

Do Pine Trees in Aspen Stands Increase Bird Diversity?

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Abstract—In the Black Hills of South Dakota, quaking aspen (*Populus tremuloides*) is being replaced by conifers through fire suppression and successional processes. Although the Black Hills National Forest is removing conifers (primarily ponderosa pine [*Pinus ponderosa*]) to increase the aspen communities in some mixed stands, Forest Plan guidelines allow four conifers per hectare to remain to increase diversity in the remaining aspen stand. We compared bird species richness in pure ponderosa pine, mixed stands dominated by ponderosa pine with quaking aspen, mixed stands dominated by aspen with ponderosa pine, and pure aspen stands. Stands dominated by ponderosa pine had lower ($P < 0.01$) bird species richness than stands dominated by aspen. Aspen in ponderosa pine stands or pine in aspen stands did not increase bird species richness ($P \geq 0.68$) over the respective pure stands. Thus, leaving ponderosa pine in aspen stands will not have the desired effect of increasing bird diversity but may have the negative effect of speeding successional processes that replace aspen with conifers.

Introduction

Quaking aspen (*Populus tremuloides*) is an important vegetation community for wildlife in the West (Buttery and Gillam 1983). The importance of this vegetation community is demonstrated by the numerous symposia and publications addressing its importance to wildlife, livestock, and recreation. In the Black Hills, aspen frequently occurs with paper birch (*Betula papyrifera*, Hoffman and Alexander 1987). Aspen comprised about 5% of the Black Hills landscape about 25 years ago (Severson and Thilenius 1976). Currently, aspen comprises 4% of the Black Hills National Forest and is being replaced by ponderosa pine (*Pinus ponderosa*) through successional processes (Revised Land and Resource Management Plan, Black Hills National Forest, Custer, SD, 1996).

Many aspen stands are old or have been invaded by conifers (Revised Land and Resource Management Plan, Black Hills National Forest, Custer, SD, 1996). To reverse this trend, the current management direction is to increase the extent of aspen and birch communities by 10% during the 10-year period applicable to the Revised Land and Resource Management Plan. Aspen in the Black Hills regenerates mostly by vegetative regeneration (Schier et al. 1985). Yet to preserve diversity, stands treated to convert mixed conifer/aspen to aspen may include up to four conifer trees per hectare (10 per acre; Revised Land and Resource Management Plan, Black Hills National Forest, Custer, SD, 1996).

Aspen stands provide habitat to some species that would not occur without it (Finch and Reynolds 1987; Mills et al. 2000; Scott and Crouch 1988). Presumably, stands of mixed conifer with aspen support the greatest diversity of wildlife (DeByle 1985b). We tested the hypothesis that including conifers in aspen stands increases bird species diversity (e.g., species richness) in the Black Hills.

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Study Area and Methods

The Black Hills encompasses approximately 15,540 km² in west-central South Dakota and east-central Wyoming. Elevation ranges from 1,450 to 1,770 m. The climate is continental with cold winters and warm summers; temperatures range from -11 to 2 °C in winter and 15 to 29 °C in summer (Orr 1959) and annual precipitation averages approximately 50 cm (South Dakota Climatological Summary, U.S. Department of Commerce, Asheville, NC).

The Black Hills National Forest is primarily a conifer forest, with approximately 84% of the forest in ponderosa pine (Hoffman and Alexander 1987). The Forest is managed in 4 to 32 ha land units (hereafter referred to as stands) in which the vegetation is relatively homogeneous. The vegetation in stands is described using the dominant vegetation type; for units forested, descriptions include average diameter at breast height (d.b.h.) categories and overstory canopy cover categories. These vegetation structural stages are described by Buttery and Gillam (1983). We used the same criteria, as did the Black Hills National Forest, for describing vegetation in stands.

The data for bird species richness come from two studies of breeding nongame birds in the Black Hills (Mills et al. 2000; Dykstra et al. 1999). Both studies used variable radius plots for counting birds (Reynolds et al. 1980). Mills et al. counted birds during 1992 and 1993 in 48 stands of ponderosa pine and 28 stands of aspen. Ponderosa pine stands included seven vegetation structural stages ranging from sapling/pole to old growth, and included all d.b.h. categories. Aspen stands included four vegetation structural stages, the shrub/seedling stage, and all overstory canopy cover (OCC) categories of sapling/poles. These stands were selected from the forest inventory database and represent the range of vegetation structural stages in ponderosa pine and aspen in the Black Hills. Mills et al. (2000) counted birds at each of three sites on 2 consecutive days, twice each year.

Dykstra et al. (1999) counted birds in 40 ponderosa pine stands in 1993 and 1994. These stands included 20 sapling/pole to mature stands of ponderosa pine with 40 to 70% OCC and 20 mature to old growth pine stands with >70% OCC. These stands were representative of the managed and unmanaged ponderosa pine forest in the Black Hills. Birds were counted at two to five sites in two sample sessions in 1993 and three sample sessions in 1994.

Bird species richness represents the number of species of passerines and woodpeckers (*Picidae*) observed ≤50 m of the count point (Hutto et al. 1986) in each stand. Birds flying overhead or birds that flew by and did not land were excluded from tallies of species richness. In the Black Hills, species accumulation curves reached an asymptote for species richness in stands at between two and three bird count sites per stand (Rumble et al., in press).

We measured the vegetation at each of the bird count sites once during each study to characterize the habitat. Mills et al. measured vegetation in five 0.04 ha circular plots—one at the bird count point and four others in the cardinal directions 30 m away. In some aspen stands that occurred in drainages, only three plots could be measured within the drainage. Dykstra et al. (1999) measured vegetation in five variable-radius (using a 20 basal area factor prism [BAF]) over 0.04 ha circular plots at each site—one at the bird count point and four in the cardinal directions 40 m away. Trees ≥15 cm d.b.h. were measured in the variable radius plots and trees <15 cm d.b.h. were measured in the 0.04 ha circular plots. Estimates of tree basal area were averaged among plots at sites and then sites in stands.

We plotted the frequency of stands in incremental basal area (BA) categories of ponderosa pine and aspen/birch. Based on the frequency plots, we evaluated four treatments that described the tree composition of stands: pure ponderosa pine stands (≤ 0.02 m²/ha of aspen, $n = 72$), ponderosa pine stands with aspen (> 0.02 m²/ha aspen/birch, $n = 16$), pure aspen stands (≤ 0.1 m²/ha ponderosa pine, $n = 12$), and aspen stands with ponderosa pine (> 0.1 m²/ha pine, $n = 16$). Most of the pure ponderosa pine stands had no aspen and most pure aspen stands had no ponderosa pine. When we evaluated the bird species richness for homogeneity of variances among these treatments using Levene's test, we found that variances did not differ ($P = 0.48$). We compared species richness among treatments using one way analysis of variance followed by Tukey's multiple range test. Because stands with more bird count sites could have more species (Hutto et al. 1986), we repeated these tests using species richness per count site. These variances also were homogeneous ($P = 0.31$). We selected $\alpha \leq 0.10$ as significant for all tests.

Results

Overstory canopy cover in these stands was similar among all stands except the pure aspen, in which it was lower ($P \leq 0.01$; table 1). Basal area of ponderosa pine differed among all treatments ($P < 0.01$). The increased ponderosa pine basal area in stands of pine with aspen reflected the increased aspen component in unmanaged pine stands in the northern portions of the Black Hills. Aspen basal area increased ($P < 0.01$) consistently among treatments from pine to aspen. Percent canopy cover of grasses and forbs also generally increased among treatments from pure ponderosa pine to pure aspen. Shrub cover varied little among treatments with one exception: percent shrub cover was higher in the pine with aspen treatment ($P < 0.02$) than the pure pine or aspen with pine treatments. Abundance of snags did not differ among treatments ($P \geq 0.24$).

Bird species richness was lowest in ponderosa pine stands (table 2). Ponderosa pine stands with aspen did not have more ($P \leq 0.10$) bird species than pure pine stands. Stands of pure aspen and aspen with ponderosa pine had more ($P \leq 0.10$) bird species than either pure ponderosa pine or ponderosa pine with aspen. Among stands dominated by aspen, those with ponderosa pine in them did not have greater bird species richness ($P \leq 0.10$). Bird species richness showed negative correlations to overstory cover (Adj. $R^2 = 0.14$, $P < 0.01$) and ponderosa pine basal area (Adj. $R^2 = 0.21$, $P < 0.01$). Bird species richness was positively correlated with aspen basal area (Adj. $R^2 = 0.10$, $P < 0.01$),

Table 1—Vegetation measurements from stands of pure ponderosa pine, ponderosa pine with aspen, aspen with ponderosa pine, and pure aspen in the Black Hills, South Dakota.^a

Variable	Ponderosa pine ($n = 72$)		Pine with aspen ($n = 16$)		Aspen with pine ($n = 16$)		Aspen ($n = 12$)	
	$\bar{x} \pm SE$		$\bar{x} \pm SE$		$\bar{x} \pm SE$		$\bar{x} \pm SE$	
Overstory cover	53.4	2.4A	58.7	3.6A	53.7	4.7A	21.0	5.2B
Ponderosa pine basal area	15.3	1.1A	22.3	1.8B	2.4	0.6C	0.1	<0.1D
Aspen basal area	<.1	<.1A	0.4	0.2B	6.7	0.9C	2.3	1.1D
Percent cover grasses	10.3	1.0A	8.1	1.2A	28.8	3.8B	30.2	2.7B
Percent cover forbs	8.9	0.7A	18.1	2.3B	27.6	2.6C	32.1	2.6C
Percent cover shrubs	20.5	1.2AC	31.0	2.0B	23.5	1.9AC	24.1	2.0AB
Number of snags/ha	11.2	1.1	6.8	1.0	9.1	1.8	7.6	4.2

^aAverages ($\pm SE$) followed by different letters are significantly different ($\alpha \leq 0.10$, MRPP test).

Table 2—Average species richness and species richness per bird count site in stands of pure ponderosa pine, ponderosa pine with aspen, aspen with ponderosa pine, and pure aspen in the Black Hills, South Dakota.^a

Stand type	<i>n</i>	Species richness	± SE	Species richness/site	± SE
Pure ponderosa pine	72	14.6	0.4A	5.2	0.1A
Ponderosa pine with aspen	16	15.5	0.7A	4.4	0.2A
Aspen with ponderosa pine	16	18.9	0.7B	6.3	0.2B
Pure aspen	12	18.3	0.7B	6.1	0.2B

^aAverages ± SE followed by the same letter do not differ ($\alpha \leq 0.10$, Tukey's multiple range test).

percent cover of grasses (Adj. $R^2 = 0.16$, $P < 0.01$), and percent cover of forbs (Adj. $R^2 = 0.20$, $P < 0.01$).

The same patterns of bird species richness were evident when data were evaluated using species richness per bird count site. Stands of ponderosa pine and ponderosa pine with aspen had similar but fewer ($P \leq 0.10$) bird species per count site than stands of pure aspen or aspen with ponderosa pine.

Despite the habitat affinities of species, very few birds were restricted to a particular vegetation community in our study and most bird species were observed a few times in habitats considered unsuitable (table 3). Nonetheless, some species demonstrated affinities for pure aspen stands: Swainson's thrush (*Cartharus ustulatus*), common yellowthroat (*Geothlypis trichas*), and mountain bluebird (*Sialia currucoides*). Others occurred mostly in pure aspen or aspen with ponderosa pine: northern flicker (*Colaptes auratus*), flycatchers (*Empidonax* spp.), MacGillivray's warbler (*Oporornis tolmiei*), ovenbird (*Seiurus aurocapillus*), red-napped sapsucker (*Sphyrapicus nuchalis*), chipping sparrow (*Spizella passerina*), American robin (*Turdus migratorius*), and warbling vireo (*Vireo gilvus*).

Discussion

Aspen communities are important habitats for wildlife in the Rocky Mountains (DeByle 1985b). Young birds require protein from invertebrates for proper growth and development (Johnson and Boyce 1990). Invertebrate abundance in both the aspen canopy and aspen understory are greater than invertebrate abundance in conifers (Schimpf and MacMahon 1985; Rumble and Anderson 1996). Thus, the positive correlation between cover of grasses and forbs and species richness likely reflects the increased food resources for birds.

Several bird species would be absent or occur in low abundance without aspen in the Rocky Mountains (Finch and Reynolds 1987; Scott and Crouch 1988). Mills et al. (2000) reported that red-naped sapsuckers, dusky flycatchers, warbling vireo, MacGillivray's warblers, and ovenbirds would likely be absent from the central Black Hills without aspen. In addition to these, our study also suggests that common yellowthroats, mountain bluebirds, other flycatchers, chipping sparrows, and American robins preferred habitats dominated by aspen within the forested landscapes of the Black Hills.

The origin of the idea for including conifers in aspen stands to increase diversity and niches for wildlife (e.g., DeByle 1985b) is unknown. In Canada, bird species richness and the abundance of some birds was greater in "old" aspen stands that also had conifers (Schieck and Nietfeld 1995). However, age of aspen was confounded by presence of conifers in the aspen in their study design in that stands of large old aspen trees also had conifers. The increased species richness

Table 3—Percent of bird counts that bird species occurred in that were conducted in ponderosa pine, ponderosa pine with aspen, aspen with ponderosa pine, and pure aspen in the Black Hills, South Dakota.

Species ^a	Ponderosa pine	Pine with aspen	Aspen with pine	Aspen
<i>Ammodramus savannarum</i>	<1	0	0	0
<i>Carduelis pinus</i>	11	23	4	5
<i>Carduelis tristis</i>	<1	3	0	0
<i>Cartharus ustulatus</i>	<1	4	3	17
<i>Certhia americana</i>	2	3	0	0
<i>Chordeiles minor</i>	<1	0	0	0
<i>Colaptes auratus</i>	4	5	14	14
<i>Contopus sordidulus</i>	3	0	<1	3
<i>Dendroica coronata</i>	68	68	51	30
<i>Dendroica petechia</i>	<1	0	0	0
<i>Empidonax difficilis</i>	<1	2	1	4
<i>Empidonax minimus</i>	0	0	4	3
<i>Empidonax oberholseri</i>	<1	2	52	57
<i>Empidonax trailii</i>	0	0	1	0
<i>Empidonax spp</i> ^a	0	<1	17	19
<i>Euphagus cyanocephalus</i>	<1	1	0	0
<i>Geothlypis trichas</i>	<1	0	4	18
<i>Icteria virens</i>	<1	0	0	0
<i>Junco hyemalis</i>	63	60	81	88
<i>Loxia curvirostra</i>	55	42	52	61
<i>Molothrus ater</i>	11	13	13	20
<i>Myadestes townsendii</i>	34	17	11	14
<i>Oporornis tolmiei</i>	<1	<1	10	17
<i>Passerina amoena</i>	0	0	3	0
<i>Perisoreus canadensis</i>	14	12	1	0
<i>Pheucticus melanocephalus</i>	<1	1	0	1
<i>Picoides arcticus</i>	2	0	<1	0
<i>Picoides pubescens</i>	5	1	9	3
<i>Picoides villosus</i>	19	15	27	15
<i>Pipilo erythrophthalmus</i>	<1	0	0	0
<i>Piranga ludoviciana</i>	26	20	19	9
<i>Poecile atricapillus</i>	47	37	64	53
<i>Poocetes gramineus</i>	<1	0	1	1
<i>Regulus calendula</i>	1	1	13	2
<i>Regulus satrapa</i>	0	0	2	1
<i>Seiurus aurocapillus</i>	17	22	54	28
<i>Setophaga ruticilla</i>	0	0	2	0
<i>Sialia currucoides</i>	5	1	6	20
<i>Sialia sialis</i>	<1	0	0	0
<i>Sitta canadensis</i>	57	57	49	28
<i>Sitta carolinensis</i>	21	7	23	6
<i>Sphyrapicus nuchalis</i>	3	1	29	22
<i>Sphyrapicus varius</i>	1	7	0	1
<i>Spizella passerina</i>	24	17	38	41
<i>Spizella pusilla</i>	<1	0	0	0
<i>Troglodytes aedon</i>	0	0	2	1
<i>Turdus migratorius</i>	20	17	50	35
<i>Tyrannus tyrannus</i>	<1	0	0	0
<i>Vireo gilvus</i>	10	21	84	88
<i>Vireo olivaceus</i>	<1	0	0	1
<i>Vireo solitarius</i>	7	1	3	5
<i>Zenaidra macroura</i>	2	0	2	1
<i>Zonotrichia leucophrys</i>	0	0	<1	0

^aSeveral *Empidonax* flycatchers were not identified to species during the counts.

in aspen/conifer stands in Canada resulted from adding species common in conifer habitats to those common in the aspen. Increasing within-stand diversity (alpha diversity) by adding conifer species to aspen habitats in a landscape dominated by conifers does not contribute to diversity at scales for which diversity should be managed (Knopf and Samson 1994). We did not observe an increase in alpha diversity when ponderosa pine occurred in aspen stands. Finch and Reynolds (1987) also did not observe increased bird species richness in stands of mixed aspen/conifer compared to spruce-fir stands in Colorado.

The decline of aspen in the Black Hills can be attributed to the control of fires since European settlement. Fire was once common in the Black Hills landscape (Brown and Sieg 1996). Historically, occasional intense fires would regenerate aspen stands through sprouting (Jones and DeByle 1985). Aspen in the Black Hills is currently regenerated by clearcutting. But grazing by livestock and wild ungulates reduces the number of sprouts (DeByle 1985a; Rumble et al. 1996), allowing conifer regeneration to increase growth (Shepperd and Jones 1985). Ponderosa pine within aspen sites indicates that aspen is seral on these sites (Mueggler 1985). Seeds of ponderosa pine typically disperse within 40 m of trees (Fowells 1965).

Conclusions

Leaving ponderosa pine in stands treated to increase aspen does not increase bird species diversity. It may, in fact, speed the seral processes of converting the site to conifers. In some areas, succession of aspen to conifers occurs within a single generation of the aspen (Mueggler 1985). If successional processes lead to dominance of ponderosa pine in aspen, then bird diversity, as measured by bird species richness, will decline to that typical of the surrounding ponderosa pine forest. Managers will need to suppress conifer succession in aspen to maintain high bird species diversity.

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