Modeling forest songbird species richness using LiDAR-derived measures of forest structure

Adrian A. Lesak [a,*], Volker C. Radeloff [a], Todd J. Hawbaker [a], Anna M. Pidgeon [a], Terje Gobakken [b], Kirk Contrucci [c]

[a] *Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, 1630 Linden Drive, Madison, WI 53706, USA*
[b] *Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway*
[c] *Ayres Associates Inc., 1802 Pankratz Street, Madison, WI 53704, USA*

ABSTRACT

Conservation of biodiversity requires information at many spatial scales in order to detect and preserve habitat for many species, often simultaneously. Vegetation structure information is particularly important for avian habitat models and has largely been unavailable for large areas at the desired resolution. Airborne LiDAR, with its combination of relatively broad coverage and fine resolution provides existing new opportunities to map vegetation structure and hence avian habitat. Our goal was to model the richness of forest songbirds using forest structure information obtained from LiDAR data. In deciduous forests of southern Wisconsin, USA, we used discrete-return airborne LiDAR to derive forest structure metrics related to the height and density of vegetation returns, as well as composite variables that captured major forest structural elements. We conducted point counts to determine total forest songbird richness and the richness of foraging, nesting, and forest edge-related habitat guilds. A suite of 35 LiDAR variables were used to model bird species richness using best-subsets regression and we used hierarchical partitioning analysis to quantify the explanatory power of each variable in the multivariate models. Songbird species richness was correlated most strongly with LiDAR variables related to canopy and midstory height and midstory density ($R^2 = 0.204$, $p < 0.001$). Richness of species that nest in the midstory was best explained by canopy height variables ($R^2 = 0.197$, $p < 0.001$). Species that forage on the ground responded to mean canopy height and the height of the lower canopy ($R^2 = 0.149$, $p < 0.005$) while aerial foragers had higher richness where the canopy was tall and dense and the midstory more sparse ($R^2 = 0.216$, $p < 0.001$). Richness of edge-preferring species was greater where there were fewer vegetation returns but higher density in the understory ($R^2 = 0.153$, $p < 0.005$). Forest interior specialists responded positively to a tall canopy, developed midstory, and a higher proportion of vegetation returns ($R^2 = 0.195$, $p < 0.001$). LiDAR forest structure metrics explained between 15 and 20% of the variability in richness within deciduous forest songbird communities. This variability was associated with vertical structure alone and shows how LiDAR can provide a source of complementary predictive data that can be incorporated in models of wildlife habitat associations across broad geographical extents.

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1. Introduction

Threats to biodiversity such as habitat loss, fragmentation, and climate change are a major concern to science and society alike. However, these threats can only be addressed, and potentially mitigated, if we can understand and predict biodiversity patterns across large areas. Modeling biodiversity over such wide geographical extents is challenging but sound knowledge of species' ecological requirements coupled with the tools provided by remote sensing can provide a framework to achieve this goal. The diversity of songbirds is positively associated with the vertical distribution of foliage among forest vegetation layers (Anderson & Shugart, 1974; MacArthur & MacArthur, 1961; Willson, 1974). Differences in behavior and partitioning of resources such as nesting and foraging habitat by songbird species are likely mechanisms driving this relationship. The strong relationship between vegetation structure and songbird diversity has been empirically shown at fine scales but whether it holds over wider areas remains relatively unexplored and how to incorporate this relationship into landscape level models of songbird population dynamics remains largely untested. Remote sensing of forest structure via LiDAR presents a unique opportunity to refine models of the broad scale distribution of biodiversity.

There are several structural components of a forest that contribute to its faunal diversity. Forest attributes such as stand age, site

productivity, species composition, and disturbance history interact to shape forest structural traits including overstory height, stem and crown density and architecture, and horizontal and vertical foliage diversity. Forest structure in turn limits the range of vegetation layers available to forest songbirds and thus ultimately the amount and type of nesting sites and foraging substrates for forest songbirds. Additionally, forest structure moderates birds' exposure to predators, brood parasites, and adverse weather conditions.

Strong preferences for the presence or absence of certain structural characteristics within a forest are well-known for many forest bird species of eastern North America. Ovenbirds (*Seiurus aurocapilla*) for instance, prefer relatively mature forests with flat topography that have an open understory and thick leaf litter covering on the forest floor (Mossman & Lange, 1982; Van Horn & Donovan, 1994). In mixed forests, a mature coniferous component is necessary for Blackburnian (*Dendroica fusca*), Black-throated Green (*Dendroica virens*), and Pine Warblers (*Dendroica pinus* [Howe & Mossman, 1996; Morse, 1976; Niemi et al., 1997]). As most songbirds are insectivorous during the breeding season in North America, their preferred location and mode of foraging are important in determining their abundance in a particular stand. Flycatchers such as the Eastern Wood-Pewee (*Contopus virens*) reach higher densities in forests with open midstories that provide space for their sallying foraging technique (Crawford et al., 1981). The Least Flycatcher (*Empidonax minimus*) on the other hand, often perches and pursues insects from smaller trees in the subcanopy (Mossman & Lange, 1982) while the Acadian Flycatcher (*Empidonax virescens*) forages lower in the forest in areas with few shrubs and saplings (Bakermans & Rodewald, 2006; Mossman & Lange, 1982). Together, these studies show that forests with a range of vertical structural elements host a greater diversity of species.

The density of forested stands can also modify the foraging behavior of flycatching species. In forests with dense canopies in central Illinois, Great-crested Flycatchers (*Myiarchus crinitus*) and Eastern Wood-Pewees use significantly more aerial gleans of canopy foliage (as opposed to their typical fly-catching technique) than in restored open-canopy oak savannahs (Hartung & Brawn, 2005). Canopy foliage gleaning species such as the Cerulean Warbler (*Dendroica cerulea*) respond positively to canopy openings and emergent canopy trees. Similarly, the Northern Parula (*Parula americana*) is positively associated with trees taller than the main canopy such as American Sycamore (*Platanus occidentalis*) (Moldenhauer & Regelski, 1996). Bird species inhabiting early-successional forests like the Chestnut-sided (*Dendroica pensylvanica*) and Golden-winged Warbler (*Vermivora chrysoptera*) show preferences for stands of regenerating saplings and shrubs and forest edges (Confer, 1992). Many forest bird species have affinities for different arrangements of forest structure and measurement of these variables is important in describing and predicting their occurrence in forests.

Broad-scale modeling of forest songbird habitat has been limited because the measurement of forest structure has generally been restricted to small sample areas. When fine-scale forest structure data are incorporated into broad-scale assessments, the data must be generalized, or scaled up, potentially introducing considerable extrapolation error. The main limitation is that accurate field measurements are costly in terms of time and resources and therefore can only be gathered on a small fraction of the trees and vegetation present in a forest, thus precluding continuous data collection over extensive areas. Developments in remote sensing technology have enabled ecologists to expand their study to scales well beyond the stand; however these advances have often been at the expense of spatial detail (Turner et al., 2003). More importantly, commonly-used remote sensing technologies largely rely on spectral data only to provide two-dimensional representations of the landscape through which forest structure can only be coarsely inferred. Complementing these planar data with a third, vertical dimension of data describing habitat structure will greatly improve the characterization of wildlife habitat and the prediction of biodiversity across broad spatial extents. LiDAR can provide a three-dimensional representation of the Earth's surface and notably, the vegetation on and above it (Lefsky et al., 1999b; Næsset et al., 2004; Nilsson, 1996). Forest structure measurements from LiDAR are highly correlated with detailed field measurements (Næsset, 2002), and with relatively simple modeling procedures, allow high-resolution mapping of forest attributes over large areas (Gobakken & Næsset, 2004; Lefsky et al., 1999a; Zimble et al., 2003).

Information about forest structure is not only valuable for forest inventories, but also for habitat assessments, but in terms of mapping wildlife habitat, the use of LiDAR is in its infancy (Vierling et al., 2008). Discrete-return LiDAR was successfully used in Delaware to derive canopy height and closure for delineation of potential Delmarva fox squirrel habitat (Nelson et al., 2005). In farmland habitat, crop heights and field boundaries have been measured with LiDAR and were used to map Sky Lark (*Alauda arvensis*) habitat (Bradbury et al., 2005). The Laser Vegetation Imaging Sensor (LVIS), a high-altitude, large footprint, waveform LiDAR scanner provides forest structure indices of canopy height and variability that explain bird species richness with moderate success (Goetz et al., 2007). The same sensor was also successfully used to estimate the mean and maximum canopy height, both important in characterizing wildlife habitat in the montane forests of the Sierra Nevada in California (Hyde et al., 2006). Furthermore, horizontal and vertical forest structure derived from discrete-return LiDAR refined habitat suitability maps for the Capercaillie (*Tetrao urogallus*) in Switzerland (Graf et al., 2009).

In addition to habitat delineation and richness estimation, habitat quality can also be related to forest structure. In England, habitat quality measured as chick body mass, declined for Great Tits (*Parus major*) and increased in Blue Tits (*Parus caeruleus*) with increasing canopy height (Hill et al., 2004; Hinsley et al., 2002). However, this dependency interacted in such a way with the weather of the early breeding season that the relationship of Great Tit chick mass with forest structure reversed in warmer springs (Hinsley et al., 2006) when Great Tits bred in taller forests with higher prey abundance but less thermal cover. This study highlights the interplay of forest structure with important abiotic factors such as weather patterns driven by climatic forcing (e.g. the North Atlantic Oscillation). These recent successes in wildlife habitat mapping with LiDAR underscore the viability of this remote sensing technique as an important resource for ecologists but the extent to which it can be used for biodiversity assessment is uncertain.

Our goal was to explore new approaches to map biodiversity over large areas by modeling species richness (i.e. number of species) of forest songbirds and the richness within guilds of ecologically similar species using discrete-return LiDAR in mixed hardwood forests typical of the temperate regions of eastern North America. Furthermore, we wanted to determine the explanatory power of a number of LiDAR-derived forest structure metrics used in our models. Forest structure is but one of many factors influencing biodiversity. However, using the high resolution and wide spatial extent provided by LiDAR data to quantify structural habitat characteristics that are ecologically relevant to forest songbirds across large spatial extents can lead to a new understanding of how formerly site-specific, field-based measurements may be accurately captured at the scale of the landscape.

2. Methods

2.1. Study area

Our study area was in the Baraboo Hills (Sauk County, WI, USA), an elliptical ring of quartzite and sandstone ridges (elevation range: 240–450 m) prized for their large blocks of contiguous forest and their diversity of natural communities. They include the largest intact

upland forest in southern Wisconsin and were designated a National Natural Landmark in 1980 by the U.S. Park Service, and a Last Great Place in 1995 by The Nature Conservancy.

By 1880, most of the forests of the Baraboo Hills had been cleared. Mixed-age forests have since replaced the original forests as a result of agricultural abandonment and the establishment of protected areas. Today, forests are largely dominated by oak (*Quercus* spp.), maple (*Acer* spp.), hickory (*Carya* spp.), and ash (*Fraxinus* spp.) with pockets of northern mixed forests containing relict stands of white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula alleghaniensis*) in protected stream gorges. Agricultural and urban land covers dominate the Baraboo River valley that bisects the ring of hills.

We sampled 118 systematically-arranged plots established within two contiguous preserves, Devil's Lake State Park and the Nature Conservancy's Baxter's Hollow Preserve (Fig. 1). The total study area was approximately 6000 ha, of which 4580 ha were forested. Plots were spaced 300 m apart along transects and parallel transects were 600 m apart. All sampling plots were located in forested habitat at least 150 m from hard forest edges and roads.

2.2. Avian field data

We recorded the species composition of the bird community using variable-radius point counts conducted at the center of each sampling plot. To ensure precise co-registration between the LiDAR data and bird point count stations, plot locations were measured using a differentially-corrected GPS achieving an average horizontal accuracy of 0.57 m (Hawbaker et al., 2010). Counts were conducted by two trained observers in favorable weather conditions between the hours of sunrise and 10:00 (UTC-05:00 h). Each point count lasted 10 min with data collection commencing immediately upon arrival at plot center. Birds were detected by sight and sound and a radial distance to a solid reflective surface (e.g. tree bole, rock) at the approximate distance of each bird was measured with a laser range finder. Two visits at each of the 118 count stations were completed during the breeding season from May 31–July 1, 2006.

Overall species richness, defined as the total number of all songbird species detected over the course of both census visits, was used as the main dependent variable in our models. Additional dependent variables reflected the number of species in different guilds defined by three sets of life history traits. Species were assigned to guilds based on the literature (Blake & Karr, 1987; Ehrlich et al., 1988; Freemark & Collins, 1992; Poole, 2005) and experience gained over the course of the study (Table 1). First, species were classified according to the height of their nest or preferred nest placement substrate. We distinguished guilds for canopy, cavity, midstory, low, and ground nesting species. Second, four foraging guilds were used in this study according to their primary foraging behavior and substrate (Ehrlich et al., 1988). Foliage gleaners take mostly insect prey from leaves, flowers, buds, and small stems and twigs of vegetation. Ground foraging birds glean food from the soil, leaf litter, and low-growing vegetation. Bark gleaners drill, flake, peck, and pry prey from bark and wood of the trunks and limbs of trees. Aerial foragers mainly sally from perches or drop onto their prey but may also hover-glean or actively pursue insects in the air. And third, species were grouped into two guilds based on their primary habitat association with regard to edges in the forest. Because all of our plots were at least 150 m away from the nearest exterior forest edge, the forest edge guild included species that breed or otherwise use the early successional, or dense shrubby vegetation found at 'interior edges' associated with single tree gaps or small (<1 ha) openings in the forest. Forest interior species nest in and use mature closed canopy forests and often require large unbroken blocks of forest habitat.

Each species was assigned to one nesting guild, one foraging guild, and one edge/interior guild. A few species defied confident classification into some guilds. Black-capped Chickadee (*Poecile atricapillus*), Tufted Titmouse (*Baeolophus bicolor*), Blue Jay (*Cyanocitta cristata*), and American Crow (*Corvus brachyrhynchos*) exhibit a wide range of preference for foraging substrate and technique and thus a dominant technique was not assigned for these species and they were left out of analyses of foraging guilds. Our habitat guilds omitted several species that could not be classified as either forest interior or edge specialists. Other species excluded were the sole members of a particular guild such as the Ruby-throated Hummingbird, a nectar feeder, and the Eastern Phoebe, the only species to nest on rocky overhangs in our study area.

2.3. LiDAR data

LiDAR data were collected using a Leica ALS50 flown before leaf emergence in April of 2005 at an average altitude of 1981 m and flight speed of 241 km/h. The pulse frequency was 34,700 Hz and the beam footprint was 68.9 cm. The average density of pulses on the ground was 0.625 pulses/m^2. We used over 40 benchmarks and 700 control points in 8 land classes to assess accuracy of lidar point locations. Control points were collected using differential GPS base stations and real-time kinematic units. The horizontal accuracy of pulses was ±0.5 m and the root mean squared error of ground-truthed vertical accuracy was 15 cm. Up to three, but more commonly one or two returns were recorded per pulse.

We created a digital terrain model (DTM) consisting of a combination of the bare-earth LiDAR point dataset and compiled breaklines. After the DTM was prepared, a triangulated irregular network (TIN) was created with vertices at points on the DTM. The TIN allowed interpolation of values between DTM points that determined where contours and elevation values should be placed. The TIN also served as continuous surface for the final digital elevation model (DEM) creation. The TIN's surface was referenced to determine the elevation for highly dense sets of points. These sets of points were then divided into cells with each cell's elevation determined by an average of all the elevations sampled within its extent. The DEM derived resulted in a raster surface with a resolution of 5 m.

To classify the dataset into ground and vegetation returns, an automated routine was used that considered each return's intensity,
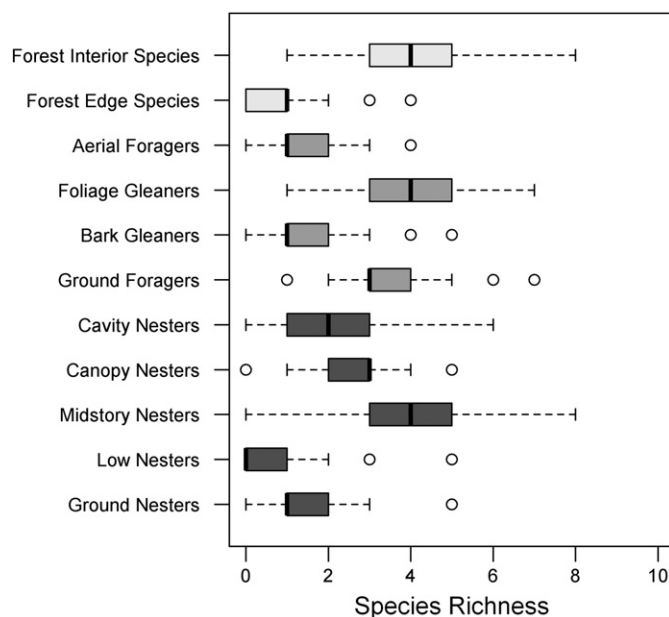

Fig. 1. Species richness of the eleven habitat, foraging, and nesting guilds. Open circles are values greater than 1.5 interquartile range widths from the first or third quartiles.

Table 1
Guild memberships of all songbird species encountered during the study classified by nest location (G, ground; L, low-shrub; M, midstory; CN, canopy; CV, cavity), foraging strategy (F, foliage glean; G, ground glean; B, bark glean; A, aerial pursuit), and habitat association (E, edge; I, interior) dashes indicate an unclassified species.

Species	Nest location guild	Foraging guild	Habitat guild	Average # detections	Standard deviation
Mourning Dove (*Zenaida macroura*)	M	G	–	0.030	0.119
Yellow-billed Cuckoo (*Coccyzus americanus*)	M	F	–	0.150	0.315
Ruby-throated Hummingbird (*Archilochus colubris*)	M	–	E	0.037	0.129
Red-bellied Woodpecker (*Melanerpes carolinus*)	CV	B	–	0.151	0.299
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	CV	B	–	0.004	0.046
Downy Woodpecker (*Picoides pubescens*)	CV	B	–	0.239	0.364
Hairy Woodpecker (*Picoides villosus*)	CV	B	I	0.138	0.251
Northern Flicker (*Colaptes auratus*)	CV	G	E	0.017	0.112
Pileated Woodpecker (*Dryocopus pileatus*)	CV	B	I	0.032	0.138
Eastern Wood-Pewee (*Contopus virens*)	CN	A	–	0.901	0.495
Acadian Flycatcher (*Empidonax virescens*)	M	A	I	0.371	0.597
Least Flycatcher (*Empidonax minimus*)	M	A	I	0.123	0.573
Eastern Phoebe (*Sayornis phoebe*)	–	A	–	0.017	0.112
Great Crested Flycatcher (*Myiarchus crinitus*)	CV	A	–	0.079	0.204
Yellow-throated Vireo (*Vireo flavifrons*)	CN	F	–	0.138	0.283
Red-eyed Vireo (*Vireo olivaceus*)	M	F	–	1.075	0.601
Blue Jay (*Cyanocitta cristata*)	CN	–	–	0.195	0.285
American Crow (*Corvus brachyrhynchos*)	CN	–	E	0.034	0.142
Black-capped Chickadee (*Poecile atricapillus*)	CV	–	–	0.380	0.456
Tufted Titmouse (*Baeolophus bicolor*)	CV	–	–	0.064	0.212
White-breasted Nuthatch (*Sitta carolinensis*)	CV	B	I	0.356	0.377
Brown Creeper (*Certhia americana*)	–	B	I	0.008	0.065
House Wren (*Troglodytes aedon*)	CV	G	E	0.008	0.065
Winter Wren (*Troglodytes troglodytes*)	CV	G	I	0.008	0.065
Blue-gray Gnatcatcher (*Polioptila caerulea*)	M	F	–	0.233	0.342
Veery (*Catharus fuscescens*)	G	G	I	0.305	0.439
Wood Thrush (*Hylocichla mustelina*)	M	G	–	0.490	0.555
American Robin (*Turdus migratorius*)	M	G	E	0.250	0.437
Gray Catbird (*Dumetella carolinensis*)	L	G	E	0.025	0.128
Cedar Waxwing (*Bombycilla cedrorum*)	M	F	E	0.079	0.193
Blue-winged Warbler (*Vermivora pinus*)	G	F	–	0.025	0.128
Chestnut-sided Warbler (*Dendoica pensylvanica*)	L	F	E	0.008	0.092
Black-throated Blue Warbler (*Dendroica caerulescens*)	L	F	I	0.004	0.046
Black-throated Green Warbler (*Dendroica virens*)	C	F	I	0.089	0.232
Blackburnian Warbler (*Dendoica fusca*)	C	F	I	0.013	0.103
Cerulean Warbler (*Dendroica cerulea*)	CN	F	I	0.064	0.191
Black-and-white Warbler (*Mniotilta varia*)	G	B	I	0.008	0.065
American Redstart (*Setophaga ruticilla*)	M	A	I	0.184	0.423
Ovenbird (*Seiurus aurocapilla*)	G	G	I	1.266	0.660
Louisiana Waterthrush (*Seiurus motacilla*)	G	G	I	0.034	0.156
Common Yellowthroat (*Geothlypis trichas*)	L	F	–	0.021	0.189
Hooded Warbler (*Wilsonia citrina*)	L	F	I	0.129	0.317
Canada Warbler (*Wilsonia canadensis*)	G	A	I	0.006	0.061
Scarlet Tanager (*Piranga olivacea*)	CN	F	I	0.451	0.459
Eastern Towhee (*Pipilo erythrophthalmus*)	G	G	–	0.021	0.137
Chipping Sparrow (*Spizella passerina*)	L	G	–	0.079	0.268
Field Sparrow (*Spizella pusilla*)	G	G	–	0.004	0.046
Song Sparrow (*Melospiza melodia*)	G	G	–	0.025	0.276
Northern Cardinal (*Cardinalis cardinalis*)	L	G	–	0.086	0.232
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	M	F	–	0.410	0.412
Indigo Bunting (*Passerina cyanea*)	L	F	–	0.038	0.187
Red-winged Blackbird (*Agelaius phoeniceus*)	L	G	–	0.017	0.184
Common Grackle (*Quiscalus quiscula*)	L	G	–	0.004	0.046
Brown-headed Cowbird (*Molothrus ater*)	–	G	–	0.629	0.484
Baltimore Oriole (*Icterus galbula*)	C	F	E	0.008	0.065
American Goldfinch (*Carduelis tristis*)	L	F	–	0.073	0.175

identity (i.e. first, second, or third return), and coordinate value. Based on these factors and the values of surrounding points, the classification routine categorized the dataset into ground and vegetation datasets which we then verified by examining the datasets in profile and oblique views, using GRIDS, TINs, and contours as a guide to reclassify any errors in the automated classification.

Each vegetation LiDAR return (i.e. each return above the ground level) was attributed horizontal coordinates and an elevation. The height of vegetation returns were calculated by subtracting the elevation of the underlying DEM pixel from the return elevation. All vegetation LiDAR returns (including first, second, and third returns) were selected within a radius of 15.24 m (50 ft) of each plot center and their heights summarized. The summary statistics calculated included the mean and coefficient of variation (*CV*) of vegetation returns, and 10% quantiles of height above ground (h_i, where i = 0, 10, 20, 30…100, see Næsset (2002)), the proportion of all returns that were above 0.9 m (p_{veg}), and the proportion of returns contained within equally-spaced height divisions (hereafter, density proportions, [p_i, where i = 10, 20, 30…100]) between 0.9 m and the maximum height value.

Previous research in the study area showed strong relationships between LiDAR data and overstory forest structure measured in the field (Hawbaker et al., 2010). Basal area, which averaged 29.1 m²/ha in our study area, was modeled by LiDAR return density and return

height variables with an R^2 of 0.46. Of trees greater than 12.7 cm (5 in.) in diameter, Lorey's mean tree height (basal area-weighted tree height) averaged 21.3 m with 25% and 75% height quartiles of 19.4 m and 23.3 m, respectively. Tree height was highly correlated with LiDAR return density and height variables at or near the top of the LiDAR return distributions ($R^2 = 0.63$). Sawtimber volume averaged 140 m³/ha in the study area and was predicted with success using cumulative LiDAR return density and return height quantiles at low and intermediate regions of the distribution ($R^2 = 0.65$). These prior results suggested that the LiDAR data, and the metrics that we used, were well correlated with important structural attributes, but the relationship between the LiDAR data and songbird diversity remained untested. We used the LiDAR height quantile variables and a modified version of the return density variables from the forest inventory study as predictors, and we also tested whether the songbirds responded to coarser structural divisions of forest physiognomy.

In addition to the 10 return proportion bins, we also attempted to characterize the three main layers of the vegetation that studies of avian habitat typically focus on, i.e., the understory, the midstory, and the canopy. Different bird species are associated with these three layers (Dickson & Noble, 1978) and we wanted to test if an estimate of the LiDAR returns in these three classes would improve the predictive power of our models.

It is important to note that the height of these three vegetation layers can differ greatly among different forests. In other words, a 15-m tall tree can be part of the midstory in a tall forest, but part of the canopy in another. This is why we did not summarize returns within absolute height thresholds, but rather the returns within aggregates of our 10 return proportion bins. Based on our field work, and natural history of the birds in our study area, we defined the understory as

$$p_{under} = \sum_{i=10}^{i=20} p_i, \tag{1}$$

where p_{under} sums the bottom two proportional density bins at each location. The midstory was defined as the summation of the third through the sixth proportional density bins,

$$p_{mid} = \sum_{i=30}^{i=60} p_i, \tag{2}$$

and the canopy by the remaining bins at the top of the density distribution,

$$p_{can} = \sum_{i=70}^{i=100} p_i. \tag{3}$$

To further capture the particular structural preferences of some bird species, the ratio of these components for each plot were calculated as well

$$r_{u:m} = p_{under} / p_{mid}, \tag{4}$$

$$r_{u:c} = p_{under} / p_{can}, \tag{5}$$

$$r_{m:c} = p_{mid} / p_{can}. \tag{6}$$

Return height diversity was calculated using the proportion of returns in each of the equally-spaced proportional density bins by means of the Shannon diversity index

$$H' = -\sum_{i=10}^{100} p_i \log p_i. \tag{7}$$

2.4. Statistical analysis

Best-subsets regression was used to derive multivariate model sets for each response variable. However; due to the number of LiDAR predictor variables and their potential collinearity, we created a subset of input variables for each analysis. Of the 35 predictor variables, we found high univariate correlations (up to $R = 0.99$) among variables of the same class (e.g. height quantiles). Therefore we chose three to five variables based on hypothesized relationships between the LiDAR variables and the ecological preferences of the songbird guild of interest.

We expected the total richness of songbirds to increase in tall, mature forests with many, well-distributed layers of foliage; therefore we selected as predictors the mean and coefficient of variation of return height, the number of non-ground returns (n_{above}), the diversity of returns across all density bins, and two upper canopy height quantiles. To support a variety of nesting and foraging guilds, a diversity of foraging and nesting sites and substrates must be present. In a mature, closed canopy forested setting, the likeliest descriptors of such conditions in our LiDAR data would be those associated with greater height, a surrogate for older or more productive forests. Therefore we predicted that more guilds would be present where the mean and variability in LiDAR return heights was higher with a high number of returns suggesting vegetation thickness and even distribution of this vegetation throughout the vertical profile of the stand. Because many of the birds nesting in the forests of our study area are canopy dwellers and nesters, we also included variables that represented a well-developed canopy, specifically h_{100}, p_{70}, p_{80}, and p_{90}.

The most common ground nesters in our study area are also associated with large, contiguous tracts of forest. The presence of ground-nesting species that use interior edges of forests (e.g. Eastern Towhee, Song Sparrow) increased the diversity of this guild. Consequently we expected ground nester richness to increase with greater mean return height, canopy height (h_{100}) as well as variables related to ample understory cover (h_{10}, p_{10}, and p_{20}). We hypothesized that low-nesting species would respond positively to vegetation density in the understory (represented by p_{10}, p_{20}, p_{under}, and $r_{u:c}$) and negatively to higher values of the lower height quantiles (h_{00}, h_{10}, h_{20}) which would suggest that the understory may also be underdeveloped. For midstory and subcanopy nesting species, we expected higher species richness where a tall canopy (Mean, h_{90}, h_{100}) occurs over ample nesting substrates immediately below (h_{50}, h_{60}, p_{mid}). We also hypothesized that richness of canopy nesters would increase in areas of tall mature forests with many vegetation returns, especially in the canopy. In models of canopy nester richness we included quantiles in the upper portion of the return distribution (h_{70} through h_{100}) density proportions p_{80} and p_{90}, the aggregated canopy density variable (p_{can}), as well as summary variables such as the mean and CV of return height, and the number of vegetation returns (n_{above}). Because canopy nesters need mature forest stands containing dead and senescent trees of sufficient diameter to allow for cavity excavation in the bole and large limbs, we chose LiDAR variables that have been shown to predict tree bole diameter in our study area (Hawbaker et al., 2010). These variables were the coefficient of variation in return height, h_{00}, h_{70}, h_{90}, h_{100}, p_{10}, and p_{90}.

The number of foraging guilds is dependent on the availability of foraging niches present on the ground, through the understory, midstory and canopy, but also in the spaces between vegetation and in the bark and wood of trees. We expect this kind of diversity of foraging locations in mature forests with heterogeneous structure. Thus we chose variables that may reflect this such as the Shannon diversity index of the proportional return density variables, the coefficient of variation in return heights, the number of vegetation returns, and the mean height of returns. Foliage gleaner diversity was expected to peak where more vegetation returns were recorded

(n_{above}), where there is an even distribution of foliage (i.e. higher Shannon index of foliage return diversity), and a large proportion of vegetation returns in the canopy where the majority of foliage gleaning species nest and forage (p_{can}). Some of the common ground foragers in our study area such as the Ovenbird, Veery (*Catharus fuscescens*), and Louisiana Waterthrush (*Seiurus motacilla*) inhabit extensive tracts of mature deciduous forests and thus we predicted they would respond positively to LiDAR variables associated with taller forests (h_{100}) but also with a low midstory layer and relatively clear understory below (negative relationship with $r_{u:m}$). Tall, large-diameter trees have greater surface area and the oaks, maples, and hickories in our study sites have deeply furrowed bark. Previous LiDAR research in the study area revealed a positive relationship between some of our LiDAR variables and tree diameter and stand basal area (Hawbaker et al., 2010). We included five of these variables in our analysis of this guild (CV, h_{00}, h_{50}, h_{70}, and h_{90}). We predicted aerial foragers would respond positively to a dense canopy (p_{80}) with a higher midstory component (h_{30} and h_{60}) and negatively to high midstory density (p_{30} and p_{50}), testing the hypothesis that forest-dwelling aerial insectivores would prefer forests with ample room to pursue insects underneath the canopy layer.

We speculated that the richness of songbird species of the forest interior would increase in tall, canopy-dominated forest with a high number of vegetation returns distributed throughout the vertical profile, and thus we included the LiDAR variables that best represent these physiognomic conditions (*Mean*, *CV*, p_{veg}, *Shannon diversity index*, h_{100}, p_{80}, p_{90}, and p_{can}). We hypothesized that richness in edge-inhabiting species would be higher in areas with a higher proportion of low LiDAR returns (p_{10} through p_{40}) indicating the dense low vegetation profile found along edges and canopy gaps. A lower mean return height could suggest greater canopy penetration and dense low

vegetation while a high *CV* may capture the variability in return heights created by non-forest cover. Fewer vegetation returns (p_{veg}) would be expected where the overstory is sparse or absent.

In addition to the variables described above, we included variables of different types (i.e. statistical summary variables, height quantile variables, density proportions, structural variables, and structural ratios) and chose variables with higher univariate correlations with the dependent variable while maintaining low collinearity with other independent variables (Table 2). The reduced variable sets included 11 to 13 predictors that were input into best subsets regression (leaps package, R version 2.7.2, R Development Core Team (2008)). We limited output models to five or fewer variables to avoid over-fitting and because model fit most commonly peaked at or below this threshold. The positive or negative relationships of predictor variables to the response variable in multivariate models were compared to those of the univariate correlations to aid interpretation.

For each response variable, all models were ranked based on the adjusted coefficient of determination (R^2_{adj}), and we analyzed the five best models in detail. In order to determine the importance of each variable in the top models selected via best subsets regression, we noted the number of times each predictor variable occurred in the five best models. We also reported the significance level for each response variable (partial p). A final measure of variable importance was obtained from hierarchical partitioning of the variables in the top model (Chevan & Sutherland, 1991). This resulted in a measure of the independent contribution (IC) of each variable when taken in the context of all permutations of other predictors in the model reported as a percentage of independent variance explained.

We examined residuals from the top models for the presence of autocorrelation in the richness estimates of each guild, among locations, by inspection of semivariograms. The majority of semivariograms were

Table 2
Correlation coefficients (Pearson's r) of variables input into best subsets regression analysis for each response variable.

Explanatory variable	Songbird richness	Nesting guild richness							Foraging guild richness					Habitat guild richness	
		# Nesting guilds	Ground	Low	Ground and low	Midstory	Canopy	Cavity	# Foraging guilds	Foliage gleaner	Ground	Bark	Aerial	Edge	Interior
Mean	0.235	0.003	0.081	−0.186	−0.073	0.291	0.240		0.046	0.150	0.146	0.034	0.257	−0.013	0.272
CV	−0.101	0.031			0.111		−0.239	0.014	−0.058		0.009	0.032	−0.160	0.036	−0.168
p_{veg}	0.203	0.085	0.075			0.284	0.222		0.164	0.171	0.026	−0.009	0.285	−0.233	0.322
H'	−0.093	−0.003					−0.197		−0.049	−0.132	0.026			0.112	−0.131
h_{00}		−0.099		−0.104				−0.012				−0.039			
h_{10}			0.017	−0.164	−0.109										
h_{20}				−0.162	−0.085	0.199									
h_{30}						0.223			0.053		0.101		0.223		
h_{40}	0.206				−0.089	0.252	0.250								
h_{50}	0.227					0.296				0.182		0.042			0.251
h_{60}	0.226			−0.205	−0.097	0.309					0.144		0.262		
h_{70}	0.237		0.090	−0.199		0.314	0.211	0.043		0.156		0.049			0.262
h_{80}	0.251		0.124			0.322	0.189				0.189				
h_{90}	0.270		0.143			0.316	0.184	0.066			0.218	0.059			
h_{100}	0.322	0.079	0.149			0.340	0.180	0.087	0.069	0.134	0.280		0.262	0.094	0.304
p_{10}			0.071	0.113	0.124			−0.043	−0.094					−0.012	
p_{20}			−0.028	0.234	0.142			0.111				0.087	−0.226	0.150	−0.210
p_{30}								0.106					−0.158	0.148	
p_{40}			−0.103	−0.104						−0.167			−0.233	0.184	−0.203
p_{50}	−0.197							−0.154	−0.092	−0.166		−0.172	−0.182		
p_{60}		0.075													
p_{70}	0.178	0.169			0.196	0.185			0.128		0.211	−0.091		0.119	
p_{80}		0.135	−0.087				0.172		0.164				0.242		0.131
p_{90}		−0.162		−0.241	−0.193		0.134	−0.047		0.100				−0.134	0.127
p_{100}		−0.069							−0.096		−0.098	0.075			
p_{under}			0.037	0.037	0.151										
p_{mid}						−0.169				−0.180		−0.082			
p_{can}							0.264			0.144			0.234	−0.124	0.194
$r_{u:m}$											−0.032	0.097			
$r_{u:c}$			0.060	0.060	0.169		−0.270	0.052	−0.104						
$r_{m:c}$						−0.191				−0.176			−0.245	0.140	−0.193

essentially flat and 95% confidence intervals overlapped at all lag distances for all semivariograms, thus no spatial structure was evident in the model residuals and the inclusion of spatial error terms was deemed unnecessary.

3. Results

We observed fifty-six songbird species from a total of 2495 individuals detected. The six most common species (Ovenbird, Red-eyed Vireo [*Vireo olivacea*], Eastern Wood-Pewee [*Contopus virecens*], Brown-headed Cowbird [*Molothrus ater*], Wood Thrush [*Hyocichla mustelina*], and Black-capped Chickadee [*Poecile atricapillus*]) accounted for 49% of detections and represented a range of nesting, foraging, and habitat guilds.

Overall songbird species richness ranged from 5 to 20 species per plot with a mean species richness of 11.7 and mode of 10 species. Midstory-nesting birds such as the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Wood Thrush represented the nesting guild with the most species, followed by canopy, cavity, ground and low nesting birds, respectively (Fig. 1). The foraging guilds were dominated by foliage-gleaning and ground-foraging species, with fewer bark and aerial foragers. On average, we observed more than twice the number of forest interior-favoring species ($\bar{x} = 3.82$, $s = 1.64$, $n = 118$) as edge specialists.

The LiDAR data revealed a spectrum of forest structure represented by a wide range of return heights and densities across the Baraboo Hills. Height of the highest quantile (h_{100}) representing the height near the top of the canopy averaged 22.9 m across all plots and ranged from 15.6 to 31.4 m. The height of the 50th quantile averaged 16.2 m suggesting a majority of LiDAR returns were reflected high in the canopy of the mature mixed hardwood forests (Fig. 2).

The average density of LiDAR returns increased steadily with height of the proportional density bins (Fig. 3) and the highest proportions of LiDAR returns occurred in the five highest height quantiles (Fig. 2). This was expected given that we sampled closed canopy mature deciduous forest where the majority of the vegetation and its supporting limbs and branches are in the canopy. The understory component of our structural composite variables had the highest degree of variation ($CV = 67\%$), the lowest variability was in the canopy ($CV = 30\%$).

Some response variables showed a measure of spatial coherence with structure metrics across the study area (Fig. 4). Species richness was high in the forest interior which often coincided with taller forests having a moderately-developed midstory. Midstory nester species richness however, showed a counterintuitive pattern where
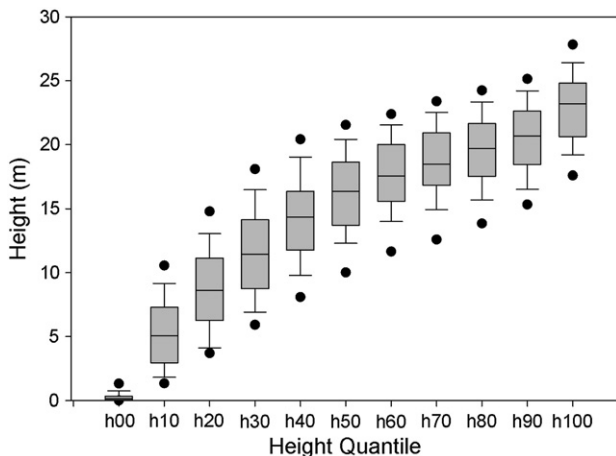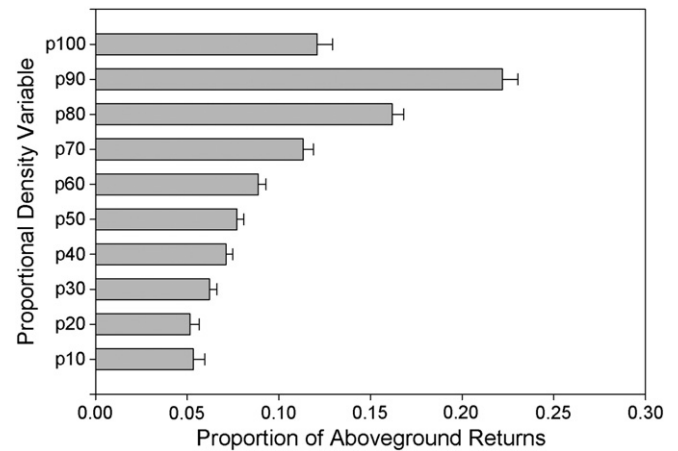

Fig. 3. Mean values (with standard error bars) of LiDAR density proportions, the percentage of LiDAR returns in 10 equally-spaced height divisions over each field plot.

higher species richness often occurred at plots with low midstory density and midstory to canopy ratios, suggesting that the availability of vegetation at this level may not be a primary habitat cue used in nest site selection by these species.

LiDAR variables associated with canopy height (h_{100}) and midstory density (p_{50}) and height (q_{60}) showed the greatest capacity to predict differences in overall songbird species richness (Table 3, $R^2 = 0.204$, $p < 0.0001$). The relationship with canopy height was positive, i.e., higher values of h_{100} resulted in higher species richness whereas height of the 60th quantile and proportional density of p_{50} were negatively related to species richness.

Some avian guilds showed greater response to LiDAR variables than others. Our models explained between 4.7 and 21.6% of the variability in richness in guilds. Some of the better-performing models encompassed all guild categories, including those for nest location, foraging technique, and habitat type.

The number of nesting guilds present in the songbird community was not explained well by LiDAR but the models of richness within a number of individual nesting guilds performed with some success. Low nesting species were most positively associated with the proportion of LiDAR returns in the understory with an independent contribution (IC) of 33.44% for p_{20} (partial $p < 0.01$) and less strongly associated with the density in p_{70} (IC = 23.95%, partial $p < 0.10$) and mean height of returns (IC = 15.26%, partial $p < 0.05$ [Table 3]). High canopy quantiles in the range of h_{80} to h_{100} (IC = 18.56–31.99%, partial $p < 0.05$,) as well as the ratio of midstory to canopy density proportions, occurred in at least 4 of the 5 top models predicting the number of midstory-nesting species. Canopy nesting species responded positively to the proportion of LiDAR returns in the composite variable that represented canopy returns (p_{can}, IC = 31.94%, partial $p < 0.01$) and h_{100} (IC = 18.17%, partial $p < 0.01$) but negatively to mean return height (IC = 19.53%, partial $p < 0.05$). Richness of ground nesting and cavity nesting species were poorly predicted by LiDAR variables.

The number of foraging guilds represented decreased with both mean LiDAR return height (IC = 21.89%, partial $p < 0.01$) and understory to canopy ratio (IC = 25.56%, partial $p < 0.01$), but increased with the highest height quantile (h_{100}, IC = 18.72%, partial $p < 0.01$). The foraging guilds with the most robust explanatory models were the ground ($R^2 = 0.149$) and aerial foragers ($R^2 = 0.216$). Ground foragers were positively associated with mean LiDAR return height (IC = 41.33%, partial $p < 0.001$), the variation in return height (CV, IC = 18.83%, partial $p < 0.01$), and the proportion of returns in the lower canopy (p_{70}, IC = 27.08%, partial $p < 0.10$). The aerial foraging guild was positively related to a range of LiDAR variables, including the proportion of vegetation in the canopy (p_{80}, IC = 23.38%, partial

Fig. 2. Box plot of LiDAR height quantiles which are the heights where each decile of the vertical lidar distribution occurs. Whiskers represent the 10th and 90th percentiles, black dots are the 5th and 95th percentiles.
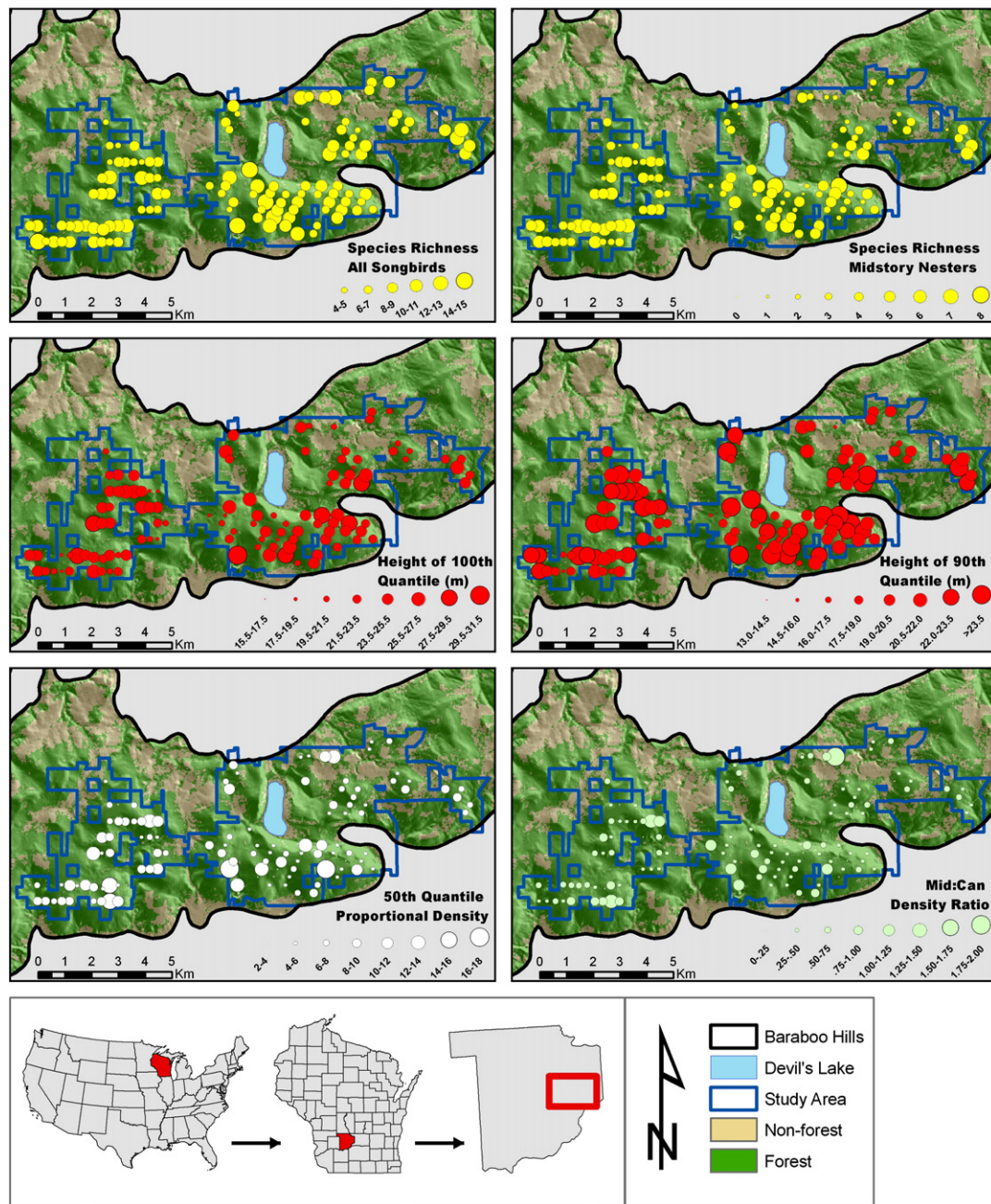
Fig. 4. Spatial distribution of total songbird richness and midstory nester richness along with four influential LiDAR predictor variables (h_{100}, h_{90}, p_{50}, $r_{m:c}$) included in their best-fitting models.

$p < 0.05$), top canopy height (h_{100}, IC = 29.85%, partial $p < 0.001$), and negatively related with understory density proportion (p_{20}, IC = 11.91%, partial $p < 0.05$) and the ratio of midstory returns to canopy returns ($r_{m:c}$, IC = 21.93%, partial $p < 0.01$) Richness of foliage gleaners and bark foragers were not well explained using LiDAR variables.

Among the better-performing models in our analyses were those for species richness of forest edge ($R^2 = 0.153$) and forest interior habitat guilds ($R^2 = 0.195$). Edge species richness was strongly negatively influenced by the proportion of LiDAR vegetation returns (p_{veg}, IC = 33.58%, partial $p < 0.01$). The proportion of returns from vegetation in the low levels of the forest (p_{20}, IC = 21.20%, partial $p < 0.01$) was an important factor positively contributing to edge species richness. Conversely, forest interior species were positively related to the proportion of vegetation returns (p_{veg}, IC = 29.49%,

partial $p < 0.10$) and were greater in number in the taller forests where h_{100} (IC = 32.13%, partial $p < 0.01$) was higher but negatively associated with LiDAR-derived indicators of the midstory, h_{50} (IC = 16.02%, partial $p < 0.05$) and $r_{m:c}$ (IC = 12.59%, partial $p < 0.05$).

4. Discussion

The bird community observed in our study is in many ways typical of those of Upper Midwestern deciduous forests, and is particularly rich in forest interior birds due to the relatively contiguous forests in the Baraboo Hills (Ambuel & Temple, 1983). Also, due to the presence of relicts of northern vegetation communities in some of the narrow protected stream valleys surveyed, species typical of more northern forests such as Blackburnian, Black-throated Green, and Canada Warblers were detected in close proximity to species with southern

Table 3

Best model results for all response variables (for all, n = 118). Bold variable names and coefficients represent those that occurred in at least 4 of the 5 top models selected using adjusted R^2 as the selection criterion in best-subsets regression. Stars indicate significance values (see footnotes). Independent contribution of each variable was determined by hierarchical partitioning, using R^2 as the goodness-of-fit criterion. Predictor variables were transformed when necessary.

Response Variable	Predictors	Coefficients	Independent Contribution (%)	R^2	R^2_{adj}	Model significance (p)
Songbird richness	(Intercept)	(8.538)[****]		0.204	0.176	<0.001
	h_{50}	0.150	10.68			
	h_{60}	**−0.307**[**]	14.52			
	h_{100}	**0.241**[****]	50.46			
	p_{50}	**−18.695**[***]	24.34			
Number of nesting guilds	(Intercept)	(6.560)[***]		0.083	0.060	0.082
	p_{veg}	1.024	8.13			
	h_{100}	0.003	4.70			
	p_{40}	**−2.890**	24.04			
	p_{90}	**−2.322**[***]	57.67			
	H'	−0.706	5.45			
Ground nester richness ($\log_{10}+1$)	(Intercept)	(0.286)[**]		0.110	0.070	0.021
	h_{70}	**−0.019**[**]	24.51			
	h_{80}	**0.021**[**]	32.28			
	p_{20}	−0.502	10.76			
	p_{40}	−0.364	12.58			
	$r_{u:c}$	0.286	19.87			
Low nester richness	(Intercept)	(−0.999)		0.142	0.104	0.004
	Mean	**0.142**[**]	15.26			
	h_{10}	−0.029	9.32			
	h_{70}	**−0.104**[**]	18.04			
	p_{20}	**5.684**[***]	33.44			
	p_{70}	**1.944**[*]	23.95			
Ground and low nester richness (sqrt)	(Intercept)	(0.545)		0.119	0.088	0.006
	Mean	**0.108**[****]	30.81			
	h_{10}	**−0.019**	12.90			
	h_{60}	**−0.077**[****]	32.22			
	p_{under}	**1.858**[**]	24.06			
Midstory nester richness	(Intercept)	(2.658)[*]		0.197	0.161	<0.001
	h_{70}	−0.313[**]	15.79			
	h_{80}	**0.663**[**]	18.56			
	h_{90}	**−0.506**[**]	19.46			
	h_{100}	**0.194**[***]	31.99			
	$r_{m:c}$	**−3.729**[***]	14.21			
Canopy richness	(Intercept)	(−0.795)		0.138	0.100	0.005
	Mean	**−0.306**[**]	19.53			
	CV	−0.086[**]	18.52			
	h_{70}	0.115[*]	11.85			
	h_{100}	**0.106**[***]	18.17			
	p_{can}	**6.906**[***]	31.94			
Cavity nester richness	(Intercept)	(2.689)[*]		0.122	0.082	0.012
	h_{00}	−0.059	2.30			
	h_{100}	**0.020**	9.25			
	p_{10}	**−10.844**[***]	26.67			
	p_{50}	**−7.250**[***]	31.68			
	$r_{u:c}$	**6.148**[***]	30.10			
Number of foraging guilds	(Intercept)	(5.869)[****]		0.108	0.068	0.024
	Mean	**−0.100**[***]	21.89			
	p_{veg}	1.812	20.05			
	h_{100}	**0.060**[***]	18.72			
	p_{50}	**−3.776**[**]	13.78			
	$r_{u:c}$	**−3.304**[***]	25.56			
Foliage gleaner richness	(Intercept)	(3.891)[***]		0.047	0.036	0.064
	h_{100}	0.019	34.67			
	p_{mid}	−2.673	65.33			
Ground forager richness	(Intercept)	(−1.877)		0.149	0.111	0.003
	Mean	**0.081**[****]	41.33			
	CV	**0.055**[***]	18.83			
	p_{veg}	−1.916	2.15			
	p_{70}	**3.556**[*]	27.08			
	p_{100}	−1.541	10.61			
Bark forager richness (sqrt)	(Intercept)	(1.737)[***]		0.055	0.022	0.168
	h_{70}	−0.050[*]	15.20			
	h_{90}	0.050[*]	17.22			
	p_{50}	**−2.278**[*]	52.16			
	p_{70}	−1.159	15.43			
Aerial forager richness (sqrt)	(Intercept)	(1.065)[**]		0.216	0.181	<0.001
	h_{30}	−0.022[**]	12.93			
	h_{100}	0.022[****]	29.85			
	p_{20}	**−1.946**[**]	11.91			
	p_{80}	**0.920**[**]	23.38			
	$r_{m:c}$	−0.928[***]	21.93			

Table 3 (continued)

Response Variable	Predictors	Coefficients	Independent Contribution (%)	R^2	R^2_{adj}	Model significance (p)
Edge species richness	(Intercept)	(−0.301)		0.153	0.115	0.002
	Mean	0.040***	17.82			
	p_{veg}	**−3.900*****	33.58			
	p_{20}	**4.411*****	21.20			
	p_{40}	2.099	14.33			
	p_{70}	**2.243****	13.07			
Interior species richness	(Intercept)	(1.445)		0.195	0.159	<0.001
	p_{veg}	**4.608***	29.49			
	h_{50}	**−0.107****	16.02			
	h_{100}	**0.109*****	32.13			
	p_{20}	−3.774	9.78			
	$r_{m:c}$	**−3.962****	12.59			

 * $p < 0.10$.
 ** $p < 0.05$.
 *** $p < 0.01$.
 **** $p < 0.001$.

core ranges such as the Hooded Warbler (*Wilsonina citrina*), Louisiana Waterthrush (*Seiurus motacilla*), and Acadian Flycatcher. This rich avifauna corresponded to a range of structural preferences in the bird community and likely enhanced the detection of patterns of variation in forest structure and songbird species' response to it.

LiDAR-derived predictors described between 4.7 and 21.6% of the variability in overall forest songbird species richness and that of several guilds. The explanatory power of our statistical models was modest, but several of the best-supported LiDAR variables within our models exhibited ecological significance congruent with demonstrated relationships between species richness and forest structure as measured via conventional, field-based methods, as well as other recent LiDAR-based studies (e.g. Cody, 1981; Goetz et al., 2007; Smith et al., 2008; Vierling et al., 2008). It is important to keep in mind that our LiDAR data were relatively low-density (by airborne LiDAR standards), multiple return, discrete LiDAR data, and thus not as information rich as full waveform LiDAR from sensors such as LVIS, or higher posting density discrete return data.

The LiDAR data in our study were collected in leaf-off conditions. This could have been a limitation, if only a small sample of returns were obtained in the canopy. However, our data showed that most of the returns were reflected by limbs and branches in the upper reaches of the return height distribution, suggesting that our LiDAR summary variables for each plot did capture forest structure well. In mixed forests in Austria, estimation of canopy heights using LiDAR acquired during both leaf-off and leaf-on seasons were nearly identical (Hollaus, 2006). Thus, while the canopy profile for leaf-on and leaf-off LiDAR are likely to differ, leaf-off LiDAR may better represent the volume and distribution of vegetation by allowing penetration of LiDAR pulses to the interior of tree canopies that would otherwise be obstructed by foliage in leaf-on conditions. We note though that our counterintuitive results for the midstory nesting species may be the result of insufficient LiDAR returns to map the midstory layer accurately. Unfortunately, we did not have field data to test this, but speculate that the typically smaller branches of midstory trees may have limited the number of LiDAR returns from this layer.

4.1. Species richness

Overall forest songbird richness was best explained by a model including upper canopy height (h_{100}; positive association) and midstory return density (p_{50}; negative association) suggesting that taller forests with a sparse subcanopy layer resulted in greater species richness in these forests. In primarily forested habitat in Maryland, songbird richness is dependent in part on canopy height and the vertical distribution of forest vegetation as derived from waveform LiDAR (Goetz et al., 2007). Tall forests with high canopy cover have also been shown to support more individuals and more species of

birds across a range of forest types in North America (James & Wamer, 1982). Forest height is important to forest songbirds potentially because of the associated higher canopy volume or the availability of diverse vegetative layers in taller forests. Layers of vegetation other than the canopy were not strongly associated with species richness and would suggest that an even distribution of foliage may not be an important driver of bird species richness in our sites. Our one foliage height diversity metric (H') rarely appeared in any of the top models despite its frequent inclusion in the reduced variable set input into the best subsets regression analysis. Canopy height and density appeared to outweigh the influence of other layers when all species are taken into account and these results reinforce the idea that forest structural characteristics measured by LiDAR can explain some of the variability in richness in forested habitats.

4.2. Nesting guilds

Among the nesting guilds, richness of low nesting species increased with understory density and low- to mid-canopy density. This concurs with findings from field-based studies elsewhere. For example, Hooded Warblers, a low shrub nesting species at our site, preferred interior forest with shrubby canopy gaps and edges in southern Ontario (Gartshore, 1988; Pasher et al., 2007). In our study area, Hooded Warbler nests in a parallel study that monitored breeding success were found in similar situations where large canopy gaps were filled with shrubs and tall herbaceous vegetation (data not shown).

High values in the 80th and 100th height quantiles in the canopy corresponded to high species richness of the midstory nesting guild. We were surprised by the decrease of richness in midstory nesting species with higher midstory to canopy ratios. However, forest species such as the Rose-breasted Grosbeak often build their nests in canopy gaps and midstory trees in interior forest habitats (Wyatt & Francis, 2002) where the surrounding midstory is comparatively less developed. Areas with a high midstory to canopy ratio would likely have tree-fall gaps or high variability in tree height and density compared to closed canopy sites. Another common midstory nester in our study, the Acadian Flycatcher, places its nest more often in areas with a more open subcanopy than would be expected from availability, presumably to accommodate their foraging behavior (sallying from a perch to capture flying insects) and to provide visibility for defense of the nest area (Whitehead & Taylor, 2002; Wilson & Cooper, 1998). Perhaps nest sites in the midstory are not limiting midstory nesting species whereas foraging habitat, prey availability, or predation risk may be more favorable in areas with higher canopy volume and sparser midstory. An alternative explanation is that forests with high, dense canopies may have masked the extent and variability of the midstory in the LiDAR data.

Species richness of canopy nesters also had significant relationships with our LiDAR structure metrics. The relationships were of limited predictive power but meaningful from an ecological standpoint in that richness in this guild was positively related to canopy density and the highest return quantile but negatively related to mean LiDAR return height. At least in part, these species respond to forest structural traits that correspond with tall, mature forest with a dense overstory but lower central distribution of vegetation returns which may lend some importance to vegetation below the canopy as well.

Cavity-nesting species also showed some sensitivity to forest structure, particularly to mid- and understory density. Although we included LiDAR variables that correlate well with larger tree diameters and tall, mature forests (Hawbaker et al., 2010) these variables were not chosen, or in the case of p_{10}, had the opposite relationship with this guild than we had hypothesized. Lower densities of LiDAR returns in the middle and bottom layers of the structural profile were indicative of higher richness in this guild. Greater numbers of cavity nesting bird species were present where the understory to canopy ratio was higher, despite this guild having a negative relationship with the density of the lowest height division. White-breasted Nuthatches, a common cavity nesting species in our study area, have been found to inhabit forest with an open understory while Downy Woodpeckers select sites with a well-developed understory (Anderson & Shugart, 1974) illustrating the complexity of habitat associations in this diverse guild.

4.3. Foraging guilds

The number of foraging guilds decreased with mean LiDAR height and with understory density relative to canopy density, and increased with h_{100}. It appears that a more even distribution of foliage above the understory with some tall trees in the canopy may support a diversity of foraging classes. Richness of ground foraging species was positively related to higher average return height and variation in return height indicating a forest with a wide distribution of vegetation throughout its vertical profile, both characteristics indicative of tall, mature, uneven-aged forests (Aber, 1979). Return density in the lower canopy was also important to this guild suggesting the importance of substantial canopy cover. In a field-based study of ovenbirds, our most common ground foraging species, successfully paired males selected territories with greater mean tree height and canopy cover (Van Horn et al., 1995). In another study, Wood Thrushes, also common ground foragers in our study, were more abundant in forested stands with a high proportion of large diameter trees and a closed canopy (Crawford et al., 1981). The somewhat counterintuitive result that ground foragers are related to tree height may reflect more the general habitat and territory requirements of the species observed in our study area, or may be related to suitable habitat conditions for their invertebrate prey, rather than a conclusion that forest structural traits facilitate their specific foraging location and behavior. For example, in southern Ontario deciduous forests, the density of both Ovenbirds and their invertebrate prey was found to be much greater in large forest tracts than small tracts (Burke & Nol, 1998); taller trees are often found in larger tracts, and thus there may be a link between the height of trees and suitable conditions for invertebrate prey of forest birds.

Aerial foragers, of which the most common representatives were the Eastern Wood-Pewee and Acadian Flycatcher; responded in ways consistent with the needs of their foraging behavior that requires unobstructed space to detect and pursue their flying prey. Aerial foragers were positively related to higher, dense canopies and negatively related to midstory and understory density suggesting that they may occupy forests that are close-canopied but open underneath. This is consistent with field studies of the Eastern Wood-Pewee (Crawford et al., 1981; Rodewald & Smith, 1998) and Acadian

Flycatcher (Bakermans & Rodewald, 2006) where open mid- and understory layers predict greater abundance of these species.

The richness of foliage-gleaning birds had a weak association with LiDAR structure variables. This diverse guild encompassed many species with a wide range of ecological requirements, the breadth of which may have confounded the response of this guild to specific structural components captured by LiDAR. That foliage-gleaning species used a common foraging technique throughout the vertical profile of the forest may have proven less influential in determining species richness than structural needs related to nesting sites, habitat type, or refuge from predators. Foliage-gleaning songbirds have been shown to partition food and nesting resources both spatially and behaviorally during the breeding season, allowing forests to support a wide range of species (MacArthur, 1958; Mills, 2007; Whitmore, 1977). Measures of species-specific abundance may help elucidate stronger patterns with forest structure among this diverse guild.

The variation in richness of the bark foraging guild was not explained by our LiDAR structure variables. Bark-foraging birds such as woodpeckers and nuthatches require large diameter trees in forests with a high number of standing dead trees (Raphael & White, 1984). In our study bark-foragers were a small guild dominated by four bird species, and 79% of the time there were two or fewer species recorded at a census point. Bark foragers are spatially and temporally restricted by their foraging substrate in forests of mixed stand age where availability of declining or recently dead trees is variable (Murphy & Lehnhausen, 1998). The bark foragers in our study feed opportunistically on dying and decaying standing dead wood, tend to have relatively large home ranges, and are habitat generalists (Conner, 1980; Jackson & Ouellet, 2002).

4.4. Habitat guilds

Edge species richness was higher on plots with a lower proportion of vegetation LiDAR returns. This is likely due to open conditions that allow penetration of the laser to the ground. Secondly, more edge-preferring species were found where the proportion of vegetation hits at low levels was comparatively higher, suggesting the presence of dense low vegetation preferred by these species in which they forage and nest. Low, dense foliage and an open overstory are important factors in determining whether Gray Catbirds (a typical edge species) occupy a particular site (Cimprich & Moore, 1995). The Indigo Bunting (*Passerina cyanea*) is another low-nesting edge species that prefers shrub- and sapling-dominated forest openings for its nesting and foraging habitats (Suarez et al., 1997). In a guild that requires habitat structure significantly different from mature closed-canopy forest, LiDAR performed capably which bodes well for detecting changes in the bird community across habitats of different types.

Interior forest bird species richness increased primarily with factors related to the amount of vegetation (p_{veg}) and canopy height (h_{100}). In field studies, interior forest species such as the Scarlet Tanager (*Piranga olivacea*) and Ovenbird have been found to use forests with high canopy height and cover (Fraser & Stutchbury, 2004; Shy, 1984; Van Horn & Donovan, 1994). Within the extensive interior forests of our study area, these structural traits were common and the limited predictive power of our models may be partly due to fact that we did not sample highly fragmented forests.

5. Conclusion

The relationships between LiDAR-derived habitat variables and bird richness measures that we found in our study were of moderate strength at best. So, is it likely that a satellite-based LiDAR sensor with much coarser resolution than our airborne LiDAR data would provide relevant information to biodiversity research? At first glance, our results would indicate that the answer to this question may be 'no',

but we caution against this interpretation because there are important differences that need to be taken into consideration.

First of all, our data were discrete-return LiDAR data, whereas other sensors record full waveform LiDAR. Studies with airborne waveform LiDAR, such as LVIS, resulted in stronger relationships than what we found here (Goetz et al., 2007). Summarizing discrete LiDAR data in pixels should minimize the difference to waveform LiDAR, but our posting density (0.625 pulses/m^2) may have been too low to fully approximate the type of information that sensors such as LVIS can provide. Second, our data was collected during leaf-off conditions. As discussed above, leaf-off data can certainly provide meaningful information about canopy structure. However, leaf-off canopy profiles will differ from leaf-on profiles, and ultimately the richest data would provide both types of data for a given pixel. Furthermore, it is during the leaf-on period when birds are making habitat selection decisions; the leaf-off data that we used may not be fully correlated with leaf-on conditions during the early breeding season. The value of multi-temporal image data is well established for optical satellite data, but the cost of data acquisition has limited the analysis of multi-temporal LiDAR data to date. A third difference to consider is that our study was conducted in mature deciduous forests that have relatively little variability in vertical structure, and LiDAR habitat models in a single vegetation types tend to exhibit low correlations (Clawges et al., 2008). Had the study included a range of habitat types such as shrublands, grassland, or actively managed forests, it is likely that the performance of our models would have been higher (Goetz et al., 2007). And last but not least, vegetation structure is only one of many factors determining species presence. Among all the factors, habitat structure is certainly important, but other factors, such as tree species composition, topography, microclimate, predator–prey relationships, and intra- and inter-species competition all affect species presence as well. Both airborne and satellite LiDAR data can therefore only provide a part of the picture.

Despite the inherent limitation of sampling a single habitat type, we attained significant models for bird species richness and richness of important guilds with selected variables that were ecologically meaningful. However, the moderate strength of the relationships that we found suggests that bird habitat models may ultimately benefit when LiDAR variables are combined with other important predictors of bird species richness. Such variables available at similarly broad scales may include measures of landscape composition and structure, land-use, disturbance history, and remotely sensed measures of productivity, habitat texture, and forest species composition (Turner et al., 2003).

LiDAR has the potential to reveal how other landscape scale variables interact with forest structure across comparable continuous extents. This is a major advantage over solely ground-based assessment, in which plot level measures either provide only a sample of the whole population, or have to be extrapolated to work at larger scales of analysis. With LiDAR data, forest structure variables can be represented as continuous surface pixel values that depend only on the resolution of the LiDAR return density to dictate their size. This presents a measure of flexibility and utility for the use of LiDAR in ecological research, which will be particularly helpful once global, space-borne LiDAR data become available. LiDAR research may also provide managers of these lands the tools necessary to determine, map, and manage habitat and biodiversity over broad areas with a high level of detail, and locate gaps in forest structural needs or characteristics.

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