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Using aerial LiDAR to assess regional availability of potential habitat for a conservation dependent forest bird

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ABSTRACT

Remotely-sensed data can inform conservation efforts that target forest wildlife, however, few spatial data products are able to quantify fine-scale aspects of structural variation within forests. Increased availability of Light Detection and Ranging (LiDAR) datasets that cover broad spatial extents and ownership types (*e.g.*, entire states) provide useful information regarding canopy and understory structure within forested landscapes. The fusion of LiDAR data with field-based species surveys can advance our understanding of species-habitat relationships and improve the effectiveness of conservation programs to recover habitat-limited species. The Golden-winged Warbler (*Vermivora chrysoptera*) is a forest-dependent songbird that nests in structurally-complex young forest across eastern North America. As with many early-successional obligates, this species has been declining for decades due, in part, to the steady loss of young forest/shrubland nesting habitat. Although conservation programs have begun restoring Golden-winged Warbler habitat, these efforts are currently limited by the inability to identify existing habitat across large spatial extents and diverse ownership patterns. Recent availability of state-wide LiDAR data for Pennsylvania provides an opportunity to overcome this limitation. From 2019 to 20, we surveyed for Golden-winged Warblers and structural vegetation at 837 sites across six forest blocks in eastern Pennsylvania. We combined these data with LiDAR derived forest structural metrics to develop statistical models to predict patterns of occupancy. Golden-winged Warbler occupancy probability was explained by models containing several LiDAR-derived structural metrics (*e.g.*, percentage of first returns between 1 and 5 m in height, structural complexity, etc.). Moreover, models fit with LiDAR-derived covariates predicted occupancy much better than those using only field-measured vegetation covariates ($\Delta AIC_c = 53.27$). Mapped predictions of Golden-winged Warbler occupancy revealed potential habitat (especially regenerating timber harvests) on both private and public lands. These results demonstrate the efficacy of LiDAR for modeling forest bird habitat associations, and how such data sources can provide a valuable tool for conservation planning.

1. Introduction

Over the past several decades, wildlife conservation efforts have increasingly used remotely sensed data to quantify ecological features (Pettorelli et al. 2014, Rose et al. 2015, Stephenson 2019) and to identify and prioritize conservation actions (Abarca et al. 2022). While many such efforts have relied heavily on coarse-scale data products like the United States National Land Cover Database (NLCD; Jin et al. 2019) and Cropland Data Layer (CDL; USDA 2021), these have been widely acknowledged as limited in their capacity to explain ecological phenomenon that operate at finer scales (*e.g.*, < 30 m) or within cover types not accurately represented therein (Wardlow and Egbert 2003, Cunningham 2006). With that in mind, one possible solution to overcome many of the challenges associated with traditional land cover rasters is

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Light Detection and Ranging (LiDAR) data (Buján et al. 2012, Yan et al. 2015). LiDAR data are three-dimensional representations of the physical world created by estimating return distances between a pulsed laser transmitted from and received by an airplane (in the case of aerial LiDAR; Verma et al. 2006). One major advantage of LiDAR data in assessments of wildlife habitat is that they can be used to describe structural attributes of habitat (e.g., variation in vegetation height) that cannot be quantified by other remotely sensed data (Atkins et al. 2018, Wilkes et al. 2018). Further, although fine-scale remotely sensed data exist for some public lands, comparable data for private lands are generally unavailable if they exist at all (Litvaitis et al. 2021). The increased availability of LiDAR data collected across large geographic extents provides valuable information about the amount and spatial contexts of wildlife habitat even in landscapes dominated by private lands.

One conservation-reliant species for which LiDAR may help inform the spatial distribution of habitat is the Golden-winged Warbler (*Vermivora chrysoptera*; Confer et al. 2020). The Golden-winged Warbler is a Nearctic-Neotropical migratory songbird that breeds across forest-dominated portions of eastern North America and winters in Central- and South America (Confer et al. 2020). Over much of the past century, populations of this songbird have declined at a rate of 1.85% per year (Hill and Hagan 1991, Sauer et al. 2020). Consequently, the species is listed as 'near threatened' by the International Union for the Conservation of Nature (IUCN), as 'threatened' by the Committee on the Status of Endangered Wildlife in Canada (OSEWIC 2006), and is currently being considered for listing under the U.S. Endangered Species Act (USFWS 2011). Although the drivers behind the Golden-winged Warbler's decline are varied, one of the most important appears to be the loss of high-quality nesting habitat (Roth et al. 2019, Confer et al. 2020). Indeed, the species nests almost exclusively in early successional woody communities (*e.g.*, young forest and reverting old fields, woody wetlands; McNeil et al. 2017, Confer et al. 2020), and, across much of the species' breeding range, the availability of these community types has dwindled (King and Schlossberg 2014).

To stem the decline of Golden-winged Warbler populations, a set of habitat best management practices were developed for the species (Bakermans et al. 2011, Roth et al. 2019), which have subsequently been implemented by several states and provinces to restore Golden-winged Warbler nesting habitat. For example, extensive work has been done on public lands in places like Pennsylvania, USA to create habitat for the species through silviculture (McNeil et al. 2018, Fiss et al. 2021). Perhaps the largest concerted effort aimed at creating Golden-winged Warbler nesting habitat has been NRCS's 'Working Lands for Wildlife' (WLFW) initiative. This federal cost-share program provides technical and financial assistance to facilitate the implementation of conservation practices on private lands in the central and southern Appalachian Mountains, which has yielded > 9,400 ha of habitat since the program's inception in 2012 (Litvaitis et al. 2021). A recent study monitored hundreds of sites enrolled in WLFW and similar efforts on public lands and found that site occupancy by Golden-winged Warblers was largely driven by landscape and regional context such as amount and type of forest (deciduous, mixed, evergreen) in surrounding landscapes and proximity to existing breeding populations (McNeil et al. 2020). This study subsequently laid the groundwork for NRCS to develop Priority Areas for Conservation (PACs) within which to prioritize the allocation of technical and financial assistance funds across the WLFW geography (Lott et al 2021).

Although remotely sensed data like the NLCD and CDL provide an excellent resource for assessing the amount of forest and forest types, they are relatively incapable of discerning Golden-winged Warbler nesting habitat (*i.e.*, young forest) from mature forest that does not support nesting Golden-winged Warblers (Jin et al. 2019, Confer et al. 2020, USDA 2021) as they lack the fine grain size necessary for habitat characterization. As such, conservation planners implementing Golden-winged Warbler best management practices can leverage traditional data products like NLCD to ascertain *broad landscapes* where conservation work may be successful (Roth et al. 2019, McNeil et al. 2020) but remain challenged if they wish to assess the presence and spatial distribution of *existing* nesting habitat from remotely sensed data sources (Webb et al. 2014). This uncertainty hampers the conservation efforts of groups like NRCS because they cannot evaluate whether sites are near potential Golden-winged warbler source populations (McNeil et al. 2020) or the amount of existing habitat within local landscapes (Bakermans et al. 2015b). Although, on public lands, ground-based vegetation surveys can be manually conducted and used to assess whether a forest stand is suitable for Golden-winged Warblers (McNeil et al. 2018), it is often impossible to do this on private lands and such site-level data are usually not mappable over broad spatial extents (*e.g.*, beyond a small focal area of sampling plots).

Given the challenges associated with identifying and quantifying early successional habitat from traditional remotely sensed data sources (*e.g.*, McNeil et al. 2020) and field surveys (*e.g.*, McNeil et al. 2018), we used recently acquired statewide LiDAR data for Pennsylvania (flown 2017–19 for our study area) to model occupancy probability of territorial Golden-winged Warblers across large spatial extents comprised of diverse ownership types. We also compared Golden-winged Warbler occupancy models fit with LiDAR-derived covariates to those fit using vegetation data collected in the field. Finally, we extrapolate our results across the NRCS's Golden-winged Warbler PACs. Specifically, our objectives were: 1. assess the degree to which LiDAR-based metrics are associated with Golden-winged Warbler occupancy, 2. assess whether Golden-winged Warbler occupancy was better predicted by field vegetation data or LiDAR metrics, and 3. predict potential Golden-winged Warbler habitat across a demographically important portion of the species' Appalachian range. We discuss these results in the context of forest bird conservation and the implementation of broad-scale habitat management efforts.

2. Methods

2.1. Study regions and forest blocks

Central to our study was the development of an occupancy model for Golden-winged Warblers in the Central Appalachian Mountains, with a focus on the Pocono Mountain region of Pennsylvania (Pike and Monroe Counties). We selected this region because it supports what is likely the densest population of Golden-winged Warblers in the Appalachian region (Fink et al. 2021) while many formerly-occupied portions of Pennsylvania are now largely vacant of the species (McNeil et al. 2020, Lott et al. 2021). By focusing our sampling within the Poconos region, we were able to identify the structural parameters that most accurately describe the habitat characteristics of Golden-winged Warblers without the inclusion of broad landscapes where the species is absent (McNeil et al. 2020).

Within the Pocono Mountains, we sampled Golden-winged Warblers within six 'forest blocks'. These forest blocks consisted of large tracts (1,118 – 4,690 ha) of public land where forest management was being implemented to benefit forest birds like the Golden-winged Warbler: State Game Lands 116, State Game Lands 180, State Game Lands 183, State Game Lands 209, State Game Lands 316, and Delaware State Forest (Fig. 1). The region overall is characterized by moderate elevation and thin, acidic soils that are poor for agriculture purposes (White & Chance 1882, Oplinger and Halma 2006). As a result, the region remains largely forested, though there exist scattered farms and developed areas (McCaskill et al. 2009). Canopy trees across the region were varied but among the most abundant were oaks (*Quercus* spp.), red maple (*Acer rubrum*), hickories (*Carya* spp.), eastern hemlock (*Tsuga canadensis*), and pines (*Pinus* spp.; Wherry et al. 1979). Understory woody plants were also varied but mountain laurel (*Kalmia latifolia*), black huckleberry (*Gaylussacia baccata*), and blueberries (*Vaccinium* spp.) were among the most common (Wherry et al. 1979).

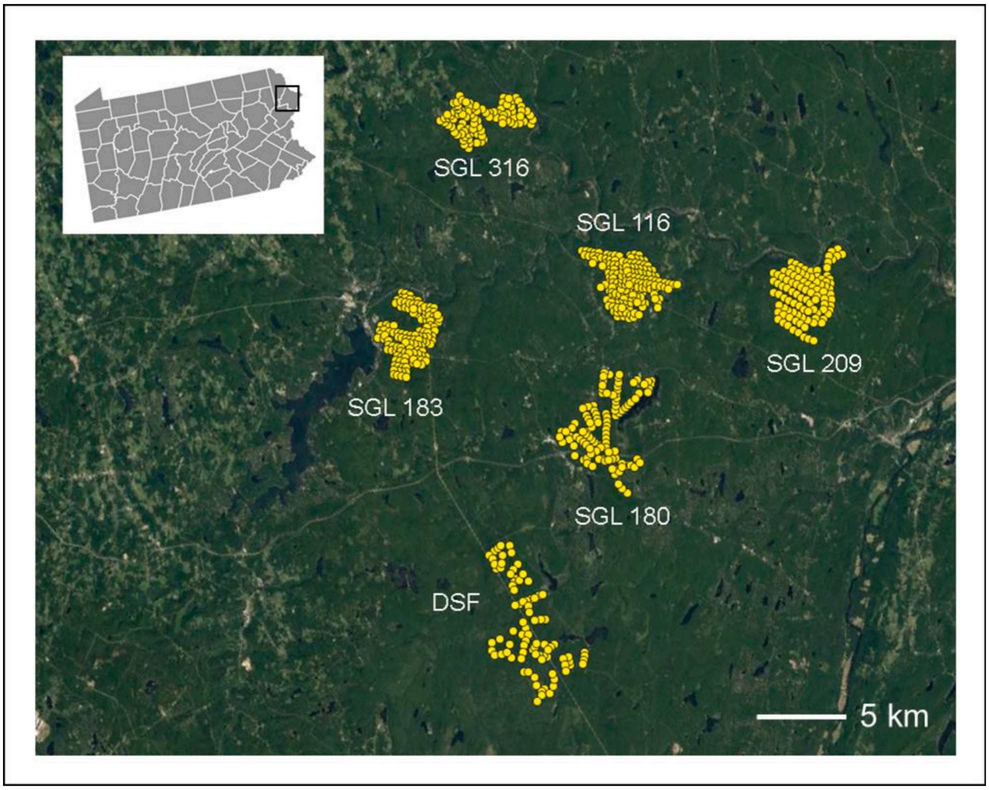

Fig. 1. Locations across Pike and Monroe Counties, Pennsylvania where we conducted point count surveys (yellow circles) within six forest blocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Golden-winged Warbler surveys

Survey locations were placed using a stratified systematic sampling scheme across the six forest blocks. More specifically, locations were placed in grids or transects (whichever maximized the number of survey locations) in each available cover type while always ensuring that each point was > 250 m from the nearest neighboring points. Our goal was to place points in each forest block such that cover types were represented relative to their prevalence in each block while remaining spatially independent. We focused on the following cover types for sampling: upland forest 0–6 years post-harvest, upland forest 7–20 years post-harvest, upland forest 21–40 years post-harvest, upland forest 41–80 years post-harvest, upland forest 81–120 years post-harvest, upland forest > 120 years post-harvest, shrub wetland, and hardwood swamp. We used shapefiles designed and provided by the Pennsylvania Bureau of Forestry (PA-DCNR) and the Pennsylvania Game Commission in ArcGIS v 10.1 (ESRI 2011) to map cover types within each of the six forest blocks. These cover type shapefiles included spatially explicit polygon data on forest type and age class depicted by two-dimensional "footprints" of each cover type, developed and maintained current by the respective state agencies (PA-DCNR and PGC). Next we created a variable number of points within each cover type, attempting to balance cover type availability with the number of sampling points. Each point was a minimum of 250 m apart to avoid double-counting individual birds on multiple survey locations (Ralph et al. 1995). We also made sure that points were > 100 m from the nearest ecotone between two cover types. For some narrow or oddly-shaped stands within a particular block, it was impossible to place points > 100 m from an edge; in this case, a point was placed in the center of the stand (*sensu* McNeil et al. 2018, 2020).

We surveyed for Golden-winged Warblers using standard avian point count surveys (Ralph et al. 1995). Briefly, these surveys involved a single observer standing at a survey point for 10 min silently recording the presence of Golden-winged Warblers detected by sight and sound. We conducted all surveys between 30 min pre-sunrise and 4 h post-sunrise. For each Golden-winged Warbler we detected, we noted the sex and estimated distance to the observer (to the nearest 5 m). For birds identified by song but not visually detected during the survey, we visually confirmed the phenotype after the survey was complete because Golden-winged Warblers can sing the songs of Blue-winged Warblers (*V. cyanoptera*), as can hybrids (Ficken and Ficken 1967). Golden-winged and Blue-winged Warblers hybridize and engage in interspecific competition when they occur in sympatry (Confer et al. 2020), thus highlighting the importance of accurate identification of the species from congeners. With that in mind, hybrids

and Blue-winged Warblers are rare across this study area, even within early successional habitats (hybrids: 3% naïve occupancy, Blue-winged Warblers: 7% naïve occupancy; McNeil et al. 2020). Prior to each survey, we also recorded survey metadata including Beaufort wind index (wind), time since sunrise (minutes), ordinal date, and cloud cover (percent, rounded to the nearest 25%; McNeil et al. 2018). Each survey location was visited twice per breeding season between 15 May and 15 June 2019–20.

2.3. Within-stand vegetation surveys

We quantified structural vegetation around each point count location using a sampling procedure where data were collected at the point location itself and at the ends of each of two randomly-selected transects (35 m in length) oriented at 0°, 120°, or 240°. This protocol yielded vegetation three sampling locations at each point count location: 1. plot center, 2. the first transect, and 3. the second transect. At each of the three locations, we conducted a 1 m^2 percent cover plot where we visually estimated the percent cover of the following vegetation strata: leaf litter, bare ground, moss, coarse woody debris, grass, herbaceous, fern, brambles (*e.g.*, *Rubus* spp.), and woody. We considered "leaf litter" to be any dead leaves and plant parts < 10 cm in diameter. Coarse woody debris was any woody plant part > 10 cm in diameter (McNeil et al. 2017). We considered "herbaceous" plants to be any monocotyledon (*e.g.*, grasses, sedges, and rushes) or herbaceous dicotyledon. Ferns were any seedless vascular plant. Our "woody" category included any sapling or shrub except *Rubus* which was its own category because of its high importance to Golden-winged Warbler ecology (Roth et al. 2019, Confer et al. 2020).

To quantify basal area, we employed the point-quarter method of sampling (Cottam and Curtis 1956) at each of the aforementioned three survey locations. Briefly, we measured the distances to the nearest tree (>10 cm diameter at breast height; DBH) using a tape measure in each of four quadrats (0-90° [NE], 91-180° [SE], 181-270° [SW], and 271-359° [NW]). If no tree was within 15 m of the point in a given quadrat, we recorded that datum as "N/A". Distance data were converted into basal area (m^2/ha) following the procedure described by Cottam and Curtis (1956). The last type of data we collected at each point location was the shrub/sapling stem density within two 1x10m plots. The two plots were each placed at one random location (0–10 m, 10–20 m or 20–30 m) along the two 35-m transects described above. Within each woody stem plot, we tallied the total number of woody stems (<10 cm in DBH) in each of two categories: short (<1.5 m) and tall (≥1.5 m tall).

2.4. LiDAR dataset and processing

LiDAR metrics used in this study were derived from previous work creating 10 × 10 m forest attribute rasters across most of the state of Pennsylvania (see Fisher et al., in review) using LiDAR datasets freely available from the USGS National Map. LiDAR datasets used to create these metrics were collected over multiple campaigns between spring 2015 and spring 2020 with the intent of targeting leaf-off conditions. LiDAR data for the Poconos region, where the occupancy model was trained, were collected during one campaign that occurred between March and November of 2019 (specifically "PA Northcentral B5 2019"). LiDAR metrics were calculated using the *lidR* package in R (Roussel et al. 2020), with all LiDAR return heights normalized based on a triangulated irregular network (TIN) algorithm to construct the digital terrain model from ground returns.

Normalized LiDAR point clouds can be distilled into a host of metrics aimed at quantifying both vertical and horizontal vegetation structural attributes (Hardiman et al., 2018). Here we targeted metrics we suspected are important to bird habitat, while also providing a broad overview of the total structure of the forest, including the upper canopy as well as the low to mid story and adjacent variability (e.g., rugosity 30 and 50 m, discussed below). In total, we selected 11 metrics, focusing on those that both had (1) little/no obvious data artifacts (*i.e.*, pronounced striping across the study area) and (2) sufficient variation that they would make useful predictors. Ultimately, we modeled Golden-winged Warbler occupancy using the following 11 metrics: 1. interquartile range ("IQR"), 2. height below which 75% of returns were recorded ("p75"), 3. height below which 90% of returns were recorded ("p90"; LaRue et al., 2022), 4. percent of *all returns* between 1 and 5 m, 5. percent of *first returns* between 1 and 5 m, 6. standard deviation of mean outer canopy height (MOCH) values at 30 m spatial resolution (*e.g.*, standard deviation of nine 10x10 m pixel values; Atkins et al., 2018), 7. standard deviation of p95 height values at 30 m spatial resolution, 8. standard deviation of p99 height values at 30 m spatial resolution, and (9, 10, 11) the same three metrics summarized in (6,7,8) but using a 50 m spatial resolution (e.g., standard deviation of 25 10x10 m pixel values) (Roussel et al. 2020). For simplification, metrics 6–11 are referred to as [*metric* rugosity *resolution*] throughout the remainder of the paper. In the context of this study, rugosity can be interpreted as a metric of surface heterogeneity (Hardiman et al., 2018).

2.5. Occupancy analyses

We used single-season occupancy models to assess ecological relationships between Golden-winged Warbler observations (only detections within 100 m of point counts) and LiDAR/vegetation data (MacKenzie et al. 2017) using the *unmarked* package in R (Fiske and Chandler 2011). To assess all occupancy models, we used the Information Theoretic approach (Burnham and Anderson 2002) and model selection with Akaike's Information Criterion adjusted for small sample size (AIC_c; Akaike 1973). Briefly, we considered models < 2.0 ΔAIC_c to be competing and model β parameter 95% confidence intervals that overlapped zero to be weak biological effects (Arnold 2010). Additionally, because we did not know the ideal scale at which to extract LiDAR data around our point count survey locations, we extracted mean LiDAR variables around each point from buffers of the following radii: 50 m, 100 m, 250 m, and 500 m. We used LiDAR data from these four levels of spatial extent to assess which was most predictive in the first stage of our occupancy analysis (describe below).

Prior to extracting LiDAR data for occupancy modeling, we masked our LiDAR rasters to exclude cover types that nesting Golden-winged Warblers are not known to use (Confer et al. 2020). We also masked non-habitat from our final predictive maps. This binary mask was done to avoid incorporating non-habitat cover types into the occupancy model and to avoid predicting occupancy to non-habitat cover types. Moreover, our model was trained using data from six forest blocks in heavily forested landscapes. For this reason, it would be inappropriate for us to predict into cover types beyond the scope of our study (*e.g.*, grasslands, urban, etc.). A composite 2020 land cover raster was extracted for our study area from Google's 'Dynamic World' land cover product (Brown et al. 2022). The Dynamic World product is a 10-m spatial resolution global land cover map that contains nine possible land cover categories: open water (0), trees (1), grass (2), flooded vegetation (3), crops (4), shrub/scrub (5), built/urban (6), barren (7), and snow/ice (8; Brown et al. 2022). We considered 'trees', 'shrub/scrub', and 'flooded vegetation' to be possible habitat types for Golden-winged Warblers and all else to be non-habitat. Thus, to create our binary mask, we converted classes 1, 3, and 4 to "1″ and all others to "N/A". We then multiplied each cell in the Dynamic World mask raster by each cell in our LiDAR layers to mask out non-habitat cover types. For each LiDAR metric, we then calculated the mean value within each of our buffer distances (50 m, 100 m, 250 m, and 500 m) using the *focal* function in the *raster* package (Hijmans and van Etten 2012) in R. Finally, we extracted values for all LiDAR metrics at each point count location for each of the four spatial extents using the raster package's *extract* function.

We began our occupancy analyses by testing single-covariate detection models for each of our survey covariates (*e.g.*, p(time of day),ψ(.) or p(cloud cover), ψ(.)). Specifically, we examined the following survey covariates: time of day, cloud cover, ordinal date, and Beaufort wind index. This model set also included an intercept-only 'null' model for comparison (p(.), ψ(.)) We limited our detection models to one detection covariate to avoid overparameterizing our models as they would only become more complex, later in the analysis (MacKenzie et al. 2017). After finding the best-ranked detection model, we incorporated any detection terms into all subsequent models. Next, we created a model set for each LiDAR metric; each of these single-metric model sets included single-covariate models for the metric at each of the four spatial scales (*e.g.*, p(best), ψ(IQR 50 m), p(best), ψ(IQR 100 m), etc.). We also created quadratic versions of each of these models, for a total of eight models in each of these sets. The result of these analyses was the best-ranked spatial scale and polynomial structure (linear/quadratic) for each variable which was carried below into the additive model selection. When a linear and quadratic model were both in the competing set (<2.0 ΔAIC_c), we defaulted to the linear structure as doing so would adhere to the rules of parsimony (Burnham and Anderson 2002). We constructed all possible combinations of covariates such that no covariates within the same model were correlated ($|r| > 0.70$; Sokal and Rohlf 1969). We followed a similar procedure to construct all possible subsets of 0–3 vegetation covariates in our vegetation occupancy model sets.

We predicted our top-ranked LiDAR occupancy model across a series of management units established by NRCS's Golden-winged Warbler Conservation Initiative: "Priority Areas for Conservation" (PACs; Lott et al. 2021). Predictions were done using the plogis() function in base R and the model's β parameter estimates (R Core Team 2021). In Pennsylvania, there are six PACs (Fig. A1): 1. Pennsylvania Wilds and Ridge-and-valley Region, 2. Allegheny Plateau, 3. Central Appalachian Region, 4. Eastern Ridge-and-valley Region, 5. High Pocono Plateau, and 6. Low Pocono Plateau. Prior to mapping our occupancy predictions across these regions, we stratified each to only include landscapes that were similar to those upon which we trained our occupancy model: > 75% forest/shrubland/wetland within 1 km of each location (Roth et al. 2019). We thus generated a focal statistics map generated by calculating the percent of these cover types within 1 km of each location across these PACs and excluded landscapes with values < 75%. Through this procedure, PAC #2 (Allegheny Plateau) had < 5% of the area available for prediction so we did not predict within this PAC (Fig. A1).

To assess the goodness-of-fit and discrimination ability of our top-ranked occupancy model, we calculated a) Briers Score and b) Area Under the Curve (receiver operating characteristic; AUC) respectively using 10-fold cross validation. The model structure was initially fit with the full dataset and then tested by iteratively fitting this model structure using 75% of the data and testing with the remaining 25% with AUC and Brier Scores each averaged over 10 runs. Additionally, we obtained coordinates for an independent dataset of 158 point locations where Golden-winged Warbler presence was confirmed through NRCS monitoring of WLFW points in the two years prior to our own sampling (2017–18; McNeil et al. 2020). We extracted our occupancy predictions at these points and calculated the proportion of points for which occupancy was estimated to be $\widehat{\psi} > 0.50$.

3. Results

From 2019 to 20, we conducted 1,674 point count surveys across 649 survey locations (n = 837 point × year combinations) over the six forest blocks and Golden-winged Warblers were detected at 69 locations (naïve occupancy probability = 0.08). The 837 samples occurred in DSF (n = 87), SGL180 (n = 106), SGL209 (n = 202), SGL116 (n = 154), SGL183 (n = 112) and SGL316 (n = 176). Across all survey locations, basal area varied from 0 – 142.4 m^2/ha (mean: 31.8 m^2/ha; Table 1). Other variables we measured also exhibited wide ranges of variation, for example, leaf litter cover: range = 0 – 94% (mean: 50.2%), herbaceous cover: range = 0 – 98.3% (mean: 6.9%), and < 1.5 m tall woody stem density: range = 0 – 173 stems/m^2 (mean: 15.6; Table 1). When we extracted LiDAR metrics for each point count location, we also observed substantial variation among points; for example, IQR at a 100 m radius varied from 0.17 to 14.95 m with a mean value of 9.29 m. Likewise, the percentage of first returns within 1–5 m in height varied from 0.25 to 39.01% (mean: 4.77%). See Table 1 for summaries of each LiDAR metric at the 100 m radius scale.

Detection probability was best explained by Beaufort wind index with no competing models; we used this survey covariate in all following occupancy models. When we tested each LiDAR metric to determine which spatial scale (50 m, 100 m, 250 m, or 500 m radius) and shape (linear vs quadratic) was most predictive, we found these varied among LiDAR metrics (Table 2, Table A1). Among the 11 metrics, seven were best predicted at the 100 m scale. Those that deviated from this pattern included percent of all returns 1–5 m and percent of first returns 1–5 m which were best predicted at the 250 m and 500 m (quadratic) scales, respectively (Table 2). Additionally, two measures of MOCH rugosity – 30 m and 50 m – best explained occupancy at the 500 m and 50 m scales, respectively. With that in mind, there was.

substantial uncertainty as to which LiDAR metrics best predicted occupancy (especially rugosity generated from MOCH) given that many were correlated and within competing models.

After excluding models that contained correlated variables, we created 151 additive LiDAR models with up to three covariates. Among them, there were six models in the competing candidate set (Table 3). The competing models all had percent of first returns 1–5 m (quadratic). Additionally, all models had a metric of p95 rugosity (either 30 m or 50 m aggregation; Table 3). Finally, all models also included one of the three measures of vegetation height (IQR, p75, or p90). With these competing models in mind, we used the top-ranked model for all model predictions explored hereafter: p(wind), ψ(p75 + percent of first returns 1–5 m^2 + p95 rugosity 30 m); see Table 3. This model predicted a negative relationship between Golden-winged Warbler occupancy probability and the height at which 75% of LiDAR returns occurred (p75; Fig. 2). The relationship between site occupancy and percent of first returns 1–5 m was a quadratic relationship peaking around 12% (Fig. 2). The relationship between occupancy and p95 rugosity exhibited the greatest magnitude of effect whereas sites with p95 rugosity values

Table 1
Summary statistics for LiDAR metrics and field-measured vegetation metrics used as covariates in our Golden-winged Warbler occupancy analyses. Shown for each variable are the minimum value, maximum value, mean, and standard error (SE).

LiDAR Metrics (Remotely sensed) Variable name	Minimum	Maximum	Mean	SE
Inter-quartile Range (IQR)	0.17	14.95	9.29	0.09
p75	0.17	17.83	9.62	0.09
p90	1.18	20.28	11.88	0.10
Percent of Returns 1–5 m	0.81	27.80	5.33	0.13
Percent of First Returns 1–5 m	0.25	39.01	4.77	0.16
MOCH Rugosity 30 m	0.26	4.34	1.48	0.02
p95 Rugosity 30 m	0.62	6.05	1.42	0.03
p99 Rugosity 30 m	0.56	6.52	1.38	0.03
MOCH Rugosity 50 m	0.38	4.99	1.68	0.02
p95 Rugosity 50 m	0.73	6.69	1.70	0.03
p99 Rugosity 50 m	0.68	6.99	1.65	0.03
Vegetation Metrics (Field-measured)				
Basal area (m^2/ha)	0.00	32.69	7.31	0.15
Leaf litter cover (%)	0.00	94.00	50.24	0.72
Bare ground cover (%)	0.00	54.33	4.94	0.25
Moss cover (%)	0.00	84.00	6.26	0.32
Coarse woody debris cover (%)	0.00	4.00	0.39	0.02
Forb cover (%)	0.00	98.33	6.90	0.43
Fern cover (%)	0.00	97.33	11.01	0.53
Rubus cover (%)	0.00	36.67	0.35	0.08
Woody cover (%)	0.00	90.00	20.20	0.60
Short woody stems (count/20 m^2)	0	173	15.65	0.74
Tall woody stems (count/20 m^2)	0	43	3.22	0.19

Table 2
Most predictive spatial scales for each of the 11 LiDAR metrics considered in this study. Each scale represents a radius (m) around each point count survey location. Variables were modeled as either linear (*e.g.*, 100 m) or quadratic (*e.g.*, 100 m^2) and scales (50 m, 100 m, 250 m, or 500 m) were assessed using the information theoretic approach. Competing models (ΔAIC_c < 2.0) are listed under "Competing spatial scales". When a linear and quadratic model were both competing at the same spatial scale, we defaulted to the linear structure.

LiDAR Metric	Best scale	Competing spatial scales
Inter-quartile Range (IQR)	100 m	100 m^2
p75	100 m	100 m^2
p90	100 m	–
Percent of Returns 1–5 m	250 m	–
Percent of First Returns 1–5 m	500 m^2	–
MOCH Rugosity 30 m	500 m	50 m, 250 m, 250 m^2, 500 m^2
p95 Rugosity 30 m	100 m	50 m, 100 m^2
p99 Rugosity 30 m	100 m	100 m^2
MOCH Rugosity 50 m	50 m	50 m^2, 100 m, 250 m, 250 m^2, 500 m, 500 m^2
p95 Rugosity 50 m	100 m	50 m, 100 m^2
p99 Rugosity 50 m	100 m	100 m^2

Table 3
Golden-winged Warbler occupancy models fit using LiDAR (Light Detection and Ranging) data covariates. The detection portion of the model is not shown. Shown are the ten top-ranked models and the null (intercept-only on occupancy) for reference. For each model, we report the number of model parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, cumulative model weight (CumWt.), and Log Likelihood (LL).

Model name	k	AIC_c	ΔAIC_c	CumWt.	LL
ψ (p75 + %first1-5 m^2 + p95Rug30m)	7	508.33	0.00	0.20	−247.10
ψ (p75 + %first1-5 m^2 + p95Rug50m)	7	508.39	0.06	0.40	−247.13
ψ (p90 + %first1-5 m^2 + p95Rug30m)	7	509.08	0.75	0.54	−247.47
ψ (p90 + %first1-5 m^2 + p95Rug50m)	7	509.64	1.31	0.65	−247.75
ψ (IQR + %first1-5 m^2 + p95Rug30m)	7	509.80	1.46	0.74	−247.83
ψ (IQR + %first1-5 m^2 + p95Rug50m)	7	509.82	1.49	0.84	−247.84
ψ (%first1-5 m^2 + p95Rug50m)	6	512.09	3.76	0.87	−249.99
ψ (%first1-5 m^2 + p95Rug30m)	6	512.67	4.33	0.89	−250.28
ψ (%first1-5 m^2 + MOCHRug50m + p95Rug30m)	7	513.09	4.76	0.91	−249.48
ψ (p75 + %first1-5 m^2 + MOCHRug50m)	7	513.33	5.00	0.93	−249.60
ψ (.)	3	626.21	117.87	1.00	−310.09

near one indicated a probability of occupancy ~ 0.0, while sites with p95 rugosity values > 6 were very likely to be occupied ($\hat{\psi} > 0.90$; Fig. 2). In the top-ranked model (as well as all competing models), none of the 95% confidence intervals for the β parameter overlapped zero. The top model also performed well (mean Brier Score = 0.07, mean AUC = 0.83) and predicted that 72% of 2017–18 test Golden-winged Warbler locations (n = 158) had $\hat{\psi} > 0.50$ (*i.e.*, were predicted to be Golden-winged Warbler habitat). When the threshold was dropped to $\hat{\psi} > 0.40$, the model predicted 82% of the test locations.

None of the field-measured vegetation variables from point count locations were correlated ($|r| > 0.70$) and, thus, we ranked all possible combinations of 1–3 covariates in addition to the null model (232 models; Table 4). As with the final LiDAR candidate set, our field vegetation models exhibited uncertainty as to which model best predicted occupancy as there were four competing models. Several variables were present in three of these four models: % leaf litter cover, % herbaceous cover, basal area^2, and # >1.5 m tall woody stems (Table 4). The top-ranked model, p(wind), ψ(%leaf litter + %herbaceous + #tall woody stems) suggested that occupancy probability was negatively related to percent leaf litter and positively associated with both percent herbaceous cover and the number of > 1.5 m tall woody stems (Fig. 2), though the β parameter 95% confidence interval on herbaceous cover overlapped zero. None of the other β parameter 95% confidence intervals for competing models overlapped zero. Still, this vegetation model was much better than a null model (Table 4). When we compared AIC_c values for our top vegetation model and our top LiDAR model, the top LiDAR model (AIC_c = 508.33) performed much better than our top vegetation model (AIC_c = 561.60; ΔAIC_c = 53.27).

Predicted occupancy probability from our LiDAR model mapped across the six forest blocks in the Poconos indicated that 5% of the land area had an occupancy probability ≥ 0.50. When we predicted this model across the five PACs of interest, we found that mean occupancy, within appropriate landscapes, varied by PAC with PAC # 4 (Eastern Ridge-and-Valley Region) hosting the greatest percentage of area being

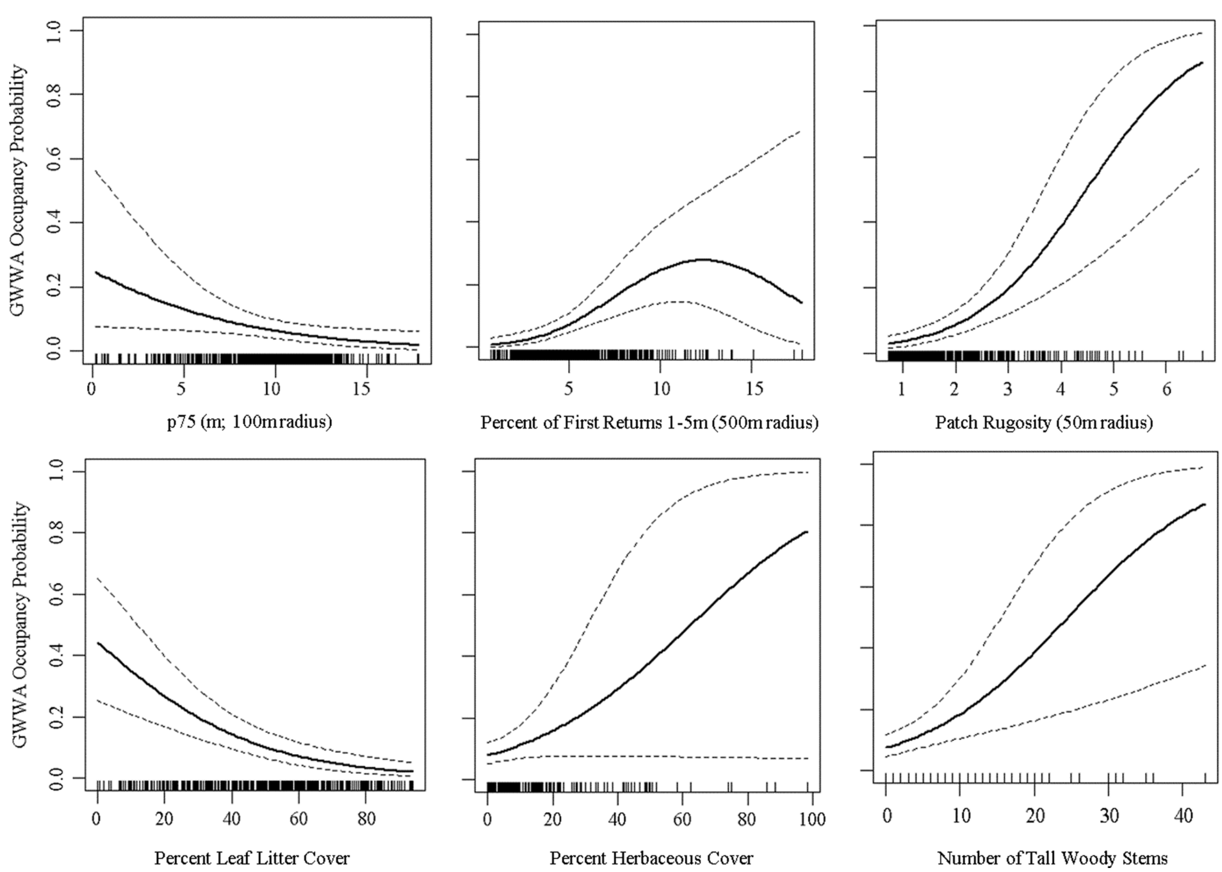

Fig. 2. Functional relationships between Golden-winged Warbler occupancy probability and habitat metrics derived from LiDAR (top row) and field-measured vegetation metrics (bottom row). Relationships plotted are derived from our best-ranked LiDAR and vegetation models, respectively. Solid lines represent functional relationships while dashed lines represent 95% confidence intervals.

Table 4
Golden-winged Warbler occupancy models fit using field-measured vegetation data covariates. Shown are the ten top-ranked models and the null (intercept-only on occupancy) for reference. For each model, we report the number of model parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, cumulative model weight (CumWt.), and Log Likelihood (LL).

Model name	k	AIC_c	ΔAIC_c	CumWt.	LL
ψ (%leaf litter + %forbs + #tall woody stems)	6	561.60	0.00	0.21	−274.75
ψ (basal area^2 + %forbs + #tall woody stems)	7	562.00	0.40	0.39	−273.93
ψ (basal area^2 + %leaf litter + #tall woody stems)	7	562.81	1.21	0.50	−274.34
ψ (basal area^2 + %leaf litter)	6	563.29	1.69	0.59	−275.60
ψ (basal area^2 + %leaf litter + % forbs)	7	564.10	2.50	0.65	−274.98
ψ (%leaf litter + %CWD^2 + #tall woody stems)	7	564.17	2.57	0.71	−275.02
ψ (%leaf litter + %*Rubus* + #tall woody stems)	6	565.00	3.39	0.75	−276.45
ψ (%leaf litter + #tall woody stems)	5	565.29	3.69	0.78	−277.61
ψ (basal area^2 + %leaf litter + % CWD^2)	8	565.33	3.73	0.82	−274.58
ψ (%leaf litter + % woody + #tall woody stems)	6	566.18	4.57	0.84	−277.09
ψ (.)	3	626.21	64.60	1.00	−310.09

potential habitat (5%) and PAC # 6 (Low Pocono Plateau) hosting the lowest percentage of area being potential habitat (3%; Fig. A2, Table A2). When we examined locations predicted to have high occupancy probability across the study area, it was readily apparent that, on public lands, many locations predicted to be potential Golden-winged Warbler habitat were known sites that had experienced recent overstory removal timber harvests (Figs. 3-4). Moreover, while public lands timber harvests were obvious and could be clearly compared to public data on timber management, private lands that had apparently experienced timber management were also predicted to have high occupancy probability (Fig. 3).

4. Discussion

Assessing the ecological needs and presence of available habitat for species of conservation concern is a persistent challenge for conservation practitioners, especially for wildlife species dependent upon ephemeral habitats such as early successional forest (Askins 2001, King and Schlossberg 2014, Litvaitis et al. 2021). While LiDAR data have been used in the past to examine forest bird habitat relationships (Goetz et al. 2007, Lesak et al. 2011), few studies have compared the value of LiDAR to field-measured habitat data. Not only did models specified with LiDAR metrics out-perform a null (intercept-only) model, they also described ecological relationships between occupancy and vegetation structure that are supported by published literature on the life history of Golden-winged Warblers (Confer et al. 2020). For example, the negative relationship between Golden-winged Warbler occupancy probability and p75 is reasonable for a species dependent upon early-successional communities (Roth et al. 2019); indeed, as canopy height increases, so will p75 (the height below which 75% of LiDAR returns are recorded). Similarly, the percent of first returns within 1–5 m being positively associated with occupancy (albeit quadratic) is also sensible as vegetation within the 1–5 m band harbors shrubs and saplings that Golden-winged Warblers require for foraging and post-fledging habitat (Bellush et al. 2016, Fiss et al. 2021). For this result, specifically, the quadratic relationship indicates an optimal percent of returns within 1–5 m (around 13%), beyond which, occupancy probability declines (though we had relatively few data points beyond 13%; Fig. 2). Finally, the relationship between occupancy and rugosity is consistent with the notion that Golden-winged Warblers require structural complexity within nesting habitat (Bakermans et al. 2015a, Wood et al. 2016, Leuenberger et al. 2017, Aldinger 2018). Ultimately, that the LiDAR patterns revealed by our top occupancy model are consistent with what is known about Golden-winged Warbler habitat, is confirmation that LiDAR-derived variables hold strong promise for predicting occupancy

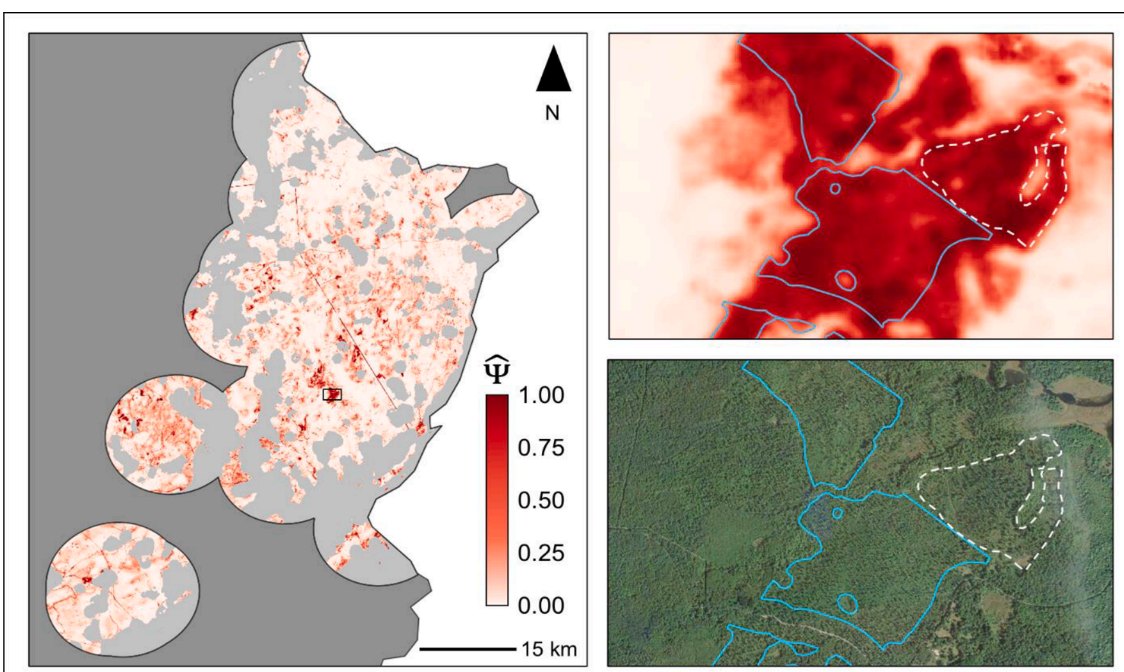

Fig. 3. A predictive map of Golden-winged Warbler occupancy probability ($\hat{\psi}$) across two of Pennsylvania's NRCS Priority Areas for Conservation (PACs; left). Close examination of areas of high predicted occupancy (upper right) coincide with timber harvest on public lands (blue polygons). Nearby private lands (e.g., white dashed lines) also depict presumed timber harvests that are also apparent from aerial imagery (lower right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

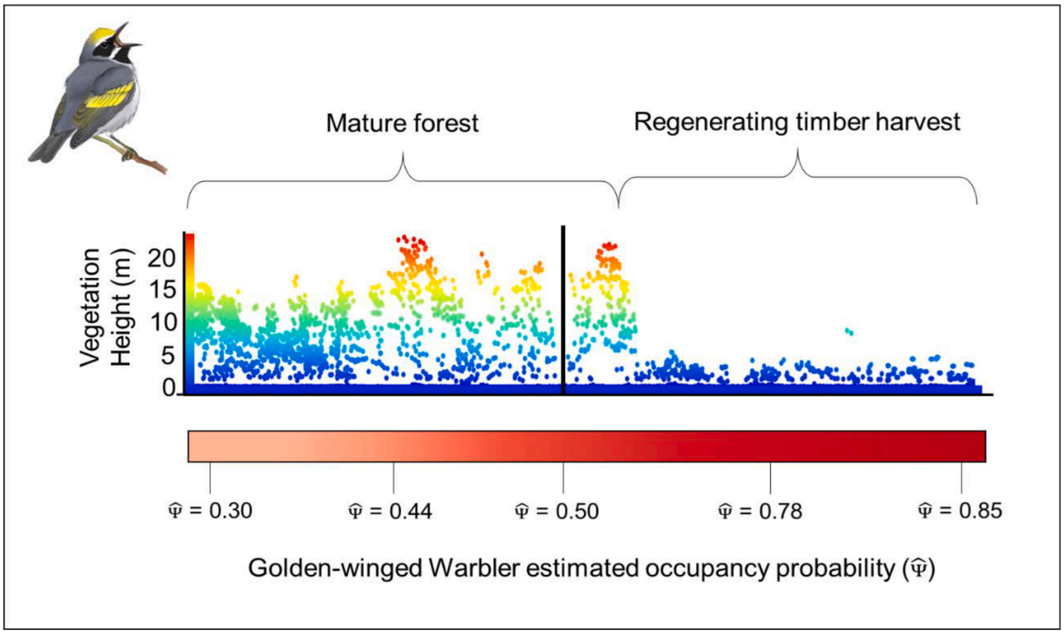

Fig. 4. Normalized vegetation height profile along a 10-m wide × 150-m long transect (above) from an area of high predicted occupancy probability ($\widehat{\psi}$; below) to low predicted occupancy from Monroe County, Pennsylvania. A vertical bar is shown where occupancy probability $\widehat{\psi} = 0.50$.

for this species, and when possible, should be incorporated into habitat assessments for the species in future work (Goetz et al. 2007, Tattoni et al. 2012, Davies and Asner 2014).

Not only did models fit with LiDAR variables describe ecologically meaningful habitat relationships but they also out-performed models specified using field-measured vegetation data. Studies on Golden-winged Warbler habitat have long relied upon field data on vegetation characteristics as a 'gold standard' for habitat quantification (*e.g.*, Confer and Knapp 1981, Klaus and Buehler 2001, Confer et al. 2003, Terhune et al. 2016, Buckardt-Thomas et al. in press). Our analyses are the first to demonstrate that LiDAR metrics can outperform field-measured vegetation data for quantifying Golden-winged Warbler habitat. The superiority of LiDAR is important for several of reasons; first, vegetation data derived from field data simply cannot be collected at all locations over broad areas (Chojnacky 2000, Tattoni et al. 2012, Campbell et al. 2018). Moreover, as our analyses demonstrate, LiDAR data provide information about habitat that would be otherwise difficult to obtain from field-measured vegetation data (Bradbury et al. 2005). In fact, is possible that the differences in predictive value we observed between the value of field-measured vegetation and LiDAR are partially driven by scale differences: Field measured vegetation sampling occurred < 50 m from each survey location while the LiDAR metrics in our top model were quantified from 100 to 250 m. Beyond the feasibility of such efforts remains also the subjectivity of field-measured vegetation data which are often impacted by individual observer biases and introduce additional uncertainty into their use in ecological modeling (Morrison 2016). However, LiDAR data generally do not provide information on plant species composition which is of key importance to many imperiled bird species like the Kirtland's Warbler (*Setophaga kirtlandii*; Bocetti et al. 2020), Cerulean Warbler (*S. cerulea*; Buehler et al. 2020) and Golden-winged Warblers (Bellush et al. 2016, McNeil et al. 2020). When data on plant species composition are required, it is likely that a "hybrid" study design would be appropriate where LiDAR data are paired with field data.

In addition to being informative from an ecological perspective, predictive maps like those produced here can also serve as valuable tools for conservation (Garabedian et al. 2017, Moudrý et al. 2021). Despite great interest in understanding declines seen in many early-successional wildlife populations, remotely sensed data products of land cover change based on timeseries of optical imagery have not proven useful for quantifying the complex structure of early-successional forest communities (Olsen et al. 1999, Xian et al. 2013). Our top-ranked occupancy model used LiDAR data to accurately delineate attributes indicative of early-successional communities upon which Golden-winged Warblers rely (Fig. 3). Mapping occupancy predictions, as we have done here, is useful for conservation because such maps can inform where a species is most likely to occur within a particular region (De Wan et al. 2009, Webb et al. 2014). This information may be helpful for conservation planning (*e.g.*, ranking of proposed locations for conservation efforts) because some shrubland bird species (including Golden-winged Warblers) are most likely to occur near aggregations of conspecifics (Roth et al. 2014, McNeil et al. 2020). Thus, it is possible that management efforts targeted near existing patches of habitat where the species may already be present could improve the efficacy of conservation efforts (Lott et al. 2021, Litvaitis et al. 2021). Alternatively, knowing where habitat is sparse provides information regarding landscapes where habitat is needed to achieve landscape-level thresholds of habitat availability (Watling et al. 2020). With this said, the value of LiDAR for mapping early-successional habitat is somewhat dependent upon regular re-collection of LiDAR across a study area due to the ephemeral nature of these communities (Askins 2001).

While the Golden-winged Warbler was the focal species in this study, it seems likely that LiDAR could inform management for other eastern forest bird species of conservation concern. In fact, previous work on more common forest bird species like the Black-throated Blue Warbler (*S. caerulescens*; Goetz et al. 2010) has already demonstrated the value of LiDAR for predicting habitat for other forest bird taxa. Many species of forest birds of conservation concern are declining due to a lack of important forest structural attributes (McShea and Rappole 2000, Parker et al. 2020, Rushing et al. 2020). To this end, LiDAR is superior to many other traditional remotely sensed data sources with information about forests like NLCD (Jin et al. 2019), CDL (USDA 2021), and the U.S. Forest Service's Forest Inventory and Analysis forest cover rasters (Chojnacky 2000) because LiDAR provides detailed information about forest structures that are important for wildlife (Tattoni et al. 2012, Vogeler et al. 2013, Dickinson et al. 2014). Cerulean Warblers, for example, breed within stands of mature, deciduous trees accompanied by small gaps in the canopy layer (Buehler et al. 2020). The Wood

Thrush (*Hylocichla mustelina*), another species of increasing conservation concern, nests in closed-canopy forest accompanied by a well-developed understory (Evans et al. 2020). It seems likely that the conservation of these species, as well as other eastern forest birds of conservation concern (*e.g.*, Eastern Whip-poor-will [*Antrostomus vociferus*], Louisiana Waterthrush [*Parkesia motacilla*], etc.) would benefit from the use of LiDAR data (Bradbury et al. 2005, Coops et al. 2021). Analyses of forest structure may indicate that bird species like Cerulean Warbler and Wood Thrush have plenty of mature forest habitat, however, as we demonstrate here, LiDAR can help refine estimates of habitat availability by incorporating aspects of forest structure, previously elusive to macroecologists. Beyond single-species studies, LiDAR has already proved useful in a community context (Goetz et al. 2007, Lesak et al. 2011), and may be valuable for understanding whole suites of declining birds (*e.g.*, shrubland species), potentially fit using community occupancy models (Kéry and Royle 2015).

4.1. Conclusion.

Although our analyses here provide a powerful demonstration of the value of LiDAR data to specify models that identify habitat for Golden-winged Warblers, there are several important caveats that should be kept in mind. For example, although we found a negative relationship between p75 (the height below which 75% of LiDAR returns occur) and occupancy probability, Golden-winged Warblers actually prefer saplings that are somewhat more advanced in size as they contribute to the structural complexity of habitat patches (Bakermans et al. 2015a, 2015b, McNeil et al. 2020); studies focused on young forest (rather than a wide suite of forest structure) would likely find a threshold below which occupancy also declines. Moreover, it is also important to keep in mind that Golden-winged Warblers may exhibit different ecological patterns in different parts of their distribution (*e.g.*, Streby et al. 2016, Fiss et al. 2021). For example, Golden-winged Warbler fledglings commonly used mature forest in the Great Lakes (Streby et al. 2016) while those in the Appalachian Mountains often stayed within early-successional habitats (Fiss et al. 2021). Finally, the LiDAR data here were collected during 'leaf-off' conditions; assessments that use LiDAR data collected during 'leaf-on' conditions would likely find different patterns, including data artifacts driven by reduced ground/low-strata returns and more canopy returns (Atkins et al., 2018). Likewise, exploration of the vast potential of alternative LiDAR forest structure metrics may provide improved predictability and insights beyond the narrow subset presented in this study. With these caveats in mind, our study also serves as a springboard for additional work. One project that seems like a natural extension beyond the analyses here would be using LiDAR to assist with the classification of different forest management regimes (e.g., shelterwoods or overstory removals; Wood et al. 2013, Dickinson et al. 2014, Roth et al. 2019). Ideally, such an effort would yield maps that depict forest, classified into relevant treatment types (Coops et al. 2021). Another area of research that is still in its infancy is using LiDAR data to describe habitat selection patterns (rather than simply occurrence) for forest-dependent wildlife (Ciuti et al., 2018). Ultimately, our results provide clear justification for the continued production of publicly available LiDAR products (in Pennsylvania and beyond) for use in wildlife conservation research.

CRediT authorship contribution statement

Darin J. McNeil: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft. **G. Fisher:** Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – review & editing. **Cameron J. Fiss:** Data curation, Investigation, Methodology, Project administration, Validation, Writing – review & editing. **Andrew J. Elmore:** Conceptualization, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – original draft. **Matthew C. Fitzpatrick:** Conceptualization, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing. **Jeff W. Atkins:** Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – review & editing. **Jonathan Cohen:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. **Jeffery L. Larkin:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121002.

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