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Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests

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Abstract

Small aspen stands are disappearing from the landscape in the Southwest, so it is important to understand their contribution to the avian community. We sampled birds in 53 small, isolated aspen stands and 53 paired plots within the ponderosa pine forest in northern Arizona, during the 1996 and 1997 breeding seasons. Bird species richness and abundance were higher in aspen than in pine. However, bird species richness and abundance did not vary with size of the aspen patch or isolation index. In addition, direct ordination of species distributions with habitat factors suggested no distinct avian communities. This suggests that aspen stands do not harbor separate populations, but rather are locations where the regional avifauna reaches high local density and richness and may be crucial to birds in years of resource scarcity. Thus it is important for avian conservation to maintain many aspen stands across the landscape, encompassing a diversity of vegetation structure and composition.

Keywords: Birds; *Populus tremuloides*; *Pinus ponderosa*; Habitat; Isolation; Area

1. Introduction

Over the past century, there has been little regeneration of quaking aspen (*Populus tremuloides*) in northern Arizona and New Mexico. This lack of regeneration is due to overgrazing of domestic livestock (ca. 1870–1910), continuing seasonal use by cattle, browsing by larger than historically present elk populations, and fire suppression (which favors succession to conifers and precludes the open conditions necessary for asexual reproduction by aspen; Krebill, 1972; Gullion, 1977; Patton and Jones, 1977; Schier et al., 1985a,b; Rowley, 1985; Shepperd and Fairweather, 1994; Baker et al., 1997; Kay, 1997; Bartos and Campbell, 1998). In northern Arizona and New Mexico, aspen exists primarily as small isolated stands within a forest dominated by ponderosa pine (*Pinus ponderosa*). With the exception of a handful of extensive, self-sustaining high-elevation sites, active management is needed to enhance and protect reproduction in order to maintain aspen in these landscapes. Aspen is important to many forest species of wildlife (Debyle, 1995). This study will determine whether small isolated aspen stands are important to the conservation of avifauna, and should be maintained as a part of the larger forest matrix.

Avian communities respond with variations in total abundance, species richness, and species composition to physical and compositional changes across landscapes. The configuration of physical structures and composition of vegetation act as cues that birds use to evaluate resources (Ricklefs, 1979, pp. 167–168). Bird species respond to these cues with patterns of habitat distribution. For example, deciduous trees, such as aspen in a coniferous matrix, may provide a unique set of resources and hence may support higher bird diversity and abundance (Winternitz, 1980; Dobkin et al., 1995; Turchi et al., 1995). Additionally, riparian areas may provide a unique arrangement of structure and composition as well as concentrating resources such as water and food, and hence should harbor a higher bird diversity and abundance (Whittaker, 1975; Stevens et al.; 1977, Szaro, 1980; Knopf, 1985; Strong and Bock, 1990). Consequently, we expect aspen stands to support a higher bird diversity and abundance than similarly sized areas in the pine matrix. Furthermore, we expect aspen associated with riparian areas to support higher bird diversity and abundance than aspen associated with hills.

The theory of island biogeography is often applied by conservation biologists to terrestrial landscapes where

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habitat occurs in patches (Brown and Dinsmore, 1988; Lomolino et al., 1989; Gustofson and Parker, 1994; Kruess and Tscharntke, 1994; Schnitzler, 1994; Kitahara and Fujii, 1997; Conner et al., 2000; Ricketts, 2001). This theory provides a general basis for evaluating the effects of patch size and isolation on species richness, and has been used to assess conservation potential for wildlife reserves in fragmented landscapes. In general, the theory of island biogeography predicts that smaller and/or more isolated patches will have lower species richness than large patches and/or close patches. Studies of forest patches in non-forested matrices have consistently found that avian communities differed markedly between forest and matrix, and that diversity and abundance of forest birds increased with patch size (e.g. Freemark and Merriam, 1986; Robbins et al., 1989; Warburton, 1997; Beier et al. 2002). Most such studies also found that isolation (distance to nearest large forest) was inversely correlated with avian abundance. However, this theory was designed for islands in a hostile matrix. We may not expect to see these predicted results for area or isolation when the matrix is permeable and is also used as breeding habitat, such as a landscape of ponderosa pine with small inclusions of aspen.

We investigated whether small aspen stands in northern Arizona supported a high richness and abundance of forest birds relative to neighboring patches. We also examined whether patch size or isolation influenced the avian community. We then assessed whether certain characteristics of aspen stands (based on size, isolation, vegetation structure, or topographic setting) were related to species richness or species composition. Finally, we describe the responses of individual species to habitat gradients, including aspen patch area and isolation, within our study area.

2. Materials and methods

2.1. The study area

We studied bird communities in small quaking aspen stands and the surrounding forest matrix in the Coconino National Forest of northern Arizona. The forest matrix was primarily ponderosa pine and ponderosa pine–Gambel oak (*Quercus gambelii*). Overstory tree species included quaking aspen, ponderosa pine, Gambel oak, Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*). Shrub species included Gambel oak, New Mexico locust (*Robinia neomexicana*), Arizona rose (*Rosa arizonica*), snowberry (*Symphoricarpos parishii*), narrowleaf cottonwood (*Populus angustifolia*), and seedlings of ponderosa pine and aspen. Elevation of our study sites ranged from approximately 2060 to 2480 m. We selected aspen stands >0.1 ha and that were surrounded by forest matrix on at least two-thirds of the stand's edge. Our study occurred during a drought. Annual precipitation was 11.8 cm in 1996 and 16.5 cm in 1997, compared to a 16-year average (1970 through 1986) of 26 cm (standard deviation 13 cm) (National Weather Service).

2.2. Sampling

We placed one plot in each aspen stand and a paired plot in the ponderosa pine forest 275 m to 950 m straight-line distance away from the edge of each aspen stand. Plots within the aspen stands were located randomly using a compass spin method for direction and table of random numbers for distance. Each pine plot was located to match the paired aspen plot in elevation, slope, aspect, and topographic setting. In the study area, aspen occurs in two topographic settings, namely hillsides and riparian areas (including drainage bottoms, canyon slopes, and springs). There were a total of 28 pairs of plots in riparian settings and 25 pairs of plots on hillside settings. Forty-eight pairs of plots, 26 riparian and 22 hill, were sampled in 1996 and 51 pairs, 27 riparian and 24 hill, were sampled in 1997. Forty-six pairs, 25 riparian and 21 hill, were sampled during both years; seven plots, three riparian and four hill, were sampled only one year. We use the term *overstory vegetation* to distinguish between aspen and pine plots, the term *topographic setting* to distinguish between riparian and hill plots, and the term *plot type* to refer to one of four combinations of tree species and topographic setting, namely aspen–riparian, pine–riparian, aspen–hill, and pine–hill.

We surveyed birds using point counts, recording all birds detected within a 50-m radius of plot center (Schieck, 1997). After arriving at the site we waited 2 min before starting the count so that the observer's breathing would slow down and their ear could attune to the ambient acoustics, and birds could acclimate to the observer's presence. We then surveyed for 8 min. All surveys were conducted within three h after sunrise. We did not sample during sustained rain or wind. We excluded birds flying overhead if they did not land in the plot. The same three observers conducted surveys both years, and were trained each spring prior to surveys. We surveyed each plot twice per breeding season (1 June–15 July), rotating observers among plots and the order of visitation with respect to time of day to control observer and temporal biases. As a measure of each species' abundance, we used the maximum of the two counts in each year, expressed as detections per hectare. Bird species richness was the number of species detected at a given plot during two point counts a year. We collected habitat data (Table 1) on 1000-m^2 plots centered on the point count station.

Table 1
Habitat variables recorded in each 20×50-m plot available as candidates for selection as independent variables in multiple regression for aspen stands only. Each plot was centered on each point count station, with long axis perpendicular to slope

Variable	Classes or measurement units; methods
Aspen as overstory	aspen trees present in overstory
Topographic setting	in riparian area or on hillside
Elevation	m; topographic maps
Aspect	degrees azimuth; hand-held compass
Slope	degrees of slope; clinometer
Area of aspen stand	ha; paced length times paced width
Distance to nearest opening >20 m radius	m; pacing (truncated at 250 m)
Distance to Nearest neighbor aspen stand	UTM coordinates
Average distance to neighboring aspen stands	Average distance to from stand to all other stands included in the study
Number of aspen in each of four diameter classes	0.1–12.7 cm dbh, 12.8–30.5 cm dbh, 30.6–45.7 cm dbh, or >45.7 cm dbh
Number of ponderosa pine in each diameter class	same as above
Number of Gambel oak[a] in each diameter class	same as above
Number of conifers (excluding ponderosa pine) in each diameter class	same as above
Total number of trees in each diameter class	by addition from previous
Aspen as percent of total trees	calculated
Number of snags in each of two diameter classes	30.6–45.7 cm dbh, >45.7 cm dbh
Canopy cover%	point intercept at 92 points, every 2 m along edge and short axis of plot
Number of shrubs	count
Number of logs in each of two size classes	small (12.8–30.5 cm diameter at center point and >1.2 m long), large (>30.6 cm diameter at center point and >2 m long)
Ground Cover% in each of six classes	(rock, soil, litter, woody debris, grass, or forb), assessed by point intercept at 92 points

[a] All deciduous trees other than aspen were included here, but 95% of such trees were Gambel oak.

2.3. Data analysis

We used a paired *t*-test ($\alpha = 0.05$) within years to determine if the aspen plots were different from their paired pine plots in bird abundance or species richness (Ott, 1993, pp. 663–709). We used a repeated measures general linear model (GLM; $\alpha = 0.05$), blocking for year, to determine if bird abundance or species richness varied between years or with overstory vegetation and topographic setting interacting with year (Neter et al., 1996, pp. 1164–1194; SPSS Inc., 1997a, pp. 145–156). We used analysis of variance ($\alpha = 0.0125$) on both bird abundance and species richness for each year to examine within year how abundance and richness varied by overstory vegetation and topographic setting (Neter et al., 1996, pp. 663–709). We tested bird abundance and species richness for normality and homogenous error variances (Kolmogorov–Smirnov test, Levene's test, respectively; SPSS Inc., 1997a, p. 358, 1997b, p. 53). We used Bonferroni correction adjustments (Neter et al., 1996, pp. 736–738) on all multiple comparisons. We used square root transformations as appropriate to meet the assumptions for a general linear model or regression.

We used forward stepwise multiple regression ($F = 4.0$ to enter, $F = 3.9$ to remove) to identify environmental factors affecting avian species richness in small aspen stands (Neter et al., 1996, pp. 347–352, SPSS Inc., 1997c, pp. 229–238). Because most plots were sampled both years (and thus years were not independent), we built individual models for 1996 ($N = 48$) and 1997 ($N = 51$).

Because responses of individual species are inherently more important and meaningful than overall diversity, we also describe the responses of individual species to habitat gradients, including aspen patch area and isolation, within our study area.

We used canonical correspondence analysis (CCA) to examine relationships between avian communities and habitat factors across our study area. This is a parametric ordination technique used to find and describe patterns in multivariate data (ter Braak, 1986; Palmer, 1993; McCune and Mefford, 1997). This technique uses a matrix of species detections and abundances and combines this with a matrix of habitat and environmental variables. This is a direct gradient analysis, meaning it is a special form of multivariate regression (multivariate regression combined with weighted averaging techniques) whereby species composition is directly related to measured environmental variables. This technique performs well even when there are skewed species distributions, extremely high noise levels, or complex sampling designs. CCA does not compress gradient extremes or generate an artificial arch, which is unlike other ordination techniques, and it performs well with nonorthogonal and collinear gradients (Minchin, 1987; Palmer, 1993).

The graph of this ordination represents complex data in fewer dimensions. The canonical axes are linear combinations of habitat variables that maximize the dispersion of the bird species in relation to these variables. We used CCA to generate graphs that show the habitat variables as vectors, and each bird species as a point in the ordination space defined by the three canonical axes. We used a Monte Carlo simulation to test the eiganvalues generated by the CCA procedure at $P=0.05$ (McCune and Mefford, 1997).

We included bird species that differed by >20% in abundance between aspen and pine and for which there were at least three detections across all plots in 1996. We chose 1996 because it had higher bird numbers and more severe drought conditions, conditions under which interspecific competition might force birds to more strongly express their habitat affinities. We also did a second ordination for only aspen stands, examining area and isolation effects on individual species.

Finally, we tested whether aspen–pine pairs, on average, harbored bird communities more similar to each other than the communities of environmentally similar plots within aspen or pine. To do so, we first computed similarity (Jaccard index) between bird communities on paired pine–aspen plots. We then sorted all plots by tree stem density; the environmental variable that best separated types of aspen and types of pine stands in the community analysis. We then computed (separately for pine and aspen) the similarity between the bird communities of each stand and the stand with the next highest stem density. We compared bird similarity between the paired plots and between environmentally similar aspen and environmentally similar pine plots using a *t*-test ($P<0.05$; Ott, 1993, pp. 260–270).

3. Results

3.1. Comparing bird abundance and richness between aspen and pine

We detected a total of 51 bird species on 102 plots during 1996 and 1997 (Appendix). Relative bird abundance ranged from 3.82 to 43.29 detections/ha in aspen (mean = 17.35) and from 1.27 to 31.83 detections/ha in the pine matrix (mean = 10.42). Species richness ranged from 3 to 17 species/plot in the aspen (mean = 9.55) and from 1 to 15 species/plot in the pine matrix (mean = 6.10).

Five of the 51 bird species were detected only in aspen stands during both years: acorn woodpecker (10 individuals), black-chinned hummingbird (eight individuals), Williamson's sapsucker (four individuals), Clark's nutcracker (three individuals), and green-tailed towhee (three individuals). Three bird species were detected only in pine stands; Cassin's finch (two individuals), Brewer's blackbird (one individual), and white-throated swift (three individuals). However, all these species have been detected at other times in both the aspen and pine (K. Griffis-Kyle and P. Beier, personal observations). The Jaccard similarity index, scaled from 0 (no overlap) to 1 (complete similarity), was 0.82, indicating the presence of many of the same bird species in both aspen and pine.

Relative bird abundance and bird species richness were higher in aspen plots than their paired pine plots during both 1996 and 1997 ($P<0.0005$ for all paired *t*-tests; Fig. 1). Relative bird abundance varied by year ($P<0.0005$) and by an interaction of overstory vegetation (i.e. aspen versus pine) and year ($P<0.02$), but not by topographic setting ($P=0.16$; GLM of abundance by year, overstory vegetation, and topographic setting), with greater bird abundance during 1996 and in aspen plots [Fig. 1(A)]. The decline in bird abundance between 1996 and 1997 coincided with a drought. The interaction reflects that bird abundance decreased more in pine (13 birds/ha in 1996 to 7 birds/ha in 1997) than in aspen (19 birds/ha in 1996 to 15.5 birds/ha in 1997). Although species richness, like abundance, was higher in aspen [Fig. 1(B)] and decreased from 1996 to 1997 ($P<0.0005$), there was no significant interaction of year with overstory vegetation ($P=0.42$) and no effect of topographic setting ($P=0.10$, GLM of richness by year, overstory vegetation, and topographic setting).

3.2. Species richness within aspen stands

The 1996 multiple regression model explained 46% (R^2) of the variation in species richness among the 48 aspen stands, and identified three variables influencing species richness in that year (Table 2). Species richness was inversely related to slope and the number of saplings (0.1–12.7 cm dbh, all species), and directly related to the number of small oak trees (12.8–30.5 cm).

The 1997 model explained 24% (R^2) of the variation in species richness among the 51 aspen stands (Table 2). Species richness increased at lower elevations and in stands with fewer saplings (0.1–12.7 cm dbh trees, all species).

The multiple regression models did not identify area of aspen patch (range 0.1–128 ha, mean 13 ha, median 4 ha), nearest neighbor distance (range 192–4825 m, mean 1466 m, median 1039 m), or mean neighbor distance (range 23–47 km, mean 30 km, median 28 km) as important factors in 1996 or 1997 (in all cases, $|r|<0.19$ and $P>0.19$). Scatterplots failed to reveal non-linear relationships or trends with either variable.

3.3. Individual species' responses to habitat variation

The habitat variables in the CCA ordination explained 50.1% of the variation in the distribution of individual bird species. The first canonical axis was positively correlated with herbaceous understory and negatively correlated with the presence of snags and small diameter aspen (Monte Carlo test, $P=0.01$)

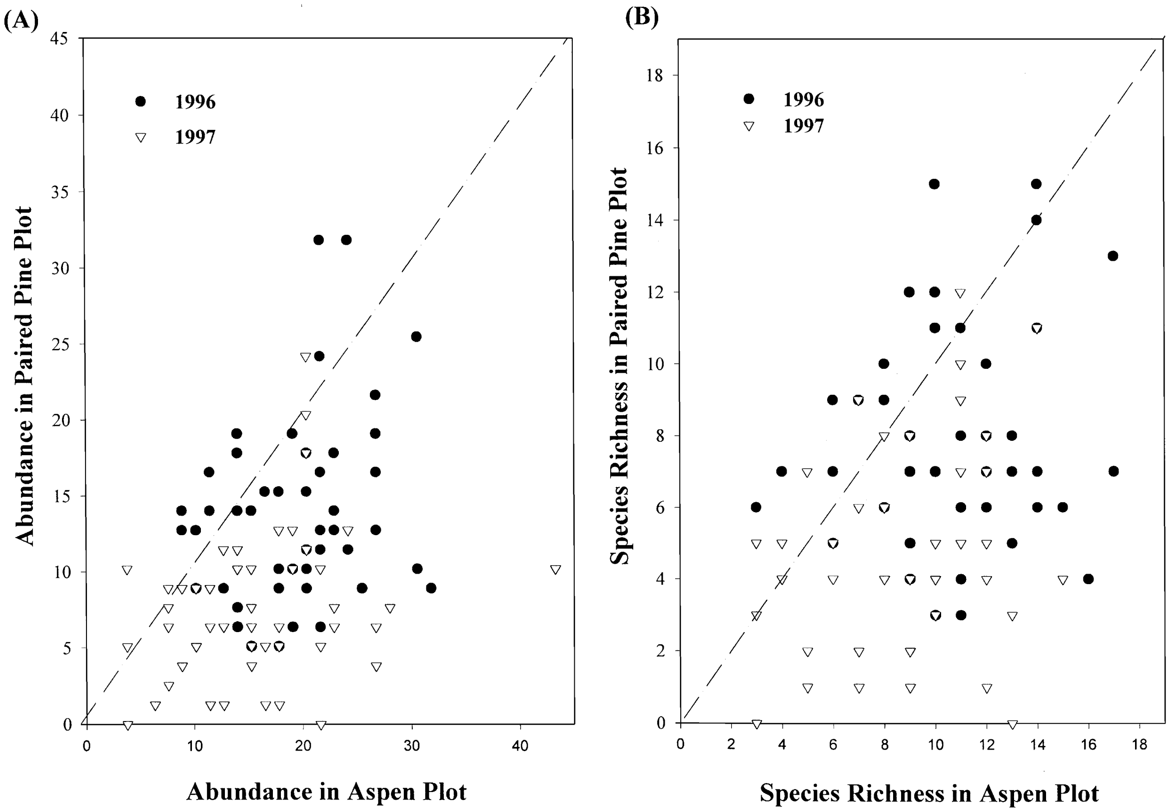

Fig. 1. A comparison between aspen–ponderosa pine pairs of plots for (A) relative bird abundance and (B) species richness in 1996 and 1997, in the northern Arizona ponderosa pine forest. Notice more points are located below the 45 degree line, indicating that in most cases the aspen plot has more birds and more bird species than the paired pine plot.

Table 2
Species richness model from a multiple linear regression for small aspen stands in northern Arizona showing the summary statistics for the final models

Factor	Coefficient	Standard error	P
1996			
Constant	12.611	0.635	0.000
Slope	−0.084	0.029	0.006
Deciduous trees (excluding aspen) 12.8 to 30.5 cm dbh[a],[b]	0.584	0.132	0.000
Total number of trees 0.1 to 12.7 cm dbh[a]	−0.019	0.006	0.002
1997			
Constant	30.221	0.635	0.004
Elevation	−0.009	0.029	0.048
Total number of trees 0.1 to 12.7 cm dbh[a]	−0.023	0.006	0.000

Years were modeled separately because of significant differences in species richness between years and independence of samples. The model for 1996 explains 46% of the variation and the model for 1997 explains 24% of the variation in species richness.

[a] Tree numbers are based on a count in a 1000 m^2 plot centered on the point count station.

[b] 215 trees out of 220 counted were Gambel oak.

(Fig. 2; Table 3). This axis accounted for 26.9% of the variation in the distribution of bird species. Virginia's warblers, violet-green swallows, brown-headed cowbirds, and chipping sparrows were associated with the positive end of axis one. Pine siskins and warbling vireos were associated with the negative end of axis one (Fig. 2).

The second canonical axis was positively correlated with herbaceous understory and negatively correlated with steep slope, litter, high canopy cover and large diameter ponderosa pine. This axis accounted for 12.5% of the variation in species distributions (Monte Carlo test, $P=0.01$; Fig. 2; Table 3). Olive-sided flycatchers, violet-green swallows, pine siskins, black-chinned

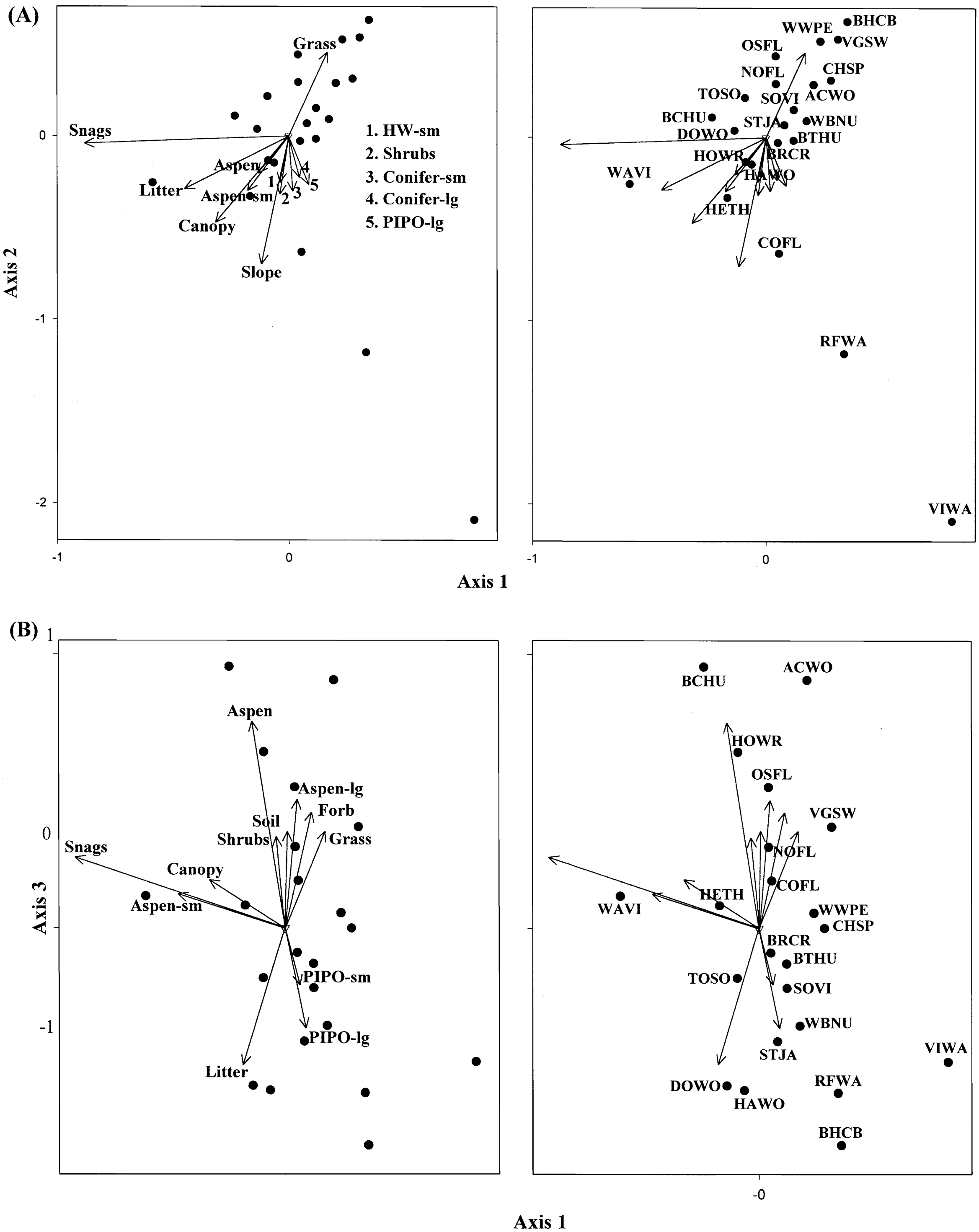

Fig. 2. This is a three-dimensional representation of bird species ordinated in relation to habitat vectors (arrows) (Table 3). The length of habitat vectors indicates their relative strength in explaining variation in the distribution of species. The distance from the origin to the perpendicular drawn from the bird species point to a habitat vector indicates how closely associated that bird is with that habitat variable. Perpendicular distance from the vector to the bird species has no relationship to the correlation between the bird species and that habitat variable. Three bird species were left off the graph to enhance readability; pine siskins which were strongly associated with snags, black chinned hummingbirds which were strongly associated with shrubs and deciduous trees other than aspen, and Virginia's warblers which were strongly associated with herbaceous cover as well as shrubs and deciduous trees other than aspen. Note that there are no distinct groups of species associated with distinct groups of habitat variables. Instead we see bird species distributed across the entire range of habitat measurements.

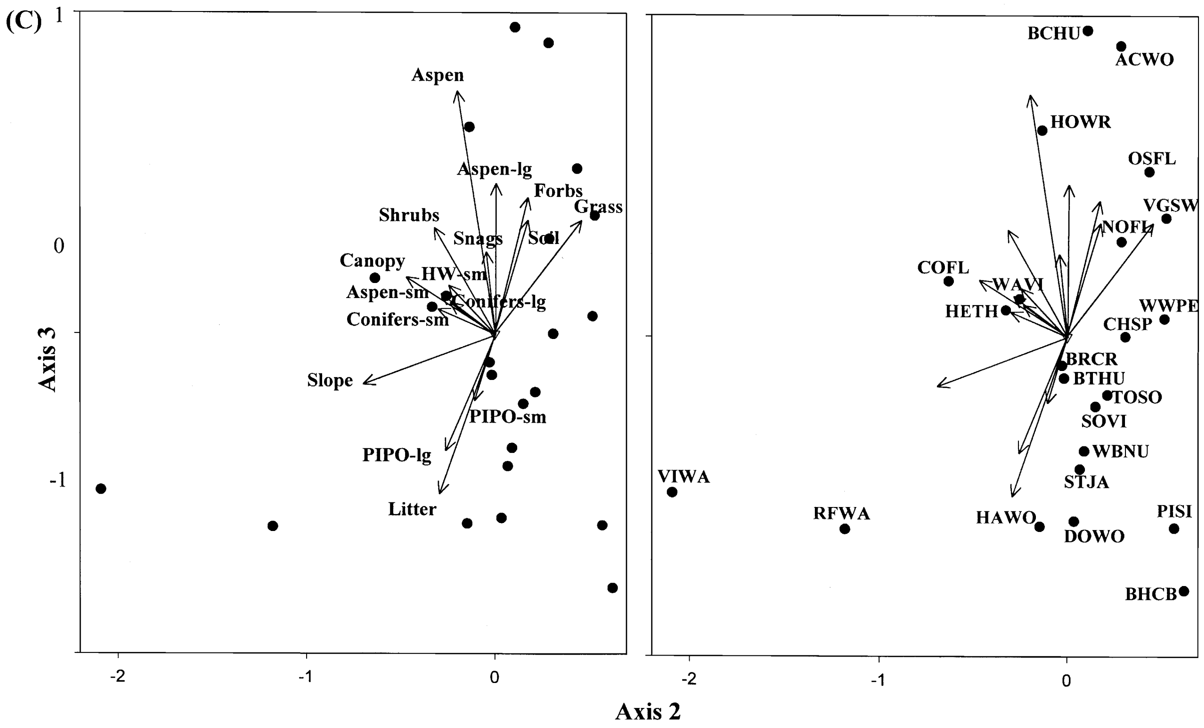

Fig. 2 (*continued*).

Table 3
Habitat variables recorded in each 20×50-m plot used in CCA analysis and their calculated correlations with axes one, two and three

Habitat variable	Description	Axis 1	Axis 2	Axis 3
Small POTR	Density of aspen 0.1–30.5 cm dbh	−0.469	−0.232	0.170
Large POTR	Density of aspen greater than 30.5 cm dbh	0.049	0.088	0.354
Small PIPO	Density of ponderosa pine 0.1–30.5 cm dbh	0.060	−0.171	−0.327
Large PIPO	Density of ponderosa pine than 30.5 cm dbh	0.089	−0.350	−0.146
Deciduous trees[a]	Density of Gambel oak	−0.034	−0.182	0.521
Coniferous trees	Density of coniferous trees, excluding PIPO	0.021	−0.247	0.295
Snags	Density of snags	−0.904	0.071	0.274
Canopy cover	% of hits of canopy for 92 point intercepts	−0.331	−0.414	0.236
Shrubs	Density of shrubs	−0.047	−0.212	0.581
Bare ground	% of hits of rock or soil for 92 point intercepts	0.060	−0.004	0.262
Litter	% of hits of litter for 92 point intercepts	−0.174	−0.476	−0.478
Herbaceous cover	% of hits of grass or forbs for 92 point intercepts	0.175	0.581	0.245
Slope	Degrees of slope, clinometer	−0.135	−0.770	0.063

[a] All deciduous trees other than aspen were included here, but 95% of such trees were Gambel oak.

hummingbirds, western wood-peewees, northern flickers, brown-headed cowbirds, and acorn woodpeckers were associated with the positive end of axis two. Virginia's warblers, red-faced warblers, cordilleran flycatchers, downy and hairy woodpeckers, hermit thrushes, and warbling vireos were associated with the negative end of axis two (Fig. 2).

The third canonical axis was positively correlated with a diverse understory, snags, and large aspen as well as other deciduous and coniferous tree species (excluding ponderosa pine) and negatively correlated with litter and ponderosa pine. This axis accounted for 10.7% of the variance in the community matrix (Monte Carlo test, $P=0.01$; Fig. 2; Table 3). Black-chinned hummingbirds, Virginia's warblers, house wrens, cordilleran flycatchers, and violet-green swallows were associated with the positive end of axis three. Chipping sparrows, Steller's jays, red-faced warblers, pine siskins, western wood-peewees, plumbeous vireos, and white-breasted nuthatches were associated with the negative end of axis three (Fig. 2).

On average, similarity between bird communities of an aspen plot and its paired pine plot (average Jaccard index = 0.289, standard deviation = 0.136) was no different than between environmentally similar aspen plots (average Jaccard index = 0.255, standard deviation = 0.010) or between environmentally similar pine plots (average Jaccard index = 0.255, standard deviation = 0.143) ($P = 0.10$ in all cases). Thus, aspen stands do not provide habitat for a different suite of birds.

3.4. Individual species' responses to area and isolation

Two canonical axes were identified, one in relation to size of aspen patch, the second in relation to nearest neighbor distance. Neither axis was statistically significant (Monte Carlo test, $P = 0.20$), and no bird species were significantly related to either patch size or isolation.

4. Discussion

Within the larger ponderosa pine forest, small aspen stands support a greater diversity and abundance of birds per hectare; a result also noted by Winternitz (1976) and Turchi et al. (1995). The high overlap between aspen and pine communities demonstrates that aspen stands do not harbor unique avian communities, but rather are locations where the regional avifauna reaches high local density and diversity. For forest birds, the scattered patches of aspen function as important landscape elements within the ponderosa pine forest matrix, not as isolated islands of habitat.

Within-patch habitat factors explained 46% (1996) and 24% (1997) of the variation in species richness among aspen stands. These low predictive values may reflect that birds were responding to arthropod abundance or other factors that we did not measure. We believe that the lower explanatory power of the 1997 model is linked to decreased competition resulting from fewer birds and a more abundant food supply. This is assuming that arthropod abundance increased with a 39% increase in precipitation and that arthropod availability further increased with a decrease in bird abundance. Thus, the 1996 model may better identify habitat characteristics important during times of greater competition.

Avian species richness decreased with increasing density of saplings (all species) in aspen stands in both 1996 and 1997; no other factor was consistently associated with species richness in aspen stands. Young (1973) and Flack (1976) noted similar patterns. High densities of saplings are characteristic of young stands with high canopy shading, depauperate understories, and an altered vertical distribution of foraging and nesting sites. We found the abundance of medium-sized Gambel oak (12.8–30.5 cm dbh) associated with higher species richness in 1996. Gambel oak is an important resource for both bird foraging and nesting in northern Arizona (Balda, 1969; Rosenstock, 1996, 1998).

Topographic setting (riparian versus hill) was not related to avian abundance or diversity in pine or aspen. This is an unexpected finding considering the importance of riparian areas to bird diversity and abundance in more xeric landscapes in the Southwest (Whittaker, 1975; Stevens et al., 1977; Szaro, 1980; Knopf, 1985; Strong and Bock, 1990). However, McGarigal and McComb (1992) similarly found no difference in bird diversity between riparian and upland sites in moist coniferous forests in Oregon and attributed this to subtle transpiration gradients between their riparian and upland sites. No riparian sites in our study have perennial water flow, and soil moisture probably differs little between upland and riparian sites. Therefore in terms of microclimate, aspen on hills may not be very different from aspen in riparian areas in the Southwest.

In our study and other studies examining patches of aspen within a forested matrix, area and isolation of aspen stands did not affect bird abundance and diversity or individual species distributions in a manner consistent with the island theory of biogeography (Yahner, 1986; Turchi et al., 1995). Traditional terrestrial application of the theory of island biogeography has been to islands of forest in a matrix of agriculture, urbanization, clearcuts, or meadows (e.g. Martin, 1980; Soulé et al., 1988; Stouffer and Bierregaard, 1995; Stratford and Stouffer, 1999; van Balen, 1999; Beier et al. 2002), i.e. habitat surrounded by nonhabitat (Ricketts, 2001). Matrix composition dramatically influences the effective isolation of habitat patches (Ricketts, 2001). In our study, the matrix of pine is so permeable as to make aspen patch area and isolation non-issues. The fact that the smallest and most isolated aspen patches had high avian diversity and abundance, in addition to the patterns of association for individual species, are consistent with the view most bird species exist as continuous populations across the pine-aspen landscape.

Researchers have long related the distribution and abundance of bird species to various aspects of their environment (Block and Brennan, 1993). Our canonical analysis revealed species associated with various aspects of forest structure and composition. We found that most of the strongest species associations were with structural factors such as herbaceous cover or the presence of snags. Nearly all of the species showed some correlation with either aspen or ponderosa pine, but this could be related to our species selection criteria for the analysis (species had to show a 20% difference in number of detections between aspen and pine plots to be included in the analysis). In addition, our results, related to both habitat structure and components, rely heavily on the theory of habitat selection. We acknowledge that other factors, such as competition, predation, and parasitism, also could influence this process (Cody, 1981; Rosenzweig, 1985).

We found several consistencies between our analyses of general patterns of avian relative abundance and species richness and patterns for individual species. The size and number of trees had a significant impact on the avian community at both of these scales of resolution. The canopy tree species also influenced individual bird species presence, albeit not as dramatically as other factors. Conversely, even though factors such as slope and understory cover may not be associated with overall avian relative abundance or species richness, they may still be significantly related to distributions of individual species. At the large scale, our results suggest there are more birds and more species in aspen stands with an additional hardwood component. However, our description of avian communities at the species scale demonstrates a much more complex relationship of diversity with the environment.

5. Conservation implications

We found that small aspen patches are an important component of the landscape to many species of birds in the Southwest. From the perspective of conservation and management of forest birds, the lack of area and isolation effects, in combination with higher bird abundance and diversity in aspen, demonstrates that even the smallest and most isolated aspen patches contribute to regional vigor of bird populations taken in the context of a larger forest system. Thus management actions (overstory thinning, burning, fencing against ungulates) to maintain several small stands of aspen can be at least as valuable as actions to conserve a single stand of the same total size. To the extent that avian control of forest insects (Marquis and Whelan, 1994) is effective outside of these high-density stands, and to the extent that they contribute potential breeders into the forest at large, several small stands may be more valuable than fewer, large stands. However, the aspen stands are not functioning as isolated habitat patches, they are adding to the diversity of forest structure within a larger system. Future research should investigate the extent to which regional stability and resilience of bird populations in the forest is enhanced by these small aspen stands.

Appendix

The 51 bird species observed, scientific names (AOU, 2001), and numbers of birds detected during breeding seasons of 1996 and 1997 in northern Arizona ponderosa pine forest matrix and quaking aspen stands. Detections are the number of individuals of a species detected per plot per year summed over a particular plot type. Bird species analyzed with the CCA are listed with their bird banding code and score for each of the canonical axes. Bird species were selected for CCA analysis based on a minimum of 20% difference in detections between aspen and ponderosa pine plots and a minimum of three detections across all plots during 1996

Species	Scientific name	Code	Plot type				Axis 1	Axis 2	Axis 3
			Aspen Hill ($N=25$)	Aspen Riparin ($N=28$)	Pine Hill ($N=25$)	Pine Riparian ($N=28$)			
Red-tailed hawk	*Buteo jamaicensis*		2	1	0	1			
Band-tailed pigeon	*Columba fasciata*		1	0	1	1			
Mourning dove	*Zenaida macroura*		2	3	1	1			
White-throated swift	*Aeronautes saxatalis*		0	0	0	2			
Black-chinned hummingbird	*Archilochus alexandri*	BCHU	2	6	0	0	−0.13307	0.531023	1.685292
Broad-tailed hummingbird	*Selasphorus platycercus*	BTHU	8	16	4	11	0.107956	−0.0123	0.168097
Acorn woodpecker	*Melanerpes formicivorus*	ACWO	13	7	0	0	0.151676	0.223198	0.012566
Downy woodpecker	*Picoides pubescens*	DOWO	4	4	2	1	−0.10779	−0.40636	0.073782
Hairy woodpecker	*Picoides villosus*	HAWO	8	11	3	7	0.02896	−0.34325	−0.21797
Northern flicker	*Colaptes auratus*	NOFL	20	24	6	6	0.046331	0.346244	0.067417
Williamson's sapsucker	*Sphyrapicus thyroideus*	WISA	3	1	0	0			
Cordilleran flycatcher	*Empidonax occidentalis*	COFL	35	46	8	18	0.04051	−0.51143	0.318648
Olive-sided flycatcher	*Contopus cooperi*	OSFL	7	6	0	1	−0.07528	0.708075	0.045878
Western wood-pewee	*Contopus sordidulus*	WWPE	38	22	9	10	0.17927	0.351399	−0.33767
Violet-green swallow	*Tachycineta thalassina*	VGSW	31	57	12	11	0.314407	0.578541	0.267694
Steller's jay	*Cyanocitta stelleri*	STJA	29	22	17	22	0.059627	−0.07509	−0.42907
Clark's nutcracker	*Nucifraga columbiana*		2	1	0	0			
American crow	*Corvus brachyrhynchos*		0	1	1	0			
Common raven	*Corvus corax*		7	10	3	5			
Mountain chickadee	*Poecile gambeli*		39	43	28	56			
Brown creeper	*Certhia americana*	BRCR	19	15	9	13	0.015253	−0.00023	−0.06462

Species	Scientific name	Code	Plot type				Axis 1	Axis 2	Axis 3
			Aspen Hill ($N=25$)	Aspen Riparin ($N=28$)	Pine Hill ($N=25$)	Pine Riparian ($N=28$)			
Pygmy nuthatch	*Sitta pygmaea*		67	56	47	66			
Red-breasted nuthatch	*Sitta canadensis*		1	3	0	0			
White-breasted nuthatch	*Sitta carolinensis*	WBNU	30	33	19	41	0.176876	0.048766	−0.25575
House wren	*Troglodytes aedon*	HOWR	43	72	5	9	−0.12036	0.097789	0.491738
Ruby-crowned kinglet	*Regulus calendula*		0	3	0	1			
Townsend's solitaire	*Myadestes townsendi*	TOSO	5	3	8	3	−0.05583	−0.1916	0.07417
Western bluebird	*Sialia mexicana*		21	6	17	21			
Mountain bluebird	*Sialia currucoides*		0	0	1	0			
Hermit thrush	*Catharus guttatus*	HETH	20	21	4	4	−0.09282	−0.26161	0.019608
American robin	*Turdus migratorius*		20	22	11	23			
Plumbeous vireo	*Vireo plumbeus*	PLVI	25	19	14	19	0.094958	0.076562	−0.27089
Warbling vireo	*Vireo gilvus*	WAVI	57	54	4	6	−0.50985	−0.25845	0.003861
Virginia's warbler	*Vermivora virginiae*	VIWA	5	6	1	6	0.649491	−1.66631	1.11562
Yellow-rumped warbler	*Dendroica coronata*		17	17	20	18			
Grace's warbler	*Dendroica graciae*		16	15	19	14			
Red-faced warbler	*Cardellina rubrifrons*	RFWA	11	25	3	18	0.18735	−0.97931	−0.38769
Olive warbler	*Peucedramus taeniatus*		2	1	0	4			
Black-headed grosbeak	*Pheucticus melanocephalus*		11	11	4	4			
Green-tailed towhee	*Pipilo chlorurus*		1	2	0	0			
Chipping sparrow	*Spizella passerina*	CHSP	2	2	4	2	0.271532	0.112452	−0.55152
Lark sparrow	*Chondestes grammacus*		3	0	2	0			
Dark-eyed junco	*Junco hyemalis*		31	34	37	43			
Western meadowlark	*Sturnella neglecta*		1	0	1	0			
Brewer's blackbird	*Euphagus cyanocephalus*		0	0	0	1			
Brown-headed cowbird	*Molothrus ater*	BHCO	5	10	12	14	0.310233	0.267036	−0.2799
Western tanager	*Piranga ludoviciana*		15	19	12	18			
Pine siskin	*Carduelis pinus*	PISI	1	7	1	1	−6.15843	0.544268	−0.37865
Lesser goldfinch	*Carduelis psaltria*		0	2	1	0			
Red crossbill	*Loxia curvirostra*		1	2	1	2			
Cassin's finch	*Carpodacus cassinii*		0	0	0	2			

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