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The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest

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Abstract

Vegetation structure is an important factor that influences wildlife-habitat selection, reproduction, and survival. However, field-based measurements of vegetation structure can be time consuming, costly, and difficult to undertake in areas that are remote and/or contain rough terrain. Light detection and ranging (lidar) is an active remote sensing technology that can quantify three-dimensional vegetation structure over large areas and thus holds promise for examining wildlife-habitat relationships. We used discrete-return airborne lidar data acquired over the Black Hills Experimental Forest in South Dakota, USA in combination with field-collected vegetation and bird data to assess the utility of lidar data in quantifying vegetation structural characteristics that relate to avian diversity, density, and occurrence. Indices of foliage height diversity calculated from lidar data were positively and significantly correlated with indices of bird species diversity, with the highest correlations observed when foliage height diversity categories contained proportionally more foliage layers near the forest floor (<5 m). In addition, lidar-derived indices of vegetation volume were significantly correlated with bird density. Using lidar-derived vegetation height data in combination with multispectral IKONOS data, we delineated five general habitat types within the study area according to the presence of prominent vegetation layers at lower levels of the forest and predominant tree type (deciduous or conifer). Habitat type delineations were tested by examining the occurrence and relative density of two bird species common to the study area that prefer lower level vegetation for foraging and nesting. Dark-eyed Juncos were significantly associated with the 0.5–2.0 m high vegetation layer in pine-dominated stands, and Warbling Vireos were significantly associated with this same layer in aspen-dominated stands. These results demonstrate that discrete-return lidar can be an effective tool to remotely quantify vegetation structural attributes important to birds, and may be enhanced when used in combination with spectral data.

Keywords: Lidar; Remote sensing; Diversity; Birds; Spectral; Habitat; Avian; Vegetation structure

1. Introduction

Ecologists have long recognized the importance of vegetation structure in the assessment of wildlife habitat. However, vegetation structure indices developed and used by ecologists are necessarily based upon field vegetation surveys, which can be time consuming, costly, and difficult or dangerous to undertake in areas that are remote and/or contain challenging terrain. Therefore, remote sensing is an attractive alternative to traditional methods used to characterize wildlife habitat (e.g. Hurlbert, 2004; Turner et al., 2003). In particular, discrete-return light detection and ranging (lidar) holds great promise for use by avian ecologists because it is an active remote sensing technology producing fine scale three-dimensional data from which vegetation structural attributes can be derived across broad landscapes (e.g. Lefsky et al., 2002).

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Researchers have begun to realize the potential for using lidar technology in studies of animal-habitat relationships (see review by Vierling et al., 2008). Recent investigations have used lidar data in habitat assessment for a diverse group of animals, including corals (Brock et al., 2004, 2006), small mammals (Nelson et al., 2005) and fish (Jones, 2006). While these studies represent lidar applications to a diversity of taxa, the majority of studies published to date address bird-habitat relationships.

Applications of lidar data in avian research have focused on 1) establishing correlations between lidar-derived and field-based estimates of vegetation structure, 2) correlating lidar-derived data with species occurrence, and 3) utilizing lidar-derived estimates to examine aspects of habitat quality. Correlations between lidar-derived and field-based estimates of vegetation structure important to birds have been demonstrated in multiple studies (e.g. Bradbury et al., 2005; Davenport et al., 2000; Hashimoto et al., 2004; Hinsley et al., 2002) in areas ranging from grasslands to forests. Relationships between vegetation structural attributes described by lidar and potential bird occurrence have also been examined (e.g. Bradbury et al., 2005). Finally, lidar data have been used to assess habitat quality for individual bird species. Working in a deciduous woodland in eastern England, Hinsley et al. (2002) examined the relation of the lidar-determined mean vegetation height around nest boxes to mean chick mass (used as a measure of habitat quality) for Great Tits (*Parus major* L.) and Blue Tits (*P. caeruleus* L.). These researchers found that for Great Tits, mean chick mass decreased with mean vegetation height, and for Blue Tits, mean chick mass increased with mean vegetation height. Hill et al. (2004) then produced a predictive map of reproductive performance in Great Tits based on a lidar-derived woodland canopy height model and a statistical relation between mean canopy height and mean nestling body mass.

In this study, we examine relations between lidar-derived vegetation height data and bird survey data. First, we examine the relationship between vegetation structure indices calculated from lidar-derived vegetation heights and corresponding field-based measurements to establish the utility of lidar data in representing vegetation structure in a pine/aspen forest occurring within the Black Hills of South Dakota, USA. Second, we examine the relation of lidar-derived vegetation structure indices with measures of bird species diversity and density. Third, we use lidar data in combination with IKONOS multispectral data to select areas within the Black Hills Experimental Forest (BHEF) containing specific vegetation composition and structural features and compare field-based estimates of bird densities among these areas for two species with known vegetation structure preferences.

This study builds upon previous efforts that have demonstrated the utility of lidar data in representing vegetation height and structure. Although previous studies have demonstrated the utility of lidar data in estimating vegetation structural attributes important to birds and designating areas of potential avian habitat based on vegetation structure, few have used bird survey data. As a result, site-level bird species diversity and density have not been examined in relation to lidar-derived vegetation metrics. Pioneering research by MacArthur and MacArthur (1961) correlated bird species diversity (BSD) with foliage height diversity (FHD). Subsequent research examined BSD and bird density in relation to other vegetation structural indices such as percent vegetation cover and vegetation volume (e.g. Erdelen, 1984; Karr & Roth, 1971; Mills et al., 1991; Willson, 1974). These studies used field-based methods to estimate vegetation heights and occurrence and produced related structural indices. To our knowledge, this study represents the first attempt to examine bird species diversity and density using bird survey data in relation to multiple lidar-derived vegetation structure indices.

2. Methods

2.1. Study area

Our study area (Fig. 1) is located in the BHEF in west central South Dakota, USA. The area ranges in elevation from 1500–1800 m above sea level and is dominated by Ponderosa pine (*Pinus ponderosa* Douglas ex Lawson), with lesser concentrated populations of Black Hills white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) (Rowell et al., 2006). Understory species common to the study area include evergreen bearberry (*Arctostaphylos uva-ursi*), Oregon grape (*Berberis repens*), choke cherry (*Prunus virginiana*), snowberry (*Symphoricarpos* spp.), and Saskatoon serviceberry (*Amelanchier alnifolia*) (Uresk & Severson, 1989).

The BHEF is a long-term silvicultural experiment site within the Black Hills, and thus contains a highly heterogeneous mosaic of structural stand stages and age classes (Rowell et al., 2006). Management and tree thinning strategies have resulted in areas ranging from dense stands of tall trees with little or no understory to highly heterogeneous stands with a more open canopy. These latter stands are more complex and contain some tall mature trees with understory vegetation of varying height, along with open areas with young trees, woody shrub species, forbs, and grasses. Some of these shrubs and young trees are under mature tree canopy and represent true understory, and others are exposed.

Birds with both eastern and western distributions occur in the Black Hills of western South Dakota (Mills et al., 2000a). Mills et al. (1995) observed 69 non-game bird species in portions of the Black Hills National Forest (BHNF) in the central Black Hills area (including the BHEF) from 1992 to 1994. Mills et al. (2000a) found that species richness was greater in aspen/birch than in Ponderosa pine in areas of the BHNF.

2.2. Remotely sensed data

Lidar data were collected over the study area on October 26, 2001 using a discrete-return Azimuth Corporation (Westford, MA) Aeroscan instrument installed on a Cessna 310 plane flown at 1666 m above mean terrain (AMT) with a forward speed of ±56.9 ms^{-1} and a scan swath of 15°. The instrument collected near infrared (1064 nm) laser returns at a nominal

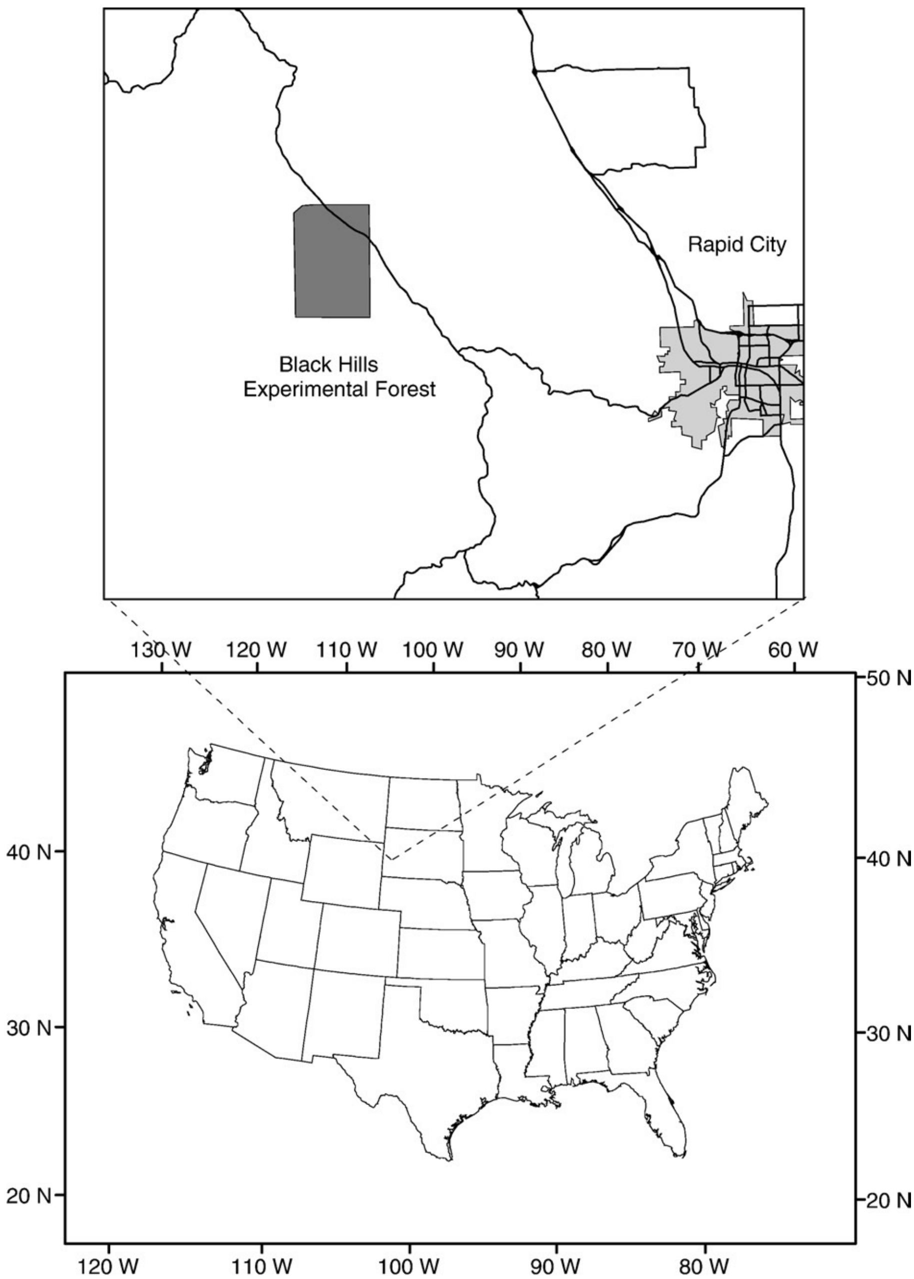

Fig. 1. Study site location.

post-spacing of 4.0 m. Laser return signals were recorded at a rate of 15 kHz and had an illuminated footprint of ~56 cm in diameter. A vertical accuracy of ±15 cm and a horizontal accuracy of ±25 cm for the return data were achieved by correcting flight lines for roll, pitch, and yaw using data obtained from the lidar sensor and inertial measurements from a dual-frequency onboard GPS antenna. Vertical accuracy of the lidar data was confirmed using GPS survey points located throughout the study area (Rowell et al., 2006).

All recorded returns (up to five per laser pulse) were used in the lidar data analysis. Using multiple-return discrete lidar allows for return signals to be potentially received from multiple vegetation layers because portions of the pulse may penetrate the upper canopy, traveling through gaps between leaves and branches. Pulse energy reaching below the canopy may strike and provide return signals from understory elements (e.g. shrubs and sub-canopy trees) and frequently also the ground surface.

Ground or 'bare earth' laser returns were delineated from aboveground (vegetation) returns by employing a combination of a 'virtual deforestation' algorithm (Haugerud & Harding, 2001) and a block minimum algorithm available in the TerraScan software suite (Terrasolid, Helsinki, Finland). Rowell et al. (2006) provide further detail regarding the surfacing procedures used for this dataset. The resulting bare earth laser returns were used to develop a triangulated irregular network (TIN) representing the land surface within a GIS. This intermediate TIN data product was used to calculate a surface that estimates an assumed slope between points to provide a ground surface representation. The bare earth TIN was then converted into a high resolution (0.25 m) raster. An Inverse Distance Weighted (IDW) interpolator was used to create a high resolution (0.25 m) raster of aboveground returns. Using the high resolution raster ensured that in most instances, adjacent returns were not aggregated into an average height value (thus preserving height values for the original returns) because they are nominally spaced at 4 m between pulses. Additionally, such a high resolution raster only marginally affects the horizontal position of the laser returns (with nominal offsets of ±0.10 m).

Vegetation heights were estimated from the lidar data by subtracting the high resolution bare earth raster from the high resolution raster of aboveground returns. The resulting 0.25 m raster of vegetation heights represented the height above land surface for the aboveground laser returns. The raster of vegetation heights was then converted back to a dataset of vectorized return heights for use in further data analysis.

Multispectral data were obtained for the study area in August 2002 using the IKONOS earth imaging satellite (http://www.geoeye.com). The IKONOS sensor records reflected radiation in four wavebands: blue (0.45–0.52 µm), green (0.51–0.60 µm), red (0.63–0.70 µm), and near infrared (0.76–0.85 µm). Multispectral data were available at 4 m resolution. A false-color composite image was produced from the data, from which patches of deciduous aspen tree cover could be delineated from areas dominated by Ponderosa pine. Image analysis benefited from the weather pattern over the period preceding data acquisition because below average precipitation resulted in complete grass senescence by the late summer. As a result, dry senesced grassy areas could be readily discriminated from areas with deciduous canopy cover using the available IKONOS bands.

2.3. Selection of field sites

In our selection of field sites, we focused on forested areas containing a layer of shrubs and/or young trees because two bird species in the BHEF upon which we later focus our analysis use this vegetation layer for foraging and/or nesting, and because we intended to test the utility of lidar in determining vegetation heights at the shrub level.

Lidar vegetation height data were subset into half-meter vertical intervals for use in identifying areas with a layer of shrubs and/or young trees. Lidar data were examined over the extent of the BHEF and used to identify areas containing vegetation at specific height intervals. Through field reconnaissance we identified two prominent vegetation layers that were not part of the mature tree canopy: 0.5–2.0 m, characterized by woody shrub species, tree seedlings, and tree saplings; and 2.0–9.0 m, characterized by tree saplings and poles, commonly Ponderosa pine and quaking aspen. Vegetation height interval summaries were examined and used to identify candidate areas where the 0.5–2.0 m vegetation layer was the dominant shrub/young tree layer as determined by percent cover, and areas where the 2.0–9.0 m vegetation layer was the dominant shrub/young tree layer. These candidate areas were then considered in the selection of sites where we would monitor birds. The 4-m IKONOS imagery was used to visually identify potential patches of deciduous trees occurring within the conifer-dominated landscape. These patch locations were subsequently verified through field visits. Lastly, using lidar data, we identified areas with few or no shrubs and/or young trees. These areas are generally open fields dominated by grasses and forbs with some scattered shrubs and trees interspersed throughout.

We defined sites as areas within a 100-m radial distance from a central bird count location. Each candidate site had to meet specific criteria to be designated as a bird point count site. Site centers were at least 200 m apart from each other and at least 100 m from a road. Forested sites contained no more than 40% tree canopy cover as determined using a densiometer at the site center, to allow for the emergence of understory species. Candidate sites that met the above criteria were stratified into three broad groups: 1) sites with a prominent 0.5–2.0 m vegetation layer, 2) sites with a prominent 2.0–9.0 m vegetation layer, and 3) sites with few or no shrubs and/or young trees. Using the IKONOS dataset, candidate sites in groups 1 and 2 were further subdivided into those dominated by Ponderosa pine and those dominated by quaking aspen, resulting in five *a priori* habitat types: 1) prominent 0.5–2.0 m vegetation layer, aspen dominated ("low aspen"), 2) prominent 2.0–9.0 m vegetation layer, aspen dominated ("high aspen"), 3) prominent 0.5–2.0 m vegetation layer, pine dominated ("low pine"), 4) prominent 2.0–9.0 m vegetation layer, pine dominated ("high pine"), and 5) few or no shrubs and/or young trees ("open"). While "low" and "high" candidate sites were defined by the dominant sub-canopy vegetation layer, some vegetation from the other sub-canopy layer was still present in many of the sites, particularly at the far end of the 100 m radial buffer. Likewise, some aspen-dominated sites contained conifers, and some pine-dominated sites contained aspen, although pine tended to be highly dominant in certain areas with no deciduous tree component.

After areas containing habitat types were identified, bird count sites were randomly selected within each of the five habitat types. Ten sites were selected per habitat type, with the exception of the "high aspen" habitat type, which contained eleven sites. Bird occurrence and vegetation survey data were collected at each of the resulting 51 sites.

2.4. Bird surveys

At each of the 51 sites, we performed variable radius point counts and recorded all birds seen or heard within a 5-minute survey. Point counts took place between 15 May and 7 July (Mills et al., 2000b) and count episodes occurred between 0600 and 1100 MDT. A total of five visits were made to each site over the two-year study; sites were visited three times in 2004 and twice in 2005. For each bird observed, we recorded species, sex, how it was detected (auditory and/or visual), and distance in meters from the observer to the bird. Birds flying over the site were noted but their numbers were not used in density estimates. The distance to each recorded bird was estimated by the observer, and recorded in one of five intervals: 0–10 m, 10–25 m, 25–50 m, 50–75 m, and 75–100 m. Observers recorded the time at the start and end of each count episode, as well as weather data (temperature, cloud cover, precipitation, and wind speed). Count episodes were suspended or not performed in periods of heavy precipitation, high winds, and/or extreme cold or heat. Observers used in this study were experienced in the visual and audible identification of birds and practiced the estimation of distances prior to conducting bird surveys. We used two observers in 2004 and two different observers in 2005, and varied count times and observers for each site to reduce temporal and observer biases.

2.5. Vegetation field data

Vegetation measurements were collected following protocols described for use in the Breeding Biology Research and Monitoring Database (BBIRD) program, a national, cooperative effort that uses standardized field methodologies for studies of nesting success and habitat requirements of breeding birds (Martin et al., 1997). Vegetation measurements were collected at each of the bird point count sites, as well as at three sites around each bird point count site. From each point count site, a field technician walked in a random direction, stopping 30 m from the point count center and establishing the second vegetation survey plot point for the site. Two additional vegetation survey plot points were established, each 30 m from the point count center, and 120° from the previous vegetation survey plot point as the field technician rotated around the point count center. This resulted in four vegetation survey points associated with each point count site, for a total of 204 vegetation survey sites. Locations of the bird count sites and vegetation survey sites were determined using a high-accuracy GPS. Differential corrections were later applied to the GPS measurements using data obtained from local reference stations. The horizontal precision of these corrected measurements ranged from 0.2 to 0.9 m and averaged 0.4 m. At each vegetation survey site we collected tree stem data within 11.3-m-radius plots as described by Martin et al. (1997).

2.6. Data analysis

2.6.1. Bird data

Bird species diversity for each count episode was calculated using the Shannon–Wiener information index ($H' = -\sum p_i \ln p_i$, where p_i is the proportion of the ith species) (MacArthur and MacArthur, 1961). A mean BSD value for each site was calculated by averaging the BSD estimates obtained for each of the five count episodes. The software program DISTANCE version 4.1 (Thomas et al., 2003) was used to estimate densities of all bird species at each point count site and to estimate densities of individual species by habitat type. DISTANCE can be used in the analysis of distance sampling data to estimate density and abundance of a population. The program was not used to estimate the density of individual species at individual point count sites because of an insufficient number of observations at that level. In these instances, a relative density was estimated based on the average number of birds per hectare that were recorded within specific radial distances of the point count center. In this paper, the term "density" is used to denote a count per unit area (Buckland et al., 2001), and is applied to counts of birds and vegetation features.

Differences in bird densities among habitat types were examined for two species common to the BHEF with a preference for the shrub/young tree vegetation layers: the Dark-eyed Junco (*Junco hyemalis*) and the Warbling Vireo (*Vireo gilvus*). We also examined the correlation of lidar-derived shrub density indices to the density of these two species at each site. The Dark-eyed Junco is a common ground-foraging and ground-nesting sparrow species that hops or walks slowly on the ground while searching for seeds and gleaning prey from the surface of the litter and lower shrub-level vegetation (Holmes & Robinson, 1988). The Warbling Vireo is a species that gleans insects and spiders from foliage. The western subspecies is commonly found in riparian areas, although it can also be found in non-riparian areas with a significant deciduous tree component (Hutto & Young, 1999).

2.6.2. Vegetation structure indices

Vegetation structure indices were calculated from the field survey and lidar-derived data to allow comparison between the two datasets. Indices related to tree stem density and tree vegetation density were calculated from the field survey data. For the tree stem density index, we counted the number of tree stems >2.0 m above ground and >8 cm at diameter breast height (DBH) within an 11.3 m radius circle centered on each survey point (Martin et al., 1997). A tree vegetation density index was calculated to provide a crude measure of the amount of tree vegetative matter that could potentially produce returns using the lidar instrument. This latter index may correspond more directly to the lidar data than the tree stem density index, because lidar returns will correspond not only to stems, but also to branches and leaves associated with the stems. The tree vegetation density index was calculated by summing the DBH of individual tree stems within the 11.3 m radius circle, under the assumption that trees with a larger DBH generally would have more vegetative matter than those with a smaller DBH. To compute a lidar-derived tree vegetation index equivalent, we counted the number of vegetation returns within the 11.3 m radius circle that were >2.0 m above ground, which provided a rough measure of the density of vegetation material present that was above the level of woody shrubs.

Relationships among lidar-determined vegetation structure indices and measures of avian diversity and density were examined using an index of shrub density, foliage height diversity (FHD), and total vegetation volume (TVV). To compute lidar-derived shrub density indices, we counted the number of vegetation returns that were between 0.5 and 2.0 m above ground within both 50 and 100 m radial buffers. The Shannon–Wiener information index was used to compute FHD ($H' = -\sum p_i \ln p_i$, where p_i is the proportion of horizontal vegetation in the ith layer (MacArthur & MacArthur, 1961)). Estimates of proportions of lidar returns within specified height intervals were produced to yield estimates of FHD within specific areas around point count sites. Six different FHD indices (Table 1) were calculated using various foliage height categories. Some of the categories were

Table 1
Pearson's product moment correlation coefficients calculated between foliage height diversity index and bird species diversity index

Buffer radius	Foliage height diversity category [a]					
	A	B	C	D	E	F
50 m	0.293*	0.340*	0.230	0.369**	0.352*	0.276*
100 m	0.183	0.355*	0.265	0.340*	0.346*	0.340*

[a] Height intervals for FHD categories: A: 0–2, 2–9, 9+ m. B: 0–2, 2–9, 9–15, 15+ m. C: 0–5, 5–10, 10–15, 15–20, 20+ m. D: 0–2, 2–5, 5–10, 10–15, 15+ m. E: 0–1, 1–2, 2–5, 5–10, 10–15, 15+ m. F: 0–2.5, 2.5–5, 5–7.5, 7.5–10, 10–12.5, 12.5–15, 15–17.5, 17.5–20, 20+ m. *$p<0.05$. **$p<0.01$.

suggested in the literature (e.g. Hashimoto et al., 2004; Willson, 1974) and others were experimental. Our FHD indices ranged from three layers of foliage for category A to nine layers for category F. For each FHD category, we calculated a separate index from the data for both a 50 m and a 100 m radial buffer around each bird point count site. Correlations were computed between FHD indices and BSD indices for all categories and for each buffer radius. The total number of vegetation lidar returns (at all heights above ground) within specified circular buffers of each bird count site was used as an estimate of TVV. Each return represents vegetation of some kind, and thus summing the number of returns gave us an estimate of the volume of vegetation present from the grass/forb/shrub layer to the maximum tree canopy height within a given area. TVV estimates were correlated with estimates of the density of all bird species present within 50- and 100-m radius circular buffers.

2.7. Statistical methods

Scatterplots were used to visually examine relationships between variables and simple linear regression was performed between a single explanatory variable and a single response variable for observed linear relations. Pearson's product moment correlation coefficient and Spearman's rank correlation coefficient were used to examine the nature (positive or negative) and significance of linear relationships between field-collected vegetation indices and lidar-derived vegetation indices, and between vegetation indices calculated from lidar data and measures of bird species diversity and density. Pearson's and Spearman's correlation coefficients and significance values were similar for relationships examined; Pearson's correlation coefficients are provided in text and figures. Correlations with p values <0.05 were considered significant. The Wilcoxon–Mann–Whitney rank-sum test was performed to determine if the relative density of birds differed between habitat types. SAS version 9.1.3 was used for statistical analysis (SAS Institute Inc., Cary, North Carolina).

3. Results

3.1. Comparison of field-collected and lidar-derived vegetation indices

Correlations between the field-based tree stem density index and the lidar-derived tree vegetation index were significant ($r^2=0.51$, $r=0.716$, $p<0.001$, $n=204$; Fig. 2a), as were correlations between the field-based tree vegetation density index and the lidar-derived tree vegetation index ($r^2=0.68$, $r=0.822$, $p<0.001$, $n=204$; Fig. 2b).

3.2. Lidar-derived vegetation structure indices and measures of avian diversity and density

All correlations computed between FHD and BSD indices were positive (Table 1). Out of 12 correlations computed, 9 were statistically significant, though FHD did not explain much of the variation in BSD (r^2 values were ≤ 0.14). FHD estimates for vegetation height categories (B, D, and E) containing proportionally more foliage layers near the forest floor correlated most strongly with BSD. Total bird density was significantly correlated with the lidar-derived index of TVV within 50 m ($r^2=0.11$, $r=0.332$, $p=0.017$, $n=51$) and 100 m ($r^2=0.10$, $r=0.310$, $p=0.027$, $n=51$) radial buffers. The relative density of Dark-eyed Juncos and Warbling Vireos was significantly correlated with the shrub density index within 50 m ($r^2=0.40$, $r=0.632$, $p<0.001$, $n=51$) and 100 m ($r^2=0.33$, $r=0.578$, $p=0.001$, $n=51$) radial buffers. We further examined the relationship between FHD and TVV and found the two vegetation indices to be significantly correlated (e.g.

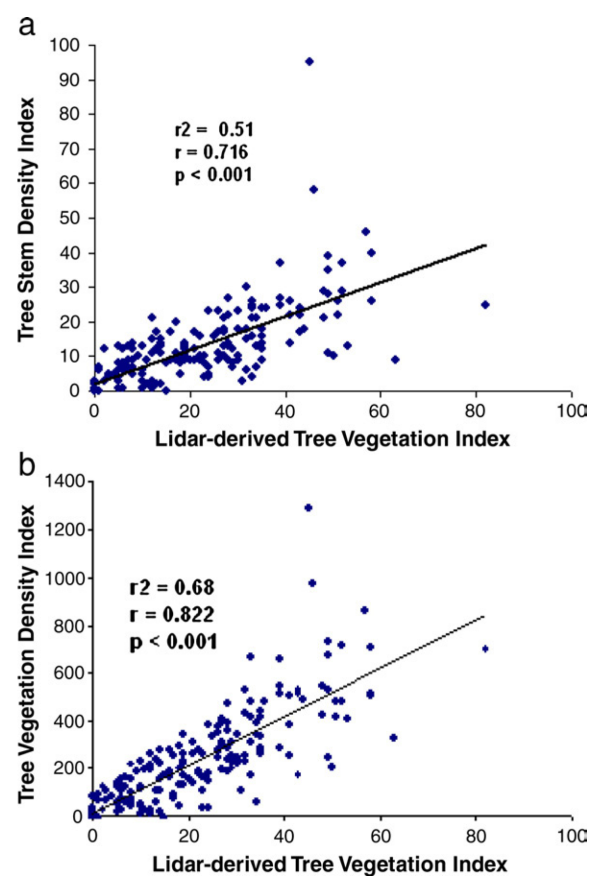

Fig. 2. Relationships between lidar-derived and field-determined vegetation structure indices: (a) lidar-derived tree vegetation index and field-determined tree stem density index, and (b) lidar-derived tree vegetation index and field-determined tree vegetation density index.

Table 2
Density estimates for birds (all species) within 100 m of point count sites, by habitat types

Habitat type	Density (birds/ha)	%CV	95% CI
"Low aspen"	46	8.3	(39, 54)
"High aspen"	36	15.3	(30, 49)
"Low pine"	20	16.7	(11, 21)
"High pine"	15	15.6	(15, 27)
"Open"	18	34.2	(9, 35)

[%CV = percent coefficient of variation; 95% CI = lower and upper bounds of 95% confidence interval].

$r=0.624$, $p<0.001$, $n=51$ for FHD height category D at a 50 m radial buffer).

3.3. Using lidar and spectral data in habitat assessment for individual species

Forty-three bird species were detected during count episodes conducted in 2004 and 2005. Total bird densities were higher at aspen-dominated sites than pine-dominated sites and those with few or no shrubs and/or young trees (Table 2). The relative density of Dark-eyed Juncos did not differ significantly between aspen-dominated and pine-dominated sites within either 50 m ($p=0.514$) or 100 m ($p=0.832$) radial buffers. Relative densities of Dark-eyed Juncos at "low pine" sites were significantly greater than those at "high pine" sites ($p=0.050$ at 50 m and $p=0.024$ at 100 m) and "open" sites ($p=0.018$ at 50 m and $p=0.045$ at 100 m). This relation generally did not hold for Dark-eyed Juncos in aspen sites. Relative densities at "low aspen" sites were not significantly different than those at "high aspen" sites ($p=0.475$ at 50 m and $p=0.567$ at 100 m). Relative densities at "low aspen" sites were significantly greater than those at "open" sites at 50 m ($p=0.010$), but not at 100 m ($p=0.339$).

Our examination showed that the relative density of Warbling Vireos was significantly greater at aspen-dominated forest sites than at pine-dominated sites within both 50 m ($p<0.001$) and 100 m ($p<0.001$) radial buffers. Relative densities were significantly greater at both the "low aspen" ($p<0.001$ at 50 m and $p<0.001$ at 100 m) and "high aspen" ($p<0.001$ at 50 m and $p<0.001$ at 100 m) sites than at "open" sites. Relative densities of Warbling Vireos at "low aspen" sites were significantly greater than those at "high aspen" sites ($p=0.030$ at 50 m and $p=0.008$ at 100 m), highlighting the importance of lower level vegetation for the species in the study area.

4. Discussion and conclusions

4.1. Lidar data can provide an alternative to field surveys for some vegetation structure indices

In this study, an index of tree vegetation volume estimated from lidar data was significantly correlated with two field-based indices. The tree vegetation density index had a higher correlation than the tree stem density index, perhaps because the tree vegetation density index came closer to representing the vegetation volume associated with trees, which may correspond better to the number of lidar returns from all parts of the tree (not just the 'bole' or main stem). Researchers using lidar data as an alternative to field-collected data need to consider a number of factors. First, users must consider the type of vegetation that is of interest. A discrete-return instrument may be useful in representing canopy heights, but may not be able to detect sub-canopy vegetation unless returns are available from laser pulses that penetrate through canopy gaps. In this study, we used all aboveground returns to characterize vegetation heights, and selected sites with a relatively open canopy. A discrete-return lidar instrument, even one producing multiple returns, may be unable to detect understory vegetation in a closed canopy forest of dense mature trees.

Users of airborne lidar also need to consider instrument specifications and settings, as well as the flying configuration used in data acquisition. For our study area, a nominal 4 m post-spacing between lidar pulses was sufficient to allow for the estimation of vegetation indices that we investigated for use in avian habitat assessment. Analyses of 1.5 m post-spacing data acquired for a portion of our study area indicated that using lidar data with a finer spatial resolution did not increase correlations between lidar-derived and field-based vegetation indices (data not shown). However, our analyses did not indicate the optimal sampling interval needed to calculate these or other vegetation indices. Researchers planning lidar data acquisition for vegetation structure analyses will need to consider the sampling interval that is most appropriate and capable of representing the vegetation of interest in a study area. A recent study by Chasmer et al. (2006) investigated how changes in emission frequencies and laser pulse properties such as laser pulse energy and pulse width determine the likelihood that laser pulses will penetrate forest canopy. An improved characterization of vegetation structure may be possible with changes in these settings, as well as through the development of new methods for modeling vegetation heights from laser pulse returns. For example, advanced methods for determining near-surface vegetation using lidar data (Hopkinson et al., 2006) may prove useful for improving habitat mapping for ground-dwelling bird species.

4.2. Lidar-derived vegetation structure indices can be used to investigate avian diversity and related factors

Our analysis showed that FHD is positively correlated with BSD; however, correlations were not statistically significant in all height categories, and corresponding r^2 values were low for all relations. The highest correlations between FHD and BSD were observed when the FHD categories used in the analysis contained proportionally more foliage layers near the forest floor (<5 m), suggesting that this layer may be important when considering the diversity of bird species in the BHEF.

Caveats concerning the use of FHD and BSD are well documented. Willson (1974), for example, found correlation between these two variables (Spearman's rank correlation $r_S=0.856$) when using a mixture of sites from forested areas and shrub-grass areas with scattered trees in Illinois, but found no correlation when examining only forested sites. Erdelen (1984) reported a regression line with $r=0.390$ ($p=0.073$) between FHD and BSD for primarily forested plots near Cologne, Germany, but the correlation was lower when three low-vegetation plots were removed from the analysis ($r=0.179$; $p=0.464$). The sites used in our study were primarily forested, but the "open" sites consisting of grasses/forbs with scattered shrubs and trees generally had lower values for both FHD and BSD and contributed to the strength of the correlations between the two variables.

Erdelen (1984) discussed how the selection of the number of vegetation height subdivisions used and differing field methods used to collect FHD data may also influence the value of this variable. Using more height layers usually results in greater values for FHD. We varied the number of layers used in calculating FHD from three to nine, which resulted in an increase in FHD values, but did not increase the value of the correlation with BSD.

It has been suggested that information indices such as FHD and BSD may lack biologically meaningful explanation (Willson, 1974) and may hide important information by combining other measures that can be examined separately (James & Rathbun, 1981). Simpler vegetation structure indices such as those related to total vegetation volume have been proposed as potentially better predictors of bird occurrence measures than FHD (e.g. Karr & Roth, 1971; Mills et al., 1991; Verner and Larson, 1989; Willson, 1974). Mills et al. (1991), for example, found that an index of TVV was strongly correlated with breeding bird density in shrub and desert habitats of the southwestern United States. We examined the relationship between total bird density and TVV in our study area using lidar data to calculate the vegetation structure index. Our correlation values were significant but considerably lower ($r=0.332$ at 50 m and $r=0.310$ at 100 m) than those reported (range $r=0.866$–0.999) by Mills et al. (1991). Higher correlations were obtained between the relative density of Dark-eyed Juncos and Warbling Vireos and the lidar-derived shrub density index ($r=0.632$ at 50 m and $r=0.578$ at 100 m). This finding supports the idea that specific layers of vegetation may be important to individual species and groups of related species (guilds). In the BHEF, Dark-eyed Juncos and Warbling Vireos are members of a guild that may be generally described as "shrub-layer foraging". Denser vegetation in this layer resulted in a higher relative density of these bird species. Willson (1974) investigated the addition of guilds with increasing vegetation height complexity and provided a discussion of related issues.

The amount of vegetation present in an area is likely related to vegetation height and vertical arrangement in many cases. We found TVV and FHD to be significantly correlated with each other. Willson (1974) found FHD to be correlated with a measure of percent vegetative cover ($r_S=0.614$). Similarly, Verner and Larson (1989) found total crown volume (an index of foliage volume) to be related to FHD in a mixed conifer forest in California.

Our analyses using FHD and TVV showed that both the amount of vegetation and its vertical structure may account for variations in the diversity and density of birds in the BHEF. Likely underlying these observations are general relations between vegetation variables, resource availability, and inter-specific interactions. Lidar data may assist in providing for more uniform estimation of vegetation structure measures such as FHD and TVV, if similar methods are used in establishing vegetation heights and calculating vegetation indices from these heights. These indices may then facilitate comparisons of bird-vegetation relationships between habitat types and geographic areas.

4.3. Habitat assessments may be enhanced by using lidar data in combination with spectral data

Previous work by Hill et al. (2004) demonstrated the ability of lidar data to assist in habitat assessment for individual bird species. Our research showed similar results, with lidar data assisting in the determination of likely habitat for Dark-eyed Juncos and Warbling Vireos, and also allowing us to make some general observations concerning vegetation abundance and structure and its relation to bird occurrence. In the BHEF, sites with a prominent 0.5–2.0 m vegetation layer had higher total bird densities than those with a prominent 2.0–9.0 m vegetation layer in both pine and aspen-dominated habitat types. Sites with few or no shrubs and/or young trees showed the greatest variation in total bird density among habitat types. These sites also showed the greatest variability in vegetation distribution, from open fields to fields interspersed with trees, and some sites were adjacent to stands of tall trees, providing an edge effect. Bird species diversity was generally higher for these sites when calculated within a 100 m buffer radius than when calculated within a 50 m buffer radius.

Both Dark-eyed Juncos and Warbling Vireos were found to be significantly associated with areas that possessed a prominent 0.5–2.0 m vegetation layer as detected by lidar. This result is consistent with previous studies involving these species. Mills et al. (1995) reported that abundance of Dark-eyed Juncos tended to decline in forested landscapes of the BHNF as overstory cover increases. Increased overstory likely causes a reduction in light reaching the forest floor, which would subsequently result in less shrubby understory and suitable nesting and foraging habitat for Dark-eyed Juncos. Airola and Barrett (1985) found that in a mixed conifer forest of the Sierra Nevada in California, the Warbling Vireo preferred foraging in the lower canopy. The Warbling Vireo is strongly associated with deciduous shrubs, and is especially common in aspen stands (Hutto & Young, 1999). Rumble and Anderson (1996) reported greater arthropod abundance in areas of aspen/birch than in areas of Ponderosa pine within a 4380 ha portion of the Black Hills. Foliage gleaners such as the Warbling Vireo may take advantage of the greater arthropod abundance in aspen stands. Panjabi (2005) reported the Warbling Vireo as having the highest density among 24 species in aspen forests of the BHNF.

Traditional passive remote sensing data sources have been shown to complement active remote sensing technology like lidar in forestry research (e.g. Hudak et al., 2002; Chen et al., 2004), and similar approaches using both types of data are being applied in ecological studies. Hill and Thomson (2005) used a combination of information from spectral data sources and canopy height data from lidar to produce thematic classes containing information on tree and shrub species composition and structure for two woodland sites in the United Kingdom. Our habitat designations made using lidar data (for determination of three-dimensional forest structure) and multispectral imagery (for determination of predominant tree type) related well to occurrences of individual species. Dark-eyed Juncos were significantly associated with the prominent 0.5–2.0 m vegetation layer in pine-dominated stands, and Warbling Vireos were significantly associated with this same layer in aspen-dominated stands. The use of the IKONOS data was integral to the success of habitat designations made for these species, and similar integration of data sources may assist researchers in future habitat assessment studies. Furthermore, landscape scale analyses such as those presented in this study can complement broader scale remote sensing analyses of relations between vegetation greenness (i.e. plant productivity) and avian species richness and diversity (e.g. Hurlbert & Haskell, 2003).

Our habitat assessments for Dark-eyed Juncos and Warbling Vireos were simplistic. We only considered vegetation structure and predominant tree type in the selection of areas where the birds were likely to occur based on their natural histories. However, other factors influence the occurrence and density of birds in particular areas. Birds use a variety of resources within their breeding sites, and while the majority of their preferred breeding sites may have specific vegetation structural characteristics, there are likely thresholds of vegetation cover and vertical complexity that the birds respond to that we did not detect in this study. At the site level, bird presence will be influenced by a number of factors, including tree and shrub species diversity, amount and configuration of overstory cover, and ground cover type (e.g. grasses, forbs, litter, and bare earth) and abundance. At the landscape level, factors such as fragmentation/edge effects, patch size, and forest management practices also influence the presence of birds. In conjunction with a consideration of these other factors, lidar may provide useful information that can increase the ability to characterize suitable habitat for a variety of species across broad spatial extents.

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