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Relationships among Vegetation Structure, Canopy Composition, and Avian Richness Patterns across an Aspen-Conifer Forest Gradient

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ABSTRACT

Ecologists have a long-term interest in understanding the relative influence of vegetation composition and vegetation structure on avian diversity. LiDAR remote sensing is useful in studying local patterns of avian diversity because it characterizes fine-scale vegetation structure across broad extents. We used LiDAR, aerial and satellite imagery, and avian field data to investigate the relative influence of vegetation structure and canopy composition on avian richness across an aspen-conifer forest gradient. Aspen enhances forest avian biodiversity but has been declining across western North America. We conducted bird surveys between 2013 and 2014 in plots with a range of aspen-conifer canopy composition. We found aspen to support higher avian richness than conifer, especially among cavity nesters. In contrast to other studies, we found weak relationships between vegetation structure and avian richness. Although primary cavity excavator richness was negatively influenced by canopy density, canopy composition was the most important variable influencing total richness and nesting guild richness. This study adds to the body of literature utilizing LiDAR-derived metrics to better understand local patterns of avian diversity, and provides perspectives on how avian communities might respond to conifer encroachment into aspen.

RÉSUMÉ

Les écologistes ont un intérêt à long terme pour comprendre l'influence relative de la composition et de la structure de la végétation sur la diversité aviaire. La télédétection lidar est utile pour étudier les patrons locaux de diversité aviaire, car elle caractérise la structure de la végétation à fine échelle sur de vastes étendues. Nous avons utilisé l'imagerie lidar, aérienne et satellitaire ainsi que des données de terrain de recensement aviaire pour étudier l'influence relative de la structure de la végétation et de la composition de la canopée sur la richesse aviaire selon un gradient de tremble-conifère. Le tremble renforce la biodiversité aviaire des forêts, mais son abondance a diminué dans l'ouest de l'Amérique du Nord. Nous avons effectué des relevés d'oiseaux entre 2013 et 2014 dans des parcelles avec une gamme variée de composition de trembles et de conifères. Nous avons constaté que le tremble favorise une richesse aviaire supérieure à celle des conifères, surtout chez les oiseaux nichant dans des cavités. Contrairement à d'autres études, nous avons constaté des relations faibles entre la structure de la végétation et la richesse aviaire. Bien que la richesse des excavateurs primaires ait été influencée négativement par la densité de la canopée, la composition de la canopée était la variable la plus importante influençant la richesse totale et la richesse de la guilde de nidification. Cette étude ajoute à la littérature existante qui utilise des mesures dérivées du lidar pour mieux comprendre les patrons locaux de diversité aviaire et elle fournit des perspectives sur la façon dont les communautés aviaires pourraient répondre à l'empiètement des conifères dans les peuplements de tremble.

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Introduction

Ecologists have long held an interest in the influence of vegetation structure (physiognomy) and vegetation species composition on avian species richness. MacArthur and MacArthur (1961) were among the earliest to find that avian species richness was more highly correlated with vegetation structure than composition. Subsequent work has shown that species richness patterns depend on structure and composition to varying degrees as a function of ecosystem type (e.g., Willson 1974; Rotenberry and Wiens 1980; Mac Nally 1990). While previous studies tend to focus on either vegetation structure or composition and not the relative roles of each, several have investigated both simultaneously but with contradictory results (Lee and Rotenberry 2005; Mac Nally 1990; MacArthur and MacArthur 1961; Rotenberry 1985; Seavy

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and Alexander 2011). Differences among previous studies have been postulated to be due to scale effects or methodology (Müller et al. 2010; Rotenberry 1985; Willson 1974) but may also involve differences in underlying response mechanisms to vegetation composition independent of vegetation structure (Lee and Rotenberry 2005).

The complexity of vegetation structure can be time consuming and expensive to quantify, especially over large areas. Recent studies investigating the role of vegetation structure in a variety of ecological contexts have largely relied on the strengths of LiDAR, an active 3-D technology with advantages in its ability to measure terrain and vegetation heights accurately and at high resolution over broad extents (Eitel et al. 2016; Hill et al. 2014; Müller and Vierling 2014). Airborne LiDAR also offers the same advantages (e.g., logistics, spatial extent, etc.) as other airborne-based remote sensing technologies relative to field efforts in the collection of environmental variables. A potential drawback to LiDAR is its cost and availability (Vierling et al. 2008). However, LiDAR has been shown to be more cost-effective than field data collection in many contexts, and a major contribution of LiDAR is the ability to incorporate structural information in predictive modeling and mapping of processes over broad extents (Müller and Brandl 2009).

LiDAR has been used to obtain a variety of terrain and vegetation structure metrics that have been used in a variety of studies addressing avian-habitat relationships, but few studies to date have used LiDAR to simultaneously investigate the relative roles of vegetation structure and composition on avian species richness patterns (see, for example, Müller et al. 2010). Müller et al. (2010) examined the relative role of physiognomy and plant species composition for birds in conifer-dominated forests in Germany. They found that forest structure was a more powerful predictor of bird communities than floristic composition, and suggest that future studies with LiDAR are needed to expand our understanding of ecological relationships. Incorporating LiDAR into such studies is important, in part because the use of LiDAR can expand the types of vegetation structural metrics that have been traditionally collected in ground-based field data efforts (e.g., Vierling et al. 2008). Due to the limited number of studies to date that have explicitly addressed interactions between vegetation composition, vegetation structure, and bird communities using LiDAR data, there also exists a broadened opportunity to expand our perspectives on how these relationships might differ across different regions and in different forest types (Müller et al. 2010).

Understanding the relative importance of vegetation structure and composition on bird communities may be particularly important in quaking aspen (*Populus tremuloides*) forests undergoing conifer encroachment because of the relative importance of aspen to bird communities. Aspen has been noted to enhance local and regional biodiversity (Bartos 2001; DeByle 1985), and conifer encroachment is one of the many factors associated with aspen decline (Bartos 2001; Kaye et al. 2005; Worrall et al. 2008). Many studies have noted that avian diversity decreases as conifers increase (Hollenbeck and Ripple 2007; Richardson and Heath 2004; Rumble et al. 2001); additionally, some nesting guilds (i.e., cavity nesters) have high diversity within aspen stands (Drever and Martin 2010; Griffis-Kyle and Beier 2003; Hollenbeck and Ripple 2007; Rumble et al. 2001). Although LiDAR has been used to address various bird-habitat relationships in aspen-pine forests (e.g., Clawges et al. 2008), it has not been used to explicitly examine relationships between bird communities, vegetation structure, and amount of conifer encroachment.

Our major objective was to examine the relative influence of forest canopy composition and vegetation structure in avian species richness and nesting guild richness across an aspen-conifer forest gradient using LiDAR-derived data. Initial studies of avian richness using LiDAR used broad habitat-based guilds (e.g., Goetz et al. 2007) while more recent studies have used a nesting-guild approach (e.g., Vogeler et al. 2014). Other work has focused on characterizing guilds presumed to be sensitive to the vegetation layers being measured (Lesak et al. 2011; Vogeler et al. 2014). Here, we used a nesting-guild approach, with a focus on the cavity and open cup nesting guilds. Similar to other studies, we hypothesize that vegetation structure of the forests, such as foliage height diversity, mean height, and the presence of a well-developed shrub layer, is important for overall bird species diversity (Flaspohler et al. 2010; Goetz et al. 2007; Hill and Hinsley 2014; Müller et al. 2009; Lesak et al. 2011; Vogeler et al. 2014). We further hypothesize that the cavity nesting guild responds more strongly to canopy composition than vegetation structure compared to the open cup nesters. Primary cavity excavators have been noted elsewhere to prefer aspen over conifer (Dobkin et al. 1995; Li and Martin 1991), in part because aspen with heart rot fungus (*Phellinus tremulae*) is relatively easy to excavate (i.e., Losin et al. 2006).

Methods

Study area

The study was conducted in the Long Valley in the west-central mountains of Idaho (Figure 1) approximately 140 km north of the Boise metropolitan area. Long Valley is a broad north-south montane valley varying from 8 km to 11 km wide and extending for 58 km; the northern edge

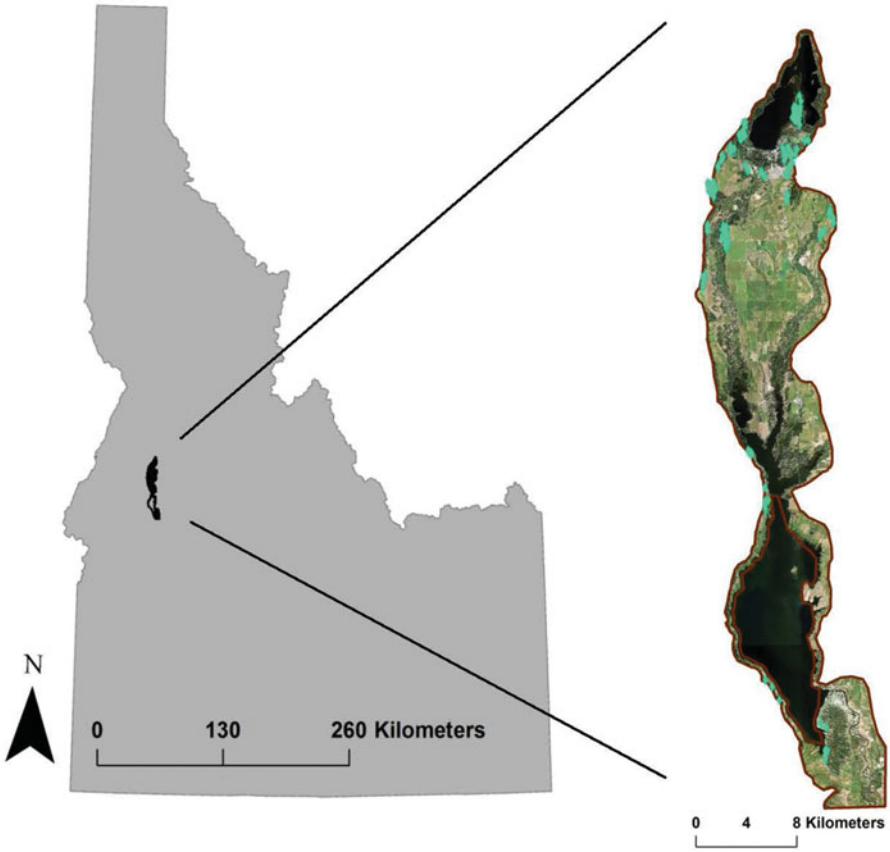

Figure 1. Locator map (left) of Long Valley study area within U.S. state of Idaho and expanded study area (right) showing distribution of field plots overlaid on 2011 NAIP imagery. Teal diamonds indicate distribution of field plots surveyed for avian species richness during 2013–2014 (combined). Brown outline on study area map depicts extent of 2012 LiDAR acquisition used to derive vegetation structure metrics.

of the valley is located in the town of McCall (44° 54′ 48″ N, 116° 6′ 15″ W), and the southern edge is 9.5 km south of the town of Cascade (44° 30′ 56″ N, 116° 2′ 37″ W). Valley floor elevation declines gradually north to south from 1,530 m at McCall to 1,450 m at Cascade. Climate in the Long Valley is characterized by warm, dry summers and moderate, wet winters (Abramovich et al. 1998). The mean January low temperature at McCall is –11°C and the mean July high temperature is 26.5°C. The mean annual precipitation at McCall is 56 cm with the bulk coming as snow (150 cm) between November and March.

The Long Valley contains a broad mosaic of habitat types and land uses. Vegetation cover types include upland and riparian forest, wetlands and wet meadows, grasslands, and sagebrush steppe. Forests are dominated by mixed second-growth conifer stands comprised of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and lodgepole pine (*Pinus contorta*; Tinkham et al. 2012; Van Daele and Van Daele 1982). Stands of quaking aspen up to approximately 2 ha are found throughout the valley in a variety of sites, often mixing with conifers. Long Valley woodlands have been cleared historically for grazing and farming (Rasmussen 1981) and more recently for recreational development. Land ownership within the study area is a mosaic of public and private. Land uses within the valley include protected lands, low to moderate intensity grazing, resource extraction, and mixed recreational uses with a small year-round population augmented by tourism.

Field plots

We located aspen, mixed aspen-conifer, and conifer stands within the LiDAR acquisition area using aerial imagery, ground surveys, and locally available information. A subset of stands were selected for sampling, which were accessible, spanned the full extent of the study area, were located in a variety of physiographic settings (Figure 1), and were generally of similar successional stages. Within selected stands we established 50-m radius (.78 ha) survey plots a minimum of 150 m apart. Plot centers were located in the field, georeferenced with a Trimble GeoXT GPS (NAD83 UTM 11N), and mapped in ArcMAP 10.1 (ESRI, 2013). Within each survey plot the proportion of the canopy comprised of aspen and conifer was estimated to the nearest 10% using high resolution imagery from the USDA National Agricultural Inventory

Program (NAIP; USDA, 2011) overlaid with a 20-m grid. Survey plots were classified as aspen-dominated (hereafter aspen), mixed aspen-conifer (hereafter mixed), and conifer-dominated (hereafter conifer) as follows:

- aspen: 80% or higher aspen canopy cover;
- mixed: between 20% and 80% aspen cover with the remainder conifer;
- conifer: 80% or higher conifer canopy cover.

We simplified the NAIP-based classification to just these 3 classes to allow for misclassification error in the 10% aspen (or conifer) class calls, thus providing a fuzzy tolerance. Three classes constituted an equitable distribution of plots between forest conditions that best represented "pure" aspen, mixed, and "pure" conifer stands, such that we could test our hypothesis concerning composition as a descriptor of avian habitat suitability. Multiple photographs taken at each plot center were used to verify the plot classification.

Avian point counts

To survey for bird species richness, we conducted 2 point counts at each survey plot across 2 field seasons; 92 plots were surveyed in 2013 and 38 plots were surveyed in 2014 for a total of 130 plots. We sampled for the presence of all cavity and open cup nesters, and followed Drever et al. (2008) by using audio broadcasts for select woodpecker species to increase woodpecker detection via callback. A standard 5-minute point count for all breeding species was followed by audio broadcasts for each of 6 commonly occurring woodpecker species in the study area: Pileated Woodpecker (*Dryocopus pileatus*), Northern Flicker (*Colaptes auratus*), Hairy Woodpecker (*Picoides villosus*), Downy Woodpecker (*Picoides pubescens*), Red-naped Sapsucker (*Sphyrapicus nuchalis*), and Williamson's Sapsucker (*Sphyrapicus thyroideus*). The broadcast portion of the count consisted of 30 seconds of calls and drums followed by 30 seconds of silent listening for each species. Survey data recorded included survey phase (silent/broadcast), species and number of individuals within the 0.79 ha (50 m radius) survey plot, temperature, wind, and cloud cover. We acknowledge the possibility that callbacks may have attracted some individuals from adjacent plots. However, 70% of the plots were greater than 200 m apart (Drever et al. 2008) and there was a high correlation between detections with point counts only and detections including callbacks ($R^2 = .87$). Point counts were conducted between late May and early July to correspond with the breeding season peak singing and territory defense period. Each plot was surveyed once early and once later in the survey period to capture variability in breeding phenology and to increase the likelihood of detecting all species present. Point counts were conducted between 6:00 AM and 11:00 AM MDT during favorable weather conditions. All avian point counts were conducted by the same observer (Swift).

Species richness calculations

We calculated total bird species richness and guild species richness at each survey plot by pooling count data from the 2 survey periods. Species recorded within 50 m of plot center were included in richness measures for analysis. Fly-overs, suspected migrants, and water birds (except for several cavity-nesting ducks) were excluded from analyses. Species were categorized into 1 of 3 nesting guilds: primary cavity excavators (PCE), secondary cavity users (SCU), and open cup nesters following Martin and Eadie (1999). Weak cavity excavators (nuthatches and chickadees) were included in total species richness and total cavity nester richness but not in the PCE or SCU guilds, as they can act as primary excavators or secondary users in different circumstances (Li and Martin 1991; Norris and Martin 2012). To compare species richness similarity among aspen, conifer, and mixed canopy composition categories, we calculated Jaccard's similarity index (Jaccard 1901). The Jaccard index ranges between 0 and 1 and rises as similarity increases among 2 groups. We compared species richness for each nesting guild and total richness across aspen, mixed, and conifer plots using a Tukey multiple comparison of means test with a significance level of $p < .05$.

LiDAR remote sensing data

We used discrete multiple-return airborne LiDAR data to generate vegetation structure metrics for our study plots (Table 1). The LiDAR data were collected on May 7, 8, and 30, 2012 by Aerometric Inc. using fixed-wing aircraft as part of the United States Federal Emergency Management Agency's Risk MAP program and provided to us by the Idaho Department of Water Resources. The LiDAR extent spanned approximately 35,750 ha (Figure 1) with a post-spacing of 1 m and a nominal point density of 0.9 m^{-2}. LiDAR point cloud data were pre-processed and error checked by the vendor with maximum GPS horizontal variance of 7.6 cm and maximum vertical variance of 9.8 cm. Comparison with 23 ground control points resulted in a 0.057 m root mean square error. LiDAR data were delivered as 225 ha tiled output in raw and classified LAS format data files projected in spatial reference North American Datum 1983 Universal Transverse Mercator Zone 11 North. We processed the vendor-supplied point cloud data using LAStools (Isenburg 2013) to generate forest structure metrics at a 10-m resolution raster grid. Plot-level metrics were calculated using Focal Statistics with a 50-m radius in ArcGIS Spatial Analyst (ESRI

Table 1. Description of explanatory metrics used for modeling total and guild-specific species richness.

Category	Variable	Description
Vegetation structure	HeightSD	LiDAR metric of the standard deviation of plot averaged height of returns (>1.37 m)
	HeightMN	LiDAR metric of plot averaged mean height of returns (>1.37 m)
	UnstDN	LiDAR metric of plot averaged percentage of returns between 1 m and 2.5 m
	CnpyDN	LiDAR metric of plot averaged percentage of returns above 2.5 m in height
Canopy composition	CnpyCM	Plot canopy classification of aspen, mixed aspen-conifer, conifer
Landscape composition	FrstCM	Percentage of 30-m map units classified as forest cover types in a 2.25-ha window around plot center

Note. Metrics include 5 plot-level (50 m radius) vegetation structure variable and a 2.25-ha landscape variable. LiDAR-derived vegetation structure and canopy composition metrics were calculated from 10-m raster grids.

2013) at each of the 130 plot centers. The LiDAR acquisition differed temporally from the bird surveys by 1–2 years; however, several studies (Hill and Hinsley 2015; Vierling et al. 2014) note that time lags up to 6 years or more are likely to have minimal effect on detecting organism-habitat relationships in undisturbed forests. We are unaware of and could not identify any major disturbances in our study plots during the study period. We compared vegetation structure across aspen, mixed, and conifer plots using a Tukey multiple comparison of means test with a significance level of $p < .05$.

Modeling covariates

We selected a priori, 4 LiDAR-derived metrics of vegetation structure (Table 1), which we hypothesized could have an influence on total bird richness, cavity-nester richness, and open cup nester richness. Mean height and standard deviation of height have been shown to be predictors of snag distribution and forest successional stage (Falkowski et al. 2009; Martinuzzi et al. 2009). These vegetation height metrics may be correlated with the presence of cavity excavators, which are sensitive to snag availability and tree diameter. Further, standard deviation of height (analogous to field-measured foliage height diversity) and mean height have been shown to positively correlate with total bird richness (Flaspohler et al. 2010; Goetz et al. 2007; MacArthur and MacArthur 1961; Müller et al. 2009). Finally, percentage of returns in vegetation layers representing shrub density and canopy density were included, as they have been shown to correlate with species richness of under-story and mid/upper-story cup nesters, respectively, which are major components of bird diversity in forested habitat (Lesak et al. 2011; Vogeler et al. 2014).

We included 2 non-LiDAR explanatory variables in our models, canopy composition (CnpyCM) and a forest landscape metric (FrstCM). The canopy composition variable represents a generalized plant community, which as noted earlier has been shown to influence avian communities. A forest landscape variable was also included to address the fact that our study plots were placed in a variety of landscape settings, broadly categorized as forest types and primarily open, non-forest types (e.g., wet meadow, grassland, cropland), which we hypothesized may also influence avian species richness across our study area. The landscape variable was calculated as the percentage of 30-m map elements within a 5×5 (2.25 ha) window around each plot center classified as National Gap Analysis Program (GAP) forest land cover types (U.S. Geological Survey 2011).

Statistical modeling

We used generalized linear models in an information-theoretic framework to test for relationships between total and guild-specific species richness measures and 6 habitat explanatory variables: 4 LiDAR-derived vegetation structure metrics, aspen-conifer canopy composition, and the forest landscape variable. We compared all subsets of the 6-variable global model with the R statistical program (R Core Team 2016) using package glmulti (Calcagno and De Mazancourt 2010). The Akaike information criterion for small samples (AICc) was calculated for all candidate models and those within 2 ΔAICc of the top model were considered to be competitive (Burnham and Anderson 1998). We calculated Akaike weights, adjusted R^2 values, and significance values for all competitive models for comparison purposes. A model-averaging approach was used with each of the 5 model sets to estimate parameters, unconditional variances, parameter importance (sum of model Akaike weights), and 95% confidence intervals (Johnson and Omland 2004) for making inferences.

Predictive mapping

We mapped predicted species richness for total species, all cavity nesters, and open cup nesters across the full study area. Mapping was accomplished by applying the top model for total species, and the cavity nester and open cup nester guilds, to input rasters using the AsciiGridPredict function of R package yaImpute (Crookston and Finley 2008). The vegetation structure rasters, standard deviation of height (HeightSD variable) and canopy density (CanopyDN variable), were derived from the

Table 2. Mean and standard deviation of plot-level total and guild-specific species richness grouped by canopy composition category.

Nesting Guild	Aspen ($n = 33$)	Mixed ($n = 41$)	Conifer ($n = 56$)	Combined ($n = 130$)
Total species ($n = 70$)	11.79 (0.42) ***a***	10.83 (0.40) ***a***	8.27 (0.36) ***b***	9.97 (0.26)
Cavity nester ($n = 19$)	5.33 (0.34) ***a***	4.34 (0.29) ***b***	2.52 (0.17) ***c***	3.81 (0.18)
PCE ($n = 6$)	2.39 (0.21) ***a***	1.66 (0.19) ***b***	0.73 (0.11) ***c***	1.45 (0.11)
SCU ($n = 7$)	1.61 (0.19) ***a***	1.02 (0.19) ***b***	0.16 (0.07) ***c***	0.80 (0.10)
Open cup ($n = 50$)	6.33 (0.32) ***a***	6.27 (0.42) ***a***	5.61 (0.28) ***a***	6.00 (0.20)

Note. Nesting guilds PCE = primary cavity excavator and SCU = secondary cavity user. Letters (***a–c***) indicate different groupings based on Tukey multiple comparison of means ($p < .05$).

original 10-m LiDAR rasters, and generated by applying the ArcGIS focal statistics function to correspond with the 50-m radius field survey plots, output to a 30-m raster. The canopy composition (aspen, conifer, mixed) raster (CnpyCM variable) was generated with 67% accuracy using a random forests classification algorithm (Breiman 2001, Liaw and Wiener 2002) trained from the 130 classified field plots and applied to 8 predictor variables selected based on the Model Improvement Ratio in the R package rfUtilities package (Evans and Murphy 2016). Six variables were generated from the LiDAR points at 30-m resolution using FUSION software (McGaughey 2015): Rumple (the best predictor), which is the ratio of canopy surface area over the ground surface area and has been shown to be an important predictor of forest canopy structure (Parker et al. 2004; Kane et al. 2010; Hudak et al. 2016); maximum height; the percentage of returns above modal height; and the percentage of returns within vertical canopy strata of 0.15 m–1.37 m, 20 m–30 m, and >30 m. The other 2 predictor variables were percent topographic slope and a Normalized Difference Vegetation Index image generated from a (2011) NAIP image. Finally, a raster of percent GAP forest cover type (FrstCM variable) in a 5 × 5 (2.25 ha) window around each map cell was generated with ArcGIS using focal statistics and raster algebra functions.

Results

Bird species richness

Overall we detected 70 bird species (see Appendix 1) within the 50-m radius point counts ($n = 130$), including 54 in aspen ($n = 33$), 50 in conifer ($n = 56$), and 56 in mixed ($n = 41$). Of the 70 total species, 43 species were found in both aspen and mixed (Jaccard = 0.64), 43 in aspen and conifer (Jaccard = 0.70), 44 in mixed and conifer (Jaccard = 0.71), and 40 in aspen, mixed, and conifer (Appendix 1). Of the 70 species total, 50 were open cup nesters, 19 were cavity nesters, and 1 was a brood parasite (Appendix 1).

Comparing species richness across aspen, mixed aspen-conifer, and conifer canopy types, we found total species richness was significantly greater in aspen and mixed than conifer with similar patterns among the cavity nesting guilds but not among open cup nesters (Table 2). Cavity-nester richness was greater in aspen and mixed than conifer with primary cavity excavators and secondary cavity users greater in aspen than mixed and greater in mixed than conifer. Species richness of open cup nesters was not significantly different between aspen, mixed, and conifer (Table 2).

LiDAR and landscape metrics

Differences in LiDAR-derived measures between aspen and conifer were significant in height metrics but not vegetation density metrics (Table 3). For example, both mean height and standard deviation of height were significantly greater in conifer than aspen and mixed plots. In contrast, understory and canopy density were not significantly different. Mixed stands, although not significantly different from aspen, were nonetheless intermediate between aspen and conifer stands as expected. The GAP forest landscape metric was significantly different between aspen and conifer and mixed and conifer but not between mixed and aspen (Table 3).

Species richness models

The confidence set of models for total species richness included 11 models; canopy composition appeared in all models and was the most important variable influencing total species richness followed by the standard deviation of vegetation height (Table 4). Competing models were all significant ($p < .001$) and had adjusted R^2 values that ranged from 0.264 to 0.277 (Table 4). Total species richness was significantly negatively correlated with conifer canopy type and negatively correlated with mixed canopy type but with the 95% CI including zero (Table 5). The total species richness predictive map (Figure 2a) was created with the top model consisting of canopy composition, standard deviation of height, and forest composition variables (Table 4).

Among the 3 cavity nester groups (all, PCE, SCU), all competitive models included canopy composition and canopy density predictor variables (Table 5). Model

Table 3. Mean, standard error, and range of (4) LiDAR-derived vegetation structure variables and the forest composition variable, grouped by canopy composition.

	Aspen ($n = 33$)	Mixed ($n = 41$)	Conifer ($n = 56$)	Combined ($n = 130$)
HeightSD (m)	3.27 (0.19) ***a***	3.70 (0.20) ***a***	4.38 (0.19) ***b***	3.89 (0.12)
	1.66–5.63	1.50–7.22	1.49–8.09	1.49–8.09
HeightMN (m)	9.27 (0.39) ***a***	10.41 (0.48) ***a***	12.91 (0.56) ***b***	11.20 (0.33)
	6.02–13.71	6.31–18.24	5.63–21.16	5.63–21.16
UnstDN	1.62 (0.33) ***a***	2.21 (0.20) ***a***	2.27 (0.25) ***a***	2.08 (0.15)
	0.11–10.37	0.56–4.55	0.17–11.34	0.11–11.34
CnpyDN	53.66 (3.01) ***a***	58.10 (2.20) ***a***	60.60 (2.21) ***a***	58.05 (1.41)
	20.48–83.09	24.32–83.94	23.46–87.95	20.46–87.95
FrstCM	14.55 (2.82) ***a***	23.41 (3.55) ***a***	41.86 (4.34) ***b***	29.11 (2.50)
	0–76.0	0–88.0	0–100.0	0–100.0

Note. Height metrics in meters, density metrics are % of LiDAR returns, forest composition is % of forest landscape (see Table 1 for definitions). Letters (***a–b***) indicate different groupings based on Tukey multiple comparison of means ($p < .05$).

confidence sets for total cavity nester richness included 5 models, PCE richness included 4 models, and SCU richness included 6 models (Table 4). In all cavity-nester groups, species richness was significantly negatively correlated with conifer and mixed canopy types although mixed had less than half the effect size of conifer (Table 5). Similarly, canopy density parameter estimates were negative for all cavity-nester guilds, while understory density was moderately important (>0.6) and negative for secondary cavity users (Table 5). Competing models in all 3 cavity-nester guilds were significant ($p < .001$) and had R^2 values that ranged from 0.308 to 0.379 (Table 4). The all (PCE and SCU combined) cavity nester richness predictive map (Figure 2b) was created with the top model consisting of canopy composition and canopy density variables (Table 4).

The confidence set of models for open cup nesters included 6 models, with canopy composition again occurring in all models (Table 5). Species richness of open cup nester was significantly negatively correlated with conifer canopy composition and negatively correlated with mixed canopy composition, and the 95% confidence interval of this variable included zero (Table 5). Species richness of this guild was positively correlated with all

Table 4. Confidence sets of total and guild-specific species richness models from all-subsets model selection.

Species Guild	Model Set	AICc	ΔAICc	*W*	adjR^2	*p*
Total species	CnpyCM HeightSD FrstCM	618.34	0	0.16	0.277	**
	CnpyCM HeightSD	618.62	0.28	0.14	0.269	**
	CnpyCM HeightMN	619.15	0.81	0.11	0.266	**
	CnpyCM FrstCM	619.43	1.09	0.09	0.264	**
	CnpyCM HeightSD UnstDN FrstCM	619.48	1.15	0.09	0.277	**
	CnpyCM HeightMN UnstDN	619.65	1.32	0.08	0.269	**
All cavity nesters	CnpyCM CnpyDN	504.47	0	0.31	0.355	**
	CnpyCM CnpyDN FrstCM	505.27	0.80	0.21	0.357	**
	CnpyCM HeightMN CnpyDN	505.29	0.82	0.21	0.357	**
	CnpyCM UnstDN CnpyDN	506.06	1.58	0.14	0.353	**
	CnpyCM HeightSD CnpyDN	506.33	1.86	0.12	0.353	**
Primary cavity excavator	CnpyCM HeightMN CnpyDN	383.14	0	0.38	0.322	**
	CnpyCM HeightSD CnpyDN	383.75	0.62	0.28	0.318	**
	CnpyCM CnpyDN	384.49	1.35	0.19	0.308	**
	CnpyCM HeightMN HeightSD CnpyDN	385.11	1.97	0.14	0.318	**
Secondary cavity user	CnpyCM UnstDN CnpyDN	343.26	0	0.28	0.379	**
	CnpyCM CnpyDN	344.01	0.75	0.19	0.370	**
	CnpyCM UnstDN CnpyDN FrstCM	344.45	1.19	0.15	0.379	**
	CnpyCM CnpyDN FrstCM	344.63	1.37	0.14	0.372	**
	CnpyCM HeightSD UnstDN CnpyDN	344.90	1.64	0.12	0.377	**
	CnpyCM HeightMN UnstDN CnpyDN	345.11	1.84	0.11	0.376	**
Open cup	CnpyCM HeightSD CnpyDN	578.36	0	0.28	0.085	*
	CnpyCM HeightSD UnstDN CnpyDN	578.64	0.28	0.24	0.091	*
	CnpyCM HeightMN UnstDN	580.02	1.66	0.12	0.073	*
	CnpyCM HeightSD UnstDN CnpyDN FrstCM	580.04	1.68	0.12	0.090	*
	CnpyCM HeightSD CnpyDN FrstCM	580.11	1.74	0.12	0.081	*
	CnpyCM HeightMN UnstDN CnpyDN	580.21	1.85	0.11	0.080	*

Note. Models within 2 AICc of top model are considered competitive (only top 6 of 11 competitive models shown for Total species). Akaike weights and adjusted coefficient of determination indicated by *W* and adjR^2, respectively.
*$p < .01$. **$p < .001$.

Table 5. Model-averaged parameter estimates for total and guild-specific species richness models within 2 AICc of top model.

Nesting Guild	Measure	Intercept	Conifer	Mixed	HeightMN	HeightSD	UnstDN	CnpyDN	ForCM
Total species	Estimate	**10.569**	**− 4.078**	− 1.168	0.035	0.205	0.033	0.001	0.006
	95% Lower	**8.872**	**− 5.327**	− 2.369	− 0.079	− 0.207	− 0.097	− 0.006	− 0.011
	95% Upper	**12.267**	**− 2.830**	0.033	0.150	0.617	0.162	0.008	0.024
	Variance	0.736	0.398	0.368	0.003	0.043	0.004	0.000	0.000
	Importance	1.000	1.000	1.000	0.323	0.652	0.235	0.132	0.468
Total cavity	Estimate	**6.577**	**− 2.722**	**− 0.902**	0.012	0.008	− 0.009	**− 0.026**	0.001
	95% Lower	**5.385**	**− 3.493**	**− 1.671**	− 0.035	− 0.036	− 0.054	**− 0.046**	− 0.004
	95% Upper	**7.769**	**− 1.951**	**− 0.132**	0.059	0.052	0.035	**− 0.006**	0.007
	Variance	0.363	0.152	0.151	0.001	0.000	0.001	0.000	0.000
	Importance	1.000	1.000	1.000	0.209	0.124	0.142	1.000	0.211
PCE	Estimate	**2.826**	**− 1.702**	**− 0.717**	0.028	0.040	*	**− 0.015**	*
	95% Lower	**1.995**	**− 2.197**	**− 1.199**	− 0.045	− 0.092	*	**− 0.030**	*
	95% Upper	**3.656**	**− 1.207**	**− 0.234**	0.101	0.172	*	**− 0.001**	*
	Variance	0.176	0.063	0.059	0.001	0.004	*	0.000	*
	Importance	1.000	1.000	1.000	0.524	0.423	*	1.000	*
SCU	Estimate	**2.903**	**− 1.273**	**− 0.458**	− 0.002	− 0.005	− 0.051	**− 0.022**	0.001
	95% Lower	**2.243**	**− 1.699**	**− 0.877**	− 0.012	− 0.032	− 0.154	**− 0.033**	− 0.003
	95% Upper	**3.562**	**− 0.848**	**− 0.039**	0.008	0.021	0.052	**− 0.012**	0.005
	Variance	0.111	0.046	0.045	0.000	0.000	0.003	0.000	0.000
	Importance	1.000	1.000	1.000	0.111	0.123	0.667	1.000	0.295
Open cup	Estimate	**3.477**	**− 1.432**	− 0.414	0.035	0.241	0.110	0.029	0.002
	95% Lower	**1.577**	**− 2.485**	− 1.443	− 0.080	− 0.121	− 0.141	− 0.003	− 0.005
	95% Upper	**5.377**	**− 0.380**	0.616	0.151	0.602	0.361	0.060	0.008
	Variance	0.921	0.283	0.271	0.003	0.033	0.016	0.000	0.000
	Importance	1.000	1.000	1.000	0.235	0.765	0.601	0.877	0.007

Note. 'Importance' is sum of weights of models including variable. 'Conifer' and 'Mixed' estimates are relative to the Aspen composition type. Bolded values indicate 95% confidence interval does not span zero.
*Variable does not appear in top models.

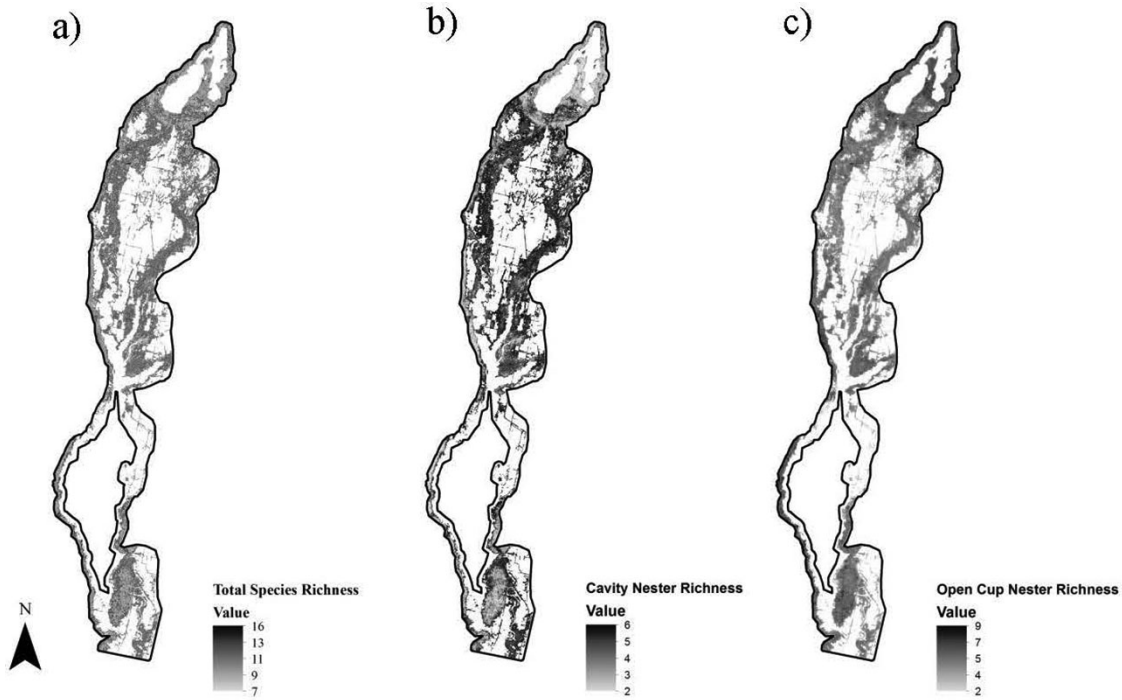

Figure 2. Predictive maps of species richness for (a) total species, (b) all cavity nesters, and (c) open cup nesters. Maps were generated with the AsciiGridPredict function of R package yaImpute by applying the top model for each richness measure to input rasters of vegetation structure, canopy composition, and GAP forest type. Black outline on maps depicts extent of 2012 LiDAR acquisition. Non-forest map cells (i.e., lakes, reservoirs, agricultural fields, and a small town) within the LiDAR footprint are indicated by a white mask where no LiDAR returns occurred above 1.37 m.

LiDAR metrics, with moderate importance for height SD and vegetation density metrics (0.60–0.87); but the effect sizes were relatively small and all 95% confidence intervals included zero (Table 5). All models were significant ($p < .05$) with R^2 values that ranged from 0.073 to 0.091 (Table 4). The open cup nester richness predictive map (Figure 2c) was created with the top model consisting of canopy composition, standard deviation of height, and canopy density variables (Table 4).

Discussion

Our objective was to evaluate the relative importance of vegetation composition compared to vegetation structural attributes for assessing bird richness at local scales (~ 1 ha). We found that total bird species richness was significantly associated with canopy composition, with species richness in aspen greater than in conifer, and cavity-nester richness in aspen greater than conifer and mixed aspen-conifer. Further, canopy composition had a stronger influence on species richness than the structural metrics included in this study. The total species richness pattern observed here concurs with several prior studies showing greater local bird richness in aspen than conifer (Griffis-Kyle and Beier 2003; Richardson and Heath 2004; Turchi et al. 1995) and studies that found no increase in bird richness in mixed versus aspen alone (Finch and Reynolds 1987; Hollenbeck and Ripple 2007; Rumble et al. 2001). Studies investigating avian richness patterns in North American grasslands and deciduous forests in Australian woodlands have also noted that vegetation composition is more important than structure at certain spatial scales (Lee and Rotenberry 2005; Mac Nally 1990; Rotenberry and Wiens 1980), while other studies (Seavy and Alexander 2011) have found that interactive effects between vegetation structure and composition are likely important. Among structural attributes we only found a significant association between canopy density and cavity nester richness.

In contrast to our study, recent studies using LiDAR-derived vegetation structure metrics have generally found a stronger association between total bird richness and vegetation structure (e.g., Goetz et al. 2007, Clawges et al. 2008, Flaspohler et al. 2010). These studies have focused on relationships between bird species richness and measures of vegetation height heterogeneity as predicted by MacArthur and MacArthur (1961). For example, total species richness has been associated with standard deviation of height (Goetz et al. 2007), foliage height diversity indices emphasizing understory (Clawges et al. 2008), understory density alone (Vogeler et al. 2014), canopy and mid-story height and density (Lesak et al. 2011), and canopy top and foliage height diversity (Weisberg et al. 2014). Our study did not have a single LiDAR-derived predictor variable that consistently appeared in all models. Variability in the relative importance of different predictor variables has been noted by Vogeler et al. (2014), which suggests different factors may be driving bird richness patterns across sites and study areas including those not easily measured by LiDAR or other remote sensing methods.

However, in examining guild species richness we found a negative association between LiDAR-derived canopy density and cavity nester richness, which concurs with several prior studies. For example, Vogeler et al. (2014) found a weak negative correlation between canopy density and the cavity nester guild in mixed-conifer forests, and Lesak et al. (2011) found a negative correlation between cavity nesters and densities of mid- and understory canopy layers in deciduous forest. Some studies suggest that the abundance of dead and decadent aspens varies with age and stand condition, which is reflected in the canopy density (Hollenbeck and Ripple 2008; Lee 1998). Therefore, the positive response of cavity excavators to snag availability provides a possible mechanism for the association between canopy density and cavity nester richness seen here.

Open cup nesters represented the majority of species in our study but we found no significant associations between species richness and vegetation structure metrics. A finer guild division of open cup nesters based on canopy stratification as used in other studies (Lesak et al. 2011) may have resulted in the detection of stronger associations. In addition, understory density appears often in guild-level analyses (e.g., Lesak et al. 2011, Vogeler et al. 2014), and it is possible that the understory was either not sufficiently variable across our sites to reveal these associations or that our chosen understory height was the height that is not ecologically relevant for this specific bird community.

In a recent and more directly comparable study of the roles of vegetation structure and composition using similar LiDAR-derived metrics, Müller et al. (2010) found structure to be a significantly stronger predictor of bird richness than both forb and tree-shrub composition. A key difference between our study and Müller et al. (2010) was our more diverse cavity nester community with 19 (vs. 7) total cavity nesters and 6 (vs. 1) primary cavity excavators. In our study, the cavity nester guild and primary cavity excavator richness were significantly correlated with canopy type (aspen greater than mixed greater than conifer). The strong association between aspen and cavity nesters, and the robust cavity nesting community in our study, may be overwhelming or confounding the species richness-vegetation structure relationships often present in other studies.

Differences among studies favoring vegetation composition or structure may also be due to the spatial scale or the diversity of the habitats being sampled (Mac Nally 1990; Rotenberry 1985). For example, it has been suggested that vegetation structure will emerge more importantly at coarser scales (e.g. across habitats) and vegetation composition at finer scales (Lee and Rotenberry, 2005). Müller et al. (2010) includes a more diverse range of elevational and habitat types than our study, which may thus account for some of the differences seen. It has been suggested that when vegetation composition emerges as an important factor in bird-habitat associations, it is likely due to food preferences or foraging strategies (Lee and Rotenberry 2005; Rotenberry 1985). Here, it appears that the aspen cavity-nester association is largely mediated by a preference for aspen as a nesting substrate by primary cavity excavators.

Conclusion

In sum, our study provides additional evidence that aspen enhances avian diversity in mixed forest settings and can play an important role in avian diversity patterns. In addition, our findings add to the ongoing discussion of the relative roles of vegetation structure and composition in avian diversity patterns and their underlying mechanisms. The ability of LiDAR to assist in improving understanding of ecological processes via the incorporation of structrural information will continue to be important in studies of wildlife-habitat relationships, and the ability to generate predictive maps of such relationships will aid conservation and management of wildlife as such models improve.

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Appendix

Listed below are bird species detected within a 50-m radius of plot centers in 2013 ($n = 92$) and 2014 ($n = 38$), in alphabetical order grouped by nesting guild. Aspen, Mixed, and Conifer columns indicate species was detected in that plot type. Nesting guilds are denoted as: 1—primary cavity excavator, 2—secondary cavity user, 3—weak cavity excavator, 4—open cup, 5—brood parasite.

Common Name	Scientific Name	Guild	Aspen	Mixed	Conifer
Downy Woodpecker	*Picoides pubescens*	1	x	x	x
Hairy Woodpecker	*Picoides villosus*	1	x	x	x
Northern Flicker	*Colaptes auratus*	1	x	x	x
Pileated Woodpecker	*Dryocopus pileatus*	1	x	x	x
Red-naped Sapsucker	*Sphyrapicus nuchalis*	1	x	x	x
Williamson's Sapsucker	*Sphyrapicus thyroideus*	1	x	x	x
American Kestrel	*Falco sparverius*	2	x	x	x
Bufflehead	*Bucephala albeola*	2	x		
European Starling	*Sturnus vulgaris*	2	x	x	x
House Wren	*Troglodytes aedon*	2	x	x	x
Mountain Bluebird	*Sialia currucoides*	2		x	
Tree Swallow	*Tachycineta bicolor*	2	x	x	x
Wood Duck	*Aix sponsa*	2	x		
Black-capped Chickadee	*Poecile atricapillus*	3	x	x	x
Chestnut-backed Chickadee	*Poecile rufescens*	3		x	
Mountain Chickadee	*Poecile gambeli*	3	x	x	x
Pygmy Nuthatch	*Sitta pygmaea*	3	x	x	x
Red-breasted Nuthatch	*Sitta Canadensis*	3	x	x	x
White-breasted Nuthatch	*Sitta carolinensis*	3		x	x
American Crow	*Corvus brachyrhynchos*	4	x	x	x

(*Continued on next page*)

Continued

Common Name	Scientific Name	Guild	Aspen	Mixed	Conifer
American Goldfinch	*Spinus tristis*	4	x	x	x
American Robin	*Turdus migratorius*	4	x	x	x
Black-billed Magpie	*Pica hudsonia*	4	x	x	
Black-chinned Hummingbird	*Archilochus alexandri*	4			x
Black-headed Grosbeak	*Pheucticus melanocephalus*	4	x	x	x
Brewer's Blackbird	*Euphagus cyanocephalus*	4	x		
Brown Creeper	*Certhia Americana*	4	x	x	x
California Quail	*Callipepla californica*	4		x	
Calliope Hummingbird	*Selasphorus calliope*	4	x		
Cassin's Finch	*Haemorhous cassinii*	4	x	x	x
Cassin's Vireo	*Vireo cassinii*	4	x	x	x
Cedar Waxwing	*Bombycilla cedrorum*	4	x	x	x
Chipping Sparrow	*Spizella passerina*	4	x	x	x
Clark's Nutcracker	*Nucifraga columbiana*	4		x	
Common Raven	*Corvus corax*	4		x	x
Common Yellowthroat	*Geothlypis trichas*	4			x
Dark-eyed Junco	*Junco hyemalis*	4	x	x	x
Dusky Flycatcher	*Empidonax oberholseri*	4	x	x	x
Evening Grosbeak	*Coccothraustes vespertinus*	4	x	x	
Golden-crowned Kinglet	*Regulus satrapa*	4		x	x
Gray Jay	*Perisoreus canadensis*	4		x	
Hammond's Flycatcher	*Empidonax hammondii*	4	x	x	x
Lazuli Bunting	*Passerina amoena*	4	x	x	x
Least Flycatcher	*Empidonax minimus*	4	x		x
Lincoln's Sparrow	*Melospiza lincolnii*	4	x	x	
MacGillivray's Warbler	*Geothlypis tolmiei*	4	x	x	x
Mourning Dove	*Zenaida macroura*	4		x	
Orange-crowned Warbler	*Oreothlypis celata*	4		x	
Osprey	*Pandion haliaetus*	4			x
Pacific Wren	*Troglodytes pacificus*	4		x	x
Pine Siskin	*Spinus pinus*	4	x	x	x
Red Crossbill	*Loxia curvirostra*	4	x		x
Red-winged Blackbird	*Agelaius phoeniceus*	4	x		
Ruby-crowned Kinglet	*Regulus calendula*	4	x	x	x
Ruffed Grouse	*Bonasa umbellus*	4	x	x	x
Song Sparrow	*Melospiza melodia*	4	x	x	x
Spotted Towhee	*Pipilo maculatus*	4	x		x
Steller's Jay	*Cyanocitta stelleri*	4		x	
Swainson's Thrush	*Catharus ustulatus*	4	x	x	x
Townsend's Warbler	*Setophaga townsendi*	4	x	x	x
Vesper Sparrow	*Pooecetes gramineus*	4		x	
Warbling Vireo	*Vireo gilvus*	4	x	x	x
Western Meadowlark	*Sturnella neglecta*	4	x		
Western Tanager	*Piranga ludoviciana*	4	x	x	x
Western Wood-Pewee	*Contopus sordidulus*	4	x	x	x
White-crowned Sparrow	*Zonotrichia leucophrys*	4	x		
Willow Flycatcher	*Empidonax traillii*	4	x		
Yellow Warbler	*Setophaga petechia*	4	x	x	x
Yellow-rumped Warbler	*Setophaga coronata*	4	x	x	x
Brown-headed Cowbird	*Molothrus ater*	5	x	x	x