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Structure and Composition of a Dry Mixed-Conifer Forest in Absence of Contemporary Treatments, Southwest, USA

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Abstract: Dry mixed-conifer forests in the Southwest occupy an important ecological and hydrological role in upper watersheds. In the absence of reoccurring fire and silvicultural treatments over the last 50 years, we quantified forest structure and composition on prevailing north and south aspects of a dry mixed-conifer forest in southcentral New Mexico using mixed models and ordination analysis in preparation for an experiment in ecological restoration. Results indicated overstory and midstory were dominated by Douglas-fir (*Pseudotsuga menziesii*) and shade tolerant/fire intolerant white fir (*Abies concolor*) with interspersed mature aspen on north aspects, and Douglas-fir and Southwestern white pine (*Pinus strobiformis*) on south aspects. Ponderosa pine (*Pinus ponderosa*), which was historically co-dominant with Douglas-fir on north and south aspects, was subdominant on south aspects and almost entirely absent on north aspects. Regeneration was dominated by white fir saplings and seedlings on north aspects while ponderosa pine was completely absent. South aspect saplings and seedlings were characterized by Douglas-fir and Southwestern white pine, but almost no ponderosa pine. Ordination analysis characterized the effect of aspect on species composition. Understanding contemporary forest structure and composition is important when planning for desired future conditions that are to be achieved through ecological restoration using silvicultural techniques designed to foster resilience.

Keywords: aspect; desired future conditions; ordination analysis

1. Introduction

Quantification of forest stand attributes and composition are important metrics in forest management. In the Southwest, mixed-conifer forests have not been researched and described as extensively as ponderosa pine (*Pinus ponderosa*) forests. Compositional complexity and mixed severity fire regimes have been cited as to why dry mixed-conifer forests in the Southwest are less understood [1,2].

A number of factors combined to change forest structure and composition, fuel conditions, and the historic natural fire regime in Southwestern forests over the last 130 years. Similar to lower elevation pine forests, frequent fire historically shaped stand development, structure, and vegetation composition in Southwestern mixed-conifer forests [3–9]. Fire acted as a natural thinning agent by reducing litter build-up, burning small trees, and thinning ladder fuels. Also, depending on weather and fuel conditions, torching and crowing (i.e., mixed-severity fire regime) on a stand scale also influenced forest development [10]. In the absence of frequent fire, a shift in overstory species dominance from shade intolerant ponderosa pine to shade tolerant white fir (*Abies concolor*) and intermediate shade tolerant Douglas-fir (*Pseudotsuga menziesii*) has been reported [11–14].

With an ever increasing interest in forest resilience in the face of fire, insect, disease [15], and increasing temperature [16], future mixed-conifer stand structure and composition are of particular interest to forest managers and stakeholders [17]. Stand structure in relation to water quantity and quality are also of interest in the arid Southwest, especially in upper elevation watersheds. In addition, stand structure is useful in determining aboveground forest carbon pools [18], biomass, and successional pathways. Understanding contemporary stand structure is essential when planning for future desired conditions that are to be achieved through ecological restoration using silvicultural techniques. For example, all National Forests in the Southwest (Region 3) are currently undergoing Forest Plan revisions. These plans, which will guide the agency for the next 10–15 years, are required to describe desired future resource conditions including stand structure. Desired future conditions must be described in terms that are specific enough to allow progress toward their achievement to be determined.

We examined stand structure and species composition of dry mixed-conifer forests in absence of frequent fire and 50+ years following harvesting activities. The objective of our analysis was to quantify current stand conditions to provide baseline context for managers considering future silvicultural prescriptions designed to achieve desired future conditions. In addition, we wanted to compare and contrast composition and stand structure characteristics between north and south aspects.

2. Materials and Methods

Three distinct sites, each with a north and south aspect, were located within the central Sacramento Mountains (approximately 32°57′ N, 105°44′ W) on the Sacramento Ranger District of the Lincoln National Forest in Otero County, New Mexico. The north-south running Sacramento Mountains cover approximately 5200 km^2. The west-facing escarpment rises 2286 m from the Tularosa Basin to the peak of Sierra Blanca (3650 m) where the majority of the land area gradually descends east toward the Pecos River. Below the alpine tundra and subalpine coniferous forest lie the two dominant cover types of the Sacramento Mountains: (1) upper montane coniferous forests composed of Douglas-fir, white fir, and ponderosa pine; and (2) lower montane coniferous forests composed of ponderosa pine, piñon pine (*Pinus edulis*), juniper (*Juniperus* spp.) and oak (*Quercus* spp.) [19]. The study areas were within the upper montane coniferous forest, also known as the dry mixed-conifer, at an elevation between 2438–2895 m. Study stands were 8–20 ha and had not been silviculturally treated for at least 50+ years (personal communication with Mickey Mauter, U.S. Department of Agriculture Forest Service). Midcentury treatments were characterized as second entry harvests. Original turn of the century harvests focused on Douglas-fir, ponderosa pine, and white fir larger than 30.48 cm in diameter [20]. Mean annual precipitation (rainfall only) for the study site region was 75.1 cm [21]. Most precipitation occurs in winter as snow (annual mean = 178.6 cm) and summer as rain (June, July, August, and September) (annual mean for 4 months = 43.1 cm). During the summer months, precipitation in the form of high-intensity, short duration afternoon thundershowers were common to the study area. Average maximum and minimum temperatures were 14.2 and 0.2 °C, respectively. Soils in the study site were generally classified as Argiborolls [22].

2.1. Study Design

We selected three sites (i.e., Benson, Fork, Pump) that were separated by ~9 km each. Each site had a north and south aspect separated by a common mountain meadow. At each site with like aspect, four units (i.e., distinct forest stands) were randomly selected from a list provided by the Forest Service. These units, 8–20 ha in size, were separated by natural terrain features (i.e., draw or meadow). Baseline data (as described below) were collected to characterize contemporary stand differences and in anticipation of future experimental research investigating the effects of four common management treatments (no management, prescribed fire, timber harvest, and harvest and burn) on north and south aspects. Baseline data were collected over the course of two growing seasons in 2006 and 2007.

2.2. Field Methods

Experimental units, each 8–20 ha in size, were overlaid with a grid of Modified-Whittaker plots [23] on 50 × 50-m spacing (50-m side of Modified-Whittaker plot was oriented perpendicular to the contour). Modified-Whittaker plots were selected for understory herbaceous measurements, the results of which are not reported in this publication. To avoid bias from surrounding stands, no sampling was conducted within 50 m of stand edge [24]. Eight randomly selected plots per experimental unit were permanently established for a total of 192 plots. Variable-radius plots determined using a 10-factor prism centered within the Modified-Whittaker plot were used to quantify overstory (>30.48 cm diameter at breast height (DBH; 1.37 m)) and midstory (>12.7–30.48 cm DBH) tree characteristics by species. Fixed-radius plots (8.92 m) nested on overstory plots were used to quantify seedling (0–2.54 cm DBH) and sapling (>2.54–12.7 cm DBH) characteristics by species. Individual tree measurements included DBH (cm), height (m), height to live crown (m), and crown area (CRN) (m^2). Estimated stand characteristics included basal area per hectare (BA) ($m^2 \cdot ha^{-1}$), trees per hectare (TPH), dominant height (DMHT), and relative spacing index (RSI). We estimated mean dominant height and relative spacing index at the stand level. Dominant height was calculated following Lorey's mean height method (i.e., sum of tree height multiplied by tree basal area for all trees, divided by basal area of stand). Lorey's mean height is not statistically different when compared to other definitions of dominant height [25]. Relative spacing is a density index which is defined as mean spacing between trees divided by dominant height [26] and was calculated as follows: $\mathrm{RSI} = \left(\sqrt{10000/\mathrm{TPH})/\mathrm{DMHT}}\right)/\mathrm{DMHT}$. Relative spacing index helps to characterize the difference in crown area as the result of variation in the ratio between diameter and quadratic mean diameter [26] and also to characterize relationships between crown and diameter of an individual tree [27].

2.3. Data Analysis

We used linear mixed models to determine differences between aspects in baseline composition and structure variables using SAS Enterprise Guide 7.1 (SAS Institute, Cary, NC, USA) [28]. The random effect was the nested effect of experimental unit within site and aspect. This allowed the intercept to vary among units within sites and aspects. The fixed effect was aspect. Significance of mixed effect model was determined by applying Kenward-Roger approximation in proc mixed. When fixed effects were significant ($P < 0.05$) multiple comparisons were tested using least-squares means. All reported P-values were two tailed. Reported means for dependent variables were summarized by aspect and calculated by averaging the 12 like-aspect stand means. We used a linear mixed model to compare mean height between overstory and midstory trees (which were based on diameter classes). Results indicated significant differences at the 0.05 level (least-squares mean test) for all comparisons including by aspect.

Dissimilarity in species stand structure (i.e., stem density and basal area) in sample sites was analyzed in ordination space using non-metric multidimensional scaling (NMDS) in Canoco 5 (Microcomputer Power, Ithaca, NY, USA) [29]. The purpose of using NMDS, an indirect gradient approach, was to show whether sample sites shared similar species compositional structure. The NMDS procedure used rank ordering of dissimilarities because this omitted issues like sensitivity to transformation associated with using absolute distance [29,30]. Distance between samples is the approximation of the rank order. The species arrow is the "optima" for each species in the NMDS space. We used Bray-Curtis distance measures to calculate sample distance and standardized sum of square differences to obtain solutions [30].

In Canoco 5, NMDS analysis is an automated process with two steps [29,30]. The first step includes calculation of distance using Bray-Curtis distance, configuration of initial principal coordinate analysis for default axis three, and optimization of NMDS configuration. The NMDS procedure configuration is a self-iterative process and computation is complete when "stress" values are minimized. Stress is a statistic term designed to measure "lack of fit" between distance in ordination space and dissimilarities.

In the second step, eigenvalues are estimated by centering response data columns (i.e., species structure) along the default for the first, second, and third axis of NMDS to show total variation. This step is called a principal component analysis rotation of NMDS. The NMDS solution for overstory basal area was based on an automatic log transformed value (logX + 1) by the software before calculating distance matrix using Bray-Curtis distance.

Species abundance curves were used to rank stem density and dominance against topographical aspect using "BiodiversityR" package [31] in R programming language (R Foundation for Statistical Computing, Vienna, Austria) [32].

3. Results

3.1. Forest Structure and Composition

Forest structure and composition of mixed-conifer stands were primarily contrasted between north and south aspects. Differences in overall tree and stand level attributes between north and south aspects are presented in Table 1. Mean individual tree height and height to live crown were significantly greater on north versus south aspects (Table 1). Differences in stand level attributes included greater dominant height and relative spacing index on north versus south aspects (Table 1). Forest structure and composition by diameter class (overstory, midstory, sapling, and seedling) on north and south aspects are presented in Tables 2 and 3.

Table 1. Mean tree and stand attributes for all diameter classes ± standard error of dry mixed-conifer forest stands, Sacramento Mountains, Lincoln National Forest, New Mexico. Data were collected over the course of two growing seasons in 2006 and 2007.

Geographical Attributes		Tree Level Attributes				Stand Level Attributes				
		Crown	DBH	Height	HLC	BA	Density	DMHT	QMD	RSI
Aspect	North	27.7 ± 1.7	41.7 ± 2.0	20.2 ^{A} ± 0.5	9.8 ^{A} ± 0.6	36.7 ± 4.2	504 ± 63	22.3 ^{A} ± 1.9	33.2 ± 0.2	0.26 ^{A} ± 0.04
	South	27.1 ± 1.1	39.9 ± 1.3	17.7 ^{B} ± 0.5	7.9 ^{B} ± 0.3	33.9 ± 1.7	460 ± 12	19.9 ^{B} ± 2.0	32.8 ± 0.3	0.23 ^{B} ± 0.03
Site	Benson	32.3 ^{A} ± 1.1	45.9 ^{A} ± 1.7	20.7 ^{A} ± 0.7	9.2 ^{AB} ± 0.7	37.6 ^{A} ± 3.4	426 ^{B} ± 39	22.9 ^{A} ± 1.9	36.1 ^{A} ± 0.2	0.24 ^{AB} ± 0.04
	Fork	24.8 ^{B} ± 1.4	40.3 ^{B} ± 1.9	17.5 ^{B} ± 0.7	7.9 ^{B} ± 0.2	28.7 ^{B} ± 0.9	402 ^{B} ± 32	20.1 ^{B} ± 2.1	32.1 ^{B} ± 0.3	0.27 ^{A} ± 0.02
	Pump	25.2 ^{B} ± 1.6	36.2 ^{B} ± 1.4	18.6 ^{B} ± 0.6	9.6 ^{A} ± 0.8	39.8 ^{A} ± 4.7	618 ^{A} ± 67	20.3 ^{B} ± 1.6	30.8 ^{B} ± 0.2	0.23 ^{B} ± 0.05

Crown area in m^2; DBH = diameter at breast height (cm); Height in meters (m); HLC = height to live crown (m); BA = stand basal area ($m^2 \cdot ha^{-1}$); Density = stems per hectare; DMHT = dominant height (m); QMD = quadratic mean diameter (cm); RSI = relative spacing index. Aspect and site column means followed by same letter or without letters were not significantly different at the 0.05 level (least-squares means test).

Table 2. Mean tree density (stems hectare^{-1}) (± standard error) by species, diameter class, and aspect of dry mixed-conifer forest stands, Sacramento Mountains, Lincoln National Forest, New Mexico.

Tree Species [a]	Diameter Class and Aspect									
	0–2.54 cm (Seedling)		>2.54–12.70 cm (Sapling)		>12.70–30.48 cm (Midstory)		> 30.48 cm (Overstory)		Total Mean	
	South	North	South	North	South	North	South	North	South	North
Conifer										
PSME	72 * ± 9	37 * ± 8	218 * ± 14	115 * ± 14	161 * ± 17	79 * ± 10	109 * ± 6	65 * ± 5	541 * ± 28	286 * ± 25
ABCO	20 * ± 6	130 * ± 23	42 * ± 12	255 * ± 26	18 * ± 6	110 * ± 12	7 * ± 2	58 * ± 5	83 * ± 20	524 * ± 42
PIST	44 * ± 5	2 * ± 1	122 * ± 12	24 * ± 4	90 * ± 12	19 * ± 5	22 * ± 2	6 * ± 1	265 * ± 22	50 * ± 8
PIPO	2 ± 1	-	4 ± 2	-	8 * ± 2	2 * ± 1	16 * ± 3	0.12 * ± 0.12	29 * ± 4	2 * ± 1
PISP	-	35 ± 21	1 * ± 0.5	35 * ± 14	-	6 * ± 2	0.24 * ± 0.24	5 * ± 1	1 * ± 0.6	74 * ± 32
Sub-total	138* ± 11	205 * ± 36	387 ± 20	428 ± 33	276 * ± 20	216 * ± 16	155 * ± 7	135 * ± 7	919 ± 36	937 ± 59
Non-conifer										
POTR	-	-	4 ± 2	4 ± 2	33 * ± 12	115 * ± 24	0.3 * ± 0.3	22 * ± 4	36 * ± 13	138 * ± 25
QUGA	9 ± 5	16 ± 7	28 ± 8	27 ± 9	7 ± 4	9 ± 3	0.16 ± 0.16	0.24 ± 0.24	43 ± 11	49 ± 15
RONE	-	3 ± 1	0.4 * ± 0.4	17 * ± 5	-	12 ± 9	-	-	0.4 * ± 0.4	40 * ± 11
ACGL	-	-	0.8 ± 0.8	1 ± 0.7	4 ± 2	3 ± 2	-	-	5 ± 2	4 ± 2
Sub-total	9 ± 5	18 ± 7	34 ± 9	48 ± 12	44 * ± 12	140 * ± 26	1 * ± 1	22 * ± 4	83 * ± 17	221 * ± 31
Total mean	147 * ± 13	223 * ± 37	422 ± 22	477 ± 36	321 ± 24	356 ± 33	155 ± 6	157 ± 8	1001 * ± 40	1159 * ± 70

[a] Scientific names: PSME = *Pseudotsuga menziesii*, ABCO = *Abies concolor*, PIST = *Pinus strobiformis*, PIPO = *Pinus ponderosa*, PISP = *Picea species*, POTR = *Populus tremuloides*, QUGA = *Quercus gambelii*, RONE = *Robinia neomexicana*, and ACGL = *Acer glabrum*. Column mean values with asterisk were significantly different at the 0.05 level (least-squares means test) between aspects within diameter class, otherwise the values were not significantly different.

Table 3. Mean basal area ($m^2 \cdot ha^{-1}$) (± standard error) by species, diameter class, and aspect of dry mixed-conifer forest stands, Sacramento Mountains, Lincoln National Forest, New Mexico. Basal area was only estimated for stems > 2.54 cm diameter at breast height.

Tree Species [a]	Diameter Class and Aspect							
	>2.54–12.70 cm (Sapling)		>12.70–30.48 cm (Midstory)		>30.48 cm (Overstory)		Total Mean ($m^2 \cdot ha^{-1}$)	
	South	North	South	North	South	North	South	North
Conifer								
PSME	0.93 * ± 0.06	0.49 * ± 0.06	5.84 * ± 0.52	2.81 * ± 0.33	17.61 * ± 0.99	10.85 * ± 0.86	24.09 * ± 1.04	13.97 * ± 0.97
ABCO	0.14 * ± 0.03	0.90 * ± 0.08	0.60 * ± 0.17	3.86 * ± 0.38	0.93 * ± 0.22	9.55 * ± 0.72	1.64 * ± 0.35	14.11 * ± 0.84
PIST	0.54 * ± 0.05	0.13 * ± 0.03	2.95 * ± 0.34	0.59 * ± 0.13	2.98 * ± 0.27	1.01 * ± 0.18	6.32 * ± 0.47	1.70 * ± 0.26
PIPO	0.02 ± 0.01	-	0.42 * ± 0.11	0.10 * ± 0.05	2.14 * ± 0.34	0.02 * ± 0.02	2.55 * ± 0.38	0.12 * ± 0.05
PISP	0.003 * ± 0.02	0.10 * ± 0.03	-	0.32 ± 0.12	0.02 * ± 0.02	0.68 * ± 0.17	0.03 * ± 0.02	1.08 * ± 0.26
Sub-total	1.63 ± 0.08	1.62 ± 0.11	9.82 * ± 0.59	7.65 * ± 0.50	23.68 ± 0.94	22.12 ± 1.10	34.64 * ± 0.95	30.98 * ± 1.09
Non-conifer								
POTR	0.04 ± 0.02	0.03 ± 0.02	0.90 * ± 0.29	4.64 * ± 0.92	0.02 * ± 0.02	2.15 * ± 0.44	0.92 * ± 0.30	6.71 * ± 1.12
QUGA	0.14 ± 0.09	0.12 ± 0.04	0.12 ± 0.06	0.29 ± 0.09	0.02 ± 0.02	0.02 ± 0.02	0.27 ± 0.09	0.43 ± 0.10
RONE	<0.000 *	0.07 * ± 0.02	-	0.29 ± 0.20	-	-	<0.000 *	0.36 * ± 0.21
ACGL	0.008 ± 0.005	0.004 ± 0.004	0.07 ± 0.04	0.10 ± 0.05	-	-	0.07 ± 0.04	0.10 ± 0.05
Sub-total	0.19 ± 0.05	0.23 ± 0.05	1.09 * ± 0.30	5.32 * ± 0.95	0.05 * ± 0.03	2.17 * ± 0.44	1.27 * ± 0.31	7.59 * ± 1.14
Total mean	1.81 ± 0.90	1.85 ± 0.14	10.73 ± 0.65	12.98 ± 1.15	23.72 ± 0.93	24.29 ± 1.04	35.90 * ± 0.97	38.58 * ± 1.27

[a] Scientific names: PSME = *Pseudotsuga menziesii*, ABCO = *Abies concolor*, PIST = *Pinus strobiformis*, PIPO = *Pinus ponderosa*, PISP = *Picea species*, POTR = *Populus tremuloides*, RONE = *Robinia neomexicana*, and ACGL = *Acer glabrum*. Column mean values with asterisk were significantly different at the 0.05 level (least-squares means test) between aspects within diameter class, otherwise the values were not significantly different.

3.1.1. Overstory

Overstory conifer stem density was slightly greater on south aspects as compared to north aspects, but with no difference in basal area (Tables 2 and 3). Non-conifer stem density and basal area were greater on north aspects owing to aspen trees (Tables 2 and 3). However, when combined there were no overstory differences between north and south aspects with regard to stem density or basal area (Tables 2 and 3). Overstory density and basal area were dominated by Douglas-fir, white fir, and aspen on north aspects and Douglas-fir on south aspects. There were essentially no sub-dominant species on north aspects (e.g., ponderosa pine density and basal area were 0.12 stems ha^{-1} and 0.02 $m^2 \cdot ha^{-1}$), and minimal sub-dominance on south aspects from Southwestern white pine and ponderosa pine. Mean overstory height (m) and crown area (m^2) of individual tree species were greater on north than south aspects, in particular Douglas-fir, white fir, and Southwestern white pine (Figure 1).

3.1.2. Midstory

Midstory conifer stem density and basal area were greater on south aspects as compared to north aspects (Tables 2 and 3). Non-conifer stem density and basal area were greater on north aspects owing to aspen trees (Tables 2 and 3). However, similar to overstory characteristics, when combined there were no midstory differences between north and south aspects with regard to stem density or basal area (Tables 2 and 3). Midstory density and basal area were dominated by aspen, white fir, and Douglas-fir on north aspects and Douglas-fir and Southwestern white pine on south aspects. There were essentially no sub-dominant species on north or south aspects. Midstory mean height and crown area are reported in Figure 1.

3.1.3. Sapling and Seedling

There were no overall sapling differences between north and south aspects with regard to stem density or basal area (Tables 2 and 3). Sapling density and basal area were dominated by white fir and Douglas-fir on north aspects, and Douglas-fir and Southwestern white pine on south aspects. Seedling density was greater on north aspects and characterized predominately by white fir. Seedlings composition on south aspects was characterized by Douglas-fir and white fir. No ponderosa pine saplings or seedlings were recorded on north aspects and only a scattering on south aspects (i.e., 4 and 2 stems ha^{-1}, respectively).

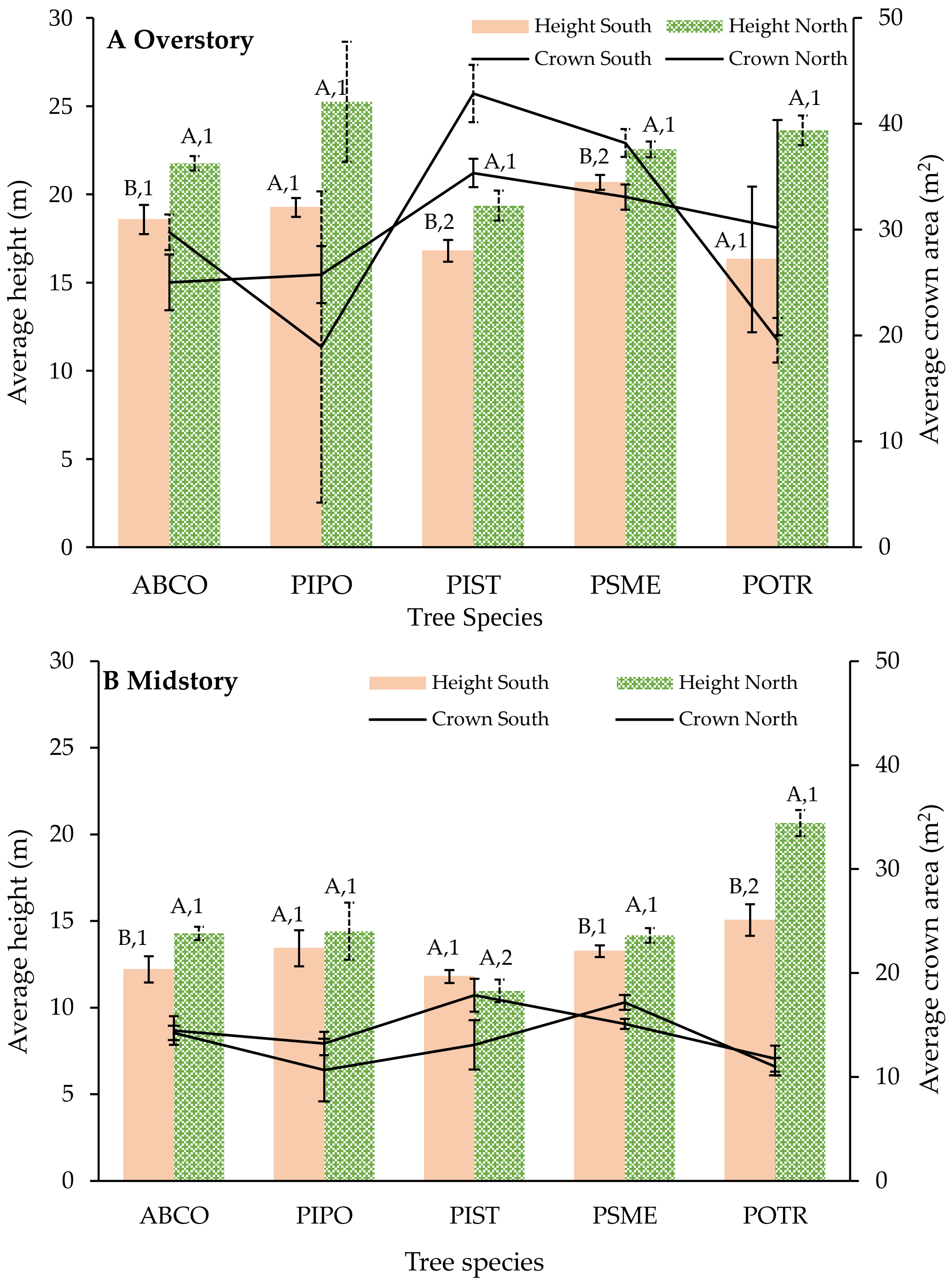

Figure 1. Mean height (m) and crown area (m^2) of selected conifer and non-conifer tree species of dry mixed-conifer forest stands, Sacramento Mountains, Lincoln National Forest, New Mexico. Different letter and number indicate significant differences at the 0.05 level (least-squares means test) between aspects for mean height and crown area, respectively. See Table 2 for list of species acronyms.

3.2. Species Rank Abundance Curves

Tree species abundance versus species rank is shown in Figure 2. These figures further illustrate stand structure and composition as described above. In particular, overstory dominance by Douglas-fir and white fir on north aspects and Douglas-fir alone on south aspects are illustrated, but also highlighted is the paucity of ponderosa pine in all other size classes. Sapling and seedling density were dominated by white fir on north aspects and Douglas-fir on south aspects (Figure 2). Aspen represents a portion of midstory structure on north aspects but without a significant presence in the overstory.

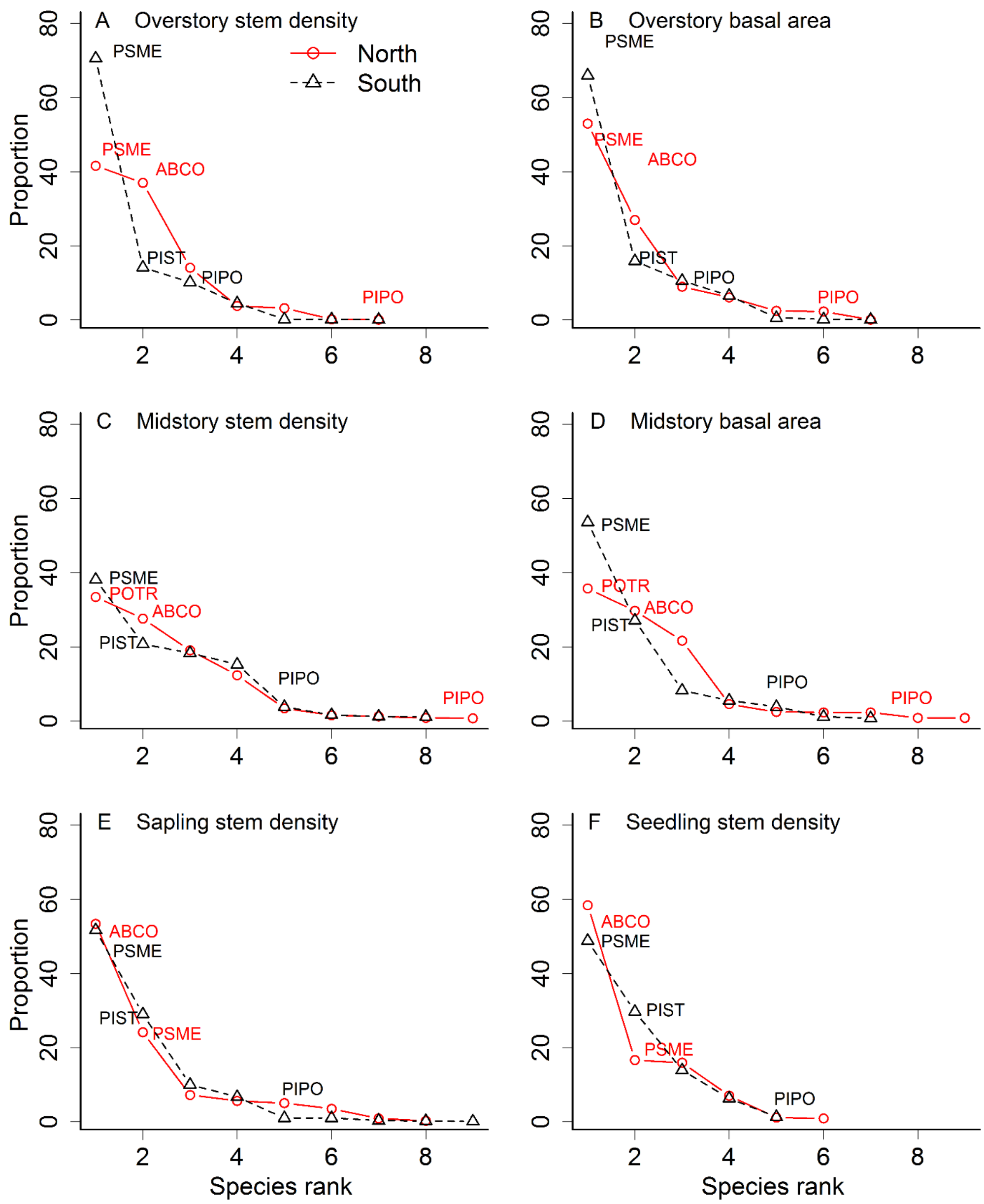

Figure 2. Species rank abundance curves showing proportion of stem density (stems ha^{-1}) (**A**,**C**,**E**,**F**) and basal area (m^2·ha^{-1}) (**B**,**D**) by tree species of dry mixed-conifer forest stands, Sacramento Mountains, Lincoln National Forest, New Mexico. The first two-ranked species and ponderosa pine are shown in the figure. See Table 2 for list of species acronyms.

3.3. Structure and Composition Variability

Nonmetric multidimensional scaling technique showed relationships in species basal area and density in relation to sample sites (Figure 3). The amount of variation explained by the first and second axis for each NMDS analysis is shown in Figure 3. The third axis explains the remaining amount of variation but is not shown. The stress statistics for all NMDS analyses were less than 0.1, indicating that reduced dimensions exhibited the greatest representation of the original patterns of samples. Species response in ordination space was similar among diameter classes with regard to aspect. Conifer species structure such as Douglas-fir, Southwestern white pine, and ponderosa pine were associated with south aspects while dominance of white fir, spruce, and aspen were associated with north aspects. The total variation explained by NMDS was 92.6% and 67.2% for overstory and midstory and 73.2% and 74.2% for sapling and seedling.

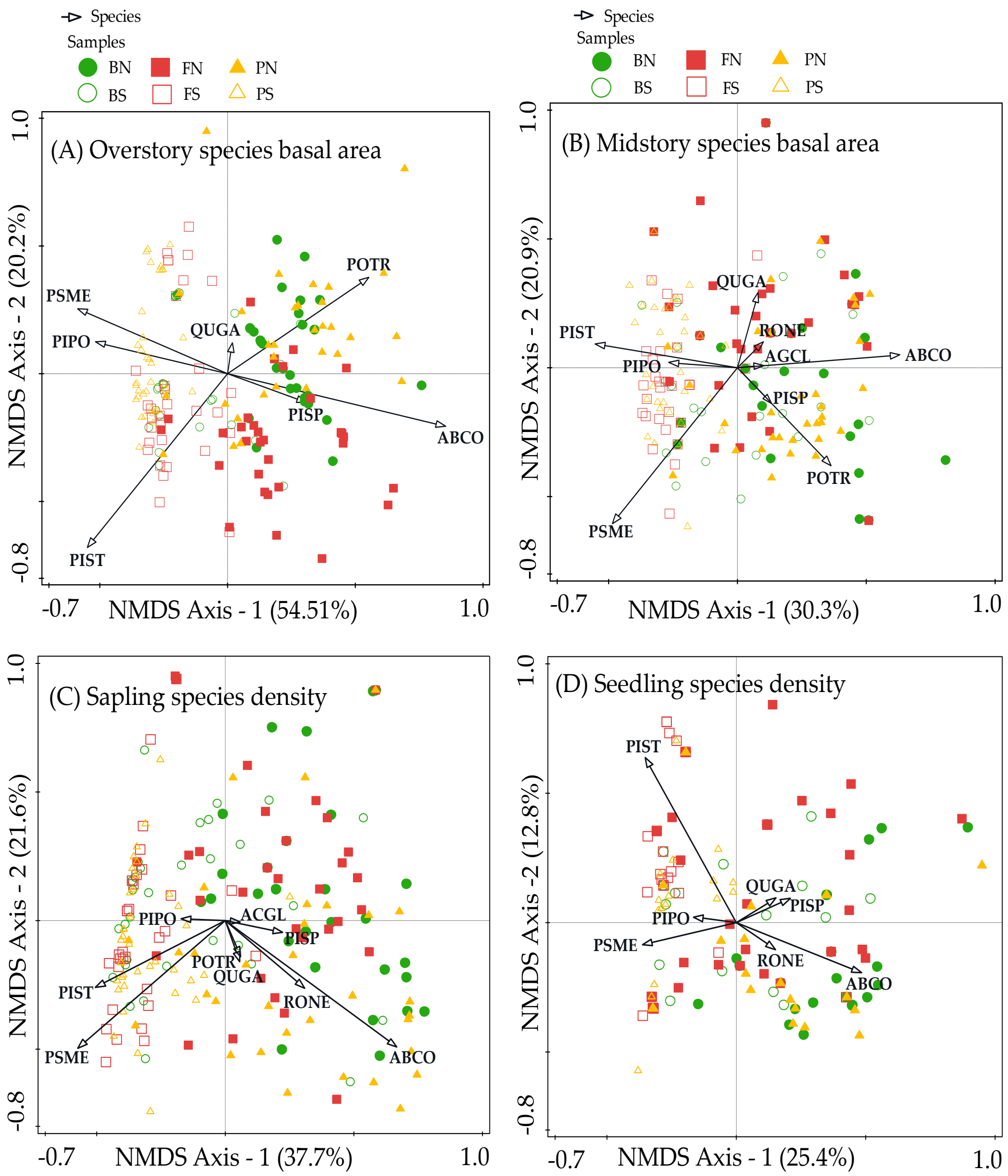

Figure 3. Biplots from non-metric multidimensional scaling method displaying species basal area ($m^2 \cdot ha^{-1}$) dissimilarities between sample sites (**A**,**B**) and species stem density (trees per ha) (**C**,**D**) dissimilarities between sample sites using *Bray-Curtis* distance measure along the first and second axis. Only biplots for the first and second axis are shown. Axis 1 shows high dissimilarity between the samples from north and south aspects (left to right), indicating high dissimilarities in species composition and structure. Axis 2 shows low dissimilarity within samples from the same aspects (top to bottom), indicating high similarity in species composition. The arrow represents the direction of the steepest increase of species value. Angle between species arrows and axis indicates the correlation. BN = Benson North, BS = Benson South, FN = Fork North, FS = Fork South, PN = Pump North, and PS = Pump South. See Table 2 for list of species acronyms.

4. Discussion

4.1. Overstory

Following a 130-year departure from the historical fire regime, as documented by Brown et al. [33], as well as 50+ years since mid-century timber harvests, present day north and south aspects have experienced an overstory compositional shift with the loss of dominant ponderosa pine (Tables 2 and 3). Multiple studies from mixed-conifer forests across the West have reported composition changes in the absence of frequent fire [7,11,14,20,34,35]. Historically, as interpreted by Kaufmann et al. [20] from General Land Office (GLO) survey notes from 1884–1941, mixed-conifer forests of the Sacramento Mountains were heterogeneous and open and dominated by Douglas-fir and ponderosa pine with varying levels of white fir and Southwestern white pine [20]. Survey accounts described mixed-conifer sites at the highest elevations in the Sacramento Mountains as being "heavy pine and fir timber", which Kaufmann et al. [20] interpreted to mean large diameter ponderosa pine and Douglas-fir.

Relative to pre-settlement conditions, increased stem density and basal area characterized current structure. Increased stem density following fire suppression has been documented in mixed-conifer forests across the Western U.S. [3,6,12,35–37]. For example, reconstructed overstory stem density on a mixed-conifer site in northern Arizona that had not had surface fire between 1887 and 1997 showed a mean increase of 514% in stem density and 92% in basal area [38]. Historically, this site was dominated by ponderosa pine and to a lesser degree white fir and characterized by a fire return interval of 5.5 years [39].

4.2. Midstory

Midstory conifer composition on north and south aspects reflected overstory composition but at greater stem densities (Tables 2 and 3). Spruce, locust, and aspen contributed to species richness on north aspects and further characterized midstory structure (Tables 2 and 3). Isolated aspen stems on south aspects occurred but only at higher elevations (e.g., >2895 m). Current aspen occurrence on north aspects were not pure stands, as historically described in GLO reports [20], but rather mixed with co- and subdominant conifer species. Aspen, an early successional species in Southwest forests, generally thrive after fire disturbance (absence concentrated elk browsing) but gradually deteriorate with age [40]. Mature aspen stems long removed from disturbance in some cases may lose vigor and become decadent [41]. Through time, chemical changes in the soil result in lower pH and nutrient content such that conditions become more suitable for conifers than aspen [41].

4.3. Sapling and Seedling

Composition of seedling and sapling reproduction was closely aligned with mature tree composition on north and south aspects, but at greater stem densities (Table 2). In the absence of frequent fire over the course of 130 years as reported by Brown et al. [33], unchecked seedling production elevated sapling and midstory densities resulting in a reverse J-shaped diameter distribution. Historic stem distribution as reported by Woolsey [42] for ponderosa pine forests in the Sacramento Mountains was bell-shaped. Ponderosa pine regeneration requires sunlight (among other attributes), as seedlings are shade intolerant. An increased abundance of intermediate shade tolerant Douglas-fir saplings may have outcompeted pine seedlings for light over the last century, resulting in a shift in species dominance away from shade intolerant species.

Of particular compositional interest, ponderosa pine seedlings and saplings were almost nonexistent on south aspects (and entirely absent on north aspects), with each comprising only 1% of stem density, while shade tolerant white fir seedlings and saplings comprised 15% and 11% of stem density on south aspects, respectively (Table 2). As noted above, historically these mixed-conifer stands were characterized in part by large diameter ponderosa pine trees. The difference in composition between these two particular species (i.e., ponderosa and white fir) on south aspects provides evidence of past unsuitable ponderosa pine regeneration conditions (i.e., lack of understory light, bare ground, and a seed source), as well as foresight into future stand composition. Under current compositional and structural conditions, ponderosa pine at the highest elevations of the Sacramento Mountains is a relic.

4.4. Structure and Composition Variability

Ordination analysis characterized species structural relationships in dry mixed-conifer forests (Figure 3). Despite the fact that our study sites only had a narrow elevational bandwidth (i.e., 500 m), significant amounts of variation in composition between aspects were observed. A contemporary study of mixed-conifer forests along the eastern slopes of the Cascades in Oregon showed that moist sites exhibited more variability in both basal area and trees per hectare than dry sites [12]. Further, greater stand structure and species composition in mixed-conifer forests in California and Oregon were associated with mesic sites regardless of fire history [43] and in the absence of harvesting and fire [13]. This phenomenon has also been reported for mixed-conifer forests in southwest Colorado [44], and the Sierra Nevada [43,45,46] and Klamath Mountains [47]. Management efforts should consider topography and associated composition when planning for desired future conditions [43].

5. Conclusions

Dry mixed-conifer forests in the Southwest occupy an important ecological and hydrological role in upper watersheds. Historically, stand structure and composition were influenced by frequent surface fire [33]. Eventually, early and mid-twentieth century harvesting prescriptions and practices also influenced stand structure and composition [20]. However, in absence of these disturbances over the course of the last 50+ years, forest composition and structure followed successional pathways toward dense, more shade tolerant, closed canopy stands. As a result, ponderosa pine basal area and density were significantly reduced as compared to historical conditions. Shade tolerance is an important factor in forest succession, especially for ponderosa pine. Silvicultural strategies designed to increase ponderosa pine should focus on increasing growth and vigor of existing trees as well as creating opportunities for regeneration (e.g., use of prescribed fire) [48].

Hanks and Dick-Peddie [49] argued that the effects of aspects, or "exposure", were the most important factor influencing mixed-conifer vegetation patterns in the White Mountains, New Mexico (a mountain range 15 km north of our study sites) in the absence of frequent disturbance. Their research indicated that aspect affected species composition and development as well as successional patterns. Our research corroborated their findings.

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