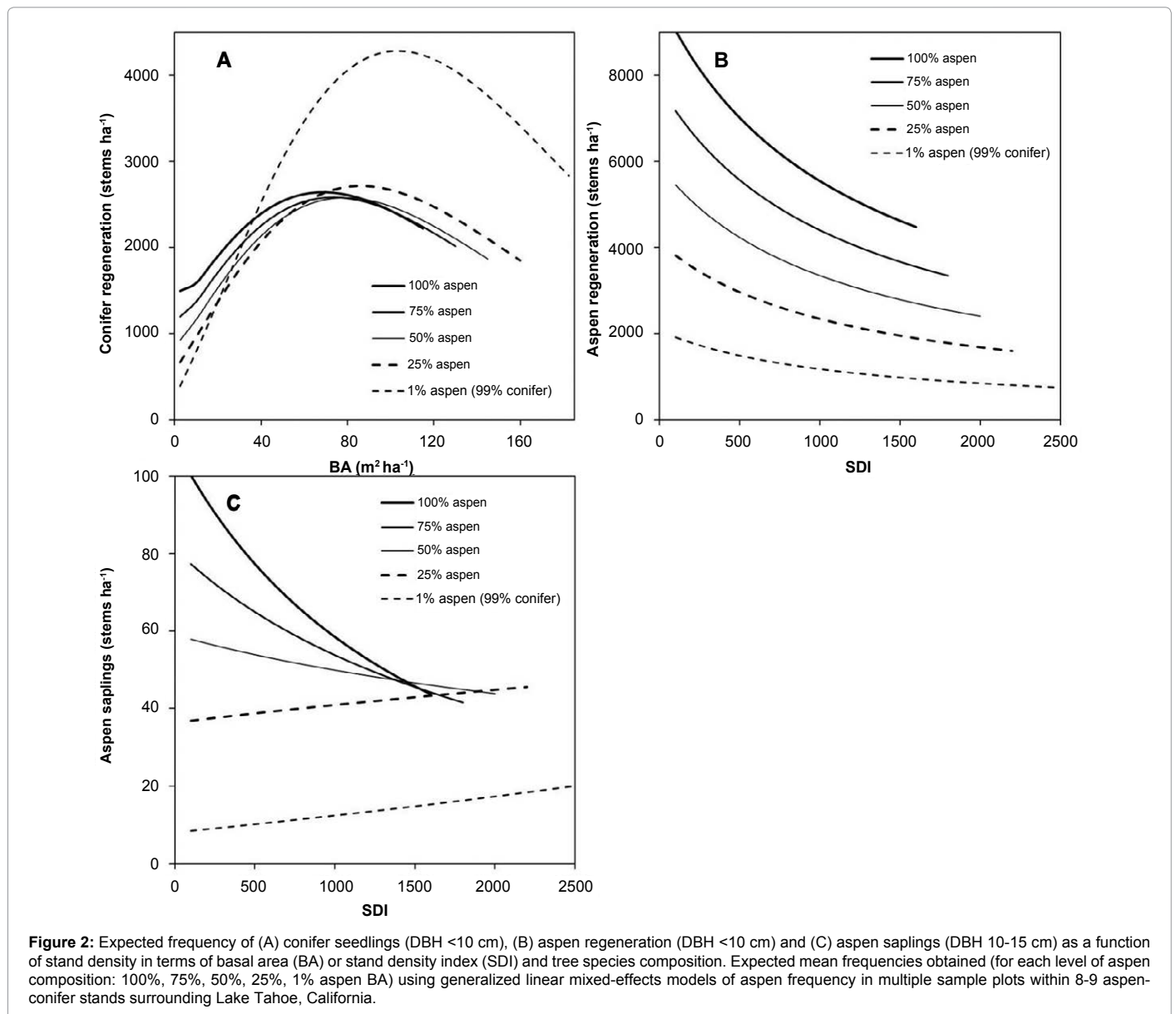
Aspen regeneration (DBH <10 cm) was most frequent in areas of lower stand density with a higher proportion of aspen BA (Figure 2b). Contrary to results from northern California where no correlations were detected [28], we specified a negative binomial distribution for aspen regeneration frequency and found that fewer aspen <10 cm DBH were counted in areas of higher stand density and areas where conifer represented a greater proportion of stand BA. However, our analysis indicated that aspen regeneration was still abundant in dense, conifer-dominated areas (>1000 stems ha⁻¹), but that these densities were 1/10ᵗʰ of those in more open areas of pure aspen.

In aspen-dominated parts of the study areas, aspen saplings (DBH 10-15 cm) were also more frequent in low-density areas and less frequent in denser areas (Figure 2c). As the proportion of conifer increased, however, fewer aspen saplings were found at any density. These findings are consistent with reported correlation of aspen sapling density and canopy openness, and the detection of repulsion between aspen saplings and neighboring white fir in northern California [28]. Smith and Smith [6] found that aspen regeneration was not long-lived and rarely advanced to the sapling stage in the presence of conifer at higher stand densities. In parts of our study areas where composition was less than a third aspen (in terms of BA), stand density no longer appeared to correlate with the occurrence of aspen saplings. In these

heavily conifer-dominated areas (i.e., BA >67% conifer), the frequency of aspen saplings appeared insensitive to stand density while declining as the proportions of conifer increased. This finding was unexpected, since conifer-dominated areas of lower density had more aspen regeneration <10 cm DBH than areas of higher density. Additionally, we expected young aspen in areas of lower density to receive more light, and grow into larger size classes, given that growth of aspen >10 cm DBH is more rapid in high light [28] at lower stand densities [14]. The discrepancy between aspen regeneration and recruitment to larger sizes, especially in areas of lower stand density where conifers dominated, merits further investigation. In the interim, our findings suggest that managers of aspen stands in the Sierra Nevada might focus their interventions in places where conifers have come to dominate, removing conifers to maintain stand density below 1000 SDI. Greater reductions in SDI are advised when the objective is to promote recruitment of young aspen to the overstory, to replace senescing aspen or enhance resilience by promoting age-class diversity within stands.

Conclusion

The degree of succession to conifer in aspen stands throughout the Lake Tahoe Basin was spatially heterogeneous. Within the nine one-hectare study areas, patches of pure aspen were rare; most common were mixed patches dominated by conifer. The regression fitted to the 99th percentile of plot SDI revealed that as composition shifted in favor of conifer, SDI increased beyond the upper limit of around 1700 for

Figure 2: Expected frequency of (A) conifer seedlings (DBH <10 cm), (B) aspen regeneration (DBH <10 cm) and (C) aspen saplings (DBH 10-15 cm) as a function of stand density in terms of basal area (BA) or stand density index (SDI) and tree species composition. Expected mean frequencies obtained (for each level of aspen composition: 100%, 75%, 50%, 25%, 1% aspen BA) using generalized linear mixed-effects models of aspen frequency in multiple sample plots within 8-9 aspen-conifer stands surrounding Lake Tahoe, California.

pure aspen. We infer from this finding that aspen were being extirpated as succession to conifer led to levels of crowding and competition in excess of what aspen could withstand. Our findings suggest that forest managers must control stand density to pre-empt competition-induced mortality among aspen growing in association with conifers that tolerate higher densities.

Counts of regeneration throughout the nine study areas correlated with stand density and species composition. Numerous conifer seedlings were becoming established in aspen-dominated areas of any density, and in conifer-dominated areas of higher density. Our analysis revealed that, on average, aspen regeneration was one order of magnitude less frequent in areas of pure conifer versus areas of pure aspen. However, aspen regeneration was still abundant in most areas. Most surprising was that aspen saplings – whose presence we assumed was associated with stand conditions favoring recruitment of aspen regeneration to the overstory – were rare, especially at high stand densities or in areas where conifers dominated.

Forest managers interested in sustaining aspen stands *in situ* over the long term will need to replace older aspen as they mature and die. If the goal of management is to foster recruitment of younger aspen to the overstory, then heavier removals of conifer (site-wide, or in patches) should provide conditions (i.e., low stand densities dominated by aspen) most favorable for regeneration and growth of young aspen beneath a partial canopy within an existing stand.

Acknowledgments

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