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RESEARCH ARTICLE

Influences of aquatic and terrestrial habitat characteristics on abundance patterns of adult wood turtles

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Abstract

Wood turtles (*Glyptemys insculpta*) are a species of conservation concern throughout their geographic distribution. Several studies have investigated individual-level habitat selection of wood turtles in the Upper Midwest in the United States, but the effects of habitat characteristics on abundance are poorly understood. This information is needed to improve landscape-level habitat management and conservation initiatives for the species. Our study aimed to identify important aquatic and terrestrial habitat characteristics and quantify their influence on abundance dynamics of adult wood turtles in the Laurentian Mixed Forest Province ecoregion of Wisconsin and Minnesota, USA. We collected standardized population survey data at 57 sites within the ecoregion between 2016 and 2022. We used *N*-mixture models with a multi-stage model selection procedure to assess the influence of aquatic and terrestrial predictors on abundance, including several 3-dimensional forest structure metrics derived from airborne Light Detection and Ranging (LiDAR) data. Several aquatic and terrestrial habitat characteristics influenced local abundance patterns of adult wood turtles. The most influential aquatic predictors were stream velocity and stream width, and the most influential terrestrial predictors were mean return height and vertical coefficient of variation of height. Abundance was high at sites containing

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comparatively narrow streams with moderate velocities. The most supported terrestrial predictors were derived from LiDAR and indicate that complex forest structures support larger wood turtle populations. Our results can be used in forest management strategies to improve habitat quality for wood turtles, such as selective tree harvesting to increase structural diversity, and potentially identify robust populations in under-surveyed areas.

KEYWORDS

forest, *Glyptemys insculpta*, LiDAR, Midwest, Minnesota, reptile, stream, Wisconsin

Habitat can be described as the environmental conditions and resources that allow for species' occupancy (Hall et al. 1997). Habitat selection theory predicts that individuals will select environments that maximize their fitness, given constraints such as availability, resource competition, and settlement costs (Rosenzweig 1981, Greene and Stamps 2001). In general, we would expect the occurrence and abundance of individuals to be positively related to habitat quality (Pérot and Villard 2009, Boyce et al. 2015, Murphy et al. 2017). Thus, identifying habitat characteristics strongly correlated with abundance patterns can indicate their importance for the species and can be used to estimate abundances across the area of inference (Boyce and McDonald 1999, Ehrlén and Morris 2015).

Wood turtles (*Glyptemys insculpta*) are a semi-aquatic freshwater species of conservation concern and are endemic to northeastern North America (Jones et al. 2021*b*). Population declines have been documented across the species' geographic distribution (Garber and Burger 1995, Daigle and Jutras 2005, Willoughby et al. 2013, Jones et al. 2021*a*), resulting in the wood turtle being classified as endangered by the International Union for Conservation of Nature and Natural Resources (IUCN; van Dijk and Harding 2011) and placed under review for federal listing under the United States Endangered Species Act (U.S. Fish and Wildlife Service 2015). In response, many state agencies have begun implementing conservation actions for the species, such as the installation of road barriers to reduce vehicular mortality and the construction, restoration, and protection of nesting sites (Wisconsin Department of Natural Resources [DNR] 2016, Jones et al. 2018, Minnesota DNR 2020). Managers are interested in incorporating broader site-level management initiatives to improve habitat quality, but few studies have assessed abundance-habitat relationships for this species.

Wood turtles are unique among North American turtles in that they require riverine systems for overwintering and regularly use rivers and streams (hereafter streams) throughout the year, but individuals are often highly terrestrial during the summer months (Ernst 1986, Kaufmann 1992, Curtis and Vila 2015, McCoard et al. 2018). Wood turtles have been documented in a wide range of stream sizes (from <3 to >50 m wide), but most populations occur in mid-sized streams (3–20 m wide), and occurrence is also positively associated with streams that contain moderate-fast currents and inorganic substrates (Jones et al. 2021*c*).

Most previous studies on wood turtle terrestrial habitat relationships have focused on individual-level habitat use and selection (Kaufmann 1992, Tingley et al. 2010, Thompson et al. 2018). Collectively, these studies indicate that wood turtles are most often found in open canopy and edge habitats within primarily forested systems, suggesting that terrestrial habitat selection is non-random (Compton et al. 2002, Arvisais et al. 2004, Brown et al. 2016, Wallace et al. 2020). Furthermore, previous studies suggest possible selection for structurally complex environments (Compton et al. 2002, Arvisais et al. 2004, Brown et al. 2016, Marchacos 2020). Variation in forest structure creates a thermally heterogeneous environment (Brokaw and Lent 1999), which could improve the thermoregulatory potential of the environment for wood turtles (Dubois et al. 2009).

Two studies in the eastern United States have assessed the influence of habitat characteristics and land use on wood turtle abundance patterns. Roberts et al. (2021) used population survey data from 293 sites across 12 states to investigate the influence of aquatic, terrestrial, and climatic variables on abundance patterns. The most supported model estimated that abundance was positively associated with the proportion of forest cover and negatively associated with traffic levels and agriculture-dominated areas within 5,500 m of the site; no aquatic variables were included in the most supported model. Willey et al. (2022) used a subset of these data (i.e., 78 sites across 9 states) to investigate further the influence of surrounding land use on the relative abundance of wood turtles (i.e., high vs. low abundance sites). High abundance sites were positively associated with proportion of forest cover and negatively associated with proportion of urban cover within 300 m and 5,500 m of survey sites, respectively. These studies indicate that broadscale changes in land use in the eastern United States have negatively affected wood turtle populations. However, wood turtle densities can vary widely over relatively small spatial scales (Jones 2009, Brown et al. 2017, Akre et al. 2019), indicating the potential for a strong influence of site-level habitat characteristics on abundance dynamics. In addition, large portions of their northern geographic distribution remain rural and forested, and these areas will likely become strongholds for the species in the future as climate and land use changes continue to reduce habitat quality across much of their southern distribution (Mothes et al. 2020, Roberts et al. 2021, Willey et al. 2022). Thus, studies focused on wood turtle abundance-habitat relationships in their northern distribution are needed to improve habitat management plans.

Our objective was to estimate the influence of aquatic and terrestrial habitat characteristics on site-level abundance of adult wood turtles in the Laurentian Mixed Forest Province (i.e., Northwoods) ecoregion of Wisconsin and Minnesota, USA. We hypothesized that abundance of adult wood turtles would vary in response to aquatic and terrestrial habitat characteristics. We predicted that abundance would be best explained using a combination of aquatic and terrestrial habitat predictors because wood turtles depend on aquatic and terrestrial habitat components, that variables characterizing the size and flow characteristics of streams would be influential, and that terrestrial variables representing structural habitat complexity, such as variation in canopy height, would be influential based on results of previous individual-level habitat use studies.

STUDY AREA

We sampled wood turtle populations across the Laurentian Mixed Forest Province in Wisconsin and Minnesota between 2016 and 2022 (Figure 1; specific sampling locations withheld in compliance with Minnesota and Wisconsin data practices for species of conservation concern). This ecological province represents a transitional zone between boreal forest to the north and deciduous forest to the south (Bailey 1980). We selected this study area because it is largely undeveloped and primarily forested, and it is a focal area for wood turtle conservation actions by the Wisconsin DNR and Minnesota DNR (Wisconsin DNR 2016, Minnesota DNR 2020). The study area includes 62,787 km of streams and approximately 39% of the land is in public ownership (U.S. Geological Survey 2022*a*, *b*). The study area has a mean elevation of 411 m above mean sea-level and a topography characterized by mostly low relief, rolling hills (Bailey 1980). This region has a humid continental climate with 4 seasons. The average annual precipitation is 800 mm and average monthly temperature ranges from −12.1°C in January to 19.1°C in July (1990–2020; PRISM Climate Group 2024).

Major land use classes in the study area include hardwood forest (40.3%), riparian (27.1%), and conifer forest (13.3%; LANDFIRE 2016). Agricultural and developed land account for only 5.4% and 4.9% of the study area, respectively (LANDFIRE 2016). Common tree species include maple (*Acer* spp.), aspen (*Populus* spp.), ash (*Fraxinus* spp.), birch (*Betula* spp.), oak (*Quercus* spp.), American beech (*Fagus grandifolia*), American elm (*Ulmus americana*), American basswood (*Tilia americana*), eastern white pine (*Pinus strobus*), red pine (*P. resinosa*), balsam fir (*Abies balsamea*), spruce (*Picea* spp.), northern white-cedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*; Curtis 1959, Wisconsin DNR 2015). Common understory shrubs include alder (*Alnus* spp.), mountain maple (*Acer spicatum*), *Viburnum* species, honeysuckle (*Lonicera* spp.), hazelnut (*Corylus* spp.), *Vaccinium* species, and holly (*Ilex* spp.; Wisconsin DNR 2015). Other turtle species native to the study area include the snapping turtle (*Chelydra*

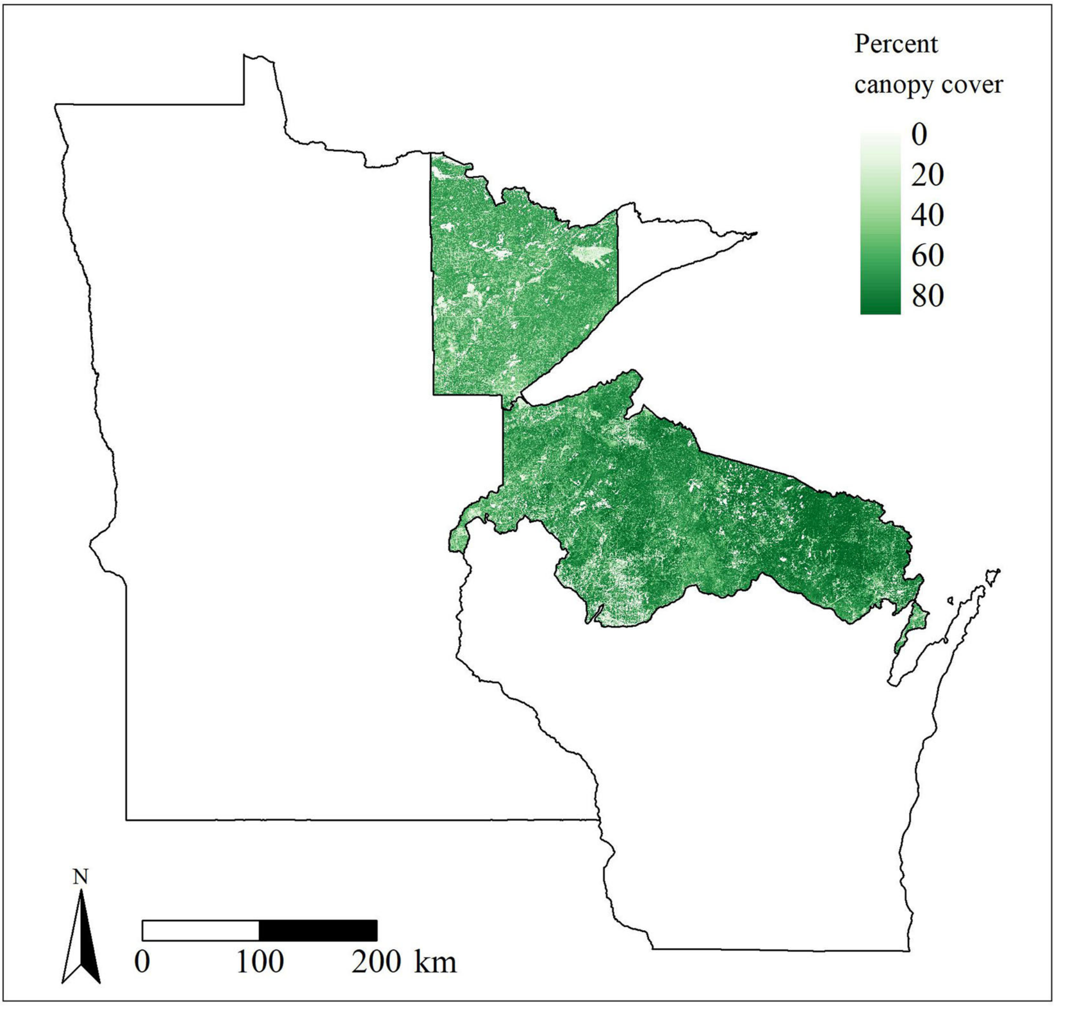

FIGURE 1 Estimated canopy cover in 2016 across the Laurentian Mixed Forest Province ecoregion of Wisconsin and counties within the geographic distribution of wood turtles in northeastern Minnesota, USA. Between 2016 and 2022, we conducted population surveys for wood turtles at 57 sites within this area to assess abundance-habitat relationships.

serpentina), painted turtle (*Chrysemys picta*), Blanding's turtle (*Emydoidea blandingii*), northern map turtle (*Graptemys geographica*), and spiny softshell (*Apalone spinifera*; Kapfer and Brown 2022).

METHODS

Population sampling

Between 2016 and 2022, we sampled wood turtle populations at 57 sites within 15 streams across 8 Hydrologic Unit Code 8 watersheds (Seaber et al. 1987), with stream selection guided by Wisconsin DNR, Minnesota DNR, and Bad River Band of Lake Superior Chippewa information needs. All sites within each watershed were sampled during the same year, with 1, 1, 2, and 4 watersheds sampled in 2016, 2018, 2021, and 2022, respectively. We selected 38 sampling sites in Wisconsin using a stratified random sampling approach designed to ensure that sites represented a range of forested and open habitats. Specifically, we delineated the streams into 1-km segments. We stratified the segments into 5 classes based on mean canopy cover within 100 m of each stream segment using the Jenks natural breaks algorithm (Jenks 1967) in ArcGIS Pro 3.0.1 (Esri, Redlands, CA, USA). We derived mean canopy cover from the National Land Cover Database 2016 tree canopy cover dataset (U.S. Geological Survey 2019*a*) and defined the 5 canopy cover classes as <43%, 43–57%, 58–66%, 67–75%, and >76% canopy cover. We then restricted potential sampling sites to state, federal, and Bad River Reservation property. We randomly selected stream segments within each study watershed across the stratification classes, using the sample_n function from the package dplyr (Wickham et al. 2023) in program R (R Core Team 2023). We sampled an additional 19 sites representing focal management areas, including sites designated for long-term monitoring and locations where management actions had previously occurred or were planned (Wisconsin DNR 2016, Minnesota DNR 2020).

We sampled populations using a standardized population survey protocol for wood turtles developed in the Midwest portion of their geographic distribution (Brown et al. 2017, Wisconsin DNR 2019). The general survey protocol consists of active searches within defined transect bands on each side of the stream, with the transect bands running parallel to the stream and spaced at 15 m intervals beginning at the stream-land interface, and each transect band searched by a single observer. We replicated surveys to estimate detection probability (*p*) and completed all replications in the spring between late April and early June. For 16 sites, we used the original protocol (hereafter S4 protocol), which included 4 transect bands, a target of 8 survey replications, and a target site (i.e., stream segment) length of 0.5 km (Brown et al. 2017). We subsequently modified the protocol for 35 sites based on results from Brown et al. (2017), which indicated that sampling effort could be reduced without affecting the accuracy of abundance estimates, and to improve data alignment with a standardized protocol used in the eastern United States (Northeast Wood Turtle Working Group 2021). Modifications included reducing the survey area to 2 transect bands, performing 3 survey replications and an additional 3 surveys if wood turtles were encountered, and expanding the target site length to 1 km (hereafter S2 protocol). For the remaining 6 sites, we used the S2 protocol with an additional survey pass per transect band conducted independently by a different observer during 4 of 6 survey replications to provide data for a separate study (Beard et al. 2024; hereafter D2 protocol). We included a categorical covariate in the statistical models to account for potential differences in detection probability among the 3 survey types.

We recorded the start time, end time, and total search time for each survey. At the start and end of each survey, we recorded weather conditions, air and water temperature, stream flow conditions, water visibility, and stream size class (see Field data below). We measured, aged, sexed, marked, photographed, and recorded the location of each wood turtle on its initial capture. For recaptured turtles, we collected mark number, location, and photographs. Measurements included midline carapace and plastron length and width, body depth, and weight (Iverson and Lewis 2018). To age the turtle, we counted annuli on plastron scutes and estimated plastron wear (Jones 2009). We recorded sex based on secondary sex characteristics, primarily plastron concavity, tail length and size, and the distance between the cloaca and the edge of the carapace (Ernst 1972). We defined juveniles as individuals with a carapace length <170 mm (Harding and Bloomer 1979). We uniquely marked turtles using marginal carapace scute notches and inserted a passive integrated transponder tag (10 mm 134.2 kHz; Biomark, Boise, ID, USA) in the inguinal cavity parallel to the bridge of the carapace (Buhlmann and Tuberville 1998).

Environmental data

We comprehensively reviewed the published wood turtle literature to identify potentially important environmental variables. We identified 57 candidate environmental variables, including 11 that we obtained through available spatial data sets, 43 that we derived from Light Detection and Ranging (LiDAR) data, and 3 that required field data collection (Appendix A). For terrestrial variables, we defined the habitat sample area as a 100-m buffer around the survey site based on previous research in the study area that found >90% of individual locations were within this distance of the stream (Brown et al. 2016). For aquatic variables, we computed mean values for the length of the survey site to represent average conditions for the stream section.

Spatial data sets

We classified all features included in the National Wetland Inventory (NWI; Wilen and Bates 1995) as open water to estimate the proportion of open water. We used the NWI riverine class to create stream polygons of each of our sites and calculated the average stream width by dividing the area by the length of the stream segment. We derived the mean and maximum percent sand from the gridded soil survey geographic database (gSSURGO; Soil Survey Staff 2021). We calculated road density as the proportion of area classified as roads in LANDFIRE's operational roads dataset (LANDFIRE 2020). We defined forest type as the most common (i.e., the mode) existing vegetation type (LANDFIRE 2016). We extracted stream order, flow, and velocity from the National Hydrography Dataset (U.S. Geological Survey 2022*b*) using all stream lines that intersected each stream segment and belonged to the same stream branch, and we calculated a weighted mean using the proportional length of the stream lines with the stream segments. We used the mean velocity and flow of June to correspond with the timing of our field data collection of velocity and flow. Using the same method, we derived the median particle size from the dataset provided by Abeshu et al. (2022). We calculated stream sinuosity as the channel length of the stream segment divided by its straight-line distance. We completed data processing and analyses using ArcGIS Pro 3.0.1 and the R packages terra (Hijmans 2023) and sf (Pebesma 2018).

Light detection and ranging data

We obtained airborne discrete-return LiDAR from various sources participating in the 3-dimensional (3D) Elevation Program (U.S. Geological Survey 2019*b*). All files met quality level 2 according to the LiDAR Base Specification, which requires aggregate nominal pulse spacing of <0.71 m, aggregate nominal pulse density >2.0 pulses/m^2, and absolute vertical accuracy of <0.10 m root mean square error (Heidemann 2019). Minnesota LiDAR was flown in 2021, and Wisconsin LiDAR between 2014 and 2019, depending on the county. LiDAR was flown during leaf-off conditions in either spring (Apr–May) or fall (Oct–Nov). Leaf-off and leaf-on LiDAR data are generally comparable for forest structure metrics, but leaf-off data may underestimate vegetation cover in deciduous forest (Hill and Broughton 2009, Parent 2014, Davison et al. 2020). To our knowledge, no tree harvesting occurred at our sites between LiDAR sampling and wood turtle sampling, and thus we assumed the derived forest structure metrics were representative of the sites during the study. We visually assessed all sites in a 3D environment to check for and filter out outliers. We processed and analyzed LiDAR data using LAStools (Isenburg 2019) and the R package lidR (Roussel et al. 2020), and the package terra (Hijmans 2023) to work with the raster outputs.

We calculated several measures of 3D vegetation structure from the LiDAR point cloud (Appendix A). We adapted the relative density canopy cover function from St. Peter et al. (2021) to calculate forest structure metrics at a 10-m resolution to capture both vertical and horizontal variation of canopy cover and height. We calculated height as the mean of all returns >1 m (hereafter mean return height), upper canopy height as the mean of all returns >5 m, and vertical variation of height as the standard deviation for both. We generated vertical leaf area density (LAD) profiles of 1-m layers for each cell (Bouvier et al. 2015). We calculated multiple measures of canopy cover, including the proportion of first returns and proportion of returns >5 m over all returns, and the mean and sum of the LAD profile. We calculated variation in vertical cover using the LAD profile's standard deviation and Shannon diversity index (Shannon 1948). We calculated understory cover as the proportion of returns and the LAD between 0.15–1 m, >1–2 m, and >2–5 m. We summarized the resulting multiband raster for each site, calculating each variable's mean and coefficient of variation (CV). For the vertical variation of height and LAD, we also divided the mean standard deviation value by the site mean to obtain the CV. After summarizing, we obtained 32 metrics, including means, horizontal variation, vertical variation, and horizontal variation of vertical variation for height and LAD (i.e., how the variation along a vertical profile varies across the site), and means and horizontal variation for canopy cover and understory cover.

We calculated the mean and CV of canopy height and deep gap fraction (i.e., proportion of cells with a height of <1 m) from a 5-m resolution canopy height model interpolated from a normalized point cloud. We used a point-to-raster method that assigns each raster cell the highest return height within the cell, so we term this canopy height as outer canopy height to differentiate it from mean return height. We calculated the vertical complexity index (van Ewijk et al. 2011), CV of height, and canopy rumple (Jenness 2004) from a normalized point cloud. Unlike the first method, this method calculates metrics directly from the area of interest rather than a grid-based approach. This variation of height can be considered an overall variation, not specifically horizontal or vertical. We also used this method to calculate alternative forms of previously mentioned metrics, including mean return height, outer canopy cover, mean LAD, vertical CV of LAD, and Shannon diversity index of LAD.

We interpolated a 5-m resolution digital surface model from classified ground points using the *k*-nearest neighbor algorithm with an inverse-distance weighting (number of nearest neighbors [k] = 10, power value [p] = 2). We calculated the slope using the 4-nearest neighbor method, ideal for flatter areas (Ritter 1987, Jones 1998). We averaged the slope along the stream segment to derive the stream gradient. We extracted each site's mean elevation, CV of elevation, and mean slope. We also calculated ground rumple index from classified ground points (Jenness 2004).

Field data

We measured stream turbidity, depth, flow, and velocity at the study sites in June 2021 and 2022, with 33, 38, and 14 sites sampled in 2021, 2022, and both years, respectively. We sampled all sites during typical weather and flow conditions and within a 2-week timeframe each year to maximize comparability among sites. We assumed that stream conditions measured in 2021 and 2022 were representative of the sites sampled for wood turtles in 2016 and 2018. For sites sampled in 2021 and 2022, there was no difference in mean velocity (t_{13} = 0.789, P = 0.444) or flow (t_{13} = 1.283, P = 0.222) based on paired *t*-tests, providing some evidence of consistency across years. We sampled turbidity using a turbidity tube and velocity profiles using a Marsh-McBirney model 2000 electromagnetic flow meter (Marsh-McBirney, Frederick, MD, USA). To maximize the accuracy of flow measurements, we chose a cross-section within each site that was a relatively straight, even channel, free of upstream obstructions (Turnipseed and Sauer 2010). We measured turbidity before velocity to avoid the influence of sediment disturbance. We divided the cross-section into ≥20 equal sections for velocity and depth, increasing the number of sections as needed based on stream width and flow. We sampled across the cross-section in the middle of each section (i.e., vertical), following standard flow measurement procedures (Turnipseed and Sauer 2010). At each vertical, we measured water depth, velocity on the streambed, and velocity at 40% of the height of the stream from the streambed. When stream depth was >0.76 m, we measured velocity at 20% and 80% of the stream height instead of 40% (Turnipseed and Sauer 2010). Four of our sites were too deep to survey all verticals, so we estimated values for the site using the National Hydrography Dataset (U.S. Geological Survey 2022*b*) and nearby stream gauge stations. We calculated the flow for the cross-section using the midsection method as described by Turnipseed and Sauer (2010). We averaged velocity, bottom velocity, and depth across the cross-section for each site.

Data analysis

We used *N*-mixture models with a removal (i.e., depletion) sampling observation process to estimate site-level abundances of adult wood turtles (Royle 2004*a*, *b*; Kéry and Royle 2016). Brown et al. (2017) reported that this approach performed well for the standardized population survey protocol based on data simulations using parameter ranges derived from empirical survey data. A subsequent empirical study reported that estimated wood turtle abundances at survey sites in Wisconsin were similar between this approach and Jolly-Seber capture-recapture models at sites where the Jolly-Seber model converged (Wisconsin DNR 2019). A recent study found that for our population sampling design, detection probability did not differ between adult males and females but was approximately 1.4 times higher for adults than juveniles (Beard et al. 2024). An important assumption of *N*-mixture models is that all individuals have the same detection probability (Veech et al. 2016). To address this bias, we restricted our count data set to adults. Thus, our study is limited to assessing the influence of habitat characteristics on adult wood turtle abundance.

For our initial set of candidate abundance predictors, we grouped variables based on ecological similarity (e.g., measures of vegetation cover) to assess multicollinearity. We inputted each variable group into a linear regression to estimate their variance inflation factors (VIF) and retained all variables with VIF < 5 for the final set of candidate abundance predictors (Daoud 2017, Shrestha 2020). For variables with VIF > 5, we created *N*-mixture models of each individual variable, ranked the models using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham et al. 2011), and retained the variable with the highest predictive power. Furthermore, if 2 versions of the same variable were still present, we retained the variable with higher explanatory power. We standardized each quantitative variable to facilitate model convergence (Kéry and Royle 2016). When ecologically appropriate, we created linear and quadratic forms of the variables. The final set of candidate abundance predictors included 34 environmental variables (Appendix A).

We used a multi-stage model selection approach to identify influential variables for detection and abundance. The overdispersion ($\hat{c}$) value for our most complex candidate model with support indicated some overdispersion ($\hat{c} = 2.18$). We ranked candidate models using Quasi-AIC_c ($QAIC_c$; Symonds and Moussalli 2011) to account for this overdispersion. We followed the build-up strategy recommended by Morin et al. (2020), where model complexity increased with each stage. Within each stage, we ranked individual variables and additive models containing individual variables with some support ($QAIC_c < 7$) and retained the most parsimonious model as the null model for subsequent stages. In the first stage, we tested survey type and mean survey air temperature as detection covariates based on a previous study that reported air temperature during the survey was the most important detection variable for our population survey design (Brown et al. 2017). For abundance predictors, we ranked aquatic and terrestrial variables in the second and third stages, respectively. As a stream-obligate species, we assumed that aquatic habitat characteristics would be more influential than terrestrial habitat characteristics.

For the most supported model, we assessed each variable's direction, magnitude, and strength of effect (85% CI; Arnold 2010). We performed *N*-mixture model analyses using the package unmarked (Fiske and Chandler 2011) and created figures using the packages ggplot2 (Wickham 2016), cowplot (Wilke 2022), and tmap (Tennekes 2018). We assessed model goodness of fit and ranked candidate models using the package AICcmodavg (Mazerolle 2020).

RESULTS

We detected wood turtles at 39 of 57 study sites and captured 310 unique adults. At sites where wood turtles were detected, we captured 1–40 unique adults (mean = 7.9 adults/site). The most supported detection submodel included air temperature (quadratic) + survey protocol (Table 1), and we used this model as our final detection model. We estimated a quadratic relationship between air temperature and detection probability, with the highest detection probability (p_{max}) at approximately 21.5°C (Figure 2). At the optimal air temperature, the estimated

TABLE 1 Model selection results to determine the most influential covariates for detection probability and abundance of adult wood turtles in the Laurentian Mixed Forest Province ecoregion of Wisconsin and Minnesota, USA, based on *N*-mixture models with a depletion sampling observation process and Quasi-Akaike's Information Criterion corrected for small sample size ($QAIC_c$) to account for overdispersion ($\hat{c} = 2.18$) and model weights (w_i). We collected standardized population survey data at 57 sites across the study area between 2016 and 2022 and tested the influence of 2 detection probability and 34 abundance variables. We used a 3-stage model selection approach with a build-up strategy. Variables coded to be a quadratic term are denoted with (q), and null models within each stage are shown as (.). For terrestrial variables, LAD represents leaf area density, SDI represents the Shannon diversity index, and VCI represents the vertical complexity index.

Models	Parameters	$QAIC_c$	$\Delta QAIC_c$	w_i
Detection probability				
Air temp (q) + survey protocol	7	449.82	0.00	0.96
Survey protocol	5	456.25	6.42	0.04
Air temp (q)	5	489.96	40.14	0.00
(.)	3	496.42	46.60	0.00
Abundance: aquatic				
Stream width + stream velocity (q)	10	407.43	0.00	1.00
Stream width + stream flow (q)	10	423.48	16.05	0.00
Stream width	8	423.87	16.44	0.00
Stream velocity (q)	9	425.42	17.99	0.00
Stream flow (q)	9	429.38	21.95	0.00
Stream depth	8	439.17	31.74	0.00
Stream sinuosity (q)	9	439.46	32.03	0.00
Stream gradient (q)	9	444.27	36.84	0.00
(.)	7	449.82	42.39	0.00
Stream bottom velocity	8	452.54	45.11	0.00
Abundance: terrestrial				
Mean return height + vertical CV of height (q)	13	390.26	0.00	0.51
Mean return height	11	393.10	2.84	0.12
Vertical CV of height (q) + SDI of LAD	13	394.24	3.98	0.07
SDI of LAD + canopy cover (>5 m)	12	394.96	4.70	0.05
Mean return height + VCI	12	395.02	4.76	0.05
Vertical CV of height (q) + canopy cover (>5 m)	13	395.43	5.17	0.04
Mean return height + canopy cover (>5 m)	12	395.49	5.23	0.04
Mean return height + SDI of LAD	12	395.94	5.68	0.03
VCI + SDI of LAD	12	396.35	6.09	0.02
SDI of LAD	11	396.72	6.46	0.02
VCI	11	397.87	7.61	0.01
Canopy cover (>5 m)	11	397.93	7.67	0.01

(Continues)

TABLE 1 (Continued)

Models	Parameters	$QAIC_c$	$\Delta QAIC_c$	w_i
Vertical CV of LAD	12	398.20	7.94	0.01
Mean vertical LAD	11	400.14	9.88	0.00
VCI + canopy cover (>5 m)	12	400.20	9.94	0.00
CV of elevation (q)	12	400.43	10.17	0.00
Mean percent sand	11	402.25	11.99	0.00
CV of canopy cover (>5 m)	11	403.31	13.04	0.00
Canopy rumple index (q)	12	403.50	13.24	0.00
Proportion open water	11	403.97	13.71	0.00
CV of SD of LAD (q)	12	405.96	15.70	0.00
CV of outer canopy cover (q)	12	406.06	15.80	0.00
LAD (0.15–1 m)	11	407.08	16.82	0.00
CV of outer canopy height	11	407.18	16.92	0.00
(.)	10	407.43	17.17	0.00
Road density	11	407.58	17.32	0.00
CV of LAD (q)	12	408.04	17.78	0.00
Ground rumple index	11	408.81	18.54	0.00
Mean elevation	11	409.33	19.07	0.00
Deep gap fraction (q)	12	409.38	19.12	0.00
Horizontal CV of LAD	11	409.43	19.17	0.00
CV of canopy cover (2–5 m)	11	409.73	19.47	0.00
Slope (q)	12	409.79	19.53	0.00
Horizontal CV of mean height	11	410.06	19.80	0.00
Overall CV of height	11	410.26	20.00	0.00
CV of SD of height (q)	12	410.35	20.09	0.00
Forest type	18	422.06	31.80	0.00

detection probability was highest for the D2 protocol ($p_{max} = 0.289$), followed by the S4 protocol ($p_{max} = 0.270$) and the S2 protocol ($p_{max} = 0.147$; Table 2).

The VIF analyses reduced the original 57 habitat characteristics to the final set of candidate abundance predictors containing 7 aquatic and 27 terrestrial variables (Appendix A). All aquatic variables except stream width and depth exhibited a quadratic relationship with abundance, and only stream bottom velocity had less support than the null model. The strongest aquatic predictors were stream width, stream velocity, and stream flow, and the most supported model was stream width (linear) + stream velocity (quadratic; Table 1). The strongest terrestrial predictors were mean return height, Shannon diversity index of the LAD profile, vertical complexity index, canopy cover >5 m, and vertical CV of height (quadratic), and the most supported model was mean return height (linear) + vertical CV of height (quadratic; Table 1).

Our final model estimated that adult wood turtle abundance ranged from 2–47 (mean = 10.1) across occupied sites. Estimated adult densities ranged from 2–95 individuals/km (mean = 15.3 individuals/km). For aquatic

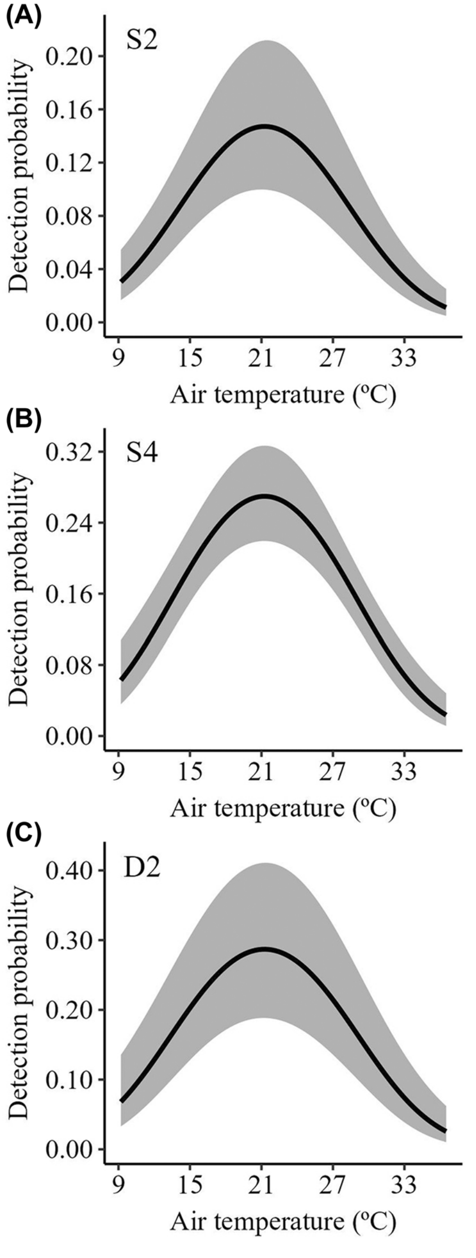

FIGURE 2 Estimated detection probability for adult wood turtles during population surveys between 2016 and 2022 in the Laurentian Mixed Forest Province ecoregion of Wisconsin and Minnesota, USA, based on survey temperature (°C) and survey protocol used, including A) single-pass with 2 transect bands (S2), B) single-pass with 4 transect bands (S4), and C) double-pass with 2 transect bands (D2). The solid gray band represents 85% confidence intervals.

variables, estimated abundance decreased as stream width increased and was highest at moderate velocities relative to our study sites (mean = 0.37 m/s; Figure 3). For terrestrial variables, estimated abundance decreased as mean return height increased and was highest at comparatively low and high levels of vertical CV of height (Figure 3). The effect size for the variables was highest for stream velocity, followed by mean return height, stream width, and vertical CV of height (Table 2).

TABLE 2 Parameter estimates (β) and confidence intervals (CI) for the most supported *N*-mixture model explaining abundance patterns for adult wood turtles in the Laurentian Mixed Forest Province ecoregion of Wisconsin and Minnesota, USA. We collected standardized population survey data at 57 sites across the study area between 2016 and 2022. Abundance covariates include stream width (linear), stream velocity (quadratic), mean return height (linear), and vertical coefficient of variation (CV) of height (quadratic). Detection probability covariates include mean survey air temperature (quadratic) and survey protocol (D2, S2, S4).

Model	Parameter	β	85% CI
Abundance	Intercept	1.822	1.595–2.049
	Stream width	−0.577	−0.818–−0.336
	Stream velocity	0.205	0.037–0.373
	Stream velocity^2	−0.814	−1.070–−0.559
	Mean return height	−0.766	−0.994–−0.538
	Vertical CV of height	−0.007	−0.102–0.088
	Vertical CV of height^2	0.231	0.157–0.304
Detection probability	Intercept	−0.912	−1.463–−0.361
	Air temperature	−0.051	−0.164–0.061
	Air temperature^2	−0.354	−0.470–−0.239
	Survey: S2	−0.847	−1.279–−0.415
	Survey: S4	−0.086	−0.634–0.463

DISCUSSION

Our results indicate that stream velocity and width strongly influence local abundance dynamics of adult wood turtles. Wood turtles are often found in slower-moving sections of moderate to fast-flowing streams (Jones et al. 2021*c*). Thus, it was unsurprising that abundance was highest at sites with moderate stream velocities in our study area. Similarly, wood turtles are generally associated with mid-sized streams (Jones et al. 2021*c*), and in our study abundance decreased from mid-sized (>7–15 m) to large streams (>15 m). Wood turtles can occupy narrower streams than we surveyed (Foscarini and Brooks 1997), and we would expect abundance to decline as stream width approaches zero. Previous research found that stream gradient had a strong negative influence on the proportion of juveniles, but not abundance, at survey sites throughout the northeastern United States (Roberts et al. 2021). We also did not find a strong effect of stream gradient on adult abundance, with the variable being ranked second lowest among candidate aquatic variables (Table 1).

Quantifying the influence of terrestrial habitat conditions on wood turtle abundance is challenging because of their high mobility and lack of unique habitat feature requirements (Brown et al. 2016, Cochrane et al. 2018). To overcome these challenges, we created and tested various LiDAR-derived metrics that could characterize the structural diversity that wood turtles appear to select based on individual-level habitat use studies and applied it at a larger scale than is feasible via field-based methods (Arvisais et al. 2004, Wallace et al. 2020). The use of LiDAR to characterize vertical forest structure in wildlife studies is still uncommon. It has primarily been used to assess habitat conditions for flying and arboreal species (Brokaw and Lent 1999, Bergen et al. 2009, Davies and Asner 2014). Relatively few studies have used LiDAR to derive vegetation structure metrics for ground-dwelling species, mainly consisting of small mammals (Jaime-González et al. 2017, Schooler and Zald 2019, Torre et al. 2022, Brocardo et al. 2023) but also ground-dwelling birds (Brocardo et al. 2023), ground beetles (Bombi et al. 2019), and reptiles (Fill et al. 2015). Many of the LiDAR-derived variables we tested had some explanatory power for adult wood turtle abundance, and the most supported model contained 2 of these variables.

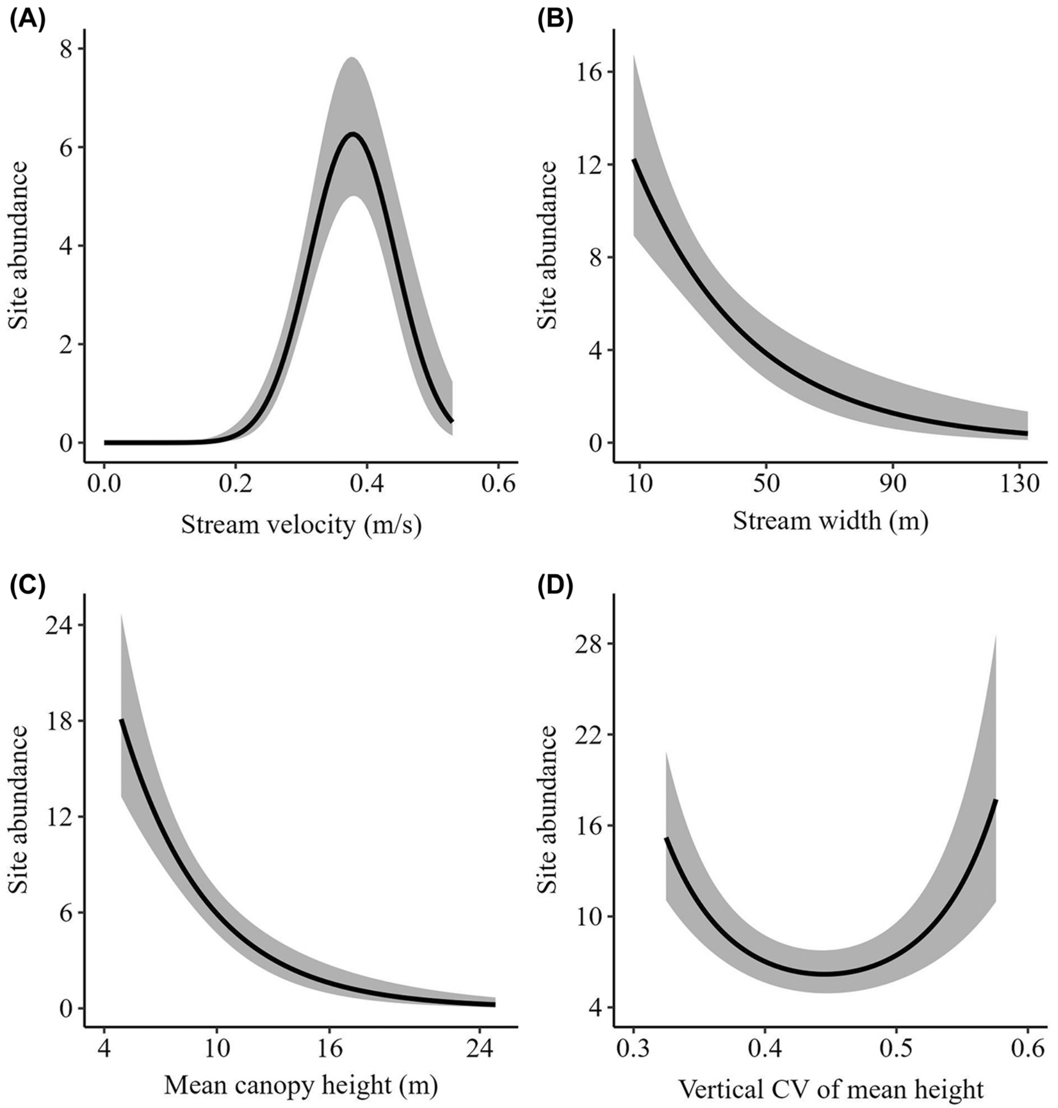

FIGURE 3 Influence of 2 aquatic variables, stream velocity (A) and stream width (B), and 2 terrestrial variables, mean canopy height (C) and vertical coefficient of variation (CV) of height (D), on site-level abundance of adult wood turtles in the Laurentian Mixed Forest Province ecoregion of Wisconsin and Minnesota, USA. These were the most supported abundance predictor variables based on our analysis of standardized population survey data collected at 57 sites between 2016 and 2022. Abundances are estimated for each variable, with the other variables held at their mean. The solid gray bands represent 85% confidence intervals.

Mean return height was the strongest terrestrial predictor and had a negative relationship with adult wood turtle abundance. Contrary to canopy height, mean return height, calculated using all LiDAR returns, also includes heights of vegetation layers under the canopy and canopy gaps. These LiDAR-derived heights are positively correlated with many field-based measurements such as biomass, volume, succession, and age (Lim et al. 2003, Zimble et al. 2003, Falkowski et al. 2009). The negative relationship between abundance and mean return height suggests that sites containing shorter forest stands and more open environments supported more wood turtles, consistent with individual-level habitat selection patterns (Arvisais et al. 2004, Brown et al. 2016). Wood turtles likely benefit from the greater basking opportunities and increased herbaceous and shrubby growth that young forests and open environments can provide (Compton et al. 2002, Dubois et al. 2009).

Wood turtle abundance was highest at the relative extremes of vertical CV of height. Variation in height, another common LiDAR metric, can indicate multistory forests (Zimble et al. 2003), canopy gaps (Ritchie et al. 1993), and mixed forests (Smart et al. 2012), and is associated with tree species diversity (Torresani et al. 2020) and biomass (Magnussen et al. 2011). Abundance was most related to the vertical CV of height, which differs slightly from more common measures of variation in height because it quantifies the variation in heights of returns in a vertical column rather than across a horizontal plane. Sites with high vertical CV of height had consistent vegetation returns between 1–20 m throughout the site and tended to be taller than average. Sites with low vertical CV of height primarily consisted of short forests with many open areas, with most vegetation returns occurring from 2–10 m. In addition, many of the low vertical CV sites were adjacent to forest patches with high vertical CV. Although the estimated relationship with vertical CV of height seems contradictory, the high abundances at both ends of the vertical CV spectrum suggest that open and low canopy environments within the broad matrix of mature forests are important. These results support previous studies that suggest wood turtles are an edge species (Kaufmann 1992, Compton et al. 2002, Arvisais et al. 2004, Wallace et al. 2020).

MANAGEMENT IMPLICATIONS

Our results highlight the importance of stream morphology and structural diversity of terrestrial habitat for supporting robust wood turtle populations. Large portions of our focal area have yet to be surveyed for wood turtles, and the abundance-habitat relationships estimated in this study can be used to direct future survey efforts toward areas that are most likely to contain robust populations. A diverse forest structure can be achieved through various forest management practices, such as selective tree harvesting to create canopy gaps and prescribed burning to promote a mosaic of understory vegetation conditions, with appropriate timing to avoid wood turtle mortality. Finally, our study supports the value of LiDAR to derive forest structure metrics as proxies for habitat features important to ground-dwelling wildlife.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This research was approved by the Minnesota DNR, Wisconsin DNR, University of Minnesota Institutional Animal Care and Use Committee (protocol number 1504-32514A), and West Virginia University Institutional Animal Care and Use Committee (protocol number 2002033297).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author and approval from the applicable state agencies. The data are not publicly available due to privacy or ethical restrictions.

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APPENDIX A: HABITAT VARIABLES

See Table A1.

TABLE A1 Candidate habitat variables for predicting abundance of wood turtles (*Glyptemys insculpta*) in the Laurentian Mixed Forest Province ecoregion of Wisconsin and Minnesota, USA.

Candidate variables[a]	Description[a]	Data source[b]	References	Final candidate variable
Aquatic variables				
Stream gradient	Slope of stream	DEM	Jones (2009), Roberts et al. (2021), Willey et al. (2022)	Y
Stream sinuosity	Ratio of channel length to straight-line length	NHD	Jones (2009), Willey et al. (2022)	Y
Stream flow	Volume of water that flows past a fixed point	NHD*, field	Willey et al. (2022)	Y
Stream velocity	Speed of stream	NHD*, field	Willey et al. (2022)	Y
Bottom stream velocity	Velocity measured on the streambed	Field		Y
Stream width	Mean stream width along length of site	NWI	Foscarini and Brooks (1997)	Y
Stream depth	Average depth across a cross-section	Field	Foscarini and Brooks (1997), McCoard et al. (2018)	Y
Stream order	Relative size of stream based on hierarchical classification of branches	NHD	Jones (2009)	
Median sediment particle size	Median particle size of bed-material sediment	Abeshu et al. (2022)	Buech et al. (1997)	
Stream visibility	Tannic, clear, or turbid	Field		
Terrestrial variables				
Ground rumple	Roughness of the ground; the ratio of surface area to the projected area	DEM	Tingley et al. (2010)	Y
Mean elevation	Mean height of ground-classified returns	DEM	Jones (2009), Tingley et al. (2010), Mothes et al. (2020)	Y

TABLE A1 (Continued)

Candidate variables[a]	Description[a]	Data source[b]	References	Final candidate variable
CV of elevation	CV of height of ground-classified returns	DEM	Tingley et al. (2010)	Y
Mean slope	Mean slope calculated using the 4-nearest neighbors method	DEM	Buech et al. (1997), Tingley et al. (2010), Mothes et al. (2020)	Y
Proportion of open water	Proportion of area classified as open water	NWI	Arvisais et al. (2004), Brown et al. (2016)	Y
Forest type	Existing vegetation type	EVT	Arvisais et al. (2004)	Y
Road density	Proportion of area classified as roads	Operational roads	Roberts et al. (2021)	Y
Mean percent sand		gSSURGO	Buech et al. (1997), Hughes et al. (2009)	Y
Max. percent sand		gSSURGO	Buech et al. (1997), Hughes et al. (2009)	
Canopy rumple	Roughness of the canopy; ratio of the surface area of the canopy and the area of the ground	Point cloud		Y
Outer canopy height	Mean height of first returns	CHM	Arvisais et al. (2004)	
CV of outer canopy height	CV of heights of first returns	CHM		Y
Mean height	Mean return height	Grid metrics*, point cloud	Arvisais et al. (2004)	Y
Overall CV of height	CV of return height	Point cloud		Y
Horizontal CV of mean height	CV of mean return height	Grid metrics		Y
Vertical CV of height	Mean CV of return height	Grid metrics	McCoard et al. (2016)	Y
CV of vertical SD of height	CV of SD of return height	Grid metrics		Y
Mean height >5 m	Mean of returns >5 m	Grid metrics	Arvisais et al. (2004)	

(Continues)

TABLE A1 (Continued)

Candidate variables[a]	Description[a]	Data source[b]	References	Final candidate variable
Horizontal CV of mean height >5 m	CV of mean of returns >5 m	Grid metrics		
Vertical CV of height >5 m	Mean of CV of returns >5 m	Grid metrics	McCoard et al. (2016)	
CV of vertical SD of height >5 m	CV of SD of returns >5 m	Grid metrics		
Vertical complexity index	A fixed normalization of Shannon diversity index applied to return points binned by height	Point cloud	McCoard et al. (2016)	Y
Deep gap fraction	Proportion of 5-m cells with a height >1 m	CHM		Y
Outer canopy cover	Proportion of first returns	Grid metrics, point cloud	Compton et al. (2002), Arvisais et al. (2004)	
CV of outer canopy cover	CV of proportion of first returns	Grid metrics		Y
Canopy cover >5 m	Proportion of returns >5 m	Grid metrics	Compton et al. (2002), Arvisais et al. (2004)	Y
CV of canopy cover >5 m	CV of proportion of returns >5 m	Grid metrics		Y
Mean of LAD	Mean LAD across height bins	Grid metrics*, point cloud		Y
Vertical CV of LAD	CV of LAD across height bins	Grid metrics, point cloud*	McCoard et al. (2016)	Y
Horizontal CV of LAD	CV of mean LAD across height bins	Grid metrics		Y
CV of vertical SD of LAD	CV of SD of LAD across height bins	Grid metrics		Y
Vertical sum of LAD	Mean of sum of LAD across height bins	Grid metrics		
CV of vertical sum of LAD	CV of sum of LAD across height bins	Grid metrics		
Shannon diversity index of LAD	Shannon diversity index applied across height bins	Grid metrics, point cloud*	McCoard et al. (2016)	Y

TABLE A1 (Continued)

Candidate variables[a]	Description[a]	Data source[b]	References	Final candidate variable
CV of Shannon diversity index of LAD	CV of Shannon diversity index applied across height bins	Grid metrics		
Canopy cover between 0.15–1 m	Mean proportion of returns between 0.15–1 m	Grid metrics	Compton et al. (2002), Arvisais et al. (2004)	
CV of canopy cover between 0.15–1 m	CV of proportion of returns between 0.15–1 m	Grid metrics		
Canopy cover between 1–2 m	Mean proportion of returns between 1–2 m	Grid metrics	Compton et al. (2002), Arvisais et al. (2004)	
CV of canopy cover between 1–2 m	CV of proportion of returns between 1–2 m	Grid metrics		
Canopy cover between 2–5 m	Mean proportion of returns between 2–5 m	Grid metrics	Compton et al. (2002), Arvisais et al. (2004)	Y
CV of canopy cover between 2–5 m	CV of proportion of returns between 2–5 m	Grid metrics		
LAD between 0.15–1 m	Mean LAD between 0.15–1 m	Grid metrics		Y
CV of LAD between 0.15–1 m	CV of LAD between 0.15–1 m	Grid metrics		
LAD between 1–2 m	Mean LAD between 1–2 m	Grid metrics		
CV of LAD between 1–2 m	CV of LAD between 1–2 m	Grid metrics		
LAD between 2–5 m	Mean LAD between 2–5 m	Grid metrics		
CV of LAD between 2–5 m	CV of LAD between 2–5 m	Grid metrics		

[a]Leaf area density, the 1-sided leaf area per unit volume, was denoted as LAD.

[b]Data sources include the National Hydrography Dataset (NHD; U.S. Geological Survey 2022*b*), National Wetland Inventory (NWI; Wilen and Bates 1995), the existing vegetation cover (EVT) layer (LANDFIRE 2016), the operational roads layer (LANDFIRE 2020), the gridded soil survey geographic database (gSSURGO; Soil Survey Staff 2021), median bed-material particle size (Abeshu et al. 2022), variables we collected in the field (field collected), and variables calculated through light detecting and ranging (LiDAR) data: LiDAR-derived canopy height model (CHM), LiDAR-derived digital elevation model (DEM), LiDAR point cloud, and LiDAR grid metrics. For variables with more than one source, the source that produced the values used in the final model selection is denoted with an asterisk.