



RESEARCH ARTICLE

Application of lidar and camera traps to model wildlife habitat

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Abstract

Many wildlife studies develop habitat models based on spatially limited, ground-based surveys. These surveys cannot adequately measure forest canopy features or characterize features at landscape scales, nor can these models be applied at larger extents, making them less useful for conservation. Lidar offers the opportunity to objectively measure habitat features across landscape-level extents, making it possible to predict landscape suitability at the level of entire states. We measured structural diversity of forest vegetation at 179 plots across Indiana, USA, at 3 radii (50 m, 100 m, and 300 m) to explore species associations with forest characteristics at different spatial scales. We developed occupancy models at each scale to predict species presence by relating detection–non-detection of wildlife species from camera traps (2019–2020) to indices of forest structure derived from aerial lidar (2016–2020). We quantified the relationship between the presence of 7 wildlife species and the 3 forest structure metrics. The effect sizes for each metric varied depending on the plot extent and species, often displaying opposite trends at different radii. Deep gap fraction had a strong positive association with species like eastern cottontail (*Sylvilagus floridanus*) at the 100-m and 300-m extents (95% credible intervals did not cross zero), but weaker relationships at 50 m. Some species also used areas with higher vegetation diversity, such as coyote (*Canis latrans*), which was positively associated

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with higher values for Gini foliage diversity at the 300-m extents. Habitat generalists did not show strong evidence of selection for specific metrics. Our study demonstrates that lidar shows great promise for habitat modeling based on its ability to characterize forest structure at landscape scales across large geographic extents. These models identify patterns of space use that are difficult and expensive to capture through traditional survey methods and have clear conservation and management applications owing to their extensive spatial coverage.

KEYWORDS

camera trap, coyote, eastern cottontail rabbit, forest structure, lidar, occupancy model, raccoon, remote sensing, squirrel, white-tailed deer, wild turkey

The ability to accurately characterize habitat is essential for successful long-term management and conservation of wildlife. Although satellites such as MODIS (Moderate Resolution Imaging Spectroradiometer) and Landsat can provide broad thematic representations (e.g., National Land Cover Database) of coarse habitat features at spatial resolutions of 250 m and 30 m, respectively, finer-resolution studies to quantify local habitat structure have until recently been limited largely to field-based and plot-level studies. Field-based measurements, such as those collected using quadrats or line transects, are useful for surveying vegetative species composition, understory structure, or individual habitat features, such as individual trees. However, it is logistically difficult to conduct such surveys over large extents. Thus, plot-level analyses necessarily restrict biological inferences to small spatial extents (Qiao et al. 2017, Frías et al. 2018, Ampacher et al. 2021) or are relegated to broader scale associations with land cover data as a proxy for habitat (Gallant 2009). Moreover, plot-level measures are often subject to measurement bias (Canning and Waltham 2021, Brice et al. 2021). Field methods are efficient when measuring ground vegetation, but measurement error increases when measuring vegetation attributes in higher vertical strata, such as canopy cover. In the field, canopy cover is primarily measured using densimeters, which can be difficult to standardize (Cook et al. 1995). Densimeters also measure only small sections of canopy within a plot. Broad-scale surveys of habitat structure are necessary for understanding how wildlife species select biotic and abiotic features across their entire home range and account for ecosystem-level interactions across variables. These studies are commonly done using coarse-resolution data from satellites like the normalized difference vegetation index (NDVI; Pettorelli et al. 2011) and lack the resolution to convey important structural differences among areas. However, habitat selection occurs at a hierarchy of scales. Fine-scale data are needed to capture local structural information important for wildlife and LiDAR (Light Detection and Ranging; hereafter referred to as lidar) can provide fine-scale data over large spatial extents. There is a fundamental need for better habitat models with new data sources to inform both management and conservation, which necessitates a shift in how we describe habitat and determine what features are selected by species.

Geographic scale is important when defining habitat. Satellite imagery has been used most frequently in intermediate to broad-scale habitat studies (Repetto et al. 2024, Rocca et al. 2020), but in recent years lidar has expanded the available range of scales under consideration. Species select resources at the level of the landscape down to individual trees (Block and Brennan 1993), and lidar can capture both. For example, lidar can quantify the percentage of vegetative cover across entire ecoregions, while also measuring the branching structure of an individual tree. Aerial lidar actively scans surface features with near-infrared lasers mounted to an aircraft and provides objective and quantitative measurements of large areas of terrestrial topography

and forest structure (LaRue et al. 2023). With lidar, researchers can calculate structural variables, which are valuable predictors of habitat use and occurrence by forest species, such as large herbivores (Neumann et al. 2015), birds (Tattoni et al. 2012, Barnes et al. 2016, Milanesi et al. 2017, Melin et al. 2018, Hagar et al. 2020), and edge predators (Kays et al. 2008). Examples of lidar metrics include tree height, percentage of canopy gaps, variety of vegetation size classes, and density of understory vegetation. This emerging technology maximizes the quality and quantity of data that researchers collect, broadens the scale of study while maintaining fine-resolution details, and minimizes human impact, bias, and time in the field.

Similarly, camera traps have revolutionized wildlife studies, enabling continuous sampling of species in their environment and collecting an unprecedented quantity of species presence data with less effort and minimal disturbance compared to classical survey methods (reviewed by Delisle et al. 2021). Together, camera data and lidar have the potential to help refine our understanding of the associations that certain species have with their environment, providing more actionable and robust insights for management and conservation decisions. Only recently have studies begun combining these 2 forms of digital technology. Focusing on 1–2 study species (Paolucci et al. 2019, Lombardi et al. 2022), these rare studies demonstrated considerable potential (Smith 2022, Killion et al. 2023) with lidar-based habitat models outperforming pre-existing habitat suitability models (Shanley et al. 2021) and field-based habitat classifications (Moreira-Arce et al. 2016). Although lidar data have been unable to predict species composition, many species selected for more structurally complex forests (de Thoisy et al. 2016, Deere et al. 2020). Yet, few papers have been published using cameras in combination with any form of lidar to examine vegetation structure.

Under the assumption that structural attributes can be proxies for broad ecosystem characteristics (LaRue et al. 2019), we tested the capability of lidar-derived forest structural metrics in predicting wildlife presence through trail camera data. We predicted that edge-dwelling species would have positive associations while forest-obligate species would have negative associations with measures of habitat fragmentation and disturbance. Additionally, we predicted that habitat generalists would not be associated with any specific structural features. We based our predicted associations between forest structure and 7 study species on their habitat needs presumed from dietary, predation-avoidance, or foraging strategies (Table 1).

STUDY AREA

We used data from camera traps originally deployed by the Integrated Deer Management Project (IDMP) in Indiana, USA. The project deployed camera traps in late winter across Indiana in 3 regional deer management units (out of the 10 units statewide), with units determined by cover, browse material, cropland, hunters, development, road density, and human populations (Swihart et al. 2020). Distribution of our sampled units included the northwestern (unit 3), south-central (unit 4), and northeastern (unit 9) portions of Indiana (Figure 1). The dominant land cover for research management units varied among units and included row-crop agriculture (unit 3, 79% agriculture), forest (unit 4, 56% forest), and a mixture of forests (8%), wetlands (13%), and agriculture (56%, unit 9; Delisle et al. 2023). Unit 3 had the largest basal area of red oak species group, the lowest sapling density, and was primarily within agricultural counties. Unit 4 had the highest sapling densities and included land within Morgan County to the Ohio River. Unit 9 included the Indiana natural lakes region, with the highest total basal area across species. All 3 units were primarily forested and unglaciated (Caudell and Vaught 2019). Elevation ranged between 300–370 m for unit 9, 140–250 m for unit 3, and 100–490 m for unit 4. Average annual precipitation was between 97–104 cm for units 3 and 9 and between 104–199 cm for unit 4 (PRISM Climate Group, Oregon State University 2022). Average annual extreme minimum temperature varied between units: unit 3 (−26.1 to −20.6°C), unit 4 (−17.8 to 15°C), and unit 9 (−23.3 to −20.6°C; U.S. Department of Agriculture 2023).

TABLE 1 For each of the 7 study species, we identified habitat associations and used these to predict which of the 3 forest structural metrics would positively or negatively influence local site presence by each species in Indiana, USA, in 2019–2020 with occupancy models. (+) denotes a predicted positive association and (–) indicates that we predict a negative association. We have listed winter home range, as camera traps were deployed during February and March.

Species	Forested habitat associations	Winter home range	Predictive metric
Coyote	Coyotes prefer fragmented rather than dense forests (Boisjoly et al. 2010) and exploit corridors for successful foraging (Atwood et al. 2004). They are opportunistic, preying primarily on rabbits, rodents, and carrion (Bekoff 1977) and using open areas for hunting and movement (Nielsen et al. 2017).	27–89 km ² (Crête et al. 2001)	Deep gap fraction (+)
Virginia opossum	Opossums are a generalist species that prefer forested land (Greenspan et al. 2018) but exploit variable ecological settings (Gardner and Sunquist 2003) and avoid agricultural and shrubby land in winter (Beatty et al. 2014). They may not often select for specific features (Beatty et al. 2016), with a diet of insects, carrion, and plant material (McManus 1974).	1.14 km ² (Gipson and Kamler 2001)	No strong associations
Wild turkey	Turkeys use edges and areas with numerous openings (Pollentier et al. 2017) for food sources (e.g., invertebrates; Kiss 2015). Predators use dense cover for nest predation, so turkeys select nesting grounds in open areas (Nielsen et al. 2017). Preferred winter habitats include large diameter, tall trees for roosting sites (Perlichek et al. 2009). They are generalist foragers (Rioux et al. 2009) and often use recently burned sites because of the increased foraging material (Martin et al. 2012).	5.41 km ² (Miller et al. 1997)	Deep gap fraction (+)
White-tailed deer	Deer use fragmented land (Cain et al. 2019) and are generalists but like a diversity of stand types (Diefenbach and Shea 2011), potentially because fawn mortality is lower in heterogeneous land (Gulsby et al. 2017). In winter, they show a preference for mixed stands (Sabine et al. 2001). Deer have diverse diets, primarily consuming grasses, forbs, and oak mast (Smith 1991).	5.2 km ² (Brinkman et al. 2005)	Deep gap fraction (+) Gini diversity (+)
Raccoon	Raccoons are a generalist species (Daniels et al. 2019, Stanton et al. 2021) that are positively associated with the proportion of forests (Chamberlain et al. 2002), but they can also occur in wetlands or grasslands (Greenspan et al. 2018). They are omnivores who eat a wide variety of food, including berries, nuts, seeds, and invertebrates, but they are not selective when resources are scarce (Lotze and Anderson 1979).	0.371 km ² (McWilliams and Wilson 2015)	No strong associations
Sciuridae	Eastern gray squirrels prefer mature, continuous woodlands with diverse understories and their	0.006 km ² (Doebel and McGinnis 1974); 0.059 km ²	Deep gap fraction (–) Gini diversity (+)

TABLE 1 (Continued)

Species	Forested habitat associations	Winter home range	Predictive metric
	diet consists of nuts, flowers, and buds (Koprowski 1994b). Fox squirrels occur in primarily open forests. Diet is similar to gray squirrels (Koprowski 1994b). Red squirrels (<i>Tamiasciurus hudsonicus</i>) use mixed conifer-deciduous stands, with ties to herbivorous density and canopy cover. They are granivores but opportunistic (Steele 1998). Southern flying squirrels (<i>Glaucomys volans</i>) are sensitive to fragmentation and need trees for food, shelter, and gliding locomotion. They disperse seeds and fungi (Howard et al. 2020) and need old growth features for nest sites (Zweep et al. 2018).	(Conner 2000); 0.006 km ² (Gurnell 1984); 0.1 km ² (Jacques et al. 2017)	Vegetation area index (+)
Eastern cottontail rabbit	Eastern cottontail rabbits occur on the edges of forests (Bertolino et al. 2011) and use dense understory cover for foraging (Cheeseman et al. 2019) and thermal insulation (Althoff et al. 1997), particularly in winter (Swihart and Yahner 1984). They are not restricted to one single land cover type but prefer a dense layer of herbaceous cover as protection from predators and as their main food source (e.g., grasses), along with woody plants (Chapman et al. 1980).	0.064 km ² (Kilpatrick and Goodie 2020)	Deep gap fraction (–) Vegetation area index (+)

METHODS

Camera trap data and processing

The IDMP collected >3.2 million photos from 1,103 camera stations over 3 years. For this study, we included data from a sample of 179 camera stations operated during 2019 and 2020 and located in both continuous and fragmented forested areas based on the 2019 National Land Cover Database (NLCD) and land classifications from field technicians. We deployed Browning Strikeforce HD or BTC-5HDE cameras (Browning, Birmingham, AL, USA) in early February and retrieved them in mid-March. Cameras were not baited and were placed a minimum of 200 m apart. Our initial dataset contained 242,899 photos across sites. We selected a 2-week period (12–25 February 2019; 9–22 March 2020) where there was overlap in deployment for all cameras, although cameras were deployed for additional time before and after these dates. When sites had species presence data for 2 years, we randomly selected 1 of the years and removed the other to ensure 1 camera detection history per location for each species. We classified the majority (79.1%) of the sites as deciduous forests, while 17.6% were mixed forests and the remaining plots were woody wetlands. We selected plots that fell within sites classified as forests by our technicians that had data for a minimum of a 2-week period. Because of this approach, our model was a measurement of probability of habitat use at each site rather than true occupancy.

Volunteers and technicians identified species present within each photo using the program DigiKam (KDE, Berlin, Germany) and analyzed tagged photo metadata from each site in program R (R Core Team 2020) using the package camtrapR version 2.0.3 (Niedballa et al. 2016). The IDMP tagged data from a 2-week winter period in February or March each sampling year. Therefore, we only included capture histories for plots deployed during this period.

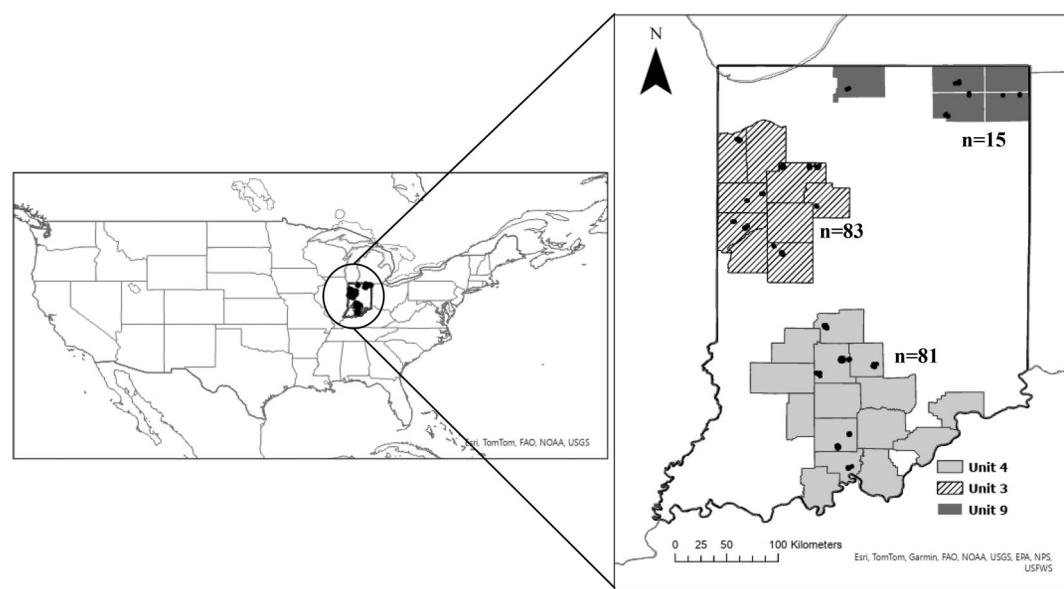


FIGURE 1 The 179 camera trap locations (black points), which collected presence-absence data (2019–2020) that we used to develop occupancy models for 7 species in Indiana, USA. Camera traps were deployed across Indiana by the Integrated Deer Management Project in 3 research units that are grouped by land cover type and level of human development. County boundaries are shown within each unit (black lines).

We processed data in *camtrapR*, which allowed for the organization of raw camera trap photos and creation of detection–non-detection matrices to be used in occupancy models. For each species, we generated a 14-day binary (0 = absence; 1 = presence) detection history to be used in our models.

Quantifying forest structure with lidar at different extents

We quantified forest structure at 3 spatial extents, treating the location of the camera trap as the center of the plot and clipping point cloud data at radii of 50 m, 100 m, and 300 m. The smallest plot radius (50 m) is twice the estimated detection range of the cameras given by the manufacturer (Browning), although the actual range is likely smaller (Delisle et al. 2023). Viewshed visibility is dependent on physical conditions at the site, such as topography, surrounding vegetation (Moll et al. 2020), and camera angle (Moeller et al. 2022). The 100-m plot extent served as an intermediary size between the largest and smallest extent and maintained a greater sample size than when we extended the radius to the largest size. The 300-m radius acted as the largest extent to limit plot overlap to reduce the potential effects of pseudo-replication on model residuals. Using 2019 NLCD data in ArcGIS Pro (Esri, Redlands, CA, USA), we determined that plots larger than 300 m in radius risked too much overlap in plot extent and percentage of non-forested land. Plots were initially spaced with a minimum of 200 m between each, and we removed those that heavily overlapped.

In R with the package *lidR* version 3.1.4 (Roussel et al. 2020), we read in the catalog of LAS tiles from the 2016–2020 Indiana statewide high-resolution aerial lidar, along with a shapefile of plot centers. Indiana lidar was flown in the spring over the course of 5 years when there was no snow on the ground and rivers were at normal heights. Units 9, 4, and 3 were scanned in 2017, 2017–2018, and 2018, respectively. Pulse spacing was 0.7 m with a positional horizontal accuracy of ± 0.36 m. We sourced Indiana 3DEP lidar from the Institute for Digital Forestry at Purdue (<https://lidar.digitalforestry.org/>).

We processed the tiles according to a systematic workflow (Figure 2). Using the clip_roi function, we clipped a fixed 400-m radius circular point cloud for each plot. Because our largest plot extent had a radius of 300 m, this ensured a minimum of a 100-m buffer for data processing to avoid interpolating on the edge of each plot while filtering data and creating the digital terrain models (DTM), which is a raster data product generated from the ground points. We then filtered outliers by removing points whose elevation values were outside of 6 standard deviations from the mean Z (height) value for the plot because these points could be random noise or outliers caused by, for example, birds. We used the lasnormalize function to automatically

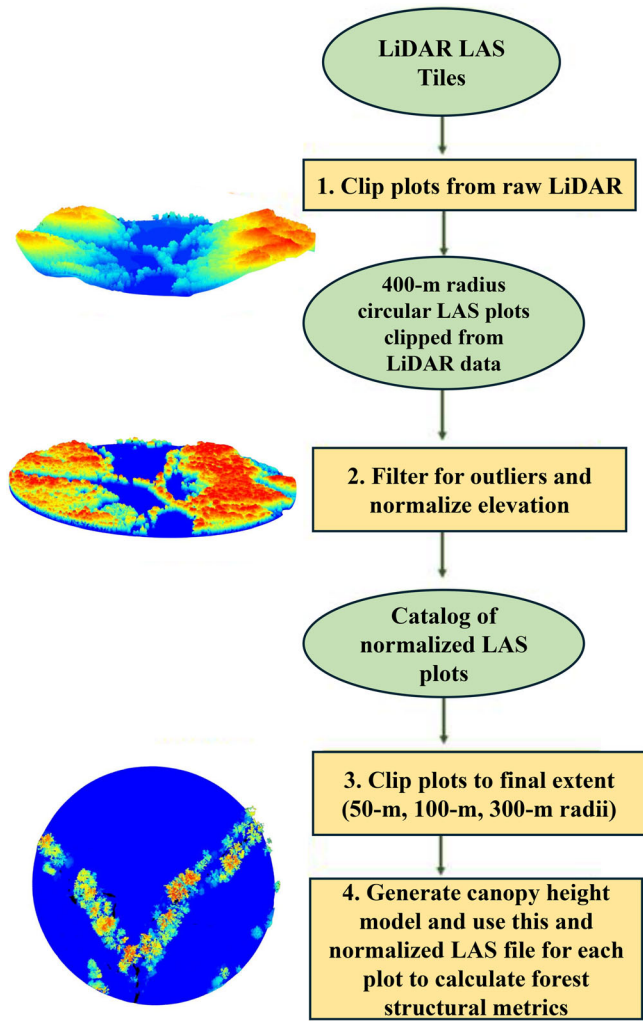


FIGURE 2 We processed aerial lidar collected in Indiana, USA (2016–2020) and used the resulting LAS data to calculate 3 forest structural metrics for use as occupancy covariates in models for 7 wildlife species. The LAS tiles are the format in which raw 3D lidar point clouds are stored. Lidar point cloud plots are on the left, with cool tones (blue, green) indicating low elevation areas, and warm tones (yellow, red) indicating high height above ground values. Ground elevation derived from a digital terrain model is subtracted from every point in the point cloud, respective of pixel and point locations. This ensures that ground points read as 0 m. A canopy height model is a rasterized version of a point cloud, in which X and Y coordinates correspond to longitude and latitude, respectively, and each pixel displays the highest height value within the area.

subtract DTM from the Z values. This accounted for variation in topography and ensured that ground points had Z values of zero.

We then clipped each plot to its final spatial extent (50 m, 100 m, 300 m) using the `clip_roi` and `lascatalog` functions, removing the extraneous buffer area. The resulting lidar point cloud has an average density of 2.54 (SD = 1.52), 2.44 (SD = 1.44), and 2.07 (SD = 1.20) points/m² on plots with a 50-m, 100-m, and 300-m radius, respectively. For each of the 3 plot sizes, we created an individual canopy height model (CHM) at a resolution of 1 m. We calculated vegetation area index (VAI) and Gini foliage diversity based on the point cloud and Z values, whereas we calculated deep gap fraction using the individual CHM for each plot.

Initially, we calculated 9 structural metrics for all 179 camera traps with 3 plot radii, including average canopy height, maximum canopy height, top rugosity (3-dimensional distribution of leaf densities), rumple (roughness of tree canopy surface), vertical complexity index, Gini coefficient of foliage (tree height inequality), vertical heterogeneity, VAI (measure of light availability), and deep gap fraction (Table S2). To minimize issues with multicollinearity, we computed Pearson product-moment correlation coefficients at each radius (Figure S1). We removed metrics that were correlated ($r > 0.40$) with all other metrics at all scales. There were ultimately 3 remaining variables: deep gap fraction, Gini coefficient of foliage, and VAI (Table S2). We ran Pearson's correlation analyses between 3 metrics at each scale to test for across-scale correlation (Figure S2). We focused primarily on the ability of forest structural metrics alone to predict species presence. We removed more traditional, well-established predictors (e.g., distance from roads, slope, elevation, percentage of different land cover classes) from the models to test the ability of structural metrics independently.

Modeling species-structure relationships

We constructed Bayesian occupancy models with the R package `ubms` version 3.0.4 (Kellner et al. 2022, 2023) to test the capability of our 3 structural metrics in predicting presence of 6 species and 1 family of wildlife: coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), Virginia opossum (*Didelphis virginiana*), eastern cottontail (*Sylvilagus floridanus*), raccoon (*Procyon lotor*), tree squirrels (Sciuridae), and wild turkey (*Meleagris gallopavo*; Table 1). Thus, we fit models for parameter estimation rather than model selection. We used all 3 structural metrics as occupancy covariates and daily temperature means and total daily precipitation (Daymet, National Aeronautics and Space Administration, Washington, DC, USA) as detection covariates. We chose temperature and precipitation as detection covariates, as these are known to vary significantly between trapping occasions and are commonly used (Thorn et al. 2009, Cooper et al. 2019). We included IDMP unit and year as random effects in early models but found that these did not explain significant amounts of variation and removed these variables.

We compared models using 1 of each of the 3 total structural variables at a time as an occupancy predictor and found negligible differences in expected log pointwise predictive density (ELPD) difference scores (< 4). For occupancy models within Bayesian frameworks, ELPD differences are used to compare model performance rather than Akaike's Information Criterion (AIC) scores (Kellner et al. 2022). This suggests that the differences between the best covariates for models were not substantial enough to be able to confidently support 1 over the other for many of the species. Therefore, we estimated parameters for global models for all species individually at all 3 scales. We then plotted standardized (z-score normalization so that average mean = 0; average SD = 1) coefficients against each other to test the directionality and effect sizes of each metric in these species-structure relationships. Global models included both detection covariates and all 3 occupancy covariates. We calculated site occupancy estimates based on the global model of detection and occupancy at each scale (Table S1).

For each of our global models, we performed MacKenzie-Bailey goodness-of-fit tests (chains = 3, iterations = 1,000; MacKenzie and Bailey 2004, Kellner et al. 2023) in R to compare the predicted and observed species presence at each plot. For occupancy models, P -values > 0.5 indicated a well-fitting model. We also plotted 95% credible intervals and judged variable importance and consistency based on whether these credible intervals

included 0. Additionally, we created traceplots for each global model to ensure convergence and plotted residual versus fitted values to visually inspect for spread and distribution.

RESULTS

Forest structure across scales

For each of the 3 forest structural metrics, means across radii were similar but increased with spatial extent (Figure 3). Average deep gap fraction ranged from 0.40 (SD = 0.18) at the 50-m radius to 0.46 (SD = 0.46) at the 100-m radius and 0.59 (SD = 0.17) at the 300-m radius. Gini foliage diversity was highest at the largest spatial extent, with an average of 0.32 (SD = 0.46). The VAI was largest at the 300-m radius as well, where it averaged 6.47 (SD = 0.46), although standard deviation was high at 50 m (SD = 1.79) and 100 m (SD = 1.25). Pearson's correlation coefficients were highest between variables at the 300-m extent (Figure S1). We retained those that we presumed to have the most ecological significance to our study species and had correlation scores <0.40 with other remaining variables (Figure S1). We tested for across-scale correlation by calculating Pearson's correlation coefficient for each

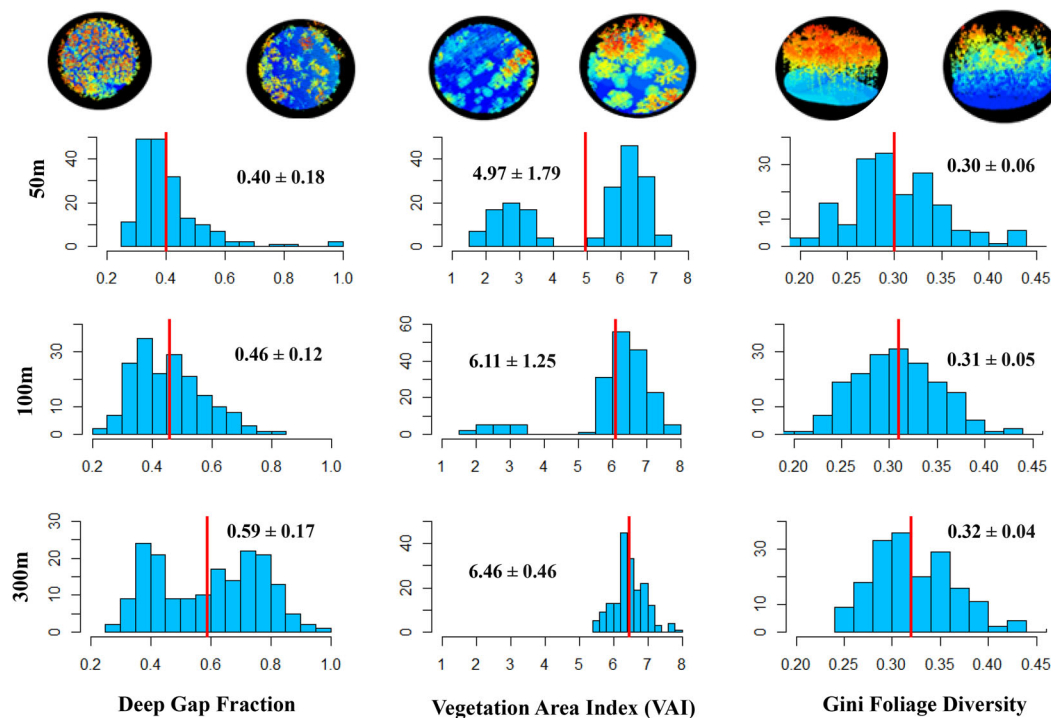


FIGURE 3 Histogram of the 3 lidar-derived forest structural metrics used in wildlife occupancy models measured across 179 camera trap plots at 3 scales (radii of 50 m, 100 m, and 300 m) in Indiana, USA, between 2016 and 2020. Three-dimensional point clouds illustrate plots with high or low values for each metric. Colors in the same LAS plots represent height above ground values for each of the pixels, with cool tones (blue, green) representing low values and warm tones (red, orange) representing high height above ground values. Plots with high deep gap fraction have greater percentages of non-forested land and edge. Plots with higher vegetation area index values have a greater number of vegetated pixels, and plots with higher Gini foliage diversity have greater structural complexity. The X and Y axes are metric values and frequencies, respectively. Mean value (red line) and standard deviation are indicated for each metric.

metric at each of the 3 scales (Figure S2). For deep gap fraction, correlation between the 50-m and 100-m extents ($P = 0.96$) and between the 50-m and 300-m extents ($P = 0.57$) were negligible ($r < 0.05$), but correlation was high between 100-m and 300-m extents ($r = 0.63$; $P < 0.001$). For Gini foliage diversity, correlation between the 50-m and 100-m extents ($P = 0.80$) and between the 50-m and 300-m extents ($P = 0.47$) were also small ($r < 0.06$), but correlation was strong between the 100-m and 300-m extents ($r = 0.84$; $P < 0.001$). For VAI, the highest correlation was between the 50-m and 100-m extents, with $r = 0.32$ ($P < 0.001$).

Detection probability

The mean daily temperature and total daily precipitation, averaged over the 2-week trapping period, were 3.64°C and 4.61 mm, respectively. Unit 3 had the highest temperature and precipitation across the trapping period (3.62°C ; 4.56 mm), followed by unit 4 (3.45°C ; 4.47 mm), and finally unit 9 (2.91°C ; 2.91 mm). Average detection probability for each species across the 14-day period was similar across units (e.g., coyote = 0.03 for all 3 units). Average detection probability was highest within unit 9 for white-tailed deer (0.28), eastern cottontail (0.07), and raccoon (0.07). For turkey (0.14) and opossum (0.05), unit 3 had the highest average detection, and Sciuridae was similar (0.02) between units 3 and 4.

Forest structure as a predictor of species presence

We examined the directionality of the relationships between each species' occurrence and the covariates in their global models (Figure 4). Eastern cottontail, and to a lesser degree raccoon, exhibited a consistent positive association with deep gap fraction, while coyote exhibited a positive relationship with tree height inequality (Gini) at the larger 2 extents. Other species did not demonstrate consistent directionality across spatial extents or strong relationships with forest structural metrics in either direction (e.g., wild turkey; Table S3).

Our best fitting models were for coyote, which had P -values of 0.31, 0.24, and 0.28 for the 50-, 100-, and 300-m radii, respectively. Wild turkey had the next best models (50-m: $P = 0.02$; 100-m: $P = 0.05$; 300-m: $P = 0.04$). All other models had negligible goodness-of-fit values ($P = 0$). A visual inspection indicated proper convergence within each traceplot and relatively even horizontal and vertical distribution of residuals.

DISCUSSION

Our study demonstrated that species display associations with certain forest characteristics that can be measured with lidar-derived metrics. There is potential for increased use of lidar in habitat modeling, particularly for characterizing forest structure at landscape scales and pairing with camera trap data. The strength of the effect of forest structural metrics on habitat use varied by species and the spatial extent of the plot (Figure 4). Some species displayed a strong relationship with measures of forest structure, such as deep gap fraction, whereas more generalist species did not (at any radius). In future studies, we recommend the incorporation of more measures of forest structure into studies of habitat use by species in forested landscapes and evaluation of their importance and utility relative to more widely used measures, particularly as documentation for new metrics becomes available.

We hypothesized that species that capitalize on openings and habitat corridors, such as coyote, white-tailed deer, and wild turkey, would have a strongly positive relationship with measures of habitat fragmentation and disturbance (Table 1). Coyotes only had a weakly positive relationship with deep gap fraction at the 50-m extent. This is contrary to previous studies, which demonstrated their use of fragmented forests for hunting and ease of movement (Table 1). At the 300-m extent, coyotes had a strong negative relationship with deep gap fraction,

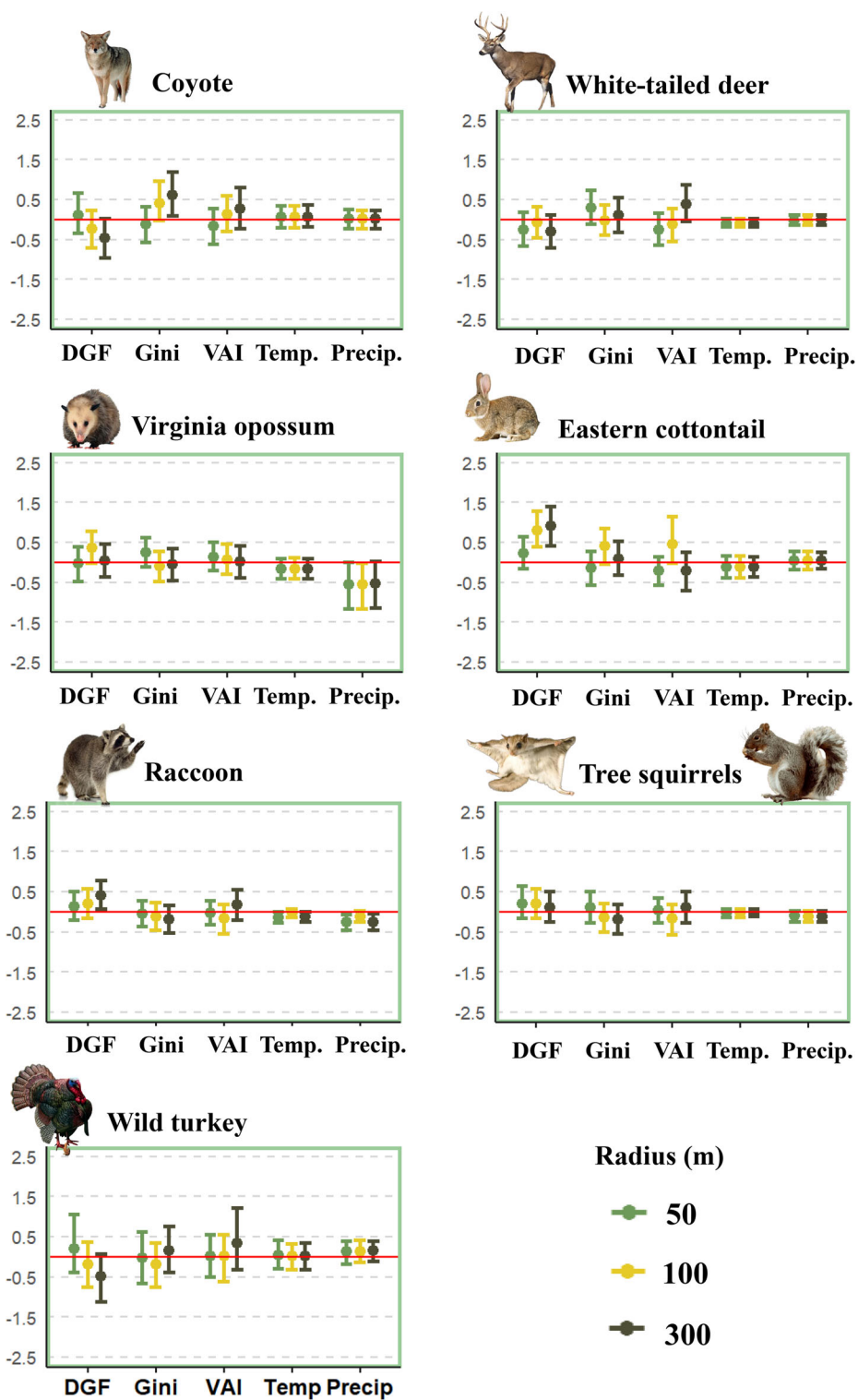


FIGURE 4 (See caption on next page).

potentially due to decreased ease of movement from increased understory vegetation density (Grandpré et al. 2011). Instead, the Gini foliage coefficient had a strong positive effect on coyote presence at the 300-m extent (95% credible interval does not cross 0). Increased vegetation diversity may support a higher prey population for hunting—an underexplored driver of coyote occurrence models to date. White-tailed deer had weakly negative relationships with lidar metrics, and wild turkey displayed weak and inconsistent relationships across the 3 radii. However, species like eastern cottontail displayed a strong association with deep gap fraction at all 3 radii (Figure 4), and 95% credible intervals did not cross 0 for the 100- or 300-m extents. While eastern cottontails require overstory coverage as protection from avian predators, they still use open grassy areas and occur on the edges of forests (Table 1). Additionally, increased light penetration to the understory creates denser shrub cover and more diverse browse material (Grandpré et al. 2011). Contrary to our hypotheses, deep gap fraction did not display strong effects on other species, such as Sciurids.

We also anticipated that habitat generalists would not strongly use specific structural features. Virginia opossums have varied diets and select for a mixture of ecological settings (Gardner and Sunquist 2003, Greenspan et al. 2018), including forested land (Table 1). Yet, for opossums, deep gap fraction, vegetation area index, and Gini foliage diversity had weak effects with 95% credible intervals that crossed zero (Figure 4). This provides evidence in support of our initial prediction that generalists like the Virginia opossum may not select strongly for specific structures. Similarly, raccoons are omnivorous generalists (Stanton et al. 2021, Daniels et al. 2019) who use forests in addition to other land cover types like grasslands (Chamberlain et al. 2002; Table 1). For raccoons, effect sizes for forest structure variables were small and most 95% credible intervals crossed 0. However, deep gap fraction was consistently positive (CI did not cross 0), and strongest at the 300-m radius, indicating that raccoons may seek more open areas at larger scales (Figure 4).

The directionality and effect size of coefficient estimates were not always consistent for each species, each variable, and each scale (Figure 4). Previous work asserts that deer prefer a diversity of stand types (Diefenbach and Shea 2011) and may experience lower fawn mortality in more heterogeneous environments (Gulsby et al. 2017), with one of the largest winter home ranges of the species we examined (Table 1). Yet, white-tailed deer shifted from a negative relationship with VAI at the 50-m extent to a positive one at the 300-m extent (Figure 4). Deer also had a positive relationship with Gini foliage diversity at the 50-m extent, with a nearly 0 effect size at 100 m and 300 m. Eastern cottontail had a strong positive relationship with VAI at the 100-m extent and a negative one at the 100-m and 300-m extents (Figure 4). Similar to other species in our study, cottontails are not restricted to one ecological setting and may select varied levels of vegetation strata and densities depending on their spatial extent (Table 1), which is consistent with their varied response to forest structure across spatial extents (Figure 4). However, VAI, Gini foliage diversity, and deep gap fraction all had strong positive effects on cottontails at the 100-m extent, a scale that more closely approximates their winter home range size (Kilpatrick and Goodie 2020). Wild turkeys were associated with high deep gap fraction at 50-m extent and low deep gap fraction at the 100-m and 300-m extents (Figure 4). Turkeys are generalists (Rioux et al. 2009) who frequent disturbed sites for foraging and more continuous forest for cover (Martin et al. 2012), which could explain their lack of consistent trends with the forest metrics we included (Table 1). Forest structure had weak effects on Sciurids, contrary to expectations (Figure 4). We analyzed squirrel images at the family level because it was difficult to assign images to the species level with the camera trap photos. Syntopic species such as eastern gray squirrel (*Sciurus carolinensis*) and fox squirrel (*S. niger*) have different habitat needs (Koprowski 1994a, 1994b) and our pooling them together may have

FIGURE 4 The standardized coefficient scores and 95% credible intervals from global wildlife occupancy models for each of the 7 species detected by camera traps in Indiana, USA, at the 50-m, 100-m, and 300-m scales for 2019–2020. Variables included deep gap fraction (DGF), Gini foliage diversity (Gini), vegetation area index (VAI), mean daily temperature (temp.), and daily precipitation (precip.).

resulted in the lack of a clear trend with any forest metric (Table 1). Future studies should further explore the ecological significance of each of these measures and their ability to characterize and identify suitable landscapes for a species, ideally with larger spatial extents and greater camera spacing.

We also identified a relationship with the 3 structural measures and size of plot extents that are reflective of stand complexity and disturbance. Gini foliage diversity index and gap fraction increased with plot size, although the changes were slight (Figure 3) because as plot size increases, so does the diversity of forest structure, and the percentage of non-forested land. The VAI also increased with plot spatial extent; however, standard deviations for the 50-m and 100-m extents were very high (Figure 3). High and low values for each of the 3 forest structure metrics represented different ecological attributes. Gini foliage diversity is often used to estimate stand age complexity based on the irregularity of tree size. Deep gap fraction can measure the amount of disturbance to a forest, and higher values for deep gap fraction could indicate a forest that has lost trees from natural or human disturbance. Lower deep gap fraction percentages indicate a more intact forest with less fragmentation and edge. The VAI measures light interception, and high values of VAI could indicate a productive forest.

Although this study demonstrated the utility of incorporating forest structural metrics into predictive models of wildlife presence, we acknowledge our limitations. Ideally, a model includes covariates for all possible factors affecting species detection probability and probability of site use. However, future models could incorporate more traditional metrics in addition to newer forest structural metrics. Additionally, we began with 9 structural metrics, but lidar-derived structural metrics are often heavily correlated, and we had to remove 6. Nonetheless, each of the 3 metrics we chose represents a unique and meaningful ecological attribute to justify its inclusion in our species models (Table 1; Figure S2). We also used lidar data that were collected ± 3 years from the deployment years of the cameras. To our knowledge, no wide-scale disturbance occurred across the region where our cameras were deployed, but it is possible that forest management occurred at some plots and influenced results. We were also unable to control differences in metrics resulting from swath overlap or scan angle variations, which could have introduced bias and inconsistencies in canopy densities (Roussel et al. 2017). The 3-dimensional elevation program (3DEP) has stringent regulations for lidar data collection to be standardized over all sites; however, it is unavoidable that some plots may fall in areas where point density is inconsistent because of this standardization. Although lidar point density has limited impacts on structural diversity metrics when the point density is sufficiently large (LaRue et al. 2022, Wang et al. 2024), future studies should be mindful of the potential implications of differences in point density on canopy estimates and could potentially filter points from overlapping swaths of scans. Furthermore, while 3DEP lidar data is completely free and open access through the United States Geological Survey, it does require significant storage space, and processing time can sometimes be several days, depending on the size and number of plots. Initial work with lidar can be challenging, as it is not as commonly used as satellite data. However, workflows, tutorials, and updates to R packages (e.g., *lidR*, *leafR*) are increasingly available and have made it possible to batch process hundreds of plots at a time.

Ecologically meaningful variables can be derived from lidar at landscape levels. This holds considerable potential for fields of ecology. However, only recently have wildlife studies begun to explore the structure of vegetation as it relates to habitat at spatial extents large enough to more accurately represent resource use (Killion et al. 2023). We recommend larger spacing between camera traps to allow for lidar plot radii to be larger while maintaining high sample sizes and considering space use of the study species or careful examination of residuals to determine whether plot overlap is an issue. Future studies can apply these models across larger extents to predict species presence based on structure outside of their study area, tailoring scale extents to be specific to each species' home range. However, studies should be mindful that patterns of use may differ in areas containing greatly different compositions of land cover types. It may additionally be useful to use a mixture of scales within the same model to account for variations in space use (Nichols et al. 2008, Fernández and Gurrutxaga 2010) or use different scales with a competing model approach. These models can identify forest structural metrics associated with wildlife species occurrence, which can then be achieved through forest management practices. For example, deep gap fraction was positively associated with eastern cottontails at the 300-m scale and could be achieved through

selective harvest of large patches. Our results add to the growing body of evidence (Moreira-Arce et al. 2016, Deere et al. 2020, Smith 2022, Killion et al. 2023) that the structural signature of a forest is an underutilized measure with potential in the field of wildlife conservation and forest management planning.

RESEARCH IMPLICATIONS

Our work tested the potential of using lidar-derived forest structural metrics to predict habitat use at forested sites across Indiana for 7 species. These metrics have rarely been used with camera traps and hold considerable potential for quantitatively measuring important ecosystem attributes, such as canopy openness. While we used only lidar-derived metrics as occupancy covariates, we recommend that future studies also incorporate more traditional metrics, such as road density, human population, or even broad habitat classifications from satellite data. Our models had poor performance for many species, possibly because they did not include important predictors or because they did not adequately account for variation in our predictors. We suggest that, rather than attempting to use the same spatial extent and predictor variables across multiple species, researchers instead select 1–2 focal species and tailor the study to each. We hope that this study can serve as a demonstration that there is space in wildlife research for the increased use of technologies like lidar, as a supplement to pre-existing methodology and variables. Lidar is particularly useful for areas where it may not be possible to perform traditional vegetation surveys because of cost or local site conditions, but it has considerable potential when combined with other datasets, such as LANDSAT or MODIS.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All methods followed guidelines for use of wild mammals in research published by the American Society of Mammalogists; however, the study was exempt from Institutional Animal Care and Use approval because the research used non-invasive survey methods, and cameras were not baited. The camera data were collected as part of a collaborative research effort between Purdue University and the Indiana Department of Natural Resources Division of Fish and Wildlife (Grant W-48-R-02). We received prior landowner approval for placement of cameras located on private lands.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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