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Projected contemporary habitat distribution and quality for wood turtles in the midwestern United States

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Abstract

Habitat suitability models (HSMs) play an important role in conservation planning by identifying areas for habitat management and guiding surveys for population discovery and monitoring. The wood turtle *Glyptemys insculpta* is a riverine turtle that uses both riparian and upland environments. Habitat loss and degradation have resulted in range-wide declines of this species throughout the United States. Previous HSMs have been developed for wood turtles; however, no published HSM we are aware of exists for their range in the midwestern United States (including parts of Iowa, Michigan, Minnesota, and Wisconsin), or has incorporated terrestrial, aquatic, and climatic variables. We developed a wood turtle HSM across their distribution in the midwestern United States using Random Forest. Modeling units consisted of 800–1,000-m stream segments and a 300-m buffer surrounding each segment. We obtained verified occurrence records from 2000–2024 from state agencies, concurrent research projects, and the community science platform iNaturalist, resulting in 1,833 segments with documented occurrence to serve as model training data. Assessment metrics indicated good model performance (area under the operator curve = 0.92, true skill statistic = 0.6704). Stream order, width, and gradient were the most influential aquatic variables, with lower stream order, lower widths, and lower

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gradient being associated with higher probability of occurrence. The most influential terrestrial variables were proportion of still water in the terrestrial environment, landscape condition index, and topographic ruggedness index, with lower proportion of still water in the terrestrial environment, moderate to high landscape condition, and lower topographic ruggedness being associated with higher occurrence probability. The majority of stream segments (68.4%) with ≥0.8 probability of occurrence currently lack documented wood turtle populations, allowing for prioritization of these streams for future surveys. These results can assist with guiding habitat management and restoration efforts in their midwestern United States range.

KEYWORDS
conservation planning, *Glyptemys insculpta*, habitat distribution, habitat suitability model, Random Forest, wood turtle

The wood turtle *Glyptemys insculpta* (Figure 1) is a species of high conservation concern across its geographic distribution that faces multiple compounding conservation threats, the most serious of which are habitat loss and degradation (Harding and Bloomer 1979, Bowen and Gillingham 2004, Steen and Gibbs 2004, Saumure et al. 2007, COSEWIC 2018). This species is under review for federal listing (Center for Biological Diversity 2012) under the United States Endangered Species Act (ESA 1973, as amended) because of perceived and documented population declines throughout its geographic distribution (Daigle and Jutras 2005, Willoughby et al. 2013). Wood turtles are currently listed at the state level in the western portion of their range as endangered in Iowa (pursuant to Iowa Administrative Code 571-77.2; Iowa Administrative Code 2023) and threatened in Michigan (pursuant to Michigan Administrative Code R. 299.1025;

FIGURE 1 Adult wood turtle *Glyptemys insculpta* on a sandy riverbank in the midwestern United States. Photo credit: Andrew Badje.

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Michigan Administrative Code 2025), Minnesota (pursuant to Minnesota Administrative Rules Chapter 6134; Minnesota Rules 2023), and Wisconsin (pursuant to Administrative Rule Chapter NR 27; Wisconsin Administrative Code 2025).

Estimating relationships between occurrence and habitat characteristics (where habitat is defined as the conditions that enable occupancy; Krausman and Morrison 2016) and then predicting occurrences at broad scales can be beneficial to wildlife managers who are engaged in wood turtle conservation. Habitat suitability models (HSMs) use spatially explicit species occurrences and environmental data to estimate relationships between species occurrence or abundance and environmental conditions. The relationships are then used to predict probability of species occurrence across a defined geographic area and time (Guisan et al. 2017). Habitat suitability models aim to quantify how environmental conditions influence occurrence or abundance of a species, which enables researchers to project past, current, or future distributions based on environmental associations (Araújo et al. 2019). An effective assessment of the distribution of a species can guide management efforts by delimiting priority regions for conservation and is particularly relevant when activities are regulated under the Endangered Species Act (Sofaer et al. 2019).

Three HSMs that we are aware of have been previously published for wood turtles. Mothes et al. (2020) developed an HSM for the portion of the wood turtle range that lies between Maine and Virginia, with Ohio at the westernmost edge of the model. Willey et al. (2022) developed their HSM for a similar range as Mothes et al. (2020) but excluded Ohio from the model. We refer to this region as the northeastern portion of the wood turtles' range in agreement with previous wood turtle studies that divided the wood turtle range in the United States into two distinct portions: the northeastern United

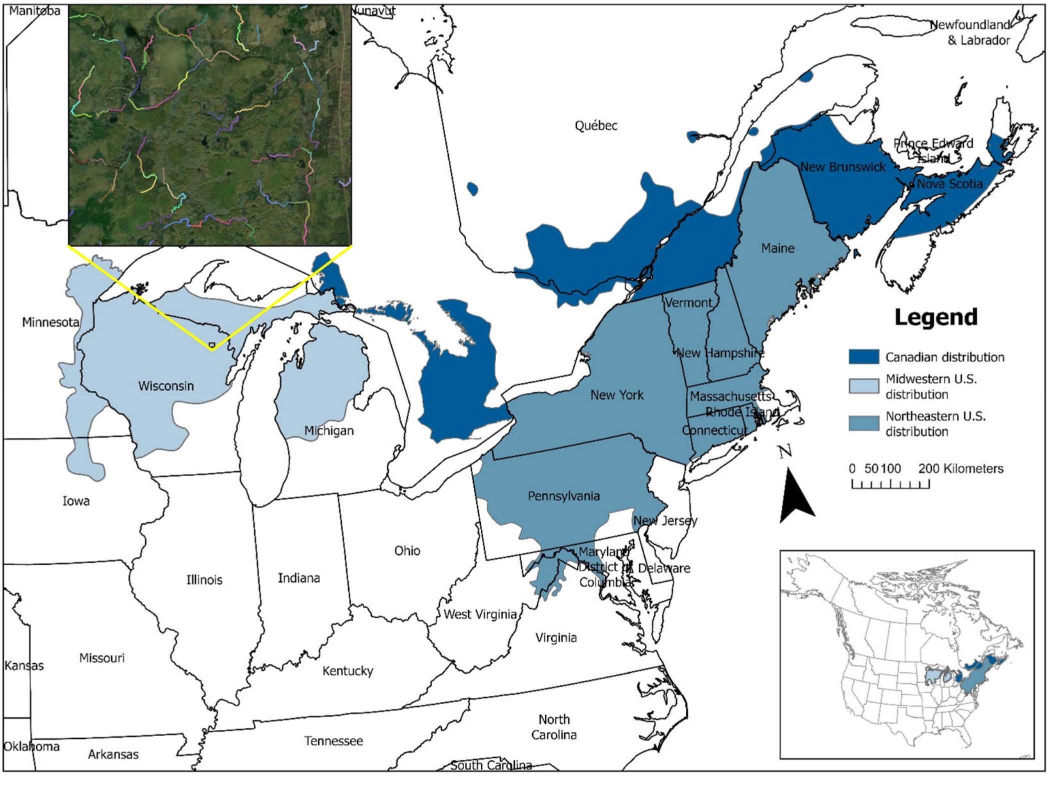

FIGURE 2 Geographic distribution of the wood turtle *Glyptemys insculpta* across the midwestern United States, northeastern United States, and Canada (produced by the Center for North American Herpetology, as published in Powell et al. 2016). We developed a habitat suitability model for wood turtles using occurrences from 2000–2024 within their distribution in the midwestern United States, which includes parts of Iowa, Michigan, Minnesota, and Wisconsin. Inset map shows an example of 800–1,000-m streamlines used as the unit of inference for the habitat suitability model (aerial imagery from Earthstar geographics).

States and the midwestern United States (Jones et al. 2015, Lapin et al. 2019, Mothes et al. 2020, Willey et al. 2022). Baker (2022) developed an HSM for the wood turtle's distribution in Atlantic Canada (Ontario, Québec, New Brunswick, and Nova Scotia; Figure 2). These three previously developed HSMs differed in purpose and modeling approach. Mothes et al. (2020) developed their model to evaluate the potential loss of habitat for this species under two alternate temperature scenarios. Willey et al. (2022) developed their model to assess the potential and current distribution of the wood turtle and estimate habitat loss. Baker (2022) aimed to improve understanding of the wood turtle's distribution in Atlantic Canada and estimate the proportion of occurrence area that is protected or identified as important by the Nova Scotia Department of Natural Resources and Renewables. Results from the previous HSMs provide a foundation for developing an HSM for the portion of the species' geographic distribution in the states of Iowa, Michigan, Minnesota, and Wisconsin. However, environmental conditions differ between the northeastern and midwestern regions of the United States and estimated relationships may not be transferable outside the model's area of inference. Thus, quantifying environmental relationships in the midwestern United States is an important component of estimating habitat abundance in the region for wood turtles. In addition to the three published HSMs, the Michigan Department of Natural Resources (MI DNR) recently developed an HSM for wood turtles that has not been published and is being used for departmental management planning (A. Cooper, Department of Fisheries and Wildlife, Michigan State University, personal communication).

Wood turtles are unusual among North American turtle species because they are strongly associated with streams and adjacent riparian areas, yet they also use surrounding riparian and upland landscapes during the summer months to forage, thermoregulate, and nest. Both terrestrial and aquatic variables are therefore important for an HSM focused on identifying relationships between habitat characteristics and occurrence for this species. Previous HSM models differed in their approaches to incorporating terrestrial and aquatic variables. Willey et al. (2022) created a stream-based model where 1-km stream segments served as the unit of inference, whereas Mothes et al. (2020) used 30-m cells in a raster-based approach, and Baker (2022) used 250-m cells in a raster-based approach. Furthermore, Willey et al. (2022) tested climatic and hydrological variables, Mothes et al. (2020) tested climatic and terrestrial variables, and Baker (2022) tested hydrological and terrestrial variables.

We quantified relationships between wood turtle occurrence and environmental characteristics, including climatic, terrestrial, and aquatic characteristics, and then used the estimated relationships to project current habitat quality for wood turtles throughout the portion of their geographic distribution that includes Iowa, Michigan, Minnesota, and Wisconsin. This information is needed by wildlife managers in the midwestern United States to help identify candidate streams and watersheds for future occurrence surveys, prioritize areas for conservation, and inform habitat management.

STUDY AREA

Our area of inference included the extant western portion of the wood turtle's distribution found in the midwestern United States (Figure 2). We used the most recent species distribution map produced by the Center for North American Herpetology (published in Powell et al. 2016) as a baseline species distribution boundary. We then made two modifications to the baseline species distribution. Firstly, we expanded the boundary to encompass the entirety of three 8-digit Hydrologic Unit Code (HUC-8) watersheds, rather than just the portions previously included, when verified occurrence records since 2000 were found outside the original baseline boundary. Secondly, we excluded a portion of the baseline distribution boundary in Wisconsin (Rock, Dane, and Green counties), which was based on two historical specimens with questionable validity (Casper 1996, Kapfer and Brown 2022). The study area encompassed portions of Iowa, Michigan, Minnesota, and Wisconsin, and includes seven Level III ecoregions (Figure 3; Western Corn Belt Plains, Northern Lakes and Forests, North Central Hardwood Forests, Driftless Area, Huron/Lake Erie Plains, Southern Michigan/Northern Indiana Drift Plains, and Southeastern Wisconsin Till Plains; U.S. Environmental Protection Agency 2024).

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FIGURE 3 Representative stream and riparian areas occupied by wood turtles in three Level III Ecoregions: the Driftless Region of Wisconsin (A); the Western Corn Belt Plains (B); and the Northern Lakes and Forests region (C; U.S. Environmental Protection Agency 2024). Photo credits: Andrew F. Badje (A); Jeffrey W. Tamplin (B); Donald J. Brown (C).

METHODS

Stream segment layer creation

We created stream segments of 800–1,000 m in length across the entirety of the study area to serve as the unit of inference for this model (n = 134,529 segments). We derived the stream segments from National Hydrography Dataset (NHD) flowlines (U.S. Geological Survey [USGS] 2022*a*), which were created at the 1:24,000 scale and represent the entire water drainage network of the United States, including both riverine and lacustrine bodies of water. We filtered this dataset to include only riverine systems in the study area that could support wood turtle populations year-round (excluding canals, ephemeral streams, and agricultural pipelines, which are not known to support wood turtle populations; Ernst and Lovich 2009). We then split the streamlines into transects, with the goal of splitting the streamlines into 1-km transects for consistency with the current survey scale for most state population monitoring programs in the United States (e.g., Badje et al. 2024), a previously published wood turtle HSM in the northeastern United States (Willey et al. 2022), and a conservation plan for wood turtles developed by the northeastern United States wildlife agencies that fall within wood turtle range (Jones et al. 2018). We included only transects that were >800 m in length in the analysis. In total, our stream segments covered 74.3% of all suitable watercourses within the study area. We obtained stream width from the NHDArea dataset and the National Wetland Inventory (USFWS 2023), which delineates the extent of surface water in larger streams and rivers. For streams that were not represented by a polygon in the NHDArea dataset, we calculated the average stream width for each stream order within that HUC-4 watershed and applied the average to all stream segments without width information (see detailed workflow in Figure 4).

Wood turtle occurrence dataset

We obtained all verified wood turtle occurrence data collected from 2000–2024 from Natural Heritage Inventory (NHI) programs in Michigan, Minnesota, and Wisconsin. The NHI datasets included occurrence points that were

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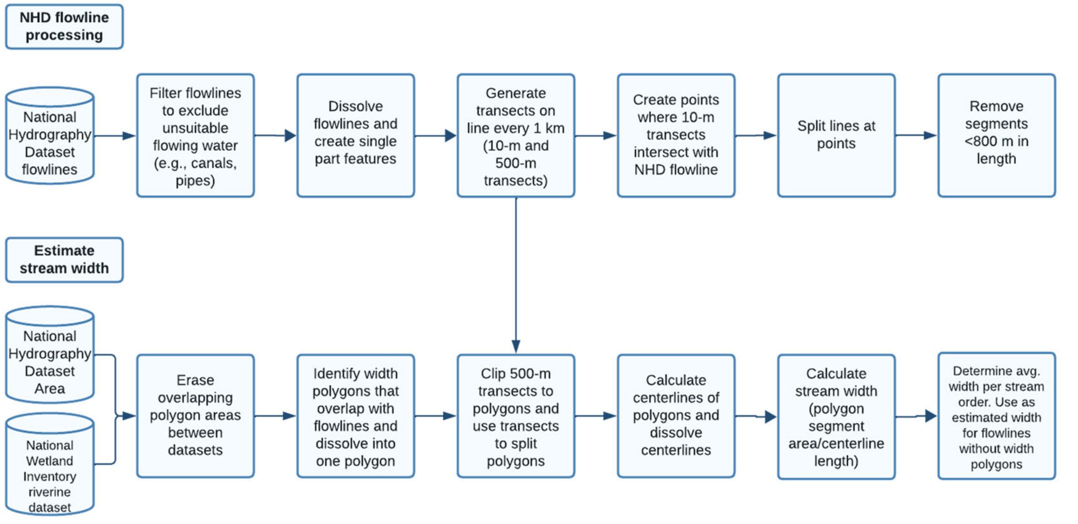

FIGURE 4 Flowchart detailing the workflow for processing National Hydrography Dataset (NHD) flowlines (U.S. Geological Survey [USGS] 2022*a*) into 800–1,000-m stream segments used as the model unit of inference for a wood turtle *Glyptemys insculpta* habitat suitability model based on occurrence records from 2000–2024 (upper flowchart), and to estimate stream width across the species' range in the midwestern United States (including parts of Iowa, Michigan, Minnesota, and Wisconsin; lower flowchart).

obtained through standardized surveys, telemetry data, and incidental captures. These occurrence records came from state wildlife agency staff members, contractors, external researchers, and members of the public. Records associated with photographs that were submitted by members of the public were verified by species experts within the appropriate state wildlife agency prior to being mapped by a state's NHI program. We excluded occurrence records prior to 2000 to ensure that observed locations reflected recent population locations and environmental conditions. We obtained additional wood turtle occurrence records from regional research projects, including a concurrent study that surveyed for wood turtle populations in river sections across northern Wisconsin from 2021–2022 (Staggs et al. 2024), population surveys in northeastern Minnesota from 2015–2018 (Cochrane et al. 2018, Berkeland 2020), and global positioning system (GPS) tracking of wood turtles in northeastern Minnesota (Cochrane et al. 2019). The Iowa wood turtle occurrence dataset represents 149 individuals and 10,449 radio telemetry locations, with population surveys from six study sites and four counties conducted over 21 years (2003–2024). Finally, we obtained 135 additional wood turtle locations that resulted in an additional 90 present stream segments through photo-vouchered observations posted to the citizen science platform iNaturalist (https://web.archive.org/web/20231210234010/https://www.inaturalist.org/projects/wood-turtles-of-the-midwest; June 2025). Observations posted to iNaturalist undergo quality assessments for species identification. Locations of sensitive species such as the wood turtle are automatically obscured until the individual user allows the coordinates to be viewed within a trusted project. Through NHI data, concurrent research study data, and iNaturalist locations, Iowa had 69 known present stream segments, Michigan had 394, Minnesota had 285, Wisconsin had 1,042, and 43 present stream segments crossed the border of one state into another.

We overlaid the stream segments with all occurrence data points to code the segments as present for wood turtles. Occurrence polygons from NHI are often created to include locational uncertainty for instances where GPS coordinates were not taken, and, therefore, some occurrence polygons overlapped with multiple stream segments. In cases where the occurrence polygon overlapped with two stream segments, both were coded as being present for wood turtles. We removed occurrence polygons from the dataset that overlapped with three or more stream segments and could not be validated with existing data. In some cases, we were able to verify that wood turtles

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were present across the entirety of the occurrence polygon using additional individual occurrence records held by project collaborators. Of the 134,529 stream segments, 1,833 were coded as known present (1.38%).

Environmental variables

We conducted a literature review of wood turtle habitat associations to develop an initial list of candidate environmental predictors (Table S1). We removed candidate predictors that could not be estimated across the area of inference using currently available spatial datasets. The final dataset consisted of 25 variables. The variables stream order, stream width (m), sinuosity, stream gradient (m/km), stream density, and stream sediment particle size (mm) represented the aquatic environmental variables dataset (Table 1). We obtained stream order from the NHD flowline dataset and calculated stream width using the NHDArea dataset and National Wetland Inventory dataset (USFWS 2023; Figure 4). We calculated sinuosity by dividing the curvilinear distance of each stream segment by the Euclidean distance of each segment. We derived stream gradient from a 1/3 arc-second resolution (~10 m) digital elevation model (DEM) from the USGS National Elevation Dataset (USGS 2022*b*; see Table 1 for details). We calculated stream density with the line density tool using all watercourses within NHD that feasibly could support wood turtle populations (i.e., stream segments that were excluded because the segment length was <800 m were included in stream density calculations). We averaged stream density across a 300-m buffer of the stream segment to represent the maximum distance that wood turtles will typically travel from their overwintering stream (Arvisais et al. 2002, Compton et al. 2002, McCoard et al. 2016). We obtained mean stream sediment particle size from the dataset provided by Abeshu et al. (2022), which was derived from NHD streamline data.

The terrestrial dataset (Table 1) included primary and secondary road density, tertiary road density, elevation (m), land cover type, distance to gravel pit (m), vegetation height (m), vegetation height standard error, percent sand, heat load index, topographic ruggedness index (TRI), percent canopy cover, canopy cover standard deviation, proportion of terrestrial environment covered by still water, landscape condition index, and ecoregion. We calculated these terrestrial variables within a 300-m buffer surrounding each stream segment, which corresponds to the distance at which turtles can be found for nearly 100% of the active period (Arvisais et al. 2002, Compton et al. 2002). We also tested the influence of percent sand, canopy cover, and canopy cover standard deviation for a 100-m buffer because wood turtle locations tend to cluster close to the stream and therefore ~90% of occurrences are within 100 m of streams (Sweeten 2008, Brown et al. 2016) and because sandy stream banks are a common nesting substrate (Harding and Bloomer 1979). These variables were ultimately included in the final model at the 300-m scale because the model's out-of-bag error rate was higher with those variables at the 100-m scale. We downloaded road layers from the United States Census Bureau TIGER/Line Shapefiles (U.S. Census Bureau 2023). We created a primary and secondary road layer for the study area, where primary roads are defined as highways that are part of the interstate or state highway systems, and secondary roads are defined as main arteries to the highway system (U.S. Census Bureau 2023). We also created a tertiary road layer for the study area in which we downloaded all roads available through the TIGER/Line dataset and then removed all primary and secondary roads from the shapefile, leaving local neighborhood roads, rural roads, city streets, private roads, gravel and dirt roads, United States Forest Service (USFS) roads, and others (U.S. Census Bureau 2023). We then used the line density tool to create two density raster layers: one for primary and secondary roads and one for tertiary roads.

We calculated average elevation from a 1/3 arc-second DEM from the National Map (USGS 2022*b*) for each buffered stream segment using zonal statistics. We derived the dominant land cover type from LANDFIRE's (2022) Existing Vegetation Type. We first used the spatial join tool to find the most dominant land cover type within every 300-m buffer. This resulted in 65 unique vegetation classifications across the modeling extent. We sorted these vegetation classifications into eight broad categories (coniferous forest, deciduous forest, mixed forest, developed, developed green space, vegetated wetland, open terrestrial, and open water; Table S2). We also used the LANDFIRE dataset to calculate distance to barren land. We used the LANDFIRE Existing Vegetation Type raster to

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TABLE 1 Aquatic, terrestrial, and climatic environmental variables tested to model habitat suitability of wood turtles *Glyptemys insculpta* in the midwestern United States (including parts of Iowa, Michigan, Minnesota, and Wisconsin) using Random Forest. The model was trained with wood turtle occurrences from 2000–2024. References include previous studies that suggested the variable could be important. The data source for the model variables, ArcGIS tools used to create the variables (extraction method), and data resolution are also provided. An asterisk (*) denotes variables that were not included in the global Random Forest model because of high collinearity.

Covariate	Literature support	Data sources (authors)[a]	Extraction method	Resolution
Aquatic variables				
Sinuosity	Ernst and Lovich (2009)	NHD (USGS)	Curvilinear distance/Euclidean distance	1:24,000
Stream density	Baker (2022)	NHD (USGS)	Line density tool	30 × 30 m
Stream gradient (m/km)	Jones (2009)	NHD (USGS); DEM (USGS)	(Max elevation – min elevation)/(curvilinear length × 0.001; Hack (1973))	1:24,000; 1/3 arc-second (~10 m)
Stream order	Ernst and Lovich (2009)	NHD (USGS)	Not applicable	1:24,000
Stream sediment particle size (mm)	Ernst and Lovich (2009)	Abeshu et al. (2022)	Spatial join	1:24,000
Stream width (m)	Ernst and Lovich (2009)	NHD (USGS); NWI (USFWS)	NHDArea/length	1:24,000
Terrestrial variables				
Canopy cover (%)	Arvisais et al. (2004)	Tree canopy cover 2023.5 (USFS Geospatial Technology and Applications Center)	Zonal statistics as table	30 × 30 m
Canopy cover standard deviation	Ernst and Lovich (2009)	Tree canopy cover 2023.5 (USFS Geospatial Technology and Applications Center)	Zonal statistics as table calculated on % canopy cover for each stream segment	30 × 30 m
Distance to gravel pit (m)	Walde et al. (2007)	LANDFIRE (USGS)	Near (analysis) tool	Not applicable
Ecoregion*	Willey et al. (2022)	Level III Ecoregions (US EPA)	Summarize within	Not applicable
Elevation (m)	Tingley et al. (2010), Mothes et al. (2020)	DEM (USGS)	Zonal statistics as table	1/3 arc-second (~10 m)

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TABLE 1 (Continued)

Covariate	Literature support	Data sources (authors)[a]	Extraction method	Resolution
Heat load index	Tingley et al. (2010)	DEM (USGS)	ArcGIS Geomorphometry & Gradient Metrics toolbox	1/3 arc-second (~10 m)
Land cover type*	Tingley et al. (2010)	LANDFIRE (USGS)	Spatial join	30 × 30 m
Landscape condition index	Willey et al. (2022)	LCI (NatureServe)	Zonal statistics as table	90 × 90 m
Percent sand (%)	Buech et al. (1997), Hughes et al. (2009)	Soil Survey Geographic Database; USDA	Spatial join	30 × 30 m
Proportion still water	Ernst and Lovich (2009)	NWI (USFWS)	Not applicable	1:12,000
Primary and secondary road density	Lapin et al. (2019)	TIGER/Line Shapefiles (US Census Bureau)	Line density tool	30 × 30 m
Tertiary road density	Lapin et al. (2019)	TIGER/Line Shapefiles (US Census Bureau)	Line density tool	30 × 30 m
Topographic ruggedness index	Ernst and Lovich (2009)	DEM (USGS)	ESRI ArcHydro toolbox add-in	1/3 arc-second (~10 m)
Vegetation height (m)*	McCoard et al. (2016)	LANDFIRE (USGS)	Zonal statistics as table	30 × 30 m
Vegetation height standard error	McCoard et al. (2016)	LANDFIRE (USGS)	Zonal statistics as table	30 × 30 m
Climatic variables				
Average July temperature (°C)	Mothes et al. (2020)	PRISM climate data (Oregon State University)	Zonal statistics as table	800 × 800 m
Mean annual precipitation (mm)	Mothes et al. (2020)	PRISM climate data (Oregon State University)	Zonal statistics as table	800 × 800 m
Minimum January temperature (°C)	Mothes et al. (2020)	PRISM climate data (Oregon State University)	Zonal statistics as table	800 × 800 m
Frost-free period length (days)	Greaves (2007), Mothes et al. (2020)	Gridded Soil Survey Geographic Database; NRCS	Zonal statistics as table	30 × 30 m

[a]DEM = digital elevation model; EPA = Environmental Protection Agency; LCI = Landscape Condition Index; NHD = National Hydrography Dataset; NWI = National Wetland Inventory; NRCS = Natural Resources Conservation Service; USDA = U.S. Department of Agriculture; US EPA = U.S. Environmental Protection Agency; USFS = U.S. Forest Service; USFWS = U.S. Fish and Wildlife Service; USGS = U.S. Geological Survey.

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select areas categorized as quarries, strip mines, gravel pits, well pads, and wind pads to derive a barren polygon, and then calculated the distance from each stream segment to the nearest barren area. We used this as a proxy variable for distance to gravel pit because female turtles commonly use gravel pits as nesting substrate (Walde et al. 2007). We derived vegetation height (m) from LANDFIRE's (2022) Existing Vegetation Height dataset, which depicts the average height of the dominant vegetation for each 30-m cell. We estimated vegetation height for vegetation categories that did not inherently contain a height value and then averaged across the buffer. We also calculated standard error of vegetation height across the buffer using zonal statistics to create a metric of structural heterogeneity. We obtained percent sand within the top 15 cm of soil at the 1:20,000 scale across the study area from the Soil Survey Geographic Database (USDA NRCS 2019), which contains soil characteristics stored in soil survey polygons, where polygons were delineated as areas dominated by one or several kinds of soil and therefore vary in size and shape. We converted the soil survey polygons to a raster and then calculated a weighted average of percent sand for each buffered stream segment.

Heat load index is an estimate of the annual direct solar radiation that accounts for latitude, slope, and aspect (McCune and Keon 2002). We calculated average heat load index from a 1/3 arc-second DEM using the ArcGIS Geomorphometry & Gradient Metrics toolbox (Evans et al. 2014). Topographic ruggedness index assesses vertical changes in a DEM between a raster cell and its adjacent cells, and we calculated it using the ArcHydro toolbox add-in (ESRI 2019). We derived total canopy cover (%) and its standard deviation from the USFS Geospatial Technology and Applications Center, which describes what percentage of a 30 × 30-m cell is covered by tree leaves, needles, branches, and stems from an aerial view (USFS 2023). We calculated canopy cover standard deviation, another metric of environmental heterogeneity, using the total canopy cover raster and the Zonal Statistics as Table tool in ArcGIS PRO for each stream segment buffer (ESRI 2019). We used the National Wetlands Inventory spatial dataset to determine the proportion of each buffer covered by still water (e.g., lakes, wetlands). This allowed us to assess the amount of land around the stream segments that lacked terrestrial habitat. We also evaluated the relative condition of natural land cover across the study area by calculating average landscape condition index (LCI) scores for each buffer using NatureServe's Landscape Condition Model (Hak and Comer 2017). This model uses map layers depicting infrastructure, land use, and anthropogenic vegetation modifications at multiple spatial scales to estimate the ecological integrity of a landscape on a scale from 0–100 (Hak and Comer 2017). Finally, we incorporated Level III Ecoregions from the U.S. Environmental Protection Agency (2024).

Candidate climatic variables (Table 1) included mean July temperature, minimum January temperature, mean annual precipitation, and length of frost-free period per year. Mean July temperature, minimum January temperature, and mean annual precipitation represent the most influential climatic variables identified by Mothes et al. (2020) and were calculated from 800 × 800-m 30-year normals (1991–2020) from the PRISM Climate Group (PRISM 2022). Length of frost-free period is calculated as the probable number of days between the last day at freezing temperature in the spring and the first day at freezing temperature in the fall, and we obtained this data from the Web Soil Survey (USDA NRCS 2019). We averaged climatic data across each 300-m buffer using zonal statistics.

Statistical analyses

Prior to building our HSM, we calculated general variance inflation factors for all candidate predictors to evaluate collinearity between predictor variables (Guisan and Zimmermann 2000, Jarnevich et al. 2015, Naimi and Araújo 2016). One of the primary objectives of this study was to identify the most influential variables for wood turtle habitat suitability, and high collinearity among predictors can reduce the accuracy of variable importance rankings (Jarnevich et al. 2015). Additionally, collinearity can be problematic when extrapolating the model results to novel geographic locations (i.e., model transfer) if the structure of the collinearity is not consistent between locations (Jarnevich et al. 2015). We considered candidate predictors with a variance inflation factor >10 to represent strong collinearity and iteratively removed variables until all remaining variables had a variance inflation

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factor <10 (Neter et al. 1989). Through this process, we removed the candidate predictors ecoregion, land cover type, and vegetation height (Jarnevich et al. 2015).

We used Random Forest (RF), which is a non-parametric, machine learning classification method to build our HSM (Breiman 2001, Prasad et al. 2006, Cutler et al. 2007). Random Forest functions by constructing large numbers of classification trees by drawing bootstrap samples from a random subset of predictors and response locations and then combining the classification trees to increase their accuracy (Breiman 2001, Prasad et al. 2006, Cutler et al. 2007). The advantages of RF classification are that it is capable of modeling complex interactions among predictor variables and is designed to minimize the overfitting that commonly occurs in classification and regression tree models (Breiman 2001, Prasad et al. 2006, Cutler et al. 2007). We used tuning on 10,000 trees to optimize the number of predictor variables sampled at each node split, which we set to six. Because we had a large imbalance between presence points (1,833 stream segments) and pseudo-absence points (132,696 stream segments), we downsampled the data to a 1:1 ratio of presence and pseudo-absence points, in which a random sampling of the pseudo-absence points was selected with replacement to build each classification tree (Valavi et al. 2021, 2022). This resulted in each individual tree having the possibility of containing a unique set of samples from the pseudoabsence class (Valavi et al. 2021, 2022). We then used backwards model selection to identify the most supported model by iteratively removing the variable with the smallest contribution to model accuracy to identify the model with the lowest out-of-bag error. We evaluated model performance with area under the operator curve, true skill statistic, sensitivity, specificity, and out-of-bag error.

We compared the importance of the predictor variables using two metrics: mean decrease in accuracy and Gini impurity (Breiman 2001). Mean decrease in accuracy quantifies the reduction in model accuracy when the values of a predictor are randomly permuted and Gini impurity reflects the average, weighted decrease in node impurity resulting from splits on a variable across all trees (Breiman 2001, Cutler et al. 2007). We examined the influence of predictor variables on habitat suitability using partial dependence plots which show the marginal effect of each predictor on the model's output while keeping other predictors constant (Friedman 2001). Partial dependence plots can offer important insights regarding habitat characteristics and their influence on the resulting habitat suitability; however, these modeled relationships should be considered exploratory in nature due to the non-linear relationships among variables in RF models.

We used the final RF model to project estimated probability of occurrence in stream segments across the focal area. Estimated probability of occurrence should be regarded as a relative probability (i.e., comparing the likelihood of one outcome to another) rather than true probability (the actual probability of an event occurring; Elith et al. 2011). We summarized occurrence probabilities on the scale of HUC-8 watersheds that were bound by this species' geographic distribution for Iowa, Michigan, and Wisconsin to maximize visual interpretability and display broad-scale patterns of habitat abundance across the landscape. For Minnesota, we summarized occurrence probabilities on the scale of HUC-4 watershed bounded by the wood turtle's geographic distribution to obscure areas with high probability of wood turtle occurrence that are on the edge of their distribution. For Minnesota, we averaged a mean of 735 stream segment probabilities for each HUC-4 watershed, and for Iowa, Michigan, and Wisconsin, we averaged a mean of 1,952 stream segment probabilities for each HUC-8 watershed. We conducted RF modeling using program R (version 4.3.1; R Core Team 2023) and the randomForest package (version 4.7.1.1; Breiman 2001); we calculated area under the operator curve with the pROC package (version 1.18.0.4; Robin et al. 2011).

RESULTS

Habitat suitability model

Backwards model selection identified the most supported model as the global model, which included 22 environmental variables (Table 1). Assessment metrics for the top model indicated strong model performance (area under the operator curve = 0.92, true skill statistic = 0.6704, sensitivity = 0.9045, specificity = 0.7660). Out-of-bag error was 9.74%, the misclassification rate for presences was 9.55%, and the misclassification rate for absences was 23.40%.

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Environmental relationships

Based on mean decrease in accuracy, stream order was the most influential variable, followed by stream width and proportion of still water in the terrestrial environment (Figure 5). Landscape condition, TRI, and stream gradient were moderately influential (Figure 5). The model estimated that probability of occurrence was higher at lower stream orders and lower stream widths (Figure 6). The model also estimated that probability of occurrence was highest when the proportion of the terrestrial environment covered by still water was low, with a sharp decline in occurrence at approximately 10% still water (Figure 6). The probability of occurrence was highest at moderate to high LCI values (LCI = 25–100) and was negatively associated with TRI (Figure 6). Probability peaked at a moderately low stream gradient (5–25 m/km) and declined at higher stream gradients.

Projected habitat suitability

We estimated that the mean probability of wood turtle occurrence across all stream segments was 0.22 ± 0.19 (range = 0–0.99). For all states other than Michigan, the majority of stream segments had a 0–0.10 probability of wood turtle occurrence, and the probability category with the fewest number of stream segments was segments with 0.91–0.99 probability of occurrence (Figure 7). Michigan followed a similar trend; however, the majority of streams segments had 0.10–0.20 probability of occurrence (Figure 7). We estimated that 10.5% of stream segments had ≥0.50

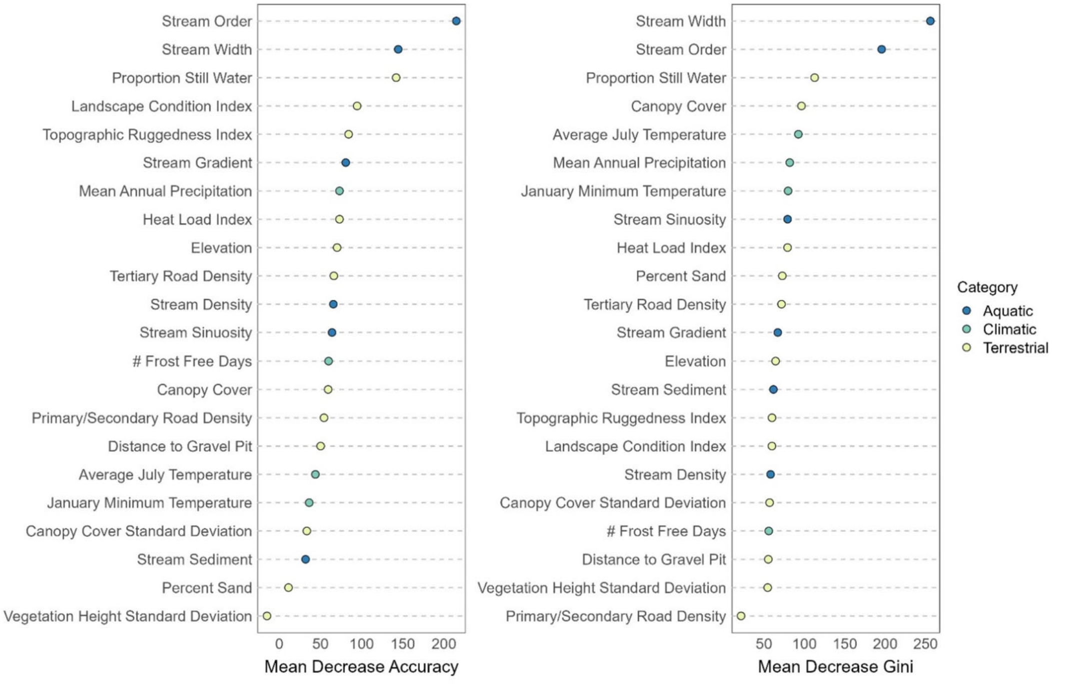

FIGURE 5 Predictor variables used to develop a global Random Forest habitat suitability model for the wood turtle *Glyptemys insculpta* based on occurrence records from 2000–2024. The plot shows each predictor's influence on mean decrease in accuracy of the model (reduction in model accuracy when the values of a predictor are randomly permuted) and mean decrease in Gini coefficient (measure of how much each variable contributes to the homogeneity of the nodes). We used this model to explain wood turtle occurrence in the midwestern United States (including parts of Iowa, Michigan, Minnesota, and Wisconsin).

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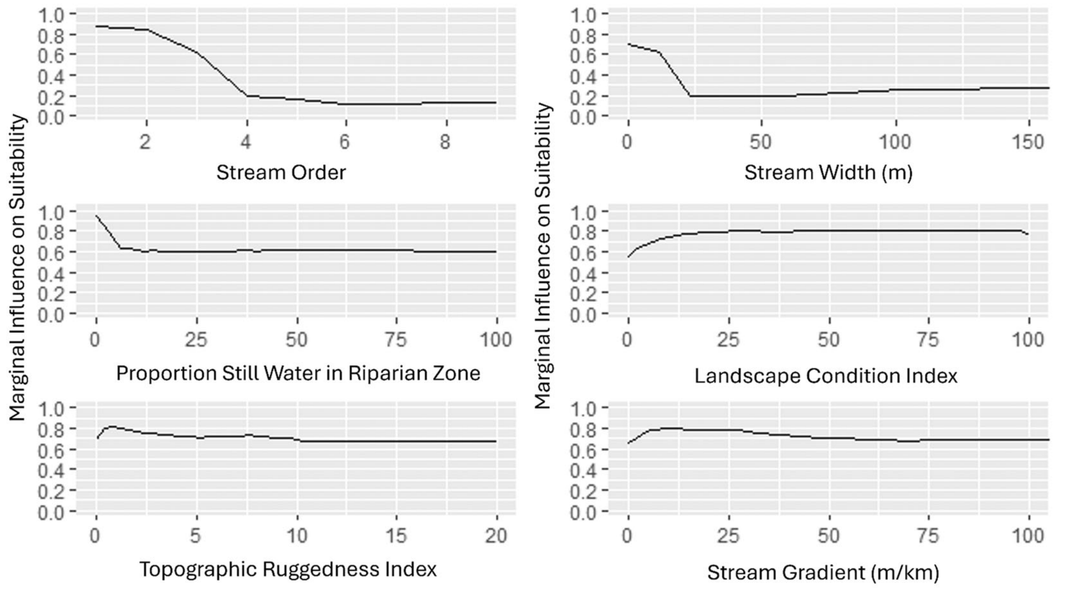

FIGURE 6 Partial dependence plots estimating relationships between the most influential environmental variables and wood turtle *Glyptemys insculpta* occurrence probability (marginal influence on habitat suitability) according to a habitat suitability model developed using occurrence records from 2000–2024 for their geographic distribution in the midwestern United States (including parts of Iowa, Michigan, Minnesota, and Wisconsin).

probability of wood turtle occurrence across the western portion of their geographic distribution, and 1.65% of stream segments were estimated to have a ≥0.80 probability of occurrence. Northeastern Wisconsin and the Lower Peninsula of Michigan had large clusters of HUC-8 watersheds with high probability of occurrence, and one HUC-4 watershed in northeastern Minnesota had high probability of occurrence (Figure 8). Iowa and western Wisconsin had large clusters of HUC-8 watersheds with low probability of occurrence (Figure 8). Of stream segments with ≥0.50 probability of occurrence, 90.0% do not currently have documented wood turtle populations according to state NHI data. Similarly, of stream segments with ≥0.80 probability of occurrence, 68.4% do not currently have documented wood turtle populations. Of stream segments with high probability of occurrence (≥0.50) but no documented populations, 33.0% were located in Michigan, 12.5% were located in Minnesota, 51.2% were located in Wisconsin, and 2.6% were located in Iowa.

DISCUSSION

The HSM developed here offers several valuable insights that can inform wood turtle management in the midwestern United States. We found that the majority of stream segments with 0.5–1.0 probability of occurrence (89.98%) and 0.8–1.0 probability of occurrence (68.18%) currently lack state agency-documented wood turtle populations. Stream segments with high probabilities of occurrence but no documented wood turtle populations could serve as priority areas for future standardized surveys, allowing for future management planning and actions to minimize habitat degradation or other anthropogenic impacts, such as road mortality. Identifying new populations could also offer opportunities to further understand metapopulation dynamics within the midwestern United States (Jones et al. 2018) and therefore guide conservation efforts that are aimed at the metapopulation level. Notably, these high-priority segments are predominantly located in Michigan and Wisconsin.

We discovered that most of the key variables influencing wood turtle occurrence are challenging or impractical to modify through wildlife management actions. Of the six most influential variables according to decrease in model

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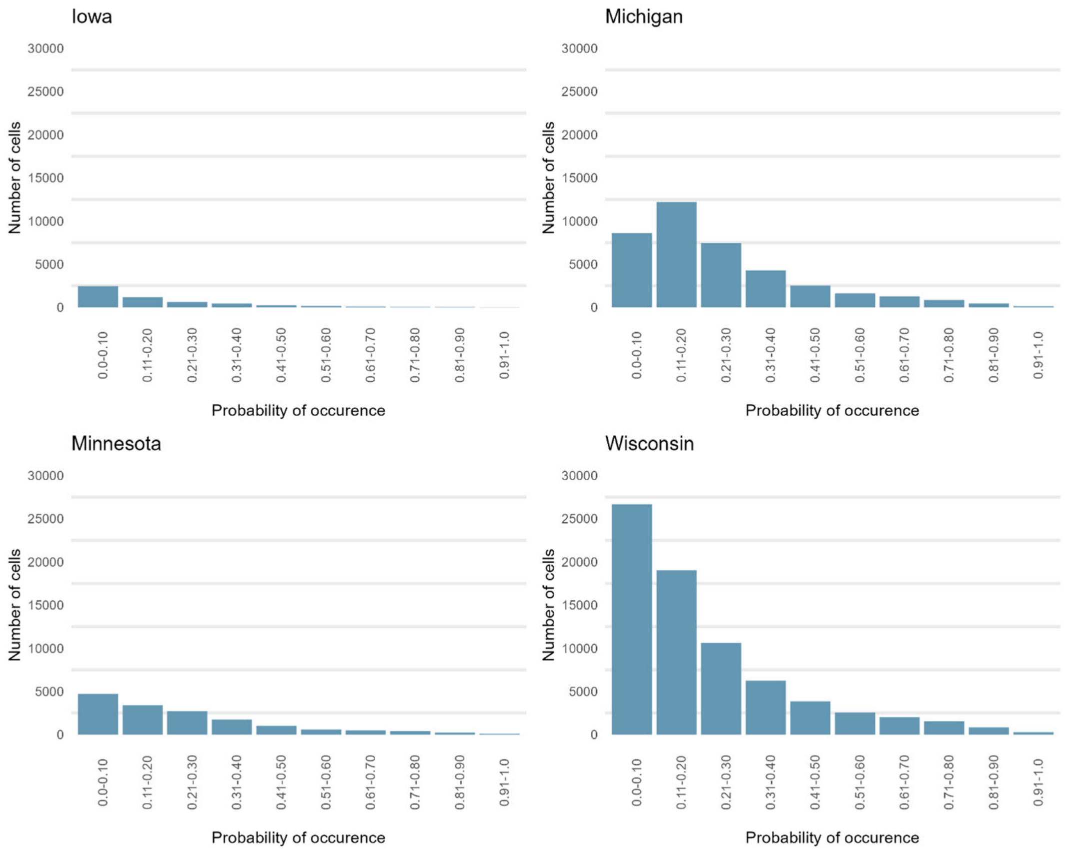

FIGURE 7 Number of stream segments within Iowa, Michigan, Minnesota, and Wisconsin and their estimated probability of wood turtle *Glyptemys insculpta* occurrence based on a habitat suitability model developed using occurrence records from 2000–2024 and including 25 aquatic, terrestrial, and climatic environmental variables. Each stream segment was 800–1,000 m in length and was derived from National Hydrography Dataset (NHD) flowlines (U.S. Geological Survey [USGS] 2022*a*).

accuracy: stream width, order, gradient, TRI, LCI, and proportion of still water in the riparian zone, only LCI and proportion of still water have the potential to be directly managed. Stream order and stream width were the two most influential variables in terms of mean decrease in model accuracy, with probability of wood turtle occurrence decreasing in large and high-order streams. Because stream width and order are typically not subject to habitat management changes, except in cases of dam removal, the creation of small, low-order streams remains largely outside of direct management control. Therefore, our results highlight the importance of conserving and restoring small and low-order streams as key wood turtle habitat. Stream gradient was negatively correlated with the probability of occurrence, indicating that wood turtles are more likely to be found in streams with lower gradients, and TRI was negatively associated with wood turtle occurrence, with higher probabilities found in streams with lower TRI. Identifying these important aquatic and terrestrial characteristics can help managers select streams with a higher likelihood of wood turtle occurrence for surveys and target areas for conservation and protection measures more effectively.

Among the environmental characteristics that can be influenced with habitat management, moderate to high LCI values were positively associated with a higher probability of occurrence. Surprisingly, probability of occurrence was nearly constant from moderate to high LCI values. This suggests that wood turtle populations can persist in landscapes

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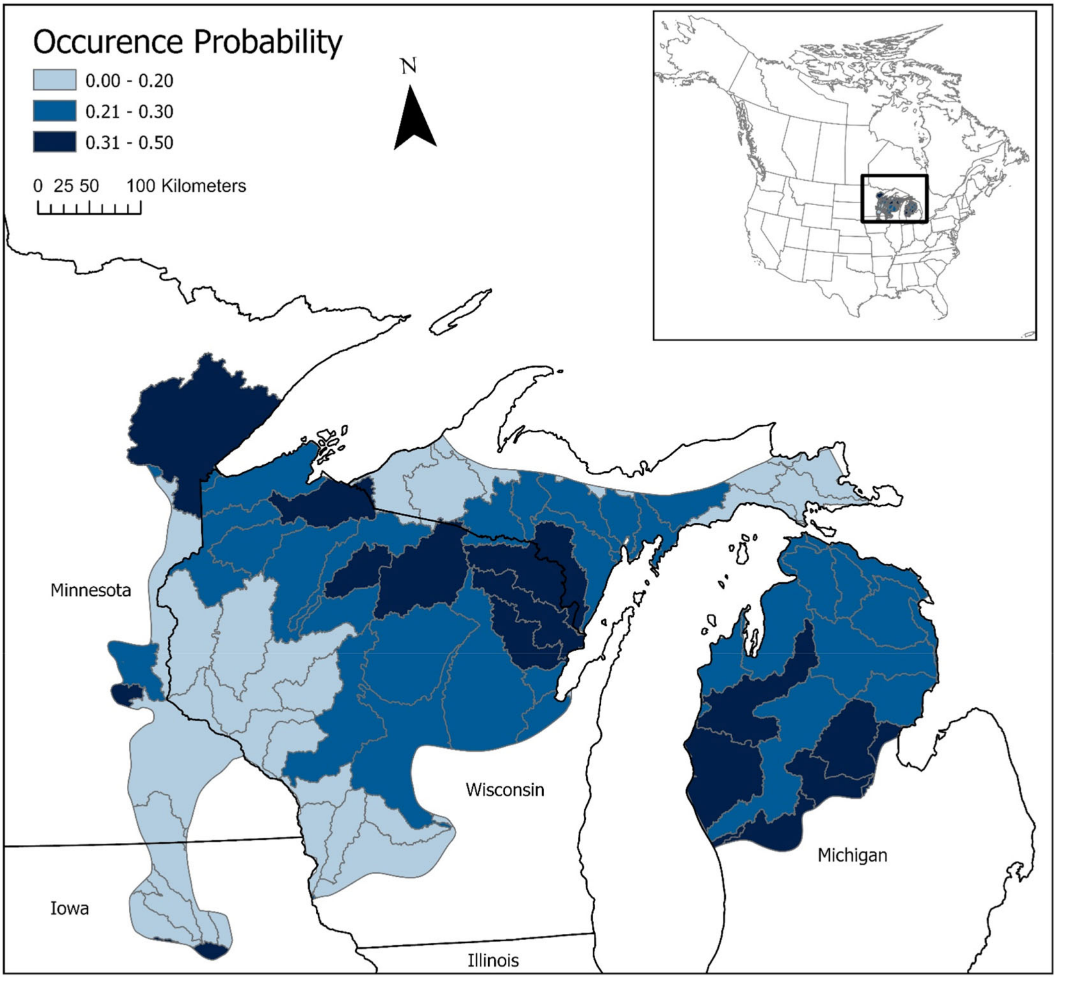

FIGURE 8 Mean probability of occurrence for the wood turtle (*Glyptemys insculpta*) summarized by HUC-8 watersheds in Iowa, Michigan, and Wisconsin, and by HUC-4 watersheds in Minnesota. We estimated probabilities using a habitat suitability model based on occurrence records from 2000–2024 and 25 aquatic, terrestrial, and climatic environmental variables. Occurrence probabilities for Minnesota were summarized on the HUC-4 watershed scale to obscure locations with relatively high probability of wood turtle occurrence that are on the distribution's edge and are easier to identify by illegal collectors.

containing substantial anthropogenic land uses (e.g., farmland), such as those found in southern Wisconsin and northern Iowa. However, we caution that populations in these lower integrity landscapes may represent ghost populations, which are populations in which high mortality rates or low recruitment rates result in a negative population growth rate, but older turtles survive and thus the population persists (Saumure et al. 2007). Conservation of this species would benefit from further investigation into how LCI and population growth rates interact. One source of still water in the riparian zone that possibly could be managed is beaver *Castor canadensis* activity. Previous research has shown that wood turtles sometimes use beaver ponds during the active season (Arvisais et al. 2004); however, little is known about the influence of beaver activity on wood turtle occurrence. Management decisions could benefit from future research evaluating how beaver-created wetlands influence wood turtle occurrence.

A companion study that estimated wood turtle abundance–habitat relationships in northern Wisconsin and Minnesota found that abundance was positively related to forest structural heterogeneity based on variables

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derived from LiDAR data (Staggs et al. 2024). We were unable to directly include those variables in this study because of a lack of LiDAR coverage across our area of inference; instead, we used vegetation height standard error and canopy cover standard deviation as metrics of structural heterogeneity. While neither of these variables were among the most influential variables for occurrence, they were supported for inclusion in the model, and creation of canopy gaps near occupied streams in mature forest stands could be a valuable management strategy to improve terrestrial habitat quality (Staggs et al. 2024).

We found that notable areas of higher probability of occurrence were in northern Wisconsin, northeastern Minnesota, and southern Michigan. Conversely, western Wisconsin, southern Minnesota, and most of the species' distribution in Iowa were associated with lower probability of wood turtle occurrence. Areas of relatively high or low probabilities were spatially clustered, which may enable wildlife managers to identify broad focal areas for conservation efforts. A joint effort by northeastern United States wildlife agencies within wood turtle distribution resulted in a conservation plan for the wood turtle that is founded on the principle of a conservation area network (Jones et al. 2018). Conservation area networks generally function as protected areas that represent relatively closed subpopulations of a species and are prioritized through a ranking system (Jones et al. 2018). A spatially explicit conservation strategy, similar to the strategy used in the northeastern United States, could identify methods and locations to attempt to stabilize the population decline of this species in the midwestern United States.

While our HSM performed well, there are several limitations that could affect accuracy and transferability to on-the-ground conditions. First, many of the data inputs to this model are derived from models themselves (e.g., stream sediment particle size, percent canopy cover), which increases the possibility of uncertainties within the input data compounding into errors in the final RF predictions (Heuvelink et al. 1989). Similarly, stream width was estimated from the NHDArea dataset and the National Wetland Inventory (USGS 2022*a*, USFWS 2023). Both datasets represent stream widths at the time of data collection. However, stream width is a highly dynamic variable that fluctuates over time; therefore, the values used here should be interpreted as proxies rather than precise measurements of actual stream width. Second, to achieve a robust occurrence dataset, we included wood turtle observation records from 2000–2024. Recent changes in local environmental conditions could result in mismatches between the occurrence and environmental data, and similarly, 30-year climate normals may not fully represent climatic relationships under contemporary rapid climate change. Third, accuracy of model estimation is reliant on representativeness of the occurrence records. As the states continue to invest in survey efforts to locate new populations, we expect the model to be updated periodically with additional occurrence data and environmental layers to improve performance. Additionally, future research could benefit from incorporating sensitivity analysis to quantify the effects of predictor variables on model predictions, thereby providing insight into how any limitations on the accuracy of the predictor variables influence the model output (Harper et al. 2011).

In summary, the insights gained from our HSM identify several important factors for wood turtle management and conservation in the midwestern United States. By focusing on high-probability stream segments that currently lack documented populations, survey efforts can be targeted to areas with the greatest potential for population discovery. While certain key variables, such as stream width and order, are challenging to alter, factors such as landscape condition and proportion of still water are potentially manageable, as are terrestrial habitat variables from the companion abundance study (Staggs et al. 2024). Our model results further highlight the importance of restoring and conserving small and low-order streams. Our results also underscore the importance of considering both aquatic and terrestrial characteristics in conservation planning. Implementing a region-specific, spatially explicit conservation strategy, similar to the conservation area network used in the northeastern United States, could enhance wood turtle conservation and management efforts and success in the midwestern United States.

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Wood Turtles of the Midwest. We also thank WVU intern C. Benson for aiding stream segment creation and environmental data processing. This research was supported by the United States Fish and Wildlife Service's Great Lakes Fish and Wildlife Restoration Act grant F21AP00170-00, the West Virginia University Arlen G. & Louise Stone Swiger Fellowship, and the USGS West Virginia Cooperative Fish and Wildlife Research Unit. Two anonymous reviewers and the Associate Editor provided comments that improved an earlier version of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this report are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

No animals were involved or handled throughout this study. This research relied on the analysis of pre-existing data which was obtained through ethically approved and lawful means, or through citizen science data collection.

DATA AVAILABILITY STATEMENT

The wood turtle occurrence data set used in this study is not available from the authors due to state threatened species data practices laws and data sharing agreement restrictions (approved by the Editor-in-Chief).

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