

Distribution of Summer Habitat for the Indiana Bat on the Monongahela National Forest, West Virginia

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Abstract: Hierarchical conservation and management of Indiana bat (*Myotis sodalis*) habitat may benefit from use of species distribution models. White-nose syndrome has caused additional declines for this endangered bat, requiring use of historical presence locations for habitat-related analyses. We created random forest presence/pseudo-absence models to assess the distribution and availability of Indiana bat habitat across the 670,000-ha Monongahela National Forest (MNF), West Virginia, USA. We collated historical roost and capture locations, both individually and in combination, to examine impacts of various biotic and abiotic predictors on roosting and foraging habitat of Indiana bats. Our final concordance map suggests that Indiana bat habitat was abundant (37.2% of the MNF) but localized, with predicted suitable areas often associated with edges of dry-calcareous forests. We observed significant variation between models, with the capture-only model independently identifying the greatest amount of potential habitat (47.8%). However, 21.9% of all potential Indiana bat habitat was identified by complete inter-model agreement. Our SDM outputs may assist land managers in identifying avoidance areas and new survey sites (i.e., capture and acoustic sampling) to support forest management activities.

Key words: *Myotis sodalis*, random forest, species distribution model

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White-nose syndrome (WNS) has been a major driver of bat mortality in North America (Cheng et al. 2021). Since its arrival in West Virginia, WNS has caused extreme population declines of several bat species, including the federally endangered Indiana bat (*Myotis sodalis*), both regionally and nationally (Cheng et al. 2021). Declines of Indiana bats have been less severe relative to other impacted species (Silvis et al. 2016), potentially driven by phased exposure, i.e., slow spatial spread of WNS through hibernacula and subsequently transmission within colonies (Maslo et al. 2017). Despite this apparent lag in spread and mortality, recent surveys suggest the species likely faces extirpation in much of its distribution, including the central Appalachians (Johnson et al. 2013, Thogmartin et al. 2013, O’Keefe et al. 2019, Johnson et al. 2021).

Previous assessments of habitat selection on the Monongahela National Forest (MNF), West Virginia, relied largely on day-roost locations of male Indiana bats associated with Big Springs Cave, captured and tracked on the Fernow Experimental Forest (FEF)

and nearby private land (Ford et al. 2002). Moreover, only one maternity colony of Indiana bats has been documented on the MNF (Keyser and Ford 2006). This is likely a function of limited survey effort relative to the size of the MNF and a lack of natural disturbance forest dynamics (i.e., fire, flood, and pests) necessary to create suitable day-roost conditions required by maternity colonies (Menzel et al. 2002). The maternity colony noted by Keyser and Ford (2006) persisted for only two summers on a parcel that, prior to the arrival of the colony, experienced a diameter-limit timber harvest (i.e., removal of high-value sawtimber) followed by an intense wildfire. These disturbances resulted in high overstory mortality and high-quality roosting conditions (e.g., trees with exfoliating bark, increased solar radiation; Johnson et al. 2010). These conditions, largely absent across much of the MNF, match forest stand structure used by Indiana bat maternity colonies across the Northeast and Mid-Atlantic (Kitchell 2002, Martin et al. 2006, Jachowski et al. 2016, St. Germain et al. 2017).

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In the Appalachian Mountains, Indiana bats select xeric forest types on upland sites that receive high levels of solar radiation (Johnson and Gates 2009, Johnson et al. 2010, De La Cruz and Ward 2016, Hammond et al. 2016). In the southern Appalachian Mountains these dry, warm areas often contain dead pine (*Pinus* spp.) used as diurnal roosts (Britzke et al. 2003). Specifically, Hammond et al. (2016) found that forests containing pine on southern aspects at 260–575 m in elevation were important Indiana bat habitat in southeast Tennessee and southwest North Carolina. Additionally, research in the Appalachian Mountains has shown that Indiana bat habitat is likely limited in the region due to extreme and sudden changes in local topography, which significantly alter local microclimates and therefore roosting temperature regimes and local prey assemblages (De La Cruz and Ward 2016, Hammond et al. 2016).

Despite the species' longstanding endangered status, recent population declines, and existing understanding of habitat characteristics, land managers in eastern North America may benefit from landscape-level habitat and distributional modeling efforts for the Indiana bat (Ford et al. 2016). Given the flexibility of presence-only SDM approaches, historical and limited current presence data enable researchers to construct reliable models assessing habitat associations and distributions of rare and declining species (De La Cruz and Ward 2016, Mi et al. 2017). Herein,

our objectives were to: 1) construct SDMs using historical presence data (i.e., roost locations, capture locations, and combination data) of Indiana bats in a random forest framework and assess model performance; 2) describe Indiana bat habitat on the MNF; 3) evaluate model agreement (i.e., roost, capture, and combination models); and 4) calculate the amount of Indiana bat habitat (i.e., foraging and roosting) on the MNF.

Methods

We examined availability of Indiana bat habitat across the 670,000-ha proclamation boundary of the MNF in eastern West Virginia (Figure 1; USFS 2011). The MNF is located in the central Appalachian Mountains, specifically the Allegheny Mountain and Upland Section and Ridge and Valley sub-physiographic provinces, and is dominated by forests varying from northern evergreen and northern hardwoods forests at higher elevations to mixed hardwood-pine and oak (*Quercus* spp.)-hickory (*Carya* spp.) forests at lower elevations (Johnson et al. 2021). See De La Cruz et al. (2023) for additional information about the study area.

Historical Capture and Roost Records

We pooled historical Indiana bat presence data accumulated from 22 July to 3 August 1997–2019 on the MNF. The U.S. Forest Service, in coordination with the U.S. Fish and Wildlife Service

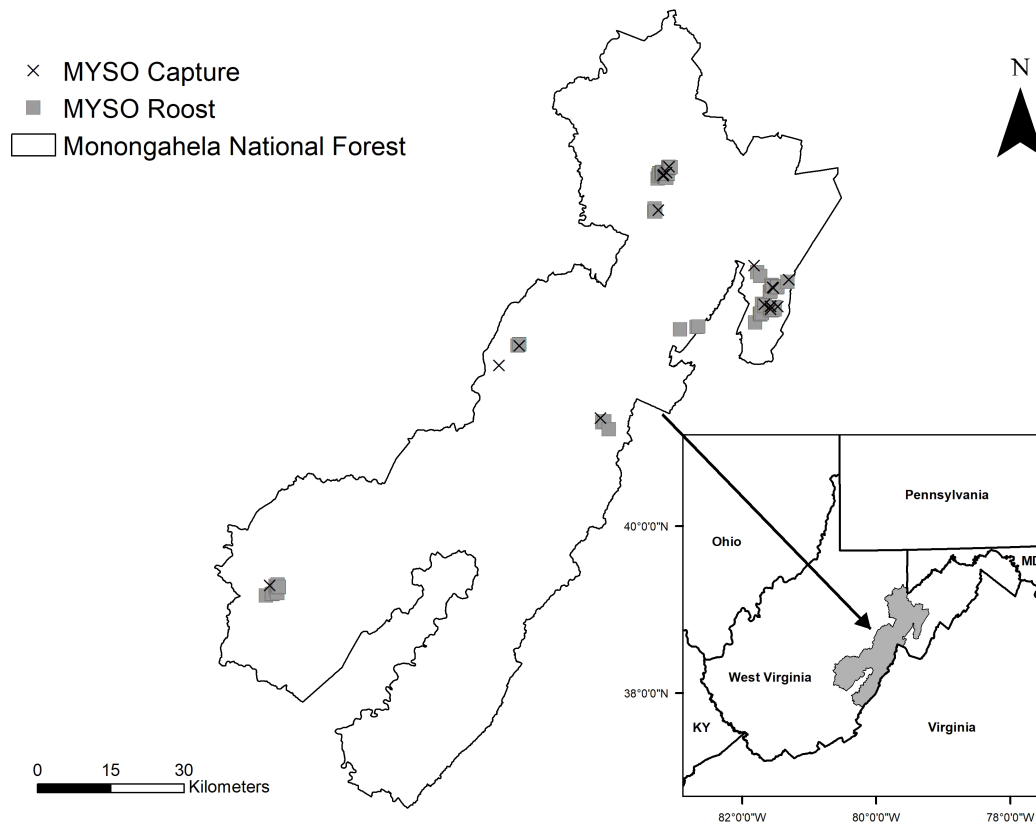


Figure 1. Approximate Indiana bat (MYSO) capture and roost location in the proclamation boundary of the Monongahela National Forest, West Virginia, 1997–2019.

(USFWS 2006), established 60 long-term monitoring sites and conducted additional capture surveys at >400 locations (≥ 30 apart) across the MNF (see Johnson et al. [2021] for details). Following Ford et al. (2016), we collapsed capture sites to unique locations when nets were >30 m apart using the BiodiversityR package in R (Kindt and Coe 2005, R Core Team 2013). From this effort, we identified $n=18$ and $n=102$ Indiana bat capture and roost locations, respectively, for inclusion in our analyses.

Habitat

We incorporated cover-type data from the West Virginia Land Use Land Cover (Strager 2020a) 5-m resolution raster dataset, which details 25 cover types, and resultant habitat diversity (Shannon diversity; H), evenness, and richness indices (De La Cruz and Ward 2016, Zuckerberg et al. 2016; see De La Cruz et al. 2023 for additional details about this dataset). Using the Forest Fragmentation of West Virginia raster dataset (Strager 2020b), we incorporated measures of forest fragmentation into SDMs, classifying forested areas as patch, edge, perforated, core (<100 ha), core (100–200 ha), or core (>200 ha); Strager 2020b). We also included canopy height (EROSC 2019), solar radiation (watt-hours per square meter), average annual temperature (PRISM Climate Group 2019), elevation (Gesch et al. 2002), aspect (i.e., cosine and sine transformations), slope degree, and distance from forest edge (0) into the forest interior (-) and into (+) non-forest cover (White et al. 2017). Terrain measures i.e., solar radiation, aspect, slope, were calculated from digital elevation models using the Spatial Analyst toolbox in ArcGIS (Version 10.3, Environmental Systems Research Institute, Redlands, CA). We standardized all raster datasets to a 30-m resolution. We calculated focal means of categorical variables using a 500-m moving window analysis, which approximates the day roost to foraging site dispersal distance of Indiana bats (Timpone et al. 2010, Pauli et al. 2015a, Cable et al. 2021).

Statistical Analysis

We fit presence/pseudo-absence random forest (RF) SDMs (Mi et al. 2017) using the sdm package in R (Naimi and Araújo 2016) to predict the availability of Indiana bat habitat on the MNF. We set the number of pseudo-absence points equal to that of known presence locations (Barbet-Massin et al. 2012) relative to data type (i.e., roost, capture, combination). To reduce both clustering and false pseudo-absences, we stipulated that all random pseudo-absence points be ≥ 1000 m from any presence point and ≥ 1000 m from any other pseudo-absence point (Olivier and Wotherspoon 2006). We removed correlated variables prior to initial modeling based on pairwise correlation (threshold = $|0.8|$). We assessed the predictive performance of our models using 10 replications of

5-fold cross-validation ($n=50$ models) of area under the curve (AUC) of the receiver operating characteristic and Cohen's Kappa (κ) statistic (Evans et al. 2011), interpreting values as described by De La Cruz et al. (2023). By measure of AUC, we quantified relative variable importance (RVI) by assessing model performance during inclusion of each variable and contrasting with omission of covariates during cross-validation (Naimi and Araújo 2016). To reduce over-fitting and improve model performance and interpretability (Evans et al. 2011), our final models contained only those landscape variables scoring greater than or equal to initial mean RVI (Naimi and Araújo 2016). We created response curves to examine the relation of probable habitat suitability to predictor variables (Evans et al. 2011).

Using predictive model averaging and “PredPrev=Obs” (i.e., predicted prevalence is equal to observed prevalence) thresholding, we created binary (i.e., suitable vs unsuitable) SDMs for all models (Freeman and Moisen 2008). We combined the binary roost, capture, and combination model rasters using spatial addition. Final concordance maps reflect habitat suitability as predicted by one or more models (i.e., capture, roost, capture and roost, combination, capture and combination, roost and combination, or all models).

Results

Predictive power of our Indiana bat capture-only SDM was good (AUC=0.86; $\kappa=0.75$) and contained aspect (cosine), distance to forest edge, elevation, landscape richness, “other” forests, and forest perforation. The most important variable to the model was forest perforations (RVI=26.8; Table 1). Based on response

Table 1. Final mean area under the curve (AUC) relative importance of select variables for Indiana bat random forest model replicates ($n=50$) derived from roosts locations, capture locations, and the combination of roost and capture locations on the Monongahela National Forests, West Virginia, 1997–2019.

Variable	Capture model	Roost model	Combination model
Aspect (cosine)	3.8	–	–
Canopy height	–	3.1	2.9
Dry calcareous forests	–	12.4	10.9
Dry oak-pine forests	–	2.7	1.6
Distance to forest edge	3.9	3.8	8.4
Elevation	4.0	–	–
Mixed mesophytic forests	–	3.9	3.5
Northern hardwood forests	–	3.8	2.4
Other forests	8.2	10.6	7.3
Pine-oak- emergent rock woodlands	–	1.6	–
Forest perforations	26.8	–	2.5
Landscape richness	7.5	–	–
Small stream riparian forests	–	–	2.2
Mean annual temperature	–	11.3	10.7

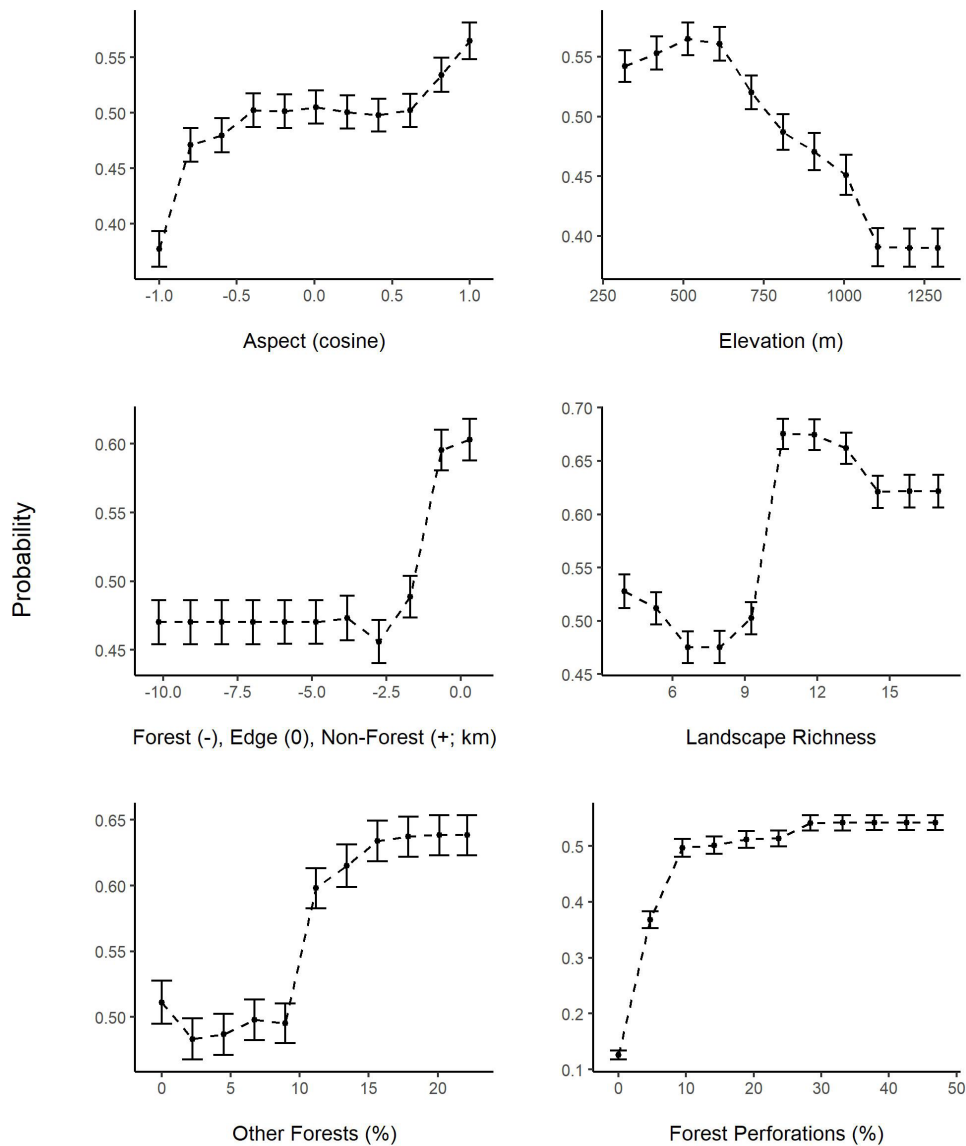


Figure 2. Predictor response curves (mean point estimates and 95% confidence interval) for $n = 50$ random forest model replicates predicting Indiana bat habitat based on capture locations on the Monongahela National Forest, West Virginia, 1997–2019.

curves, foraging habitat suitability was highest where forest perforations comprised $\geq 10\%$ of the landscape (Figure 2). Generally, the model described foraging habitat as “other” forests ($\geq 10\%$; RVI=8.2) at lower elevations (< 750 m; RVI=4.0) on southern slopes (RVI=3.8). These areas typically displayed greater landscape richness (≥ 10 cover types; RVI=7.5) and were farther from forest interiors (RVI=3.9; Figure 2).

The model created using roost-only data displayed excellent predictive capacity (AUC=0.94; $\kappa = 0.81$) and, similar to our capture SDM, contained distance to forest edge and “other” forests. Additionally, the model contained canopy height, dry calcareous forests, dry oak-pine forests, mixed mesophytic forests, northern hardwood forests, pine-oak-emergent rock forests, and mean

annual temperature. The most important variable was dry calcareous forests (RVI=12.4; Table 1), with roosting habitat located in areas containing $\geq 2.5\%$ of the cover type (Figure 3). Based on our roost-only SDM, Indiana bat habitat was positively associated with northern hardwood ($\geq 10\%$; RVI=3.8) and “other” forests ($\geq 10\%$; RVI=10.6), in warmer areas (≥ 8 C annually; RVI=11.3) that contained forest canopies ≥ 15 m tall (RVI=3.1). Roosting habitat was also negatively associated with forest interiors (RVI=3.8) and contained little mixed mesophytic forests ($\leq 30\%$; RVI=3.9), pine-oak-emergent rock forests ($\leq 5\%$; RVI=1.6), and dry oak-pine forests ($\leq 40\%$; RVI=2.7; Figure 3).

Similar to our roost-only SDM, predictive power of our combination model (i.e., capture and roost records) was good to excellent

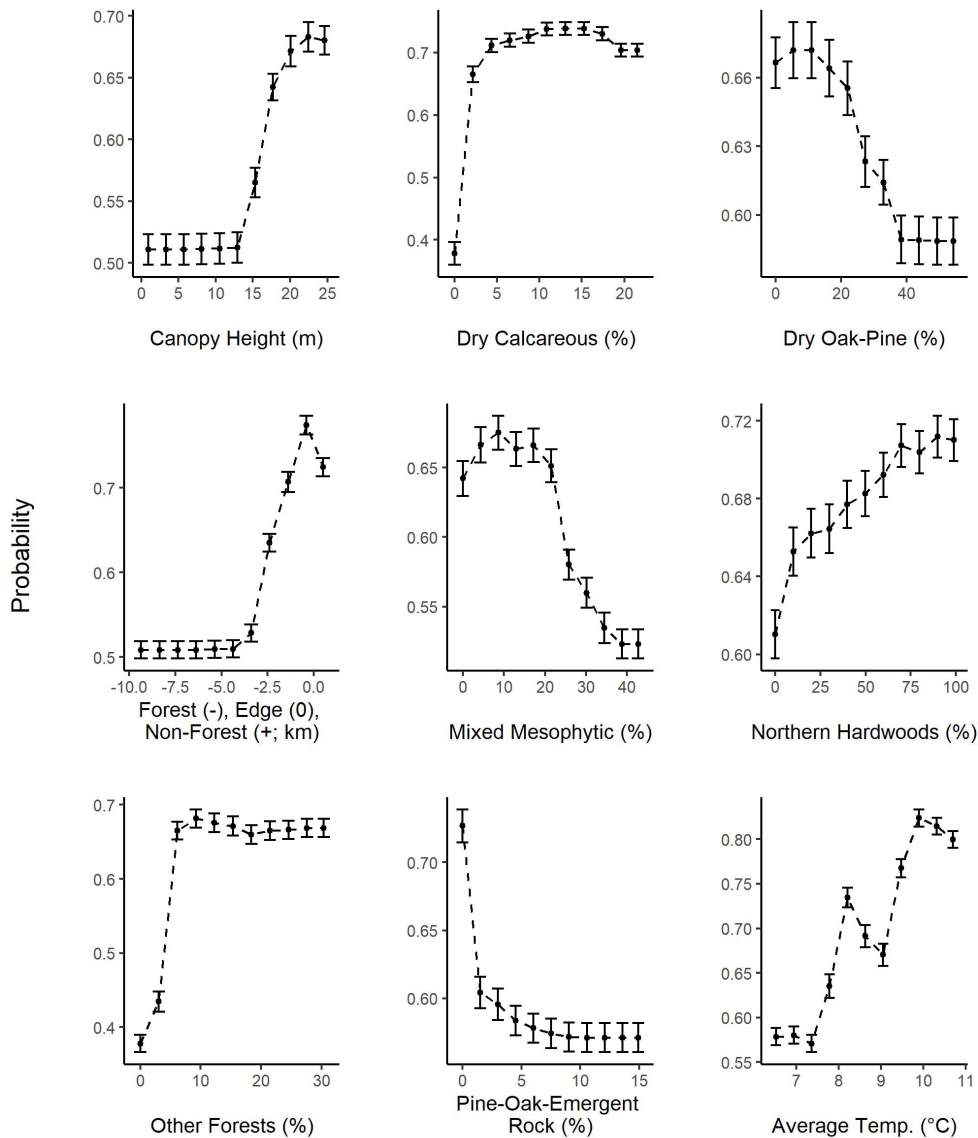


Figure 3. Predictor response curves (mean point estimates and 95% confidence interval) for $n = 50$ random forest model replicates predicting Indiana bat habitat based on roost locations on the Monongahela National Forest, West Virginia, 1997–2019.

(AUC = 0.93; $\kappa = 0.78$) and also contained distance to forest edge, dry oak-pine forests, and “other” forests. In addition to these predictors, the combination model contained canopy height, dry calcareous forests, mixed mesophytic forests, northern hardwood forests, forest perforations, small stream riparian forests, and mean annual temperature. The most influential variable was dry calcareous forests (RVI = 10.9; Table 1), with suitable areas containing $\geq 2.5\%$ of the cover type (Figure 4). Based on our combination SDM, Indiana bat habitat was positively associated with forest perforations ($\geq 10\%$; RVI = 2.5) of northern hardwood ($\geq 10\%$; RVI = 2.4) and “other” forests ($\geq 5\%$; RVI = 7.3) averaging ≥ 8 C annually (RVI = 10.7) and containing trees ≥ 15 m tall (RVI = 2.9). Additionally, habitat suitability was negatively associated with forests

interiors (RVI = 8.4), mixed mesophytic forests ($\geq 30\%$; RVI = 3.5), and small stream riparian forests ($\geq 5\%$; RVI = 2.2; Figure 4).

Indiana bat habitat, as determined by summary totals of binary capture-only ($P \geq 0.54$), roost-only ($P \geq 0.48$), and combination ($P \geq 0.47$) models, was localized yet readily abundant on the MNF (37.2% of the forest, 248,600 ha; Figure 5). The capture-only model identified 47.8% (118,725 ha) of the potential Indiana bat habitat available across the MNF. Furthermore, complete agreement between models accounted for 21.9% (54,350 ha) of potential habitat, with all other models and additive combinations accounting for $< 10\%$ of Indiana bat habitat on the MNF (Table 2).

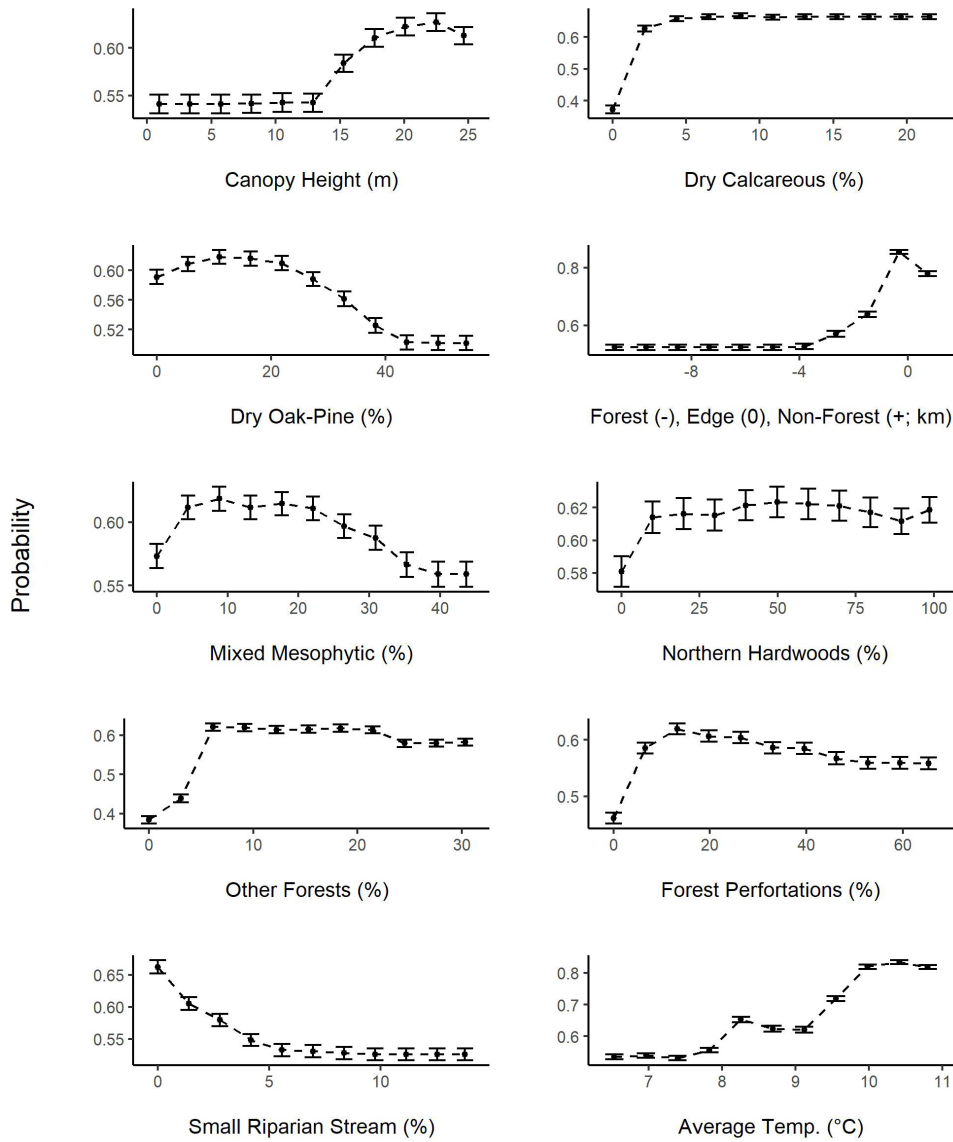


Figure 4. Predictor response curves (mean point estimates and 95% confidence interval) for $n = 50$ random forest model replicates predicting Indiana bat habitat based on both capture and roost locations on the Monongahela National Forest, West Virginia, 1997–2019.

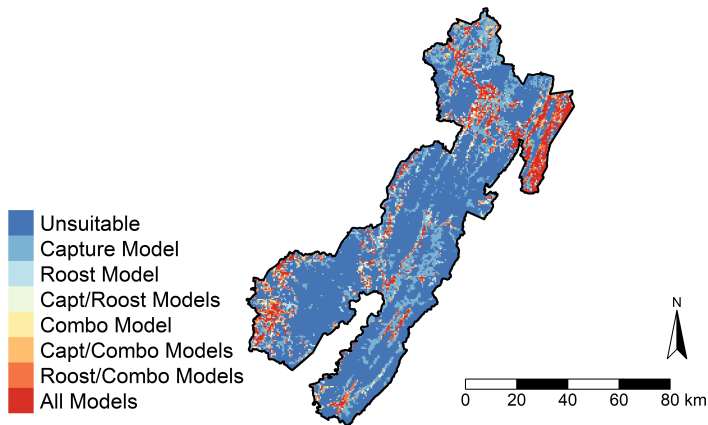


Figure 5. Indiana bat habitat suitability concordance map on the Monongahela National Forest, West Virginia, 1997–2019.

Table 2. Total contribution of models and model agreement regarding Indiana bat habitat on the Monongahela National Forest, West Virginia, 1997–2019.

Model	Total hectares	Percent total	Percent suitable
Unsuitable	418,725	62.7	–
Capture model	118,725	17.8	47.8
Roost model	17,250	2.6	6.9
Capture/roost models	10,725	1.6	4.3
Combination model	8600	1.3	3.5
Capture/combination models	16,825	2.5	6.8
Roost/combination models	22,125	3.3	8.9
All models	54,350	8.1	21.6

Discussion

On the MNF, previous Indiana bat research largely only occurred on the FEF and nearby areas (Ford et al. 2002, Ford et al. 2005, Johnson et al. 2010), typical of the localized nature of historical bat research in the high Allegheny Mountains of West Virginia (De La Cruz and Ward 2016, Johnson et al. 2021). Our MNF-wide modeling may enable natural resource managers to avoid or mitigate impacts to, or enhance, Indiana bat habitat and can assist the U.S. Forest Service in meeting regulatory requirements for the Endangered Species Act relative for this species (Ford et al. 2016, Hammond et al. 2016). Specifically, our results suggest that Indiana bat habitat is abundant and therefore not a limiting factor on the MNF. Pre-WNS, Indiana bat presence and abundance in the central Appalachian Mountains was not considered to be high, suggesting perceived impacts from land management actions were inconsequential (Brack et al. 2002).

Indiana bats typically roost in larger forest patches with diverse canopy conditions and tree species assemblages and, perhaps more importantly, in areas where disturbance such as fire or flooding have created specific day-roost conditions (Carter and Feldhamer 2005, Johnson et al. 2010). Our capture-only model is consistent with this pattern and highlights a positive relation between foraging habitat suitability and increasing landscape richness – typically a function of forest disturbance (Belote et al. 2009). Moreover, all models suggest that suitability improves as distance from unbroken interior forests increases, perhaps indicating that the MNF lacks the frequent and dynamic forest disturbances necessary to create a localized shifting mosaic of high-quality Indiana bat habitat. Indiana bats often select roosting habitats close to foraging sites and generally select forests of similar structure throughout their range (Jachowski et al. 2014). Similar to other findings (USFWS 2007, Johnson et al. 2010), our capture-only and combination models suggest that Indiana bat habitat suitability improves with increasing proportion of forest perforations, and all models support use of medium to very tall (10–25 m) forests.

Southerly aspects significantly influence both male and female Indiana bat roost-site selection in the Northeast, as well as the central and southern Appalachian Mountains where summer temperatures are cooler than in the species' range in the Midwest and Southeast (Watrous et al. 2006, Johnson et al. 2010, Loeb and Winters 2013). Similar to Hammond et al. (2016), our capture-only model identifies south-facing slopes as Indiana bat foraging/commuting habitat and also indicates that habitat suitability increases with decreasing elevation. Depending on latitude, the thermoregulatory requirements of Indiana bats result in an elevational stratification of habitats at local scales. Higher elevations are cooler, more thermally variable, and receive greater precipitation,

all factors that can inhibit fetal development and reproductive productivity (Brack et al. 2002). Our roost and combination SDMs also suggest that forests often associated with southwest-facing sideslopes, particularly dry calcareous forests, serve as Indiana bat habitat. Dry calcareous forests, a cover-type largely comprised of species frequently used as day-roosts (e.g., shagbark hickory [*C. ovata*] and white oak [*Q. alba*]), occur on drier, warmer slopes at lower elevations where fire return intervals are low relative to the MNF landscape (Thomas-Van Gundy et al. 2007). Similar to results of previous research in the central and southern Appalachian Mountains (De La Cruz and Ward 2016, Hammond et al. 2016), our roost-only and combination models also highlight the importance of ambient temperature and suggest that habitat suitability improves with increasing average annual temperature. Warmer areas may allow bats to maintain higher diurnal body temperature or provide ready access to more productive foraging habitats (Carter et al. 2002, Kurta et al. 2002, Murray and Kurta 2004, Ford et al. 2005, Johnson et al. 2010, Timpone et al. 2010). Indiana bats forage selectively in high-canopy forests, along 2nd and 3rd order forested streams (Ford et al. 2005), and along both warmer ridges (De La Cruz and Ward 2016, Hammond et al. 2016) and bottomlands (Brack et al. 2002, Menzel et al. 2005, Jachowski et al. 2014) where arthropod prey can be more abundant or available to bats.

On and adjacent to the FEF, Indiana bats select hickories, oaks, and maples as day-roost trees (Johnson et al. 2010). However, our roost-only and combination models suggest increasing habitat suitability associated with greater proportions of northern hardwood forests, particularly the Allegheny sub-type comprised largely of red oak, red maple (*A. rubrum*), and American beech (*Fagus grandifolia*). This suggests that models containing roost locations also highlight some foraging habitat close to diurnal sites (Carter et al. 2002, Kurta et al. 2002, Murray and Kurta 2004, Timpone et al. 2010, De La Cruz and Ward 2016). On the MNF, dry-oak pine forests often contain both white pine (*Pinus strobus*) and paradoxically mesic species such as eastern hemlock (*Tsuga canadensis*), two tree species infrequently used as roosts by Indiana bats (Silvis et al. 2016). Logically, our analyses suggest that the presence of dry-oak pine (i.e., roost-only model) and mixed mesophic forests (i.e., roost-only model, combination model) are negatively associated with Indiana bat habitat in our study area. Although pine is generally considered a preferred roost genera in the Southeast (Britzke et al. 2003, Hammond et al. 2016, St. Germain et al. 2017), our roost-only model suggests that the pine-oak-emergent rock forests in the context of the MNF are negatively associated with Indiana bat roosting habitat. This is perhaps in part due to the stunted trees (≤ 10 m tall) that characterize this low productivity cover type in the central Appalachian setting (Schuler and McClain 2003). This

result, along with the significance of topographic features, demonstrates the need for region specific modeling efforts and conservation based on information collected locally (De La Cruz and Ward 2016, Hammond et al. 2016)

Riparian areas serve as important foraging areas for Indiana bats in the region (Owen et al. 2004); however, our combination model supports the work of Ford et al. (2005), Hammond et al. (2016), and O’Keefe and Loeb (2016) in that habitat suitability decreases with increasing proportion of small stream riparian forests, likely a product of poor thermal conditions, low arthropod production, and highly cluttered foraging space (De La Cruz and Ward 2016). Despite this, all three Indiana bat models suggest that Indiana bat habitat is associated with high proportions of the spectrally unique but non-specific “other” forest cover-type. Qualitatively, this cover-type is more available than small stream riparian forests but is often indicative of forest ecotones on the MNF, specifically field, road, and large stream/river forest edges. Such areas likely serve as flight corridors and link roosting and foraging habitats (Murray and Kurta 2004).

Historical sampling sites, often established during regulatory consultation, are non-randomly distributed and are often associated with highly productive movement corridors (e.g., trails, roads) and foraging areas (e.g., streams, wetlands). This non-random sampling (i.e., sampling along roads) and searching bias (i.e., telemetry tracking to roosts), potentially promoted clustering of presence records and may be present in our models. However, De La Cruz and Ward (2016) found that Indiana bats selected road corridors as commuting and foraging habitat in the eastern West Virginia mountains, supporting use of these data and covariates (i.e., roads) for modeling. Moreover, for capture data the average distance between sites was 6751 m, although roost sites used for modeling were somewhat clustered (\bar{x} = 250 m). Omitting some roost sites to reduce this clustering would not be warranted biologically. Colonies of reproductive Indiana bats switch between roosts every 2 to 6 days (Silvis et al. 2016) but potentially less often in mountainous regions (Britzke et al. 2003). Roost switching by Indiana bats appears associated with a social fission-fusion dynamic (Silvis et al. 2014) and suggests the need to evaluate the distribution of roosting habitat in relation to areas of high roost density.

Models created using differing presence data (i.e., roost and capture points), separately and in combination, often produce variable results and constitute very different aspects of bat ecology (Pauli et al. 2015b, Ford et al. 2016). As seen for parallel modeling of northern long-eared bat (*Myotis septentrionalis*) habitat on the MNF (De La Cruz et al. 2023), capture (i.e., nocturnal foraging selection) and roost (i.e., diurnal roost selection) models often contained differing covariates, and when variables were shared

importance measures were dissimilar. This illustrates the need both to assess habitat selection specific to ecological need and to address these habitat requirements individually when devising species conservation and management plans. Because our concordance models combine individual binary model determinations, final mapping products likely represent a conservative estimate of habitat availability and are likely suited for identifying conservation needs concerning state and federal project consultation.

Active management (e.g., timber harvesting, prescribed burning, trail and road construction, natural gas production) on the MNF may negatively impact remaining populations of Indiana bats from roost removal and foraging habitat alterations (Loeb and O’Keefe 2014, Silvis et al. 2015). However, our findings can be used for forest management planning on the MNF and surrounding areas in the eastern mountains of West Virginia, specifically by assisting land managers in identifying avoidance areas and new survey sites (i.e., capture and acoustic sampling) to support forest management activities (USFS 2011). Due to the historical and current rarity on the MNF, collection of additional, high-value (i.e., captures, roosts) Indiana bat presence records appears highly unlikely and demonstrates the value of historical records in development of SDMs for species conservation (Ford et al. 2016). Future research examining post-WNS Indiana bat occupancy and detection probabilities, on the MNF and throughout the eastern mountains of West Virginia, may facilitate final concordance map validation and is likely to assist resource managers in monitoring population trends.

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