The Influence of Canopy Composition and Vegetation Structure on Avian Richness and Red-naped Sapsucker Occupancy Across an Aspen-Conifer Forest Gradient

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Charles E. Swift

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Authorization to Submit Thesis

This thesis of Charles E. Swift, submitted for the degree of Master of Science with a Major in Environmental Science and titled "The Influence of Canopy Composition and Vegetation Structure on Avian Richness and Red-naped Sapsucker Occupancy Across an Aspen-Conifer Forest Gradient," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Vegetation structure and composition are central to understanding avian-habitat relationships. Vegetation structure can be challenging to measure; however, 3-D LiDAR remote sensing provides a robust solution. My study utilized LiDAR-derived vegetation metrics to examine the relative influence of vegetation structure and canopy composition on 1) avian richness patterns and 2) occupancy of a cavity excavator, the Red-naped Sapsucker (*Sphyrapicus nuchalis*), across an aspen-conifer forest gradient in west-central Idaho. Quaking aspen (*Populus tremuloides*) enhances forest biodiversity but has been declining across western North America, often due to conifer encroachment. My study found evidence that 1) aspen has greater avian richness than conifer and mixed aspen-conifer, especially among cavity nesters and 2) conifer encroachment in aspen may be one mechanism that reduces occupancy of Red-naped Sapsuckers. Understanding vegetation-wildlife associations increases our ability to respond appropriately to habitat changes, such as declining aspen, and enhances our knowledge of the influence of vegetation on wildlife.

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Dedication

This work is dedicated to my wife Deb and daughter Iris for their love, support, and patience and for the many adventures we have had and are yet to come. And to my parents, David and Suzanne Swift, for their love and support, and for all the family camping trips and hikes that set me down this path.

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Thesis Introduction

The importance of vegetation in avian-habitat relationships has been recognized as a central concept in ornithology (Rotenberry 1985, Block and Brennan 1993). Vegetation characteristics influence avian occupancy and diversity patterns and vegetation can be measured in a variety of ways for examining these associations. Vegetation manipulation is a primary tool of wildlife management and this fact highlights the importance of understanding the role of vegetation in wildlife-habitat relationships.

Measureable characteristics of vegetation can be broadly categorized as pertaining to 1) plant species composition and 2) vegetation structural characteristics such as the vertical distribution of vegetation (e.g. Rotenberry 1985). From this general understanding avian ecologists have developed a long term interest in the relative influence of vegetation structure and composition on avian species richness patterns. For example, MacArthur and MacArthur (1961) found that avian species richness was more highly correlated with vegetation structure than vegetation composition. Subsequent research as sought to clarify the often complex relationships between vegetation structure, vegetation composition, and avian species diversity. Vegetation structure can also be an important attribute in understanding single-species habitat relationships, especially for species important for ecological integrity and/or of conservation concern.

The complexity of vegetation structure can be challenging to measure, however, a maturing remote sensing technology, LiDAR (Light Detection and Ranging) has provided a robust solution to this problem. LiDAR is a 3-D “active” remote sensing technology capable of measuring vegetation at high resolution over large spatial extents. LiDAR has similar advantages to other forms of remote sensing in terms of its abilities to measure large, often remote areas, and more economically than field collection of these environmental attributes (Müller et al. 2010). LiDAR-derived vegetation and terrain metrics have been combined with field-based data to examine and model a wide range of animal-habitat relationships (e.g. Vierling et al. 2008) and is likely to become more widely available in the future.

For the purposes of my thesis, I used LiDAR-derived vegetation metrics to examine the relative influence of vegetation structure and canopy composition on 1) avian richness and 2) occupancy of a cavity excavator, the Red-naped Sapsucker (*Sphyrapicus nuchalis*), across an aspen-conifer forest gradient in west-central Idaho. The Red-naped Sapsucker is an ecologically important primary cavity excavator that provides sap wells and cavities for food and nesting to a variety of other wildlife species (Daily et al. 1993, Martin and Eadie 1999). Red-naped Sapsuckers use both conifer-dominated and aspen-dominated habitat for breeding (Walters et al. 2014) making them an ideal subject for study in this aspen-conifer setting.

The relative influence of vegetation composition and structure on avian species richness and occupancy might be particularly important in forests undergoing conifer encroachment. For example, quaking aspen (*Populus tremuloides*) is recognized for enhancing forest biodiversity but has been declining across much of western North America (DeByle 1985, Bartos 2001). Changes to disturbance patterns, such as fire suppression practices, can result in accelerated conifer invasion and reduced aspen regeneration, potentially affecting the persistence of aspen in some forested landscapes (Strand et al. 2009a). Due to aspen’s biodiversity benefits to overall forest biodiversity, the effect of declining aspen may be particularly evident where aspen occurs within a conifer matrix and where aspen often represents a relatively small proportion of forest cover (Hollenbeck and Ripple 2007).

My study is novel in several respects. First, few studies to date have simultaneously investigated the relative influence of vegetation structure and composition on avian species richness patterns using LiDAR remote-sensing (Müller et al. 2010). Similarly, only 2 prior studies (Vierling et al. 2013, Holbrook et al. 2015) have examined Red-naped Sapsucker occupancy using LiDAR-derived metrics, both in conifer-dominated forest. Finally, few studies to date have investigated avian diversity patterns in aspen-conifer forest using LiDAR-derived vegetation metrics (Clawges et al. 2008).

Considering the potential effects of large-scale habitat changes on biodiversity, it is important to gain a greater understanding of wildlife-vegetation associations. For example, understanding vegetation-wildlife associations will increase our ability to respond appropriately to habitat changes, such as declining aspen. Understanding the varying influence of both vegetation structure and composition on wildlife is important in ensuring that habitat management practices do not have unintended consequences. Finally, examining the relative influence of vegetation composition and vegetation structure on avian diversity patterns enhances our understanding of the role of vegetation in these relationships, a central concept in avian science.

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Chapter 1: Relationships among Vegetation Structure, Canopy Composition, and Avian Richness Patterns across an Aspen-Conifer Forest Gradient

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Abstract

Ecologists have had a long-term interest in understanding the relative influence of vegetation composition and vegetation structure on avian diversity patterns. Vegetation structure can be challenging to measure; however, 3-D LiDAR remote sensing provides a robust solution to this problem. We used LiDAR-derived vegetation structure metrics and avian field data to investigate the relative influence of vegetation structure and canopy composition on avian richness patterns across an aspen-conifer forest gradient. Aspen enhances forest biodiversity but has been declining across western North America, often due to conifer encroachment. We conducted bird surveys between 2013 and 2014. We found aspen to have higher avian richness than conifer and mixed aspen-conifer, especially among cavity nesters. In contrast to a number of prior studies, we found weak relationships between vegetation structure and avian richness, although canopy density was negatively associated with cavity nester richness. Primary cavity excavators, key parts of complex cavity-user webs, are often associated with aspen. Our data provide evidence that vegetation composition has a greater influence on avian richness than vegetation structure in this context, and that cavity nester richness plays a large role in the diversity patterns observed. This study further highlights the potential effects of aspen declines on forest biodiversity.

Introduction

Ecologists have long held an interest 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; Müller et al., 2010; Rotenberry, 1985). Differences among previous studies have been postulated to be related to scale effects or methodology (Willson 1974, Rotenberry 1985, Müller et al. 2010) 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 challenging to quantify. Recent studies investigating the role of vegetation structure in wildlife-habitat relationships have largely relied on the strengths of LiDAR, a maturing laser-based remote sensing technology. LiDAR is an active 3-D technology with advantages over passive 2-D remote sensing in its ability to measure terrain and vegetation heights accurately and at high resolution compared with commonly available remote sensing products. 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 drawback to LiDAR is the initial cost outlay and availability (Vierling et al. 2008), however LiDAR has been shown to be more cost-effective than field data collection (Müller and Brandl 2009) and has the added benefit of quantifying ecologically meaningful structural variables that are impossible to measure using other methods. LiDAR has been used to obtain a variety of terrain and vegetation structure metrics resulting in the development of robust wildlife-habitat models for species richness, species distribution, and habitat quality (Hinsley et al. 2006, Goetz et al. 2007, Vogeler et al. 2014, Ackers et al. 2015). However, few studies to date have simultaneously investigated the relative roles of vegetation structure and composition on avian species richness patterns using LiDAR remote-sensing (Müller et al. 2010).

The relative influence of vegetation composition and structure on avian communities might be particularly important in forests undergoing conifer encroachment. For example, quaking aspen (*Populus tremuloides*) is widely recognized as an important component of western forests with multiple benefits including enhancement of local and regional biodiversity (DeByle 1985, Bartos 2001). Aspen has been shown to support high avian species richness and abundance, including cavity excavators and their attendant cavity user communities (Rumble et al. 2001, Griffis-Kyle and Beier 2003, Hollenbeck and Ripple 2007, Drever and Martin 2010). Unfortunately, however, aspen has also undergone sharp declines in western North America, with great efforts made to understand the causes. Aspen declines are thought to be caused largely by changes in disturbance regimes and resultant conifer encroachment, but also from herbivory, drought, and other factors (Bartos 2001, Kaye et al. 2005, Worrall et al. 2008).

Our major objective was therefore 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. 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. 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 particular focus on the cavity and open cup nesting guilds. We hypothesized that these guilds may be sensitive to different aspects of vegetation composition and structure across the aspen-conifer habitat gradient occurring in our study area. Multiple studies in mixed forests with both conifer and aspen components have shown (1) a clear preference among cavity nesters for aspen as a nesting substrate, and (2) a positive correlation between cavity excavators and overall bird richness (Li and Martin 1991, Martin and Eadie 1999, Drever and Martin 2010). Further, other work has shown that avian diversity does not increase in conifer-encroached aspen stands and ultimately decreases as conifers increase (Rumble et al. 2001, Hollenbeck and Ripple 2007). Although many of these studies have examined the relationship among vegetation structure, composition, and bird communities using field collected data, the use of LiDAR allows for the inclusion of vertical structure variables that are often difficult, if not impossible, to measure over broad extents (Vierling et al. 2008). We thus hypothesized that in our study area bird species richness would be higher in aspen than in conifer due to cavity nester preference for aspen. Further, we speculated that the strength of the aspen-cavity nester association observed elsewhere would result in canopy composition having a greater influence on avian richness versus vegetation structure in the aspen-conifer forests studied here.

Methods

Study Area

The study was conducted in the Long Valley in the west-central mountains of Idaho (Figure 1.1) approximately 140 km north of Boise metropolitan area. Long Valley is a broad north-south montane valley varying from 8 to 11km wide and extending for 58 km; the northern edge 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 1530 m at McCall to 1450 m at Cascade. Valley terrain is gently to moderately sloped except steeply sloped along a portion of the North Fork of the Payette River and along glacial moraines south of McCall (Rasmussen 1981). The surrounding mountains rise to elevations between 2000 and 2500 m.

Weather in the Long Valley is characterized by warm, dry summers and moderate, wet winters with the bulk of precipitation at valley elevations coming in the form of snow (Abramovich et al. 1998, U.S. Department of the Interior 2002). The mean January low temperature at McCall is -11 degrees C (22 degrees F) and the mean July high temperature is 26.5 degrees C (80 degrees F). The mean annual precipitation at McCall is 56 cm with the majority coming as snow (150 cm) between November and March.

Vegetation cover types in the study area include upland and riparian forest, wet meadows and grasslands, and sagebrush steppe. Wetlands are present within the margins of Cascade Lake as well as isolated locations throughout the valley. Conifer forests are mostly mixed second-growth and comprised of primarily ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and lodgepole pine (*Pinus contorta*)

(Van Daele and Van Daele 1982, Tinkham et al. 2012). Stands of quaking aspen up to ~2 ha in area 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 in Long Valley is a broad mix of public and private. Public lands are owned and managed by the State of Idaho as well as federal entities in a patchwork with private lands. Extensive conifer-forests from valley edges to surrounding mountains are owned and managed primarily by the U.S. Forest Service but also by private timber/land management companies. Land use within the valley includes protected lands, low to moderate intensity grazing, resource extraction, and mixed recreational uses with a small year round population augmented by tourists and second-home owners.

Field Plots

We located candidate aspen and mixed aspen-conifer stands within the LiDAR acquisition area using aerial imagery, ground surveys, and locally available information. Conifer stands were located near selected aspen and mixed aspen-conifer stands. Stands spanned the full extent of the study area in a variety of physiographic settings (Figure 1.1) 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 (ESRI 2013). Within each survey plot the proportion of the canopy comprised of aspen and conifer was estimated to the nearest 10% using moderate resolution imagery from the USDA National Agricultural Inventory Program (USDA 2011) overlaid with a 20 m grid. Survey plots were classified as aspen-dominated (hereafter aspen), mixed aspen-conifer, and conifer-dominated (hereafter conifer) as follows:

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

Multiple photographs taken at each plot center were used to inform the classification.

Avian Point Counts

To survey for bird species richness we conducted two point counts at each survey plot across two field seasons; 92 plots were surveyed in 2013 and 38 plots were surveyed in 2014 for a total of 130 plots. We sampled for presence of all cavity and open cup nesters, and followed Drever (2008) by using audio broadcasts for select woodpecker species to increase woodpecker detection via callback. A standard five minute point count for all breeding species was followed by audio broadcasts for each of six commonly occurring woodpecker species in the study area: Pileated Woodpecker (*Dryocopus pileatus*), Northern Flicker (*Colaptes auratus*), Hairy Woodpecker (*Picoides villosus*), Downy Woodpecker (*Dyrobates 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, number of individuals, (closest) distance of each individual to the observer, temperature, wind, and cloud cover. 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 two 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 one of three 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 aspen-conifer 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 two groups. We compared species richness for each nesting guild and total richness across aspen, mixed, and conifer plots using Tukey multiple comparison of means with a significance level of $p < 0.05$ (Table 1.2).

LiDAR Remote Sensing Data

We used discrete multiple-return airborne LiDAR data to generate vegetation structure metrics for our study plots (Table 1.1). The LiDAR data were collected over three days between May 7 and May 31, 2012 by Aerometric Inc. using fixed-wing aircraft as part of the United States Federal Emergency Management Agency's (FEMA) Risk MAP program and provided to us by the Idaho Department of Water Resources. The LiDAR extent spanned approximately 35,750 ha (Figure 1.1) 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 RMSE. LiDAR data were delivered as 225 ha tiled output in raw and classified LAS point data formats 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^2 resolution raster grid. Plot-level metrics were calculated using Focal Statistics with a 50 m radius in ArcGIS Spatial Analyst (ESRI 2013) at each of the 130 plot centers. The LiDAR acquisition differed temporally from the bird surveys by 1-2 years, however several studies (Vierling et al. 2014, Hill and Hinsley 2015) 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 Tukey multiple comparison of means and used a significance level of $p < 0.05$ (Table 1.3).

Statistical Modeling

We selected a priori 4 LiDAR-derived metrics of vegetation structure (Table 1.1) that 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 important predictors of snag distribution and forest successional stages (Falkowski et al. 2009, Martinuzzi et al. 2009) which may be correlated with cavity-nester communities due to their sensitivity 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 (MacArthur and MacArthur 1961, Goetz et al. 2007, Müller et al. 2009, Flaspohler et al. 2010). Finally, 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 two non-LiDAR explanatory variables in our models, canopy composition (aspen, mixed aspen-conifer, conifer) and a forest landscape metric. The canopy composition type represents a generalized plant community as well as specific attributes of canopy tree species that may drive habitat relationships. The forest landscape variable was included to address the fact that our study sites were placed in a variety of landscape settings (e.g. forest edge, forest interior, meadow, urban/residential, etc.) which we hypothesized may influence richness across our study area. The landscape variable was calculated as the percentage of 30 m map elements within a 5x5 (2.25 ha) window around each plot center classified as GAP forest land cover types (U.S. Geological Survey 2011).

We used general linear models in R (R Development Core Team 2013) with package glmulti (Calcagno and Mazancourt 2010) to compare all subsets of the 6-variable universal model in an information-theoretic model selection framework (Burnham and Anderson 1998). 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 used a model-averaging approach to estimate parameters, unconditional variances, and 95% confidence intervals (Johnson and Omland 2004) for making inferences. We performed regression diagnostics on the universal models and calculated adjusted R^2 and significance values for all competitive models for comparison purposes.

Results

Bird Species Richness

Overall we detected 70 bird species (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 aspen-conifer (*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 one 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 aspen-conifer than conifer with similar patterns among the cavity nesting guilds but not among open cup nesters (Table 1.2). 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 . The cavity-nester guild includes weak cavity excavators which were not considered in the PCE-only or SCU-only groups. Species richness of open cup nesters was not significantly different between aspen, mixed, and conifer in ANOVAS although model-averaged parameter estimates (Table 1.5) differed slightly in showing a significant lower species richness in conifer compared to aspen.

LiDAR and Landscape Metrics

Differences in LiDAR-derived measures between aspen and conifer were significant in height metrics but not vegetation density metrics (Table 1.3). For example, both mean height and standard deviation of height were significantly greater in conifer than aspen and mixed aspen-conifer plots. In contrast, understory and canopy density were not significantly different. Mixed aspen-conifer 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 1.3).

Species Richness Models

The total species richness model confidence set included 11 models with canopy composition predictor variable occurring in all models (Table 4). Standard deviation of height occurred in 7 models but was not significant. Total species richness was significantly negatively correlated with conifer canopy type (Table 1.5). Total richness was also negatively correlated with mixed aspen-conifer however the 95% CI included zero (Table 1.5). Competing models were significant ($p < 0.001$) and had adjusted R^2 values that ranged from

0.264 to 0.277 (Table 4). The total species richness predictive map (Appendix 2) was created with the second-highest model consisting of canopy composition and standard deviation of height variables.

Among the cavity richness guilds, all competing models included canopy composition and canopy density predictor variables (Table 4). Model 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 guilds species richness was significantly negatively correlated with conifer and mixed aspen-conifer canopy types although mixed aspen-conifer had less than half the effect size of conifer (Table 1.5). Competing models in all 3 cavity-nester groups were significant ($p < 0.001$) and had R^2 values that ranged from 0.308 to 0.379 (Table 4). The cavity nester richness predictive map (Appendix 2) was created with the top model consisting of canopy composition and canopy density variables.

The open cup nester guild model confidence set included 6 models with canopy composition occurring in all models (Table 4). Cup nester richness was significantly negatively correlated with conifer canopy composition (Table 1.5). Open cup richness was also negatively correlated with mixed aspen-conifer canopy but the effects were less than half of conifer and 95% confidence interval included zero (Table 1.5). Cup nester richness was positively correlated with all LiDAR metrics but the effect sizes were relatively small and all 95% confidence intervals included zero (Table 1.5). All models were significant ($p < 0.05$) with R^2 values that ranged from 0.073 to 0.091 (Table 4). The open cup nester richness predictive map (Appendix 2) was created with the top model consisting of canopy composition, standard deviation of height, and canopy density variables.

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 (Turchi et al. 1995, Griffis-Kyle and Beier 2003) and studies that found no increase in bird richness in mixed aspen-conifer versus aspen alone (Finch and Reynolds 1987, Rumble et al. 2001, Hollenbeck and Ripple 2007). 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 (Rotenberry and Wiens 1980, Mac Nally 1990, Lee and Rotenberry 2005). 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 under-story canopy layers in deciduous forest. Evidence suggests that within aspen dominated stands the abundance of dead and decadent aspens varies with age and stand condition which is reflected in the canopy density (Lee 1998, Hollenbeck and Ripple 2008). 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 not sufficiently variable across our sites to reveal these associations.

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 (versus 7) total cavity nesters and 6 (versus 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 aspen-conifer 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 (Rotenberry 1985, Mac Nally 1990). 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 (Rotenberry 1985, Lee and Rotenberry 2005). 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.

In demonstrating the importance of canopy composition relative to vegetation structure in the avian patterns observed, our data provide evidence that the association between cavity-nesters and aspen largely drives the diversity patterns across the aspen-conifer gradient in our study area. Woodpeckers are considered ecosystem engineers and critical members of cavity nest webs (Martin and Eadie 1999) and are therefore likely to have an important role in avian community patterns. This is of particular consequence considering the state of aspen decline in western North America. Aspen declines have been noted in many parts of western North America, and may result in changes to avian communities at the local and landscape scale. Aspen declines can be caused by a range of factors from herbivory to climate change, although in our study as elsewhere the likely primary cause is conifer encroachment due to fire suppression (Bartos 2001, Strand et al. 2009b). Conifer encroachment is of particular concern where aspen is enmeshed in a conifer forest matrix. Strand et al. (2009) found aspen stands in a mixed-conifer matrix are susceptible to conifer encroachment under current fire suppression practices, and are likely to suffer additional significant declines in the coming century. Additionally it has been estimated that aspen make up less than 5% of western North American forests outside of Colorado and northern Utah (Hollenbeck and Ripple 2008), an historically low value. If our finding that aspen stands serve as a driver in maintaining local cavity nester communities is true elsewhere across western North America, it is likely that continued aspen presence in these landscapes will aid in the maintenance of forest biodiversity at broader scales.

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. Predictive maps have potential utility in management and conservation activities when used in the proper context and with an understanding of their limitations. The ability to make use of LiDAR remote sensing was central to shedding light on the patterns observed here and highlights the need for more widely available LiDAR datasets in the future.

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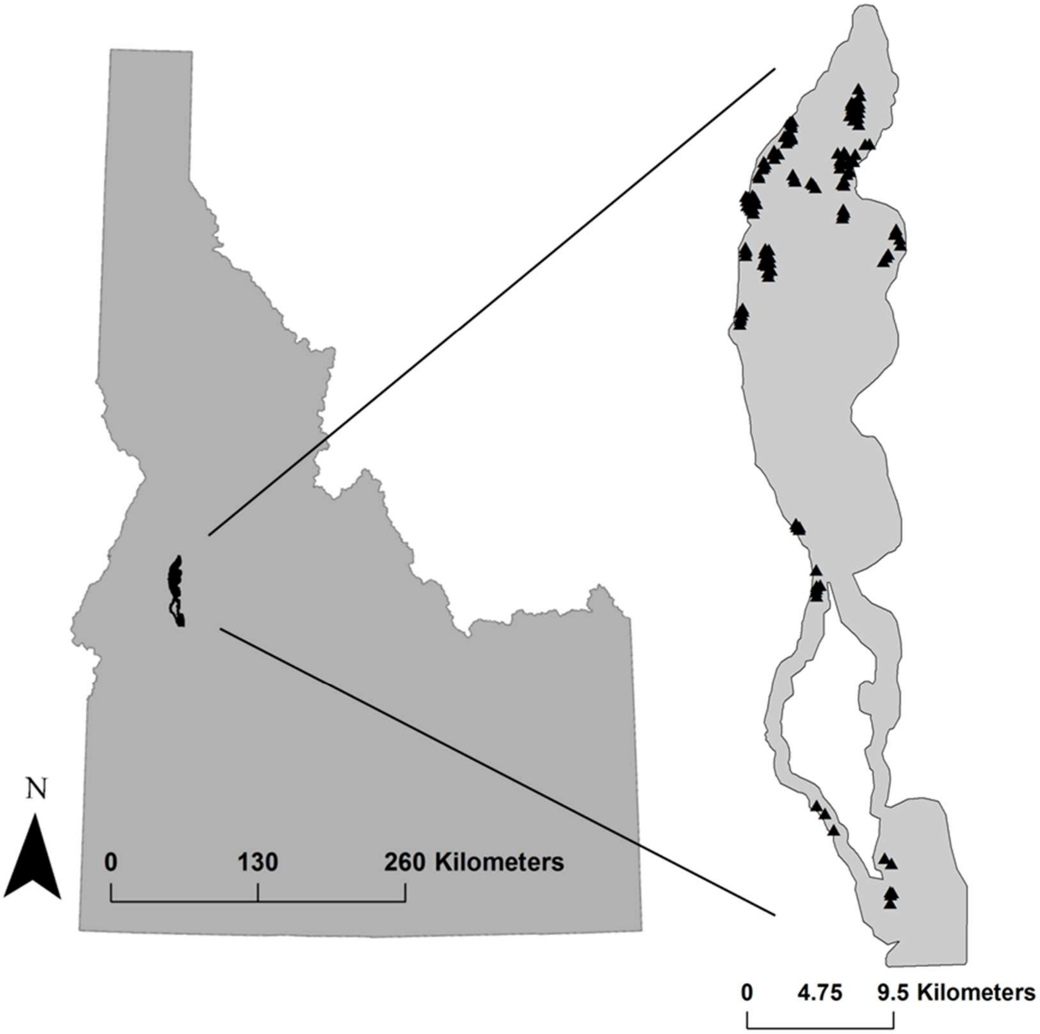

Figure 1.1. Map of Long Valley study area, black triangles indicate field plots.

Table 1.1. Description of 5 plot-level (50 m radius) and 1 landscape (150 m^2 buffer) explanatory variables..

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

Table 1.2. Summary of total and guild-specific species richness by canopy composition, mean (se).

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***	.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)

Letter groupings (a-c) differ, PCE=Primary Cavity Excavator, SCU=Secondary Cavity User.

Table 1.3. Summary of explanatory variables by canopy composition, mean (se)/range.

	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: , letter groupings (***a-b***) differ (Tukey multiple comparison of means, p < .05).

Table 1.4. Confidence set of models within 2 AICc of top model (only top 6 models for Total Species).

Species Guild	Model Set	AICc	ΔAICc	*W*	adjR^2	*p*
Total Species	CnpyCM HeightSD FrstCM	618.34	0	0.10	0.277	**
	CnpyCM HeightSD	618.62	0.28	0.08	0.269	**
	CnpyCM HeightMN	619.15	0.81	0.06	0.266	**
	CnpyCM FrstCM	619.43	1.09	0.06	0.264	**
	CnpyCM HeightSD UnstDN FrstCM	619.48	1.15	0.05	0.277	**
	CnpyCM HeightMN UnstDN	619.65	1.32	0.05	0.269	**
All Cavity Nesters	CnpyCM CnpyDN	504.47	0	0.18	0.355	**
	CnpyCM CnpyDN FrstCM	505.27	0.80	0.12	0.357	**
	CnpyCM HeightMN CnpyDN	505.29	0.82	0.12	0.357	**
	CnpyCM UnstDN CnpyDN	506.06	1.58	0.08	0.353	**
	CnpyCM HeightMN CnpyDN FrstCM	506.33	1.86	0.07	0.353	**
Primary Cavity Excavator	CnpyCM HeightMN CnpyDN	383.14	0	0.17	0.322	**
	CnpyCM HeightSD CnpyDN	383.75	0.62	0.13	0.318	**
	CnpyCM CnpyDN	384.49	1.35	0.09	0.308	**
	CnpyCM HeightMN HeightSD CnpyDN	385.11	1.97	0.07	0.318	**
Secondary Cavity User	CnpyCM UnstDN CnpyDN	343.26	0	0.18	0.379	**
	CnpyCM CnpyDN	344.01	0.75	0.12	0.370	**
	CnpyCM UnstDN CnpyDN FrstCM	344.45	1.19	0.10	0.379	**
	CnpyCM CnpyDN FrstCM	344.63	1.37	0.09	0.372	**
	CnpyCM HeightSD UnstDN CnpyDN	344.90	1.64	0.08	0.377	**
	CnpyCM HeightMN UnstDN CnpyDN	345.11	1.84	0.07	0.376	**
Open Cup	CnpyCM HeightSD CnpyDN	578.36	0	0.12	0.085	*
	CnpyCM HeightSD UnstDN CnpyDN	578.64	0.28	0.11	0.091	*
	CnpyCM HeightMN UnstDN	580.02	1.66	0.05	0.073	*
	CnpyCM HeightSD UnstDN CnpyDN FrstCM	580.04	1.68	0.05	0.090	*
	CnpyCM HeightSD CnpyDN FrstCM	580.11	1.74	0.05	0.081	*
	CnpyCM HeightMN UnstDN CnpyDN	580.21	1.85	0.05	0.080	*

Note: *W* = Akaike Weight, adjR^2 = adjusted coefficient of determination, ** = $p < .001$, * = $p < .01$.

Table 1.5. Model-averaged parameter estimates for 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
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
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	*
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	**2.903**	**-1.273**	**-0.458**	-0.002	-0.005	-0.051	**-0.022**	0.001
	Variance	0.111	0.046	0.045	0.000	0.000	0.003	0.000	0.000
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

Note: Conifer and Mixed are Canopy Composition categories and are relative to the Aspen. Bolded values indicate 95% confidence interval does not span zero, * = variable does not appear in top models.

Chapter 2: Influence of Canopy Composition and Vegetation Structure on Red-naped Sapsucker (*Sphyrapicus nuchalis*) Occupancy Across an Aspen-Conifer Forest Gradient

Abstract

Red-naped Sapsuckers (*Sphyrapicus nuchalis*) are considered ecosystem engineers as they alter their environment by making cavities and sap wells subsequently used by other species for nesting and food. Sapsuckers use conifer and deciduous habitats for breeding but show a preference for quaking aspen (*Populus tremuloides*) when present. Aspen enhances forest biodiversity but has been declining across western North America making it important to understand the potential effects of aspen declines on cavity excavator populations. Conifer encroachment into aspen results in a loss of aspen regeneration as well as changes to vegetation structure in aspen stands. Vegetation structure can be challenging to measure; however, 3-D LiDAR remote sensing provides a robust solution to this problem. We used LiDAR-derived vegetation structure metrics and avian field data to investigate the relative influence of vegetation structure and canopy composition (aspen-dominated, mixed aspen-conifer, or conifer-dominated) on Red-naped Sapsucker occupancy across an aspen-conifer forest gradient. We surveyed for sapsuckers between 2013 and 2014 in west-central Idaho. We found sapsucker occupancy to be significantly associated with aspen-dominated canopy composition. We also found sapsucker occupancy was negatively associated with canopy and understory density and positively association with foliage height diversity. These results suggest that sapsuckers are responsive to similar vegetation structure characteristics across the

aspen-conifer gradient and that sapsuckers may be disproportionally affected by aspen declines in conifer matrix habitats.

Introduction

Quaking aspen (*Populus tremuloides*) is an important component of montane forests in western North America with multiple benefits to forest biodiversity (Flack 1976, DeByle 1985, Bartos 2001). Aspen enhances forest vertebrate diversity by providing habitat for a diverse assemblage of breeding birds including a suite of functionally important cavity nesting species (Swift et al. in review, Winternitz 1980, Finch and Reynolds 1987, Turchi et al. 1995, Griffis-Kyle and Beier 2003). The short-lived nature of aspen, prevalence of aspen heart rot (*Phellinus tremulae*) in live aspen, as well as the frequency of aspen snags within stands, all makes aspen trees and aspen stands attractive to primary cavity excavators (Hart and Hart 2001, Losin et al. 2006, Hollenbeck and Ripple 2008). Cavity excavators in turn act as “ecosystem engineers”, altering their environment by excavating nest cavities subsequently used by a diverse community of secondary cavity users (Martin and Eadie 1999) and resulting in a potentially robust cavity nester community.

Quaking aspen, however, are declining in many areas of the West with declines expected to continue into the future under current climate projections and disturbance regimes (Strand et al. 2009a, Rehfeldt et al. 2009). The causes of aspen decline vary range-wide but are thought to include, individually or in combination, herbivory, climate change (drought), conifer encroachment, and changes in disturbance regimes (Bartos 2001, Kaye et al. 2005, Worrall et al. 2008). Aspen requires fire for regeneration and slowing conifer encroachment, and thus, fire is ultimately tied to aspen’s persistence on the landscape (Kay 1997, Bartos

2001). Changes in disturbance regimes, such as fire suppression practices, can result in reduced aspen regeneration and accelerated conifer invasion into aspen stands (Strand et al. 2009a). These changes, therefore, not only play an important role in ongoing aspen declines, but potentially impact forest biodiversity through the loss of benefits that aspen provides (Strand et al. 2009b). The biodiversity impacts from aspen declines may be particularly evident where aspen occurs in conifer matrices, and where aspen often represents a small proportion of forest cover (Hollenbeck and Ripple 2007) .

Research on the effects of conifer encroachment and aspen decline on avian diversity has generally focused on overall species richness (Rumble et al. 2001, Richardson and Heath 2004, Hollenbeck and Ripple 2007) and not specific guilds such as cavity excavators and cavity nesters. While the importance of aspen to cavity nesters has been widely noted (Li and Martin 1991, Dobkin et al. 1995, Norris and Martin 2010, Drever and Martin 2010), the influence of conifer encroachment on the cavity nester guild has been examined in a smaller number of studies. For example, Swift et al. (in review) found significantly higher cavity nester richness in aspen than conifer and mixed aspen-conifer in a conifer-dominated forest setting. Further, a recent aspen restoration project involving treatment through removal of conifers in conifer-encroached aspen stands, resulted in the increase of 7 focal aspen bird species including several cavity nesters, suggesting conifer encroachment had negatively impacted populations of the cavity-nesting guild (Campos and Burnett 2014).

Conifer encroachment in aspen may also directly impact individual bird species including those important for ecosystem function. For example, the Red-naped Sapsucker (*Sphyrapicus nuchalis*), a medium-sized migratory woodpecker, is considered an ecosystem engineer and possibly a keystone species (Daily et al. 1993, Robles and Martin 2013). Red-naped Sapsuckers (hereafter RNSA) alter their environment by excavating nest holes which are subsequently used by a suite of secondary cavity users. Additionally, they drill sap wells for food that are used by a suite of additional species which feed on sap and the insects it attracts (Daily et al. 1993, Walters 1996). In mixed conifer-deciduous forests, RNSA are known to use both conifer and deciduous habitat types but show a preference for deciduous trees, including birch and aspen, when available (Walters 1996, McClelland and McClelland 2000).

In addition to tree species preferences, RNSA may also be sensitive to aspects of vegetation structure. For example, research has shown RNSA occupancy to be positively associated with foliage height diversity and understory density (Vierling et al. 2013, Holbrook et al. 2015), negatively associated with upper canopy density (Holbrook et al. 2015), positively associated with availability of large diameter trees (McClelland and McClelland 2000), and sensitive to landscape configuration (Lawler and Edwards 2002, Sadoti and Vierling 2010). Conifer encroachment of aspen can result in structural alteration of both canopy and understory vegetation (Stam et al. 2008) as well as directly causing the decline of aspen through the loss of aspen regeneration (Bartos 2001, Kaye et al. 2005).

Changes to aspen due to conifer encroachment, may therefore affect the presence of RNSA both through the direct loss of aspen over time and more immediately through structural changes within aspen stands. The majority of prior research on RNSA habitat requirements has been conducted in aspen-dominated forest while fewer studies (McClelland and McClelland 2000, Vierling et al. 2013, Holbrook et al. 2015) have been conducted in conifer forest or across an aspen-conifer gradient as in our study. Our primary objective was to investigate the relative influence of canopy composition and vegetation structure on RNSA occupancy and assess the possible impacts of conifer encroachment on RNSA populations across the aspen-conifer forest gradient in our study area. We hypothesized that RNSA occupancy would be greater in aspen than mixed aspen-conifer or conifer and that vegetation structure, especially upper canopy density, may also influence RNSA occupancy in our study area. Because fine scale vegetation structural data can be labor and time intensive to gather, we utilize LiDAR (Light Detection and Ranging) to gather these data (Vierling et al. 2008, Muller et al. 2009). This represents the first study to simultaneously investigate the influence of vegetation structure and canopy composition (aspen, mixed aspen-conifer, conifer) on RNSA occupancy.

Methods

Study Area

The study was conducted in the Long Valley in the west-central mountains of Idaho (Figure 2.1) approximately 140 km north of the the Boise metropolitan area. Long Valley is a broad north-south montane valley varying from 8 to 11km wide and extending for 58 km; the northern edge 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 1530 m at McCall to 1450 m at Cascade. Valley terrain is gently to moderately sloped except steeply sloped along a portion of the North Fork of the Payette River and along glacial moraines south of McCall (Rasmussen 1981). The surrounding mountains rise to elevations between 2000 and 2500 m.

Weather in the Long Valley is characterized by warm, dry summers and moderate, wet winters with the bulk of precipitation at valley elevations coming in the form of snow

(Abramovich et al. 1998, U.S. Department of the Interior 2002). The mean January low temperature at McCall is -11 degrees C (22 degrees F) and the mean July high temperature is 26.5 degrees C (80 degrees F). The mean annual precipitation at McCall is 56 cm with the majority coming as snow (150 cm) between November and March.

Vegetation cover types in the study area include upland and riparian forest, wet meadows and grasslands, and sagebrush steppe. Wetlands are present within the margins of Cascade Lake as well as isolated locations throughout the valley. Conifer forests are mostly mixed second-growth and comprised of primarily ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and lodgepole pine (*Pinus contorta*) (Van Daele and Van Daele 1982, Tinkham et al. 2012). Stands of quaking aspen up to 1.5 ha in area are found throughout the valley in a variety of sites, often mixing with conifers, and becoming less common above the valley floor. Long Valley woodlands have been cleared historically for grazing and farming (Rasmussen 1981) and more recently for recreational development.

Land ownership in Long Valley is a broad mix of public and private. Public lands are owned and managed by the State of Idaho as well as federal entities in a patchwork with private lands. Extensive conifer-forests from valley edges to surrounding mountains are owned and managed primarily by the U.S. Forest Service but also by private timber/land management companies. Land use within the valley includes protected lands, low to moderate intensity grazing, resource extraction, and mixed recreational uses with a small year round population augmented by tourists and second-home owners.

Field Plots

We located candidate aspen and mixed aspen-conifer stands within the LiDAR acquisition area using aerial imagery, ground surveys, and locally available information. Conifer stands were located near selected aspen and mixed aspen-conifer stands. Stands spanned the full extent of the study area in a variety of physiographic settings (Figure 2.1) 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 (ESRI 2013). Within each survey plot the proportion of the canopy comprised of aspen and conifer was estimated to the nearest 10% using moderate 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, and conifer-dominated (hereafter conifer) as follows:

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

Multiple photographs taken at each plot center were used to inform the classification.

Avian Point Counts

To survey for RNSA presence we conducted two point counts at each survey plot across two field seasons; 92 plots were surveyed in 2013 and 38 plots were surveyed in 2014 for a total of 130 plots. We sampled for presence of all cavity and open cup nesters, and followed Drever (2008) by using audio broadcasts for select woodpecker species to increase woodpecker detection via callback. A standard five minute point count for all breeding species was followed by broadcasts for each of six commonly occurring woodpecker species in the study area: Pileated Woodpecker, Northern Flicker, Hairy Woodpecker, Downy Woodpecker, RNSA and Williamson's Sapsucker. 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, number of individuals, (closest) distance of each individual to the observer, temperature, wind, and cloud cover. Point counts were conducted between late May and early July to correspond with the peak RNSA breeding 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 detection. Point counts were conducted between 6:00 AM and 11:00 AM MDT during favorable weather conditions. We included RNSA detections within 50 m of plot center in statistical analyses to conform closely to 50 m vegetation measures and to avoid duplicate counting of individuals. All plot centers were a minimum of 150 m apart, and all avian point counts were conducted by the same observer (Swift).

LiDAR Remote Sensing Data

We used discrete multiple-return airborne LiDAR data to generate vegetation structure metrics for our study plots (Table 2.1). The LiDAR data were collected over three days between May 7 and May 31, 2012 by Aerometric Inc. using fixed-wing aircraft as part of the United States Federal Emergency Management Agency's (FEMA) Risk MAP program and provided to us by the Idaho Department of Water Resources. The LiDAR extent spanned approximately 35,750 ha (Figure 2.1) 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 RMSE. LiDAR data were delivered as 225 ha tiled output in raw and classified LAS point data formats 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^2 resolution raster grid. Plot-level metrics were calculated using Focal Statistics with a 50 m radius in ArcGIS Spatial Analyst (ESRI 2013) at each of the 130 plot centers. The LiDAR acquisition differed temporally from the bird surveys by 1-2 years, however several studies (Vierling et al. 2014, Hill and Hinsley 2015) note that time lags between bird data collection and LiDAR acquisitions of 6-10 years 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 Tukey multiple comparison of means and used a significance level of $p < 0.05$ (Table 2.3).

Occupancy Modeling

We built occupancy models using an apriori set of 5 explanatory variables which we hypothesized could influence RNSA occupancy. Predictor variables included canopy composition and a suite of 4 LiDAR-derived vegetation structure metrics: mean height, standard deviation of height, understory density and canopy density (Table 2.1). All variables were examined for collinearity before proceeding with the analysis. LiDAR-derived mean height and standard deviation of height (i.e. foliage height diversity; MacArthur and MacArthur, 1961) have been identified as predictors of snag diameter class distribution and forest successional stages (Falkowski et al. 2009, Martinuzzi et al. 2009) and are potentially influential on the presence of cavity excavators. Foliage height diversity, identified in prior studies in conifer-dominated forest associated with RNSA occupancy (Vierling et al. 2013, Holbrook et al. 2015) may be related to varied foraging strategies of RNSA and availability of insect prey, an important food source during the breeding season (Walters et al. 2014). Vegetation density measures may also be influential in RNSA presence and therefore explanatory in these models. For example canopy density between 20 and 30 m (Holbrook et al. 2015) and vegetation density > 2.5 m (Swift et al. in review) have been shown to be be negatively associated with cavity excavator occupancy and richness. Vegetation density may be negatively associated with RNSA occupancy for predator avoidance and potential impact on foraging via aerial fly-catching (Walters et al. 2014, Holbrook et al. 2015). The canopy composition type represents a generalized plant community as well as specific attributes of canopy tree species that may influence RNSA occupancy. For example RNSA are known to show an affinity for aspen in mixed conifer-deciduous forests (Li and Martin 1991).

We used a hierarchical modeling framework following MacKenzie et al. (2002) to jointly estimate RNSA occupancy (ψ) and detection probability (p). This method accounts for imperfect detection probability (i.e. $p < 1$) which can otherwise produce biased model results (Gu and Swihart 2004). Model evaluation and selection was conducted in the R program (R Development Core Team 2013) using package ‘unmarked’ (Fiske and Chandler 2011) which implements the MacKenzie et al. (2002) hierarchical occupancy model. Based on preliminary analysis, we included the visit (i.e. first/second) as a covariate in estimating RNSA detection probability (p). To model RNSA occupancy, we compared the null model and all subsets of the 5-variable universal occupancy model using an information-theoretic model selection framework (Burnham and Anderson 1998). The Akaike information criterion for small samples (AICc) was calculated for all candidate models and those within 2 AICc of the top model were considered to be competitive (Burnham and Anderson 2002). We used a model-averaging approach to estimate parameters, standard errors, and 95% confidence intervals (Johnson and Omland 2004) for making inferences. Model averaging was implemented using R package AICcmodavg (Mazerolle 2015). Occupancy plots for canopy and understory density for each canopy type (Figure 2.2) were generated in R using function predict from R package unmarked (Fiske and Chandler 2011).

Results

Differences in LiDAR-derived measures between aspen and conifer were significant in height metrics but not vegetation density metrics (Table 2). For example, both mean height and standard deviation of height were significantly greater in conifer than aspen and mixed aspen-conifer plots. In contrast, understory and canopy density were not significantly different. Vegetation structure metrics within mixed aspen-conifer stands, although not significantly different from aspen, had intermediate values between aspen and conifer stands as expected.

Red-naped Sapsuckers were detected on at least one visit in 19 of 33 aspen plots (57.6 %), 18 of 41 mixed aspen-conifer plots (43.9 %), 11 of 56 conifer plots (19.6 %), and 48 of 130 plots overall (36.9%) (Table 2.3). RNSA presence was significantly greater in aspen and mixed aspen-conifer than conifer (Table 2.3). Among LiDAR-derived vegetation metrics, mean height was significantly greater in occupied stands in aspen and canopy density was significantly lower in occupied stands in mixed aspen-conifer (Table 2.3). Canopy density and understory density were significantly lower in occupied plots overall (Table 2.3).

The RNSA occupancy model confidence set included three models with 3-4 parameters each (Table 4). The canopy composition, understory density, and canopy density predictor variables were included in all three top models (Table 2.4). Based on model averaged parameter estimates, RNSA occupancy was significantly negative in conifer relative to aspen and weakly negative in mixed aspen-conifer relative to aspen (Table 2.5). Among LiDAR-derived vegetation structure metrics, RNSA occupancy was weakly negative in both canopy and understory density and weakly positive in both mean height and standard deviation of height (Table 2.5). The survey visit (e.g. first/second), included as a detection covariate, was positive, suggesting that RNSA were more likely to be detected on the second visit which is later in the breeding season (Table 2.5).

Discussion

We found RNSA occupancy to be strongly associated with canopy composition as we hypothesized. The higher occupancy of RNSA in aspen than conifer in our study area concurs with what is known about cavity nesters in general and RNSA in particular (Crockett and Hadow 1975, Li and Martin 1991, Daily et al. 1993, Dobkin et al. 1995, Walters 1996). The ease of excavating generally softer and more disease prone aspen wood appears to be a key factor for sapsucker preference for nesting in aspen. In addition, RNSA prefer drilling sap wells into trees such as aspen, willow, and spruce (Daily et al. 1993). However, RNSA also use conifer-dominated stands, including in our study, and are known to nest in diseased and broken-topped softer conifer species (McClelland and McClelland 2000). Therefore it may be informative to compare other habitat characteristics, such as vegetation structure, across conifer and aspen types.

We used LiDAR-derived vegetation metrics to assess the influence of vegetation structure on RNSA occupancy in the aspen-conifer gradient in our study. Vierling et al. (2013) found a positive association between foliage height diversity and RNSA occupancy using LiDAR derived variables in a conifer-dominated forest, and Holbrook et al. (2015) also used LiDAR metrics to assess RNSA occupancy in this forest type. We also found a positive association between RNSA occupancy and foliage height diversity and negative associations between RNSA occupancy and canopy and understory density. Although these three vegetation structure associations were weak in our study, they all concur in direction with those found by Holbrook et al. (2015) who hypothesized they may be due to foraging strategies, prey availability, and predator avoidance. We also found RNSA occupancy had a weak positive association with mean height, perhaps due to availability of suitable nest trees in older stands (Walters et al. 2014). These findings suggest that similar vegetation structure characteristics may play a role in RNSA occupancy patterns across habitat types. Differences in strength between our findings and Holbrook et al. (2015) may be partially scale-dependent, as they found 4 ha the most useful scale for measuring vegetation structure which differs from the 0.75 ha scale in our study. We also used a more liberal definition of canopy (> 2.5 m) across all 3 canopy types in our density metrics compared to the upper canopy density (20-30 m) in conifer used by Holbrook et al. (2015). In addition, factors influencing RNSA occupancy may vary across habitat types due to differences in resource availability, potential predators and/or nest-site competitors. For example, differences in cavity placement, territory size, and resource use have been noted between conifer and aspen for RNSA (Walters 1996, McClelland and McClelland 2000).

Considering the biodiversity benefits of aspen in conifer forest matrix settings, it is important to understand the effects on bird communities of ongoing conifer encroachment. Of the studies that have investigated the effects of conifer encroachment on birds, the majority suggest both bird diversity as well as abundance of some species are likely to be negatively impacted (Finch and Reynolds 1987, Rumble et al. 2001, Hollenbeck and Ripple 2007). For example recently Swift et al. (in review) found bird species richness was strongly associated with canopy composition across an aspen-conifer gradient, with total species richness in aspen greater than in conifer, and cavity nester richness greater in aspen compared to conifer and mixed aspen-conifer. As noted above RNSA occupancy appears to be negatively associated with increases in canopy and understory density across the aspen-conifer gradient. Although few studies have examined vegetation structure changes to aspen resulting from conifer encroachment (Stam et al. 2008) it is likely that understory and then canopy density increase as conifers invade. Elsewhere it has been suggested that cavity nesters track structural changes in aspen (Hollenbeck and Ripple 2008) and this is also likely to occur in aspen undergoing conifer encroachment.

Primary cavity excavators play a functionally important role in forest ecosystems as key parts of cavity nest webs (Martin and Eadie 1999). In mixed conifer-deciduous forests cavity excavators occupy a variety of habitat types, but have a preference for habitats with deciduous trees, especially aspen. In this study we found RNSA occupancy to be greater in aspen than conifer but also weakly associated with a number of height and density vegetation structure metrics. The Red-naped Sapsucker is an ideal candidate to examine the influences of vegetation changes along the aspen-conifer gradient because of its occurrence in all three canopy types. As conifer encroachment continues to affect aspen, understanding the factors that influence Red-naped Sapsucker occupancy will have important implications for gauging its presence in forest landscapes as well for the suite of secondary users reliant on the sap wells and nest cavities it provides.

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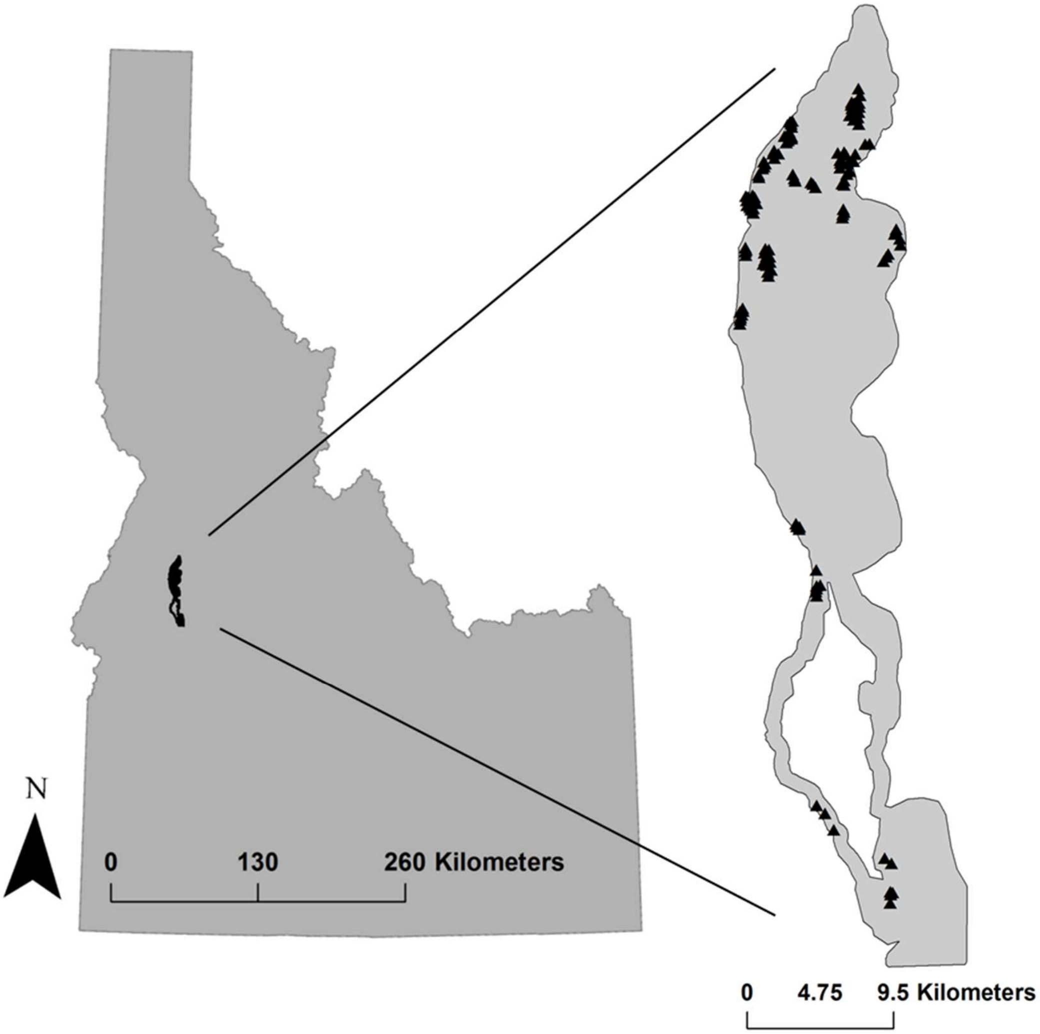

Figure 2.1. Map of Long Valley study area, black triangles indicate field plots.

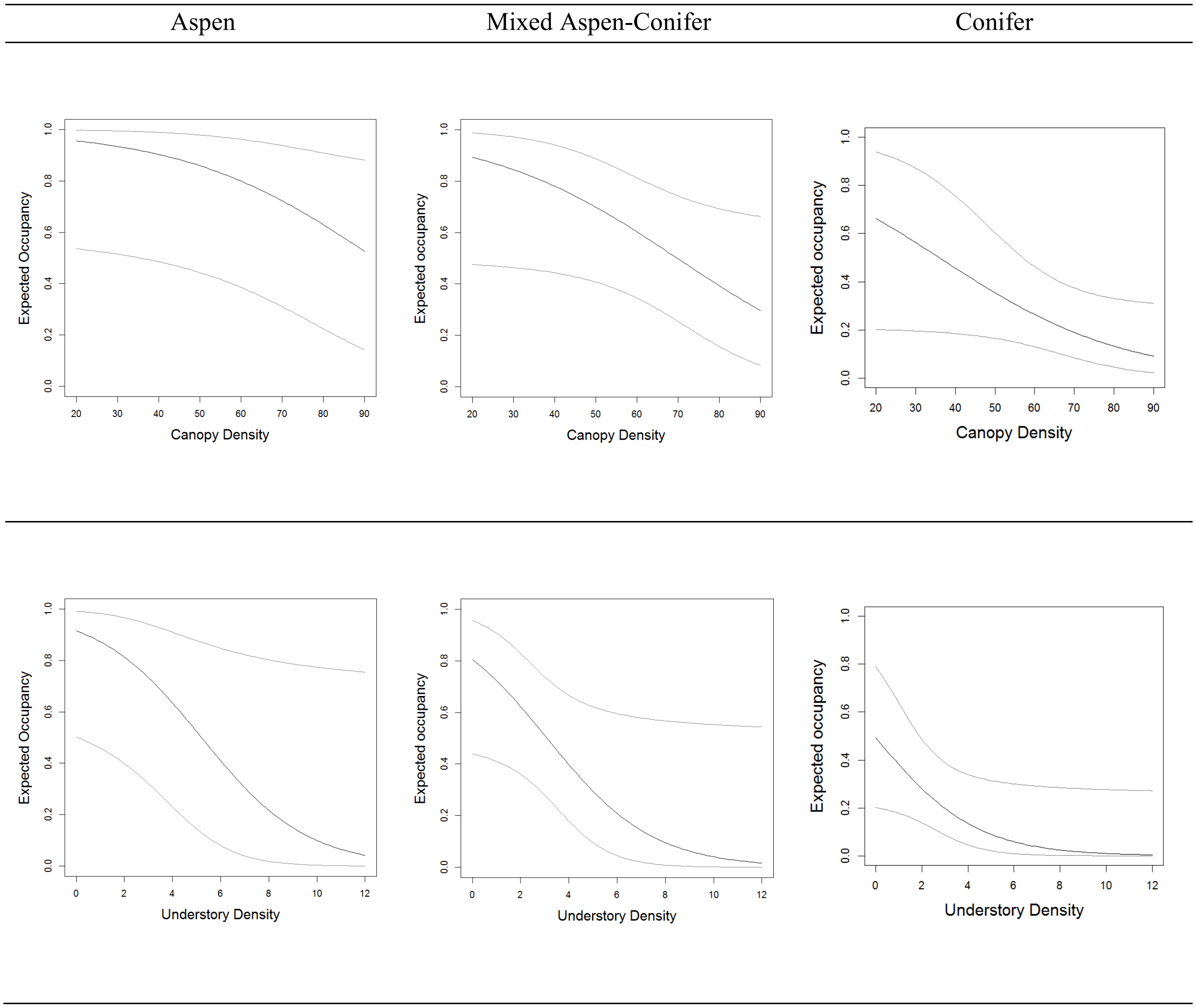

Figure 2.2. Predicted RNSA occupancy based on the top occupancy model for each Canopy Composition Type (Conifer, Mixed Aspen-Conifer, Conifer) for Canopy Density and Understory Density. Dark line indicates predicted occupancy, lighter lines indicate bounds of 95%.

Table 2.1. Description of 5 plot-level (50 m radius) explanatory variables.

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

Table 2.2. Summary of explanatory variables (Mean (se)/Range) by canopy composition, letter groupings (a-c) differ (Tukey multiple comparison of means, p < .05).

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

Table 2.3. Summary of LiDAR-derived predictor variables (Mean (se)) for Red-naped Sapsucker presence and absence by canopy composition, * indicates means differ (Tukey multiple comparison of means, p < .1).

CnpyCM	Occupancy	HeightSD (m)	HeightMN (m)	UnstDN	CnpyDN
Aspen	Present (n=19)	3.53 (0.26)	**9.85 (0.53) ***	1.28 (0.22)	54.27 (3.73)
(n=33)	Absent (n=14)	2.92 (0.25)	**8.49 (0.51) ***	2.09 (0.73)	52.83 (5.13)
Mixed	Present (n=18)	3.95 (0.37)	10.70 (0.90)	1.99 (0.26)	**52.87 (3.46) ***
(n=41)	Absent (n=23)	3.51 (0.20)	10.19 (0.51)	2.37 (0.30)	**62.19 (2.57) ***
Conifer	Present (n=11)	3.93 (0.41)	12.11 (1.02)	1.74 (0.29)	55.92 (5.63)
(n=56)	Absent (n=45)	4.49 (0.21)	13.01 (0.65)	2.40 (0.30)	61.75 (2.39)
Combined	Present (n=48)	3.78 (0.20)	10.69 (0.47)	**1.65 (0.15) ***	**54.12 (2.30)***
(n=130)	Absent (n=82)	3.95 (0.15)	11.50 (0.44)	**2.34 (0.22) ***	**60.35 (1.75)***

Table 2.4. Confidence set of Red-naped Sapsucker occupancy models within 2 AICc of top model, intercepts not shown, W = Akaike Weight.

Model Set	AICc	ΔAICc	*W*
ψ(CnpyCM + UnstDN + CnpyDN), p(visit)	264.99	0	0.49
ψ(CnpyCM + HeightMN + UnstDN + CnpyDN), p(visit)	265.75	0.76	0.33
ψ(CnpyCM + HeightSD + UnstDN + CnpyDN), p(visit)	266.93	1.95	0.18

Table 2.5. Model-averaged parameter estimates for RNSA occupancy models within 2 AICc of top model. Conifer and Mixed are Canopy Composition categories, parameter estimates are relative to the Aspen Canopy Composition. Bolded values indicate 95% confidence interval.

	Predictor Variables (ψ)							Detection Variables (p)	
Measure	Intercept	Conifer	Mixed	HeightSD	HeightMN	UnstDN	CnpyDN	Intercept	Visit
Estimate	4.79	-2.59	-1.08	0.12	0.12	-0.46	-0.05	-0.98	0.61
Lower (CI)	0.49	**-4.64**	-3.00	-0.29	-0.08	-0.93	-0.10	-2.1	0.09
Upper (CI)	9.09	**-0.54**	0.84	0.52	0.32	0.01	0	0.14	1.31
SE	2.19	1.05	0.98	0.21	0.10	0.24	0.03	0.57	0.36

Thesis Conclusions and Future Work

The purpose of my thesis was to examine the relative influence of vegetation structure and canopy composition on avian richness and occupancy of a primary cavity excavator, the Red-naped Sapsucker, in an aspen-conifer forest setting. Cavity excavating woodpeckers and aspen are vital components of forests ecosystems in western North America and cavity excavators have an affinity for aspen. Cavity excavators are also key parts of complex cavity nest webs (Martin and Eadie 1999) and Red-naped Sapsuckers excavate sapwells which are used by additional species for food. Aspen provides many benefits to forest ecosystems and have important cultural values but are declining in many parts of western North America. Aspen declines have the potential to impact forest biodiversity at multiple scales therefore it is important to examine avian habitat relationships in aspen and conifer where they occur together.

The main findings of my research were as follows:

Chapter 1: In this chapter I used LiDAR-derived vegetation metrics to investigate the relative influence of vegetation structure and canopy composition on avian richness patterns across an aspen-conifer forest gradient. I found aspen to have higher avian richness than conifer and mixed aspen-conifer, especially among cavity nesters. In contrast to some prior studies, I found weak relationships between avian diversity and vegetation structure. I also found that cavity nester diversity was negatively associated with canopy density. This chapter provides further evidence that aspen enhances forest avian diversity and that conifer encroachment may negatively affect avian richness in aspen. This chapter also adds to the ongoing discussion around the relative role of vegetation structure and vegetation composition in avian-habitat relationships.

Chapter 2: In this chapter I used LiDAR-derived vegetation metrics to investigate the relative influence of vegetation structure and canopy composition on Red-naped Sapsucker occupancy across an aspen-conifer forest gradient. I found that Red-naped Sapsucker occupancy had a strong association with canopy composition as was hypothesized and previous research has suggested. Red-naped Sapsucker occupancy was significantly greater in aspen than conifer and weakly greater in aspen than mixed aspen-conifer. Red-naped Sapsucker occupancy also had a negative association with canopy and understory density across canopy types. This relationship suggests a possible mechanism for reduced Red-naped Sapsucker occupancy in aspen undergoing conifer encroachment. This chapter adds to knowledge of a functionally important avian cavity excavator in aspen and conifer forests and the potential implications for its presence in aspen undergoing conifer encroachment.

Considering the ongoing widespread declines in aspen (Bartos 2001, Strand et al. 2009) it is important to continue investigating avian-aspen habitat associations and the potential effects of conifer encroachment and aspen decline on forest avian diversity. Aspen has a dynamic presence on the landscape and successional stage may also play a role in avian-habitat associations. Therefore further research should be directed to understanding the relationships between aspen successional stage and avian richness/occupancy. Cavity excavators are likely to track ongoing changes of succession and disturbance in aspen (Hollenbeck and Ripple 2008) which has implications for avian richness and abundance at local and landscape scales. Finally identifying occupancy thresholds for species closely tied to aspen can inform aspen-related management activities.

Empirical research can also be coupled with experimental treatments of conifer-encroached aspen. For example, recent efforts have shown a positive effect on some bird species tied to aspen (Campos and Burnett 2014). Mapping aspen extent and condition and predicting future landscape composition in regions like my study area, the Long Valley, will greatly assist in understanding the potential impacts of changes to aspen on avian diversity and other wildlife. In addition, public agencies and advocacy organizations can be encouraged to highlight the issues with aspen decline and their potential remedies though public education and outreach where appropriate. In conclusion, this project has provided an excellent opportunity to study a central concept in avian science in a dynamic natural system with application to a pressing conservation issue.

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Appendices

Appendix 1. Bird species detected within 50 m radius of plot centers in 2013 (n=92) and 2014 (n=38) with associated nesting guild and canopy class each was detected in. Nesting guild codes: 1 – primary cavity excavator, 2 – secondary cavity user, 3 – weak excavator, 4 – open cup, 5 – brood parasite.

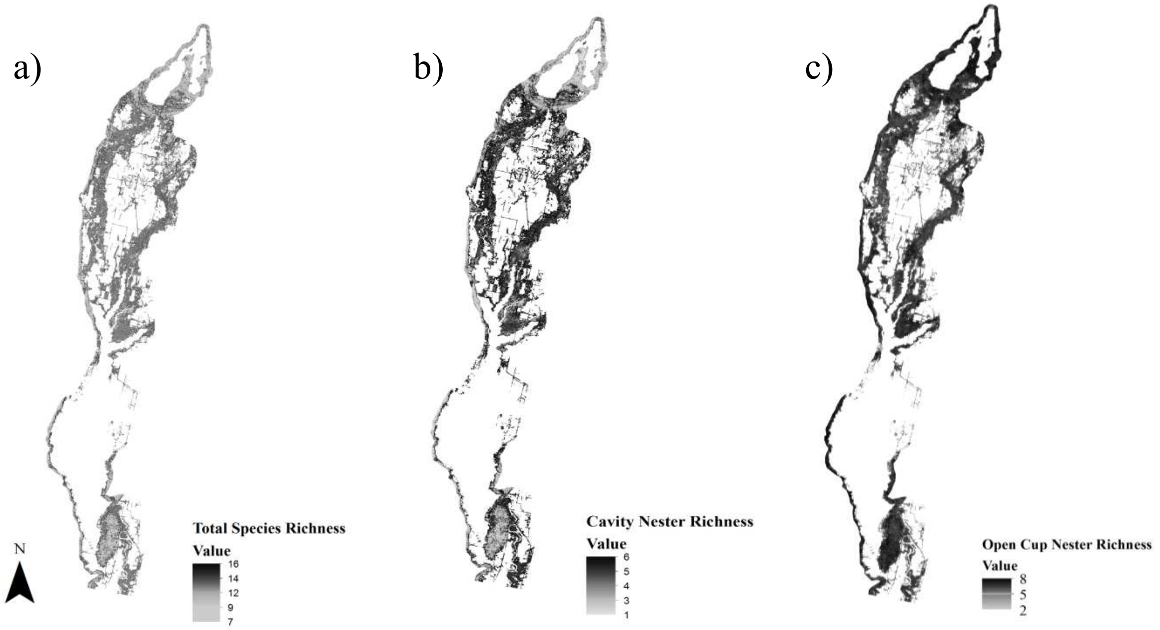
Common Name	Scientific Name	Guild	Aspen	Mixed	Conifer
Wood Duck	*Aix sponsa*	2	x		
Bufflehead	*Bucephala albeola*	2	x		
California Quail	*Callipepla californica*	4		x	
Ruffed Grouse	*Bonasa umbellus*	4	x	x	x
Osprey	*Pandion haliaetus*	4			x
Mourning Dove	*Zenaida macroura*	4		x	
Black-chinned Hummingbird	*Archilochus alexandri*	4			x
Calliope Hummingbird	*Selasphorus calliope*	4	x		
Williamson's Sapsucker	*Sphyrapicus thyroideus*	1	x	x	x
Red-naped Sapsucker	*Sphyrapicus nuchalis*	1	x	x	x
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
American Kestrel	*Falco sparverius*	2	x	x	x
Western Wood-Pewee	*Contopus sordidulus*	4	x	x	x
Willow Flycatcher	*Empidonax traillii*	4	x		
Least Flycatcher	*Empidonax minimus*	4	x		x
Hammond's Flycatcher	*Empidonax hammondii*	4	x	x	x
Dusky Flycatcher	*Empidonax oberholseri*	4	x	x	x
Cassin's Vireo	*Vireo cassinii*	4	x	x	x
Warbling Vireo	*Vireo gilvus*	4	x	x	x
Gray Jay	*Perisoreus canadensis*	4		x	
Steller's Jay	*Cyanocitta stelleri*	4		x	
Black-billed Magpie	*Pica hudsonia*	4	x	x	
Clark's Nutcracker	*Nucifraga columbiana*	4		x	
American Crow	*Corvus brachyrhynchos*	4	x	x	x
Common Raven	*Corvus corax*	4		x	x
Tree Swallow	*Tachycineta bicolor*	2	x	x	x
Black-capped Chickadee	*Poecile atricapillus*	3	x	x	x
Mountain Chickadee	*Poecile gambeli*	3	x	x	x
Chestnut-backed Chickadee	*Poecile rufescens*	3		x	
Red-breasted Nuthatch	*Sitta Canadensis*	3	x	x	x

Appendix 1 (cont). Bird species detected within 50 m radius of plot centers in 2013 (*n*=92) and 2014 (*n*=38) with associated nesting guild and vegetation type each was detected in. Nesting guild codes: 1 – primary cavity excavator, 2 – secondary cavity user, 3 – weak excavator, 4 – open cup, 5 – brood parasite.

Common Name	Scientific Name	Guild	Aspen	Mixed	Conifer
White-breasted Nuthatch	Sitta carolinensis	3		x	x
Pygmy Nuthatch	*Sitta pygmaea*	3	x	x	x
Brown Creeper	*Certhia Americana*	4	x	x	x
House Wren	*Troglodytes aedon*	2	x	x	x
Pacific Wren	*Troglodytes pacificus*	4		x	x
Golden-crowned Kinglet	*Regulus satrapa*	4		x	x
Ruby-crowned Kinglet	*Regulus calendula*	4	x	x	x
Mountain Bluebird	*Sialia currucoides*	2		x	
Swainson's Thrush	*Catharus ustulatus*	4	x	x	x
American Robin	*Turdus migratorius*	4	x	x	x
European Starling	*Sturnus vulgaris*	2	x	x	x
Cedar Waxwing	*Bombycilla cedrorum*	4	x	x	x
Orange-crowned Warbler	*Oreothlypis celata*	4		x	
MacGillivray's Warbler	*Geothlypis tolmiei*	4	x	x	x
Common Yellowthroat	*Geothlypis trichas*	4			x
Yellow Warbler	*Setophaga petechia*	4	x	x	x
Yellow-rumped Warbler	*Setophaga coronata*	4	x	x	x
Townsend's Warbler	*Setophaga townsendi*	4	x	x	x
Spotted Towhee	*Pipilo maculatus*	4	x		x
Chipping Sparrow	*Spizella passerina*	4	x	x	x
Vesper Sparrow	*Pooecetes gramineus*	4		x	
Song Sparrow	*Melospiza melodia*	4	x	x	x
Lincoln's Sparrow	*Melospiza lincolnii*	4	x	x	
White-crowned Sparrow	*Zonotrichia leucophrys*	4	x		
Dark-eyed Junco	*Junco hyemalis*	4	x	x	x
Western Tanager	*Piranga ludoviciana*	4	x	x	x
Black-headed Grosbeak	*Pheucticus melanocephalus*	4	x	x	x
Lazuli Bunting	*Passerina amoena*	4	x	x	x
Red-winged Blackbird	*Agelaius phoeniceus*	4	x		
Western Meadowlark	*Sturnella neglecta*	4	x		
Brown-headed Cowbird	*Molothrus ater*	5	x	x	x
Brewer's Blackbird	*Euphagus cyanocephalus*	4	x		
Cassin's Finch	*Haemorhous cassinii*	4	x	x	x
Red Crossbill	*Loxia curvirostra*	4	x		x
Pine Siskin	*Spinus pinus*	4	x	x	x

Appendix 1 (cont). Bird species detected within 50 m radius of plot centers in 2013 (*n*=92) and 2014 (*n*=38) with associated nesting guild and vegetation type each was detected in. Nesting guild codes: 1 – primary cavity excavator, 2 – secondary cavity user, 3 – weak excavator, 4 – open cup, 5 – brood parasite.

Common Name	Scientific Name	Guild	Aspen	Mixed	Conifer
American Goldfinch	*Spinus tristis*	4	x	x	x
Evening Grosbeak	*Coccothraustes vespertinus*	4	x	x	



Appendix 2. Species richness predictive maps generated from top models based on forest canopy composition and the following Lidar-derived vegetation metrics a) standard deviation of height, b) canopy density, c) standard deviation of height and canopy density. Areas in white indicate water bodies and non-forested areas.

Appendix 3. Correlation matrix for species richness and RNSA model explanatory variables (see table 1.1 for variable definitions).

	HeightMN	HeightSD	UnstDN	CnpyDN	FrstCM	CnpyCM
HeightMN	1.00					
HeightSD	0.63	1.00				
UnstDN	-0.15	0.07	1.00			
CnpyDN	0.55	0.00	0.00	1.00		
FrstCM	0.52	0.24	-0.08	0.34	1.00	
CnpyCM	0.42	0.34	0.14	0.16	0.40	1.00

Appendix 4. Red-naped Sapsucker predicted occupancy. Generated from top RNSA occupancy model (Table 2.4). Areas in white indicate water bodies and non-forested areas.