

Tricolored Bat Spatiotemporal Occurrence Patterns and Current Core Use Areas in the Monongahela National Forest, West Virginia

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Abstract: White-nose syndrome (WNS), caused by the fungal pathogen *Pseudogymnoascus destructans* (*Pd*), has led to widespread declines in tricolored bat (*Perimyotis subflavus*) populations across the eastern United States. Management actions have largely focused on increasing overwinter survival rates of *Pd*-infected bats through directly manipulating hibernacula. Maintenance of high-quality active-season habitat is also an important component of bat population recovery because it can result in higher body fat composition during the overwintering period and therefore increase survival rates of individuals affected by WNS. We aimed to provide spatial information to wildlife managers in the Monongahela National Forest (MNF) in West Virginia by identifying MNF locations containing high-quality active-season tricolored bat habitat. We created a habitat suitability model (HSM) using pre-*Pd* occurrence data and the ensemble learning algorithm Random Forest (RF) to quantify spatial variation in summer habitat suitability for tricolored bats in MNF. We then estimated how the species' spatial distribution changed after *Pd* became endemic to the MNF using indicator kriging models and combined the HSM results with indicator kriging results to identify current core use areas within the MNF. Across the study area, the landscape was classified as 8.2% least suitable habitat, 62.6% low suitability, 25.4% moderate suitability, and 3.8% high suitability. The estimated average probability of tricolored bat occurrence across the study area declined from 34.6% to 10.2% following onset of WNS. We identified three core use areas after *Pd* became endemic for the tricolored bat in the MNF, which encompassed 114.9 ha. The results of this study can be used by managers to identify focal locations and habitat characteristics for conservation and restoration of tricolored bat habitat.

Key words: core use areas, habitat suitability model, indicator kriging, tricolored bat, white-nose syndrome

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White-nose syndrome (WNS), caused by the fungal pathogen (*Pseudogymnoascus destructans* [*Pd*]), is a major threat to multiple species of hibernating bats in North America (Lorch et al. 2011, Hoyt et al. 2021). White-nose syndrome was first detected in a New York cave in 2006, after which the disease spread rapidly across eastern North America (e.g., Ingersoll et al. 2016, Perry and Jordan 2022). Typically, hibernating bats experience periods of torpor lasting from days to weeks, interrupted by arousal periods in which the metabolic rate increases, and body temperature rises to normal, however, WNS interferes with this process (Geiser 2004, Reeder et al. 2012). Bats infected with *Pd* develop lesions on the muzzle, ears, tail, and wings, with wing lesions causing dehydration and electrolyte depletion (Cryan et al. 2010, Verant et al. 2014). These physiological stresses cause more frequent arousals from torpor and greater energetic demands for healing, depleting fat stores and ultimately increasing mortality (Reeder et al.

2012). White-nose syndrome has been linked to high fatality rates at hibernacula and declines in the abundance and distribution of affected species (Francl et al. 2012, Ingersoll et al. 2016, O'Keefe et al. 2019, Hoyt et al. 2021, Johnson et al. 2021).

Research and management efforts for WNS have largely focused on increasing over-winter survival, including manipulating hibernaculum microclimate to reduce fungal growth rate and thus severity of infections (e.g., Sewall et al. 2023, Turner et al. 2022) and treating affected bats with probiotic bacteria (e.g., Cheng et al. 2017). Previous studies have documented higher survival rates in WNS-affected bats with greater fat stores prior to hibernation (Cheng et al. 2019, Haase et al. 2021), suggesting that the quality of foraging and roosting habitats used during the active season could influence winter survival probabilities for WNS-affected bats (Wilcox and Willis 2016, Frick et al. 2023). Thus, forest management actions that maintain or enhance key roosting and foraging

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habitats could help reduce the impacts of WNS on bat populations (Silvis et al. 2016, Johnson et al. 2021). Recent studies in South Carolina and Tennessee have aimed to identify suitable bat foraging and roosting habitats to inform the management actions for the purposes of increasing pre-hibernation fat stores (Cable and Willcox 2024, Rosales 2024).

The tricolored bat (*Perimyotis subflavus*) historically was a common bat species in the eastern United States (Stevens et al. 2017, Loeb and Winters 2022, Perry and Jordan 2022). As of 2021, *Pd* had spread to approximately 60% of the geographic distribution of the tricolored bat (Cheng et al. 2021), with >50% declines documented in populations following invasion (e.g., Powers et al. 2015, O’Keefe et al. 2019, Perea et al. 2022). Due to the observed rapid decline, in 2022 the U.S. Fish and Wildlife Service proposed to list the tricolored bat as federally endangered under the Endangered Species Act (USFWS 2022). In response, natural resource managers with the Monongahela National Forest (MNF), West Virginia, are prioritizing understanding the status and trend of tricolored bats on the MNF and the identification of core use areas where habitat quality could be maintained or enhanced for tricolored bats. Johnson et al. (2021) reported that tricolored bats accounted for 6.2% of bats captured on the MNF during summer mist net surveys between 2003 and 2008 (pre-*Pd*), with occurrence documented at a mean of 44% of sites surveyed each year. The first detection of *Pd* in a West Virginia hibernacula was in 2009 (Francl et al. 2012), and by 2019 tricolored bats had declined to account for 2.5% of bats captured and were detected at only 21% of surveyed sites. The estimated occurrence and relative abundance trends indicated the population was stabilizing but recovery was not yet occurring (Johnson et al. 2021).

The goals of this study were to identify locations on the MNF that contain high-quality active-season habitat for tricolored bats, estimate spatially explicit changes in occurrence following the invasion of *Pd*, and identify core use areas where habitat conservation or restoration actions could provide the greatest benefits for the species. We first created a tricolored bat habitat suitability model (HSM) using pre-*Pd* occurrence data (2003–2008) and classified suitable locations as low, moderate, and high suitability for tricolored bats. We then estimated the spatial distribution of tricolored bats on the MNF during three time periods: the pre-*Pd* period (2003–2008), *Pd* invasion period (2011–2014), and *Pd* endemic period (2015–2019) using indicator kriging models. Finally, we combined the HSM and indicator kriging model for the *Pd* endemic period to estimate *Pd* endemic core use areas on the MNF.

Methods

Study Area

The study area encompassed the MNF, which is managed by the U.S. Forest Service (USFS) and includes 687,966 ha in the Allegheny Mountains of eastern West Virginia (Figure 1). The study area is topographically complex, with elevations ranging from approximately 275–1480 m. The MNF is underlain by sedimentary rock and contains extensive cave systems (USFS 2011). Water resources are also abundant, with more than 950 km of perennial streams (USFS 2011). The MNF is primarily forested, including mixed mesophytic, northern hardwood, and oak-hickory forest types, with red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*) stands prevalent at higher elevations.

Occurrence Data

We obtained summer occurrence records for tricolored bats on the MNF from mist-net surveys conducted at 283 sites between 2003 and 2019 (Figure 1). The standardized MNF mist-net bat monitoring program during this period consisted of 60 long-term monitoring sites, with additional sites surveyed annually to assist with management plans and activities (Johnson et al. 2021). Mist-net sites were distributed across all primary forest types on the MNF, ranging from early successional areas to mature forests, with nets placed in potential travel corridors, foraging areas, or drinking areas (Johnson et al. 2021). Of 250 mist-net sites that were sampled prior to *Pd* invasion, 56 were located within 15 m of a stream (Figure 1). Each site sampling event consisted of at least two mist-nets sampled for two nights, with a minimum of 5 h of sampling each night. Each site was surveyed in 1 to 10 years over the study period and a minimum of 20 sites were sampled annually (Johnson et al. 2021). For the HSM, we restricted the response data set to occurrence records collected from 2003–2008 ($n = 250$ sites), prior to the invasion of *Pd*. We excluded occurrence records collected after *Pd* was first detected in West Virginia in 2009 (Francl et al. 2012) because our goal was to model tricolored bat occurrence based solely on environmental variables, and the spread of *Pd* may have confounded the relationships between occurrence and the environmental variables. For the indicator kriging models, we restricted the response data set to sites that were sampled during all three focal periods (pre-*Pd* [2003–2008], *Pd* invasion [2011–2014], and *Pd* endemic [2015–2019]; $n = 41$ sites) to avoid introducing sampling-related biases associated with differing locations and levels of effort among the focal periods. We did not include detection data in 2009–2010 because *Pd* was actively spreading throughout the study area at this time and this could obscure spatial distribution patterns in the *Pd* invasion period. The input data

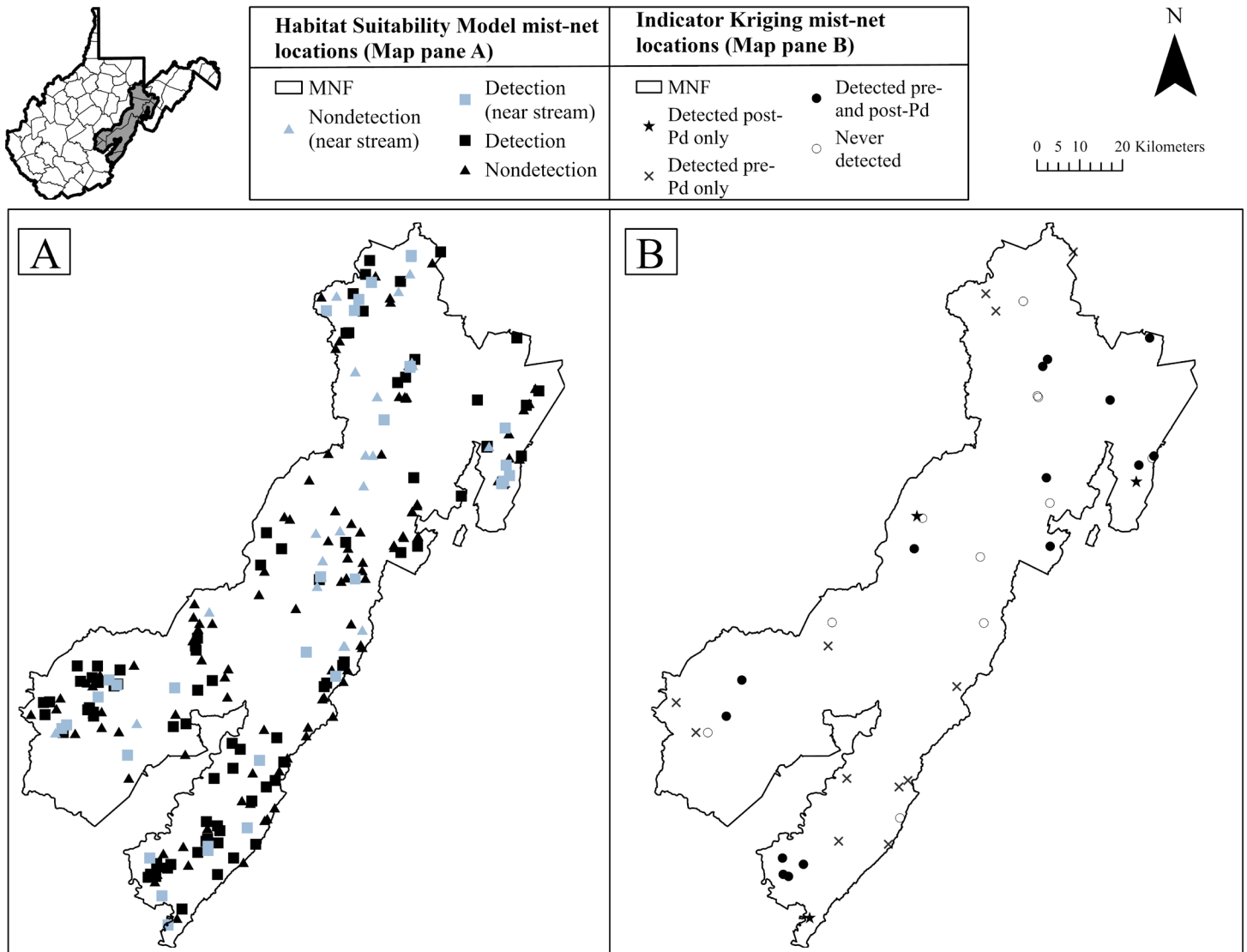


Figure 1. (a) Mist-net survey locations ($n = 250$) and tricolored bat (*Perimyotis subflavus*) detections from 2003–2008 in the Monongahela National Forest (MNF), West Virginia. The resulting detection dataset was used to develop a MNF habitat suitability model for tricolored bats. Survey locations within 15 m of streams are shown in blue, and those farther than 15 m are shown in black. (b) Mist-net survey locations ($n = 41$) and detections used to evaluate shifts in spatial distribution for tricolored bats with Indicator Kriging, with locations restricted to sites that were sampled during each of three focal periods (pre-*Pseudogymnoascus destructans*, the *Pseudogymnoascus destructans* invasion period, and *Pseudogymnoascus destructans* endemic period).

for indicator kriging models was the mean number of captures per site during each of the three focal time periods.

Habitat Suitability Modeling

Predictor Variables To identify candidate environmental predictors, we reviewed the scientific literature for tricolored bat habitat associations. Based on this review, we identified 21 candidate variables that represented a broad spectrum of environmental factors, including climatic conditions, terrain attributes, existing vegetation characteristics, and distances to relevant environmental features (Appendix, Table A1). Climatic variables included 30 arc-second annual mean temperature and annual precipitation

(1970–2000) obtained from the WorldClim database (Fick and Hijmans 2017). Terrain variables included slope degree and elevation, which were calculated from a 30-m digital elevation model (LANDFIRE 2020a). We computed the geodesic distance to the nearest stream and nearest lentic waterbody according to the National Hydrography Dataset [NHD; 1:24,000 scale; U.S. Geological Survey (USGS) 2023] using the Near Tool in ArcGIS PRO (ESRI 2023).

We represented vegetation characteristics and structure in multiple ways. We derived forest types from the 2008 USFS National Forest Type Dataset 250-m raster (Ruefenacht et al. 2008). Within our study area, there were 22 distinct forest types. We obtained

estimates for forest structure variables from 250-m rasters obtained through the 2023 USFS Forest Inventory and Analysis Program (USFS 2023), including total quadratic mean diameter, total stand density index, total basal area, tree frequency, and trees per acre. We obtained percent canopy cover from a 30-m canopy cover raster from the 2021 National Land Cover Database (Coulston et al. 2012, 2013). We used 30-m Existing Vegetation Cover (LANDFIRE 2020b) and Existing Vegetation Height (LANDFIRE 2020c) rasters to represent percent cover of the live canopy layer and average height of dominant vegetation, respectively. Finally, we represented forest configuration using a 9-m raster from the 2020 National Agricultural Imagery Program Forest Fragmentation of West Virginia (Strager and Maxwell 2020). This dataset classifies the landscape into different configuration categories, including patch, edge, perforated, small core (<101 ha), medium-sized core (101–202 ha), large core (>202 ha), and non-forested.

We considered several variables to represent moisture and productivity gradients, including Topographic Wetness Index (TWI), Integrated Moisture Index (IMI), Heat Load Index (HLI), Normalized Difference Vegetation Index, and Normalized Difference Moisture Index. Topographic Wetness Index and IMI are measures of the relative wetness of a point on a landscape. Topographic Wetness Index was derived from the 2020 LANDFIRE 30-m digital elevation model by combining the upslope contributing area and the local slope, where the upslope contributing area is the area of the landscape that drains into a given point and the local slope is the slope of the land at that point (Beven and Kirkby 1979, Sørensen et al. 2006). In contrast, IMI was calculated based on hillshade, curvature, flow accumulation, and soil water capacity (Iverson and Prasad 2003) using a 2020 LANDFIRE 30-m digital elevation model and a 150-m soil water capacity layer (Boiko et al. 2021). We created the IMI and TWI rasters using the raster calculator in ArcGIS PRO. For both IMI and TWI, higher values indicate wetter areas. We derived HLI from a 2020 LANDFIRE 30-m digital elevation model using the spatialEco package in Program R (Evans and Murphy 2023, R Core Team 2023). Heat Load Index was estimated based on slope, aspect, and latitude, and represents the heat accumulation in a specific area, with higher HLI values representing areas with higher heat stress (McCune and Keon 2002). We calculated the Normalized Difference Vegetation Index as a measure of vegetation health and density. We calculated the Normalized Difference Moisture Index from 30-m satellite or aerial imagery downloaded from 2020 USGS Landsat data (Earth Resources Observation and Science Center 2020). This index represents moisture content in vegetation and soil by quantifying the difference in near infrared and shortwave infrared reflectance, which are sensitive to changes in moisture levels (Gao 1996). We calculated the

mean of each raster-based environmental variable for each raster cell using the Zonal Statistics as Table tool in ArcGIS PRO. We conducted environmental variable calculations and manipulations in Program R (version 4.2.3) and ArcGIS PRO (ESRI 2023).

Modeling Framework and Predictor Variable Selection We created a 30 m x 30 m cell grid (1:60,000 scale) across the MNF and resampled all other environmental data layers to match this spatial resolution. We used the Random Forest (RF) method to develop a HSM using pre-Pd tricolored bat occurrence data (2003–2008) and predict relative summer habitat suitability across the MNF (Breiman 2001). Random forest modeling is a decision tree-based ensemble learning method, where multiple decision trees are constructed, each using a subset of the predictor and response data. The bootstrap ensemble approach minimizes model overfitting and the excluded samples (i.e., out-of-bag data) within the analysis can be used to assess model performance (Breiman 1996, Breiman 2001). Individual variable importance is derived by permuting out-of-bag predictor values and measuring the resulting misclassification rate increments.

For the RF models, we tested performance of models using the observed non-detection locations as absence points and using background locations as pseudo-absence points. To create pseudo-absence points, we generated random points across the MNF and filtered them to exclude those falling within a 1-km buffer around presence points to avoid spatial autocorrelation (De La Cruz et al. 2023). We found that using pseudo-absence points had substantially higher explanatory power (AUC = 0.89) than observed non-detection locations (AUC = 0.64), and thus we used pseudo-absence points for the final analysis. While this approach is well supported by previous research (e.g., Barbet-Massin et al. 2012, Iturbide et al. 2015), estimated suitability for occurrence should be regarded as a relative measure of suitability (Elith et al. 2011). To address class imbalance in our dataset, we used down-sampling to reduce the majority class to the same size as the minority class, mitigating bias towards the majority class. We then matched the predictors with the balanced class distribution, preventing the underlying distribution from skewing the model towards overpredicting the majority class (Valavi et al. 2021, Valavi et al. 2022).

We used recursive feature elimination to determine which candidate predictor variables had strong support for inclusion in the HSM (Guyon et al. 2002). This method identifies and removes unimportant predictors by iteratively splitting the data into training and testing data sets and assessing model performance with different combinations of predictors. Using this analysis, we identified 9 of the 21 candidate predictors as useful predictors of tricolored bat occurrence, including annual mean temperature, TWI, distance to

lentic waterbody, distance to stream, elevation, HLI, USFS forest type, forest fragmentation, and canopy cover. We used these variables to construct the HSM.

Model Parameterization, Performance, and Predictions Two important parameters in RF models are the number of trees constructed and the number of variables considered at each split. We selected the number of trees by monitoring the stabilization of the out-of-bag error rate, and the number of variables considered at each split was set as the square root of the total number of predictor variables, with a minimum value of 2 (Cutler et al. 2007). We evaluated model performance primarily using the out-of-bag error rate, which provides an estimate of the model's generalization error. Additionally, we examined the area under the receiver operating characteristic curve (AUC), sensitivity, specificity, and overall accuracy to characterize model performance.

We created partial dependence plots to estimate the influence of individual predictors on habitat suitability. These plots represent the marginal effect of each predictor on the predicted outcome when keeping the other predictors constant (Friedman 2001). We calculated the importance of the predictor variables using Gini impurity, which measures the total decrease in node impurities from splitting on the variable, averaged over all trees. While partial dependence plots can offer valuable insights for habitat associations, the modeled relationships should be considered exploratory in nature due to the potentially complex non-linear relationships among variables in RF models.

To assist with visualization of habitat suitability across the MNF, we classified cells into four classes (least suitable, low suitability, moderate suitability, and high suitability) using a fixed probability threshold from the RF model's predicted probabilities. We used an integrated approach combining model predictions and performance metrics. We first generated suitability scores for each data point's likelihood of belonging to the positive class (suitable habitat) using predictive models. We then calculated the performance metrics sensitivity, specificity, false negative rate, and false positive rate at various threshold levels to evaluate the effect of threshold adjustments on model performance. Least suitable habitat represented values less than the threshold defined by low suitability habitat. Low suitability habitat represented the threshold where the false negative rate was below 5%, prioritizing the minimization of false negatives. Moderate suitability habitat represented the threshold where the false negative rate ranged between 5% and 15%, with the goal of balancing false negatives and positives. High suitability habitat represented the threshold where the false positive rate was below 5% and the false negative rate was above 15%, prioritizing the minimization of false positives (Jarnevich et al. 2016). We

calculated all RF analyses and performance metrics using program R (version 4.3.1).

Spatial Distribution Patterns

We used kriging models to evaluate changes in tricolored bat spatial distribution patterns. We filtered the standardized MNF mist-net data to include only sites that were sampled in each of three focal time periods: pre-*Pd* (2003–2008), *Pd* invasion (2011–2014), and *Pd* endemic (2015–2019) to avoid introducing sampling-related biases associated with differing locations and levels of effort among the focal periods. Out of the 60 long-term monitoring sites, 41 were sampled in each of these time periods. For the 41 sites, we calculated the mean number of captures at each site during each time period and used these values as the input data for the spatial distribution analysis.

We created an interpolated distribution probability map for each time period using indicator kriging (Johnston et al. 2001). Indicator kriging belongs to a group of spatial interpolation methods called kriging that use sampled data points to estimate the value of a variable across a specified spatial distribution (Glacken and Blackney 1998, Johnston et al. 2001). Indicator kriging is a non-parametric approach to interpolation in which continuous data are assigned to binary variables according to whether they do or do not exceed a set threshold. The binary variables are then used to estimate probabilities of belonging to a specified class across the entire spatial distribution (Glacken and Blackney 1998, Johnston et al. 2001). We set the threshold for class delineation to 0 and evaluated model performance using root mean square of standardized error, which measures the average distance between the predicted and actual values (Chai and Draxler 2014). We used ArcGIS Desktop to create indicator kriging models (ESRI 2021).

Core Use Areas

We delineated potential core use areas in the *Pd* endemic period for tricolored bats in the MNF by overlapping high suitability habitat ($\geq 77\%$ as identified by the HSM) with areas identified by the indicator kriging model as having a moderate ($\geq 50\%$) or high ($\geq 75\%$) probability of occurrence in the *Pd* endemic period. We applied the Boundary Clean tool in ArcGIS PRO to the classified suitability raster created with the HSM to simplify identification of larger, contiguous core use areas. We converted the indicator kriging raster cells with $\geq 50\%$ and $\geq 75\%$ probability of occurrence to polygons and overlaid them on the high suitability habitat polygons from the HSM. We considered high suitability habitat polygons that overlapped with moderate probability of occurrence polygons ($\geq 50\%$ probability) to be priority 2 core use areas; high

suitability habitat polygons that overlapped with high probability of occurrence polygons ($\geq 75\%$ probability) were considered to be priority 1 core use areas.

Results

Habitat Suitability Model

The final random forest model yielded an overall accuracy of 84.8%, with a sensitivity of 78.3% (true positive rate) and a specificity of 91.3% (true negative rate). The AUC value was 0.89. The positive and negative predictive values were 90.0% and 80.8%, respectively. We created a map depicting tricolored bat habitat suitability across the MNF, ranging from 0 (least suitable) to 1 (highly suitable) using the model predictions (Figure 2). We categorized habitat suitability into four levels based on suitability values: least suitable (0.000–0.144), low suitability (0.145–0.484), moderate suitability (0.485–0.769), and high suitability (0.770–1.000). Across the study area, we classified the landscape as 8.2% least suitable, 62.6% low suitability, 25.4% moderately suitable, and

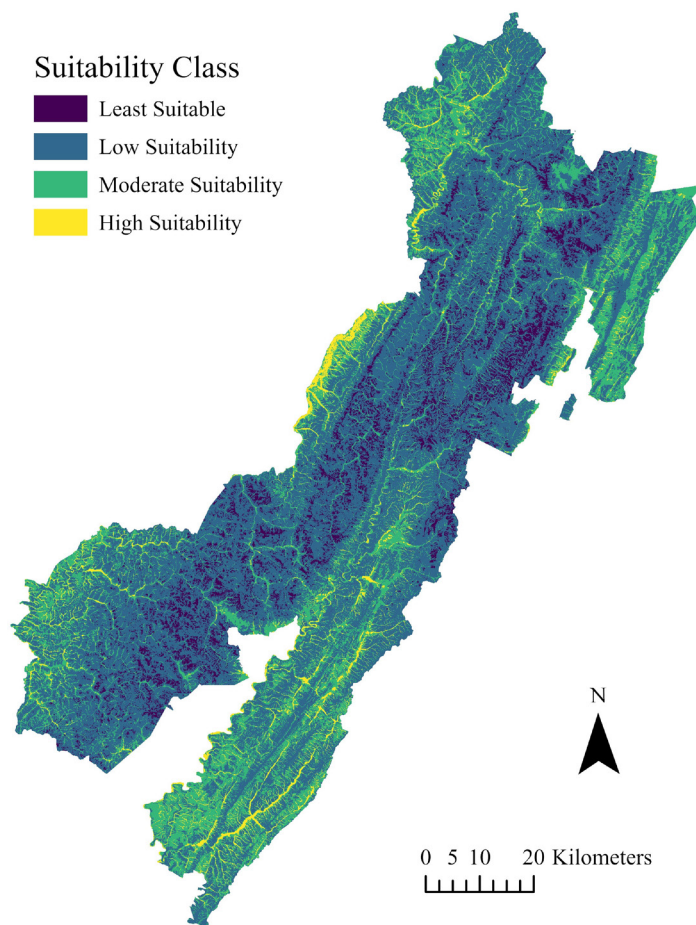


Figure 2. Relative summer habitat suitability for tricolored bats (*Perimyotis subflavus*) across the Monongahela National Forest, West Virginia, as predicted using a random forest model. See text for definition of suitability classes.

Table 1. Environmental variables used in the tricolored bat (*Perimyotis subflavus*) habitat suitability model for the Monongahela National Forest, West Virginia, as ranked by Gini impurity and relative variable importance.

Variable	Mean decrease in Gini	Relative variable importance
Distance to stream	9.90	1.00
Topographic wetness index	8.21	0.83
Annual mean temperature	7.29	0.74
Elevation	6.43	0.65
Heat load index	6.11	0.62
Distance to waterbody	5.68	0.57
National Land Cover Database canopy cover	4.87	0.49
USFS forest type	4.35	0.44
National Agricultural Imagery Program forest fragmentation	2.73	0.28

3.8% highly suitable habitat (Figure 2). For 115 sites where presence was observed, 0.9%, 11.3%, 54.8%, and 33.0% were within the least suitable, low suitability, moderate suitability, and high suitability habitat classes, respectively.

The variable distance to stream had the greatest mean decrease in Gini and relative variable importance, followed by TWI, annual mean temperature, and elevation (Table 1). The partial dependence plots indicated negative relationships with distance to stream and elevation, positive relationships with TWI, canopy cover, and annual mean temperature, and an intermediate relationship with HLI (Figure 3). The partial dependence plots also indicated that occurrence was positively associated with hardwood forests (particularly the oak-hickory forest type) and edge/perforated configurations (Figure 3).

Spatial Distribution Patterns

Performance of all indicator kriging models was high, with the pre-*Pd*, *Pd* invasion, and *Pd* endemic models having RMSE values of 1.01, 0.89, and 0.87, respectively. Estimated mean probability of occurrence across the MNF declined from 34.6% in pre-*Pd* to 17.4% in *Pd* invasion and declined further to 10.2% in *Pd* endemic (Figure 4). We estimated that 0.46% of the landscape had $\geq 70\%$ probability of tricolored bat occurrence pre-*Pd* and was approximately the same in *Pd* invasion (0.45%), but declined to 0.02% in *Pd* endemic (Figure 4). Pre-*Pd*, 11.5% of the landscape was estimated as having $\geq 50\%$ probability of tricolored bat occurrence, declining to 3.86% in *Pd* invasion and 0.21% in *Pd* endemic (Figure 4).

Core Use Areas

We identified three spatially distinct core use areas for the tricolored bat in the MNF (Figure 5). These spatially separated core use areas contained 20.3 ha, 43.9 ha, and 50.7 ha of priority 2 core

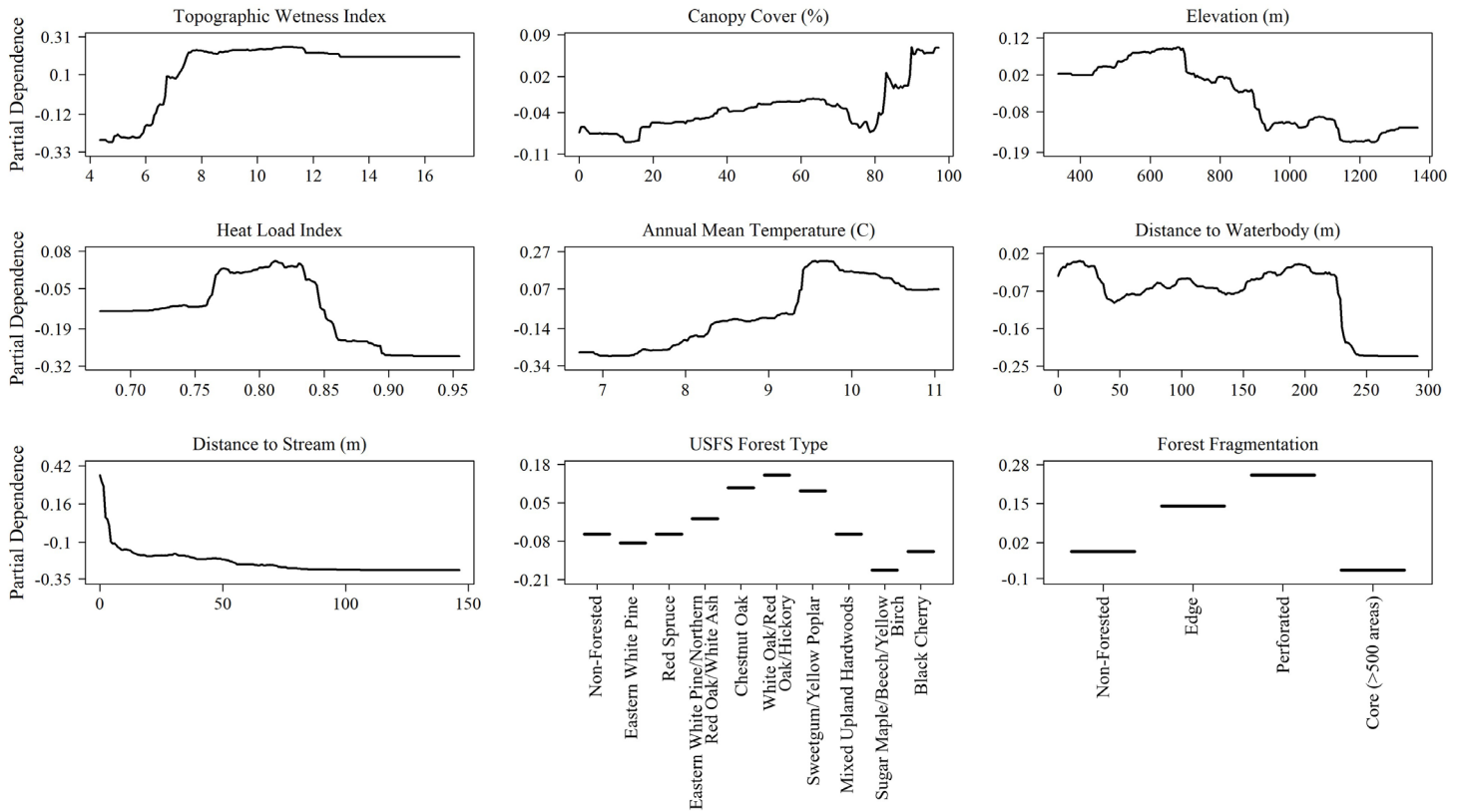


Figure 3. Partial dependence plots showing estimated relationships between the nine most influential environmental variables in a tricolored bat (*Perimyotis subflavus*) habitat suitability model for the Monongahela National Forest in West Virginia, and occurrence probability. These plots represent the marginal influence each variable on habitat suitability as predicted by the random forest model.

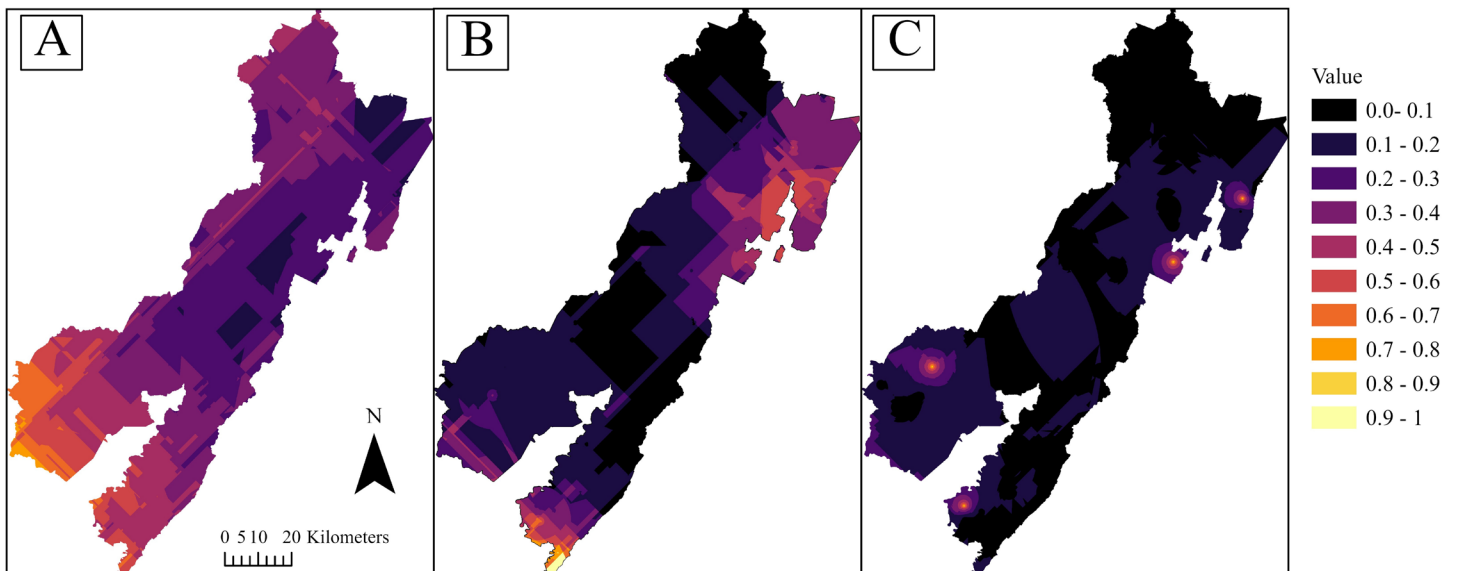


Figure 4. Distribution probability maps interpolated with indicator kriging for the tricolored bat (*Perimyotis subflavus*) in the Monongahela National Forest, West Virginia for three focal time periods: (a) pre-*Pseudogymnoascus destructans* (2003–2008), (b) the *Pseudogymnoascus destructans* invasion period (2011–2014), and (c) *Pseudogymnoascus destructans* endemic period (2015–2019).

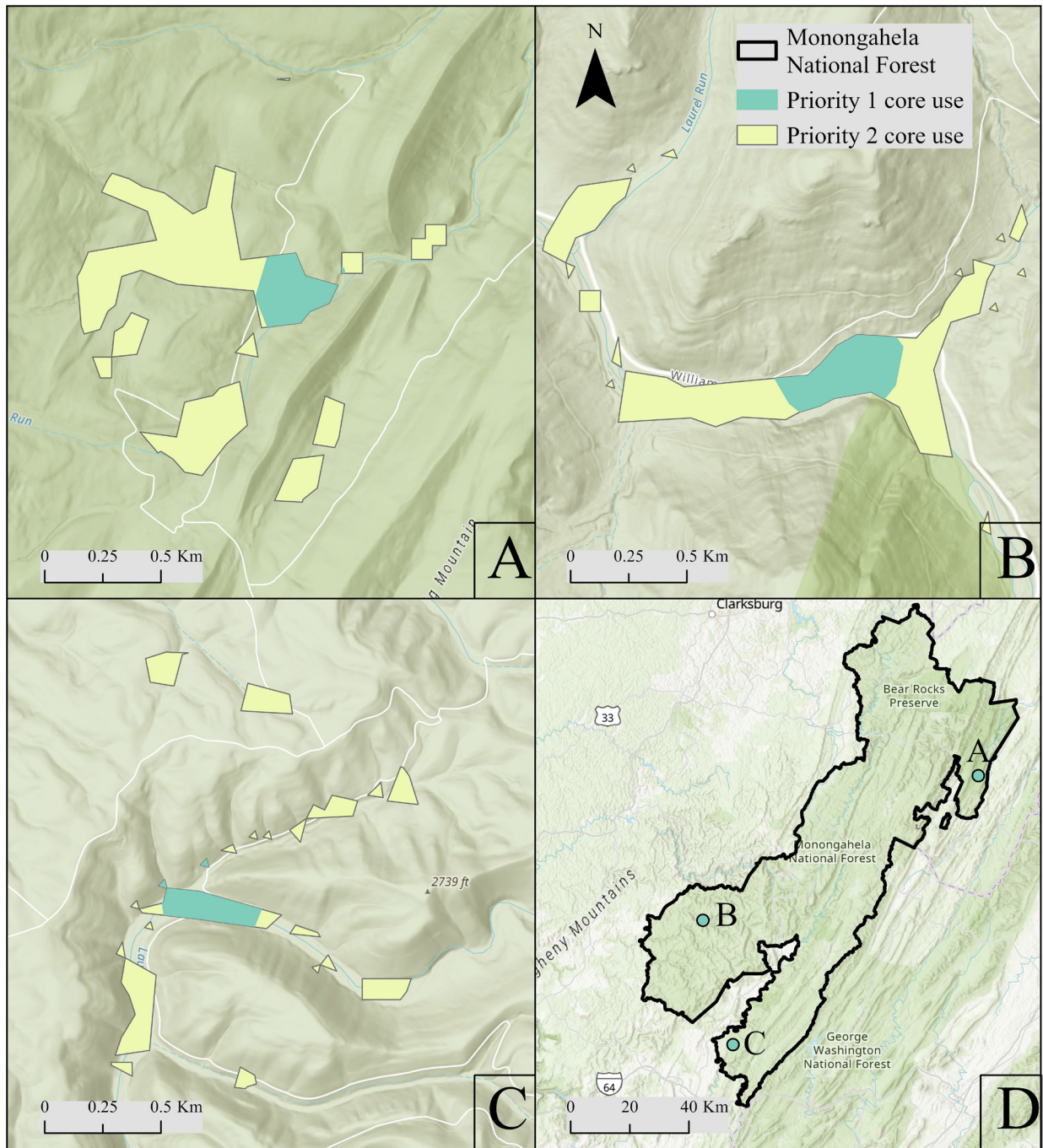


Figure 5. Priority 1 core use areas (indicated in green) and priority 2 core use areas (indicated in yellow) for tricolored bats (*Perimyotis subflavus*) in the Monongahela National Forest (MNF), West Virginia. See Methods for description of core use area definition procedures. Core use areas are located in (a) the northeastern MNF (b) the southwestern MNF, and (c) the southern MNF. Altogether, priority 2 core use habitats encompass 116.8 ha of the MNF and priority 1 core use areas encompass 22.2 ha of the MNF (d).

use habitat. We also identified a spatially distinct area of potential core use near 38°37'22.3896" N, 79°33'54.972" W. However, this area was not designated as a priority 1 or 2 core use area due to its small total size (1.98 ha) and high spatial fragmentation. The core use areas were located near Spruce Knob-Seneca Rocks Recreation Area (38°47' 44.9628" N, 79°19'20.9712" W), near

Laurel Fork (37°58'22.746" N, 80°17'33.972" W) and near the Williams River and town of Dyer (38°21'0.504" N, 80°23'53.6352" W; Figure 5). We estimate that during *Pd* endemic, there were 114.9 ha of priority 2 core use habitat within the MNF and 22.0 ha of priority 1 core use habitat. The largest contiguous priority 1 core use area was 10.5 ha, located near the Williams River and town of Dyer.

Discussion

We found that approximately 30% of the MNF represents moderate- or high-quality habitat for tricolored bats. Distance to stream and TWI were the most influential variables for habitat suitability, likely reflecting tricolored bat usage of riparian areas for foraging, drinking, and roosting (O’Keefe et al. 2013). Additionally, distance to lentic waterbody was a moderately influential variable, furthering reinforcing the strong relationship between insectivorous bats and water sources, and all three core use areas were located adjacent to a lentic waterbody. Previous studies have reported that tricolored bats select foraging ranges with more open water and wetlands (Thames 2020) and closer proximity to second- or third-order streams (Ford et al. 2005, Cox 2019). Further, roost selection is influenced by availability of water (Carpenter 2017, Quinn and Broders 2007) and adjacent stream density (Thames 2020). Likewise, the positive association with TWI is consistent with previous research that found increased foraging activity for this species in wetter areas (Allagas 2020). Our study underscores the important role that riparian zones play in ensuring the persistence of tricolored bat populations. Our finding that occurrence was higher at lower elevations is also consistent with previous studies (Ford et al. 2005, Carpenter 2017, Cox 2019).

The indicator kriging models estimated a substantial decline in spatial occurrence of tricolored bats on the MNF from pre-*Pd* (34.6%) to *Pd* endemic (10.2%), with no sign of a population recovery as of the *Pd* endemic time period. This is consistent with other studies that have monitored tricolored bat population trends after *Pd* invasion (e.g., Powers et al. 2015, Carpenter 2017, O’Keefe et al. 2019, Perea et al. 2022), although Perea et al. (2022) did note that populations stabilized at low densities. This species is widely distributed and can be found from Canada to Central America which makes it unlikely that this species will become extinct in the wild; however, tricolored bats have been extirpated from multiple locations in the eastern United States (USFWS 2021), and our indicator kriging models point to the possibility of extirpations occurring across the MNF.

Multiple metrics of model performance indicated that the HSM model performed well. However, several limiting factors of this study could reduce its potential applicability to real-world settings. Firstly, we developed the HSM using tricolored bat occurrence records from 2003–2008, which is the time period directly before *Pd* invasion in West Virginia. However, the remotely collected environmental variables used in the model were collected over several different time periods, with climatic data being averaged over a 30-year period (1970–2000), canopy cover being averaged over a 36-year period (1985–2021), forest type composition being collected from 2014–2018, and all remaining variables being estimated for

a single year from 2020–2023 (Table A1). The variables that were estimated based on a single year of data collection from 2020–2023 were incorporated in the model because they were the best available according to resolution, temporal, or data availability factors. Thus, there is a potential mismatch between the on-the-ground conditions present when the occurrence dataset was collected and the environmental data used to develop the HSM. Additionally, some of the data inputs (e.g., DEM, LANDFIRE’s existing vegetation cover) are derived from models themselves. Potential model-based uncertainties in the input data could compound into prediction errors in the HSM. Future analyses could benefit from incorporation of in-situ environmental data collection.

Several recent studies have suggested that maximizing pre-hibernation fat reserves and enhancing post-hibernation foraging opportunities could aid the recovery of bat species affected by WNS (Wilcox and Willis 2016, Johnson et al. 2021, Frick et al. 2023). Managing high-quality active-season habitat is one potential strategy for increasing fat accumulation. Therefore, we aimed to improve our understanding of the habitat characteristics associated with tricolored bat occurrence and to identify areas on the MNF where the species is comparatively more prevalent. Currently, there is a deficit of research exploring which active season management actions may have a positive effect on the individual health and population stability of bats. Strategies to increase insect abundance in core bat habitats may include habitat protection from development and riparian restoration (Harris 2018, Frick et al. 2023). Frick et al. (2023) found that using UV lights to lure calorie-rich moths to focal areas enhanced bat foraging opportunities. Additionally, Wilcox and Willis (2016) have suggested that the incorporation of artificially warmed bat houses during the spring and summer months could help *Pd*-infected bats overcome energetic immune costs associated with WNS. Future research is necessary to evaluate the efficacy of active season habitat management to improve survival rates for WNS-affected bats. The identified core use areas represent potential key locations for tracking population trends and testing efficacy of active habitat management actions.

For species and populations undergoing rapid declines due to novel diseases, the use of habitat-based approaches to estimate spatial distribution changes has limited value unless pathogen presence can be linked to specific habitat features. However, it is also difficult to accurately estimate spatial distributions using spatial interpolation models unless intensive systematic sampling occurs across the area of inference, and thus ground-truthing is needed to validate our predictions of contemporary core use areas in the MNF. In this study, we used a novel approach to identify post-decline core use areas that combined a pre-decline habitat-based model with post-decline interpolation models. This approach

assumes that tricolored bats are likely to have a greater probability of persistence in higher quality habitat while accounting for where the species has been observed post-decline. Our estimation approach could increase the potential utility of HSMs developed for other species that are undergoing rapid population declines.

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Literature Cited

- Allagas, P. L. 2020. Assessing the impact of restored wetlands on bat foraging activity over nearby farmland. Master's thesis, East Tennessee State University, Johnson City.
- Amorim, F., V. A. Mata, P. Beja, and H. Rebelo. 2015. Effects of a drought episode on the reproductive success of European free-tailed bats (*Tadarida teniotis*). *Mammalian Biology* 80:228–236.
- Barbet-Massin, M., J. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3:327–338.
- Bellamy, C. and J. Altringham. 2015. Predicting species distributions using record center data: multi-scale modeling of habitat suitability for bat roosts. *PLoS ONE* 10:e0128440.
- _____, C. Scott, and J. Altringham. 2013. Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. *Journal of Applied Ecology* 50:892–901.
- Beven, K. J. and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin* 24:43–69.
- Boiko, O., S. Kagone, and G. B. Senay. 2021. Soil properties dataset in the United States: U.S. Geological Survey data release. <<https://doi.org/10.5066/P9TI3IS8>>. Accessed 1 October 2025.
- Breiman, L. 1996. Bagging predictors. *Machine Learning* 24:123–140.
- _____. 2001. Random forests. *Machine Learning* 45:5–32.
- Cable A. B. and E. V. Willcox. 2024. Summer habitat for the female tricolored bat (*Perimyotis subflavus*) in Tennessee, United States. *Journal of Mammalogy* 105:667–678.
- Carpenter, G. M. 2017. Bat population status and roost selection of tri-colored bats in the Great Smoky Mountains National Park in the era of white-nose syndrome. Master's thesis, University of Tennessee, Knoxville.
- Chai, T. and R. R. Draxler. 2014. Root mean square error (RMSE) or mean absolute error (MAE). *Geoscientific Model Development Discussions* 7:1525–1534.
- Cheng, T. L., A. Gerson, M. S. Moore, J. D. Reichard, J. DeSimone, C. K. Willis, W. F. Frick, and A. M. Kilpatrick. 2019. Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. *Journal of Animal Ecology* 88:591–600.
- _____, H. Mayberry, L. P. McGuire, J. R. Hoyt, K. E. Langwig, H. Nguyen, K. L. Parise, J. T. Foster, C. K. R. Willis, A. M. Kilpatrick, and W. F. Frick. 2017. Efficacy of a probiotic bacterium to treat bats affected by the disease white-nose syndrome. *Journal of Applied Ecology* 54:701–708.
- _____, J. D. Reichard, J. T. H. Coleman, T. J. Weller, W. E. Thogmartin, B. E. Reichert, A. B. Bennett, H. G. Broders, J. Campbell, K. Etchison, D. J. Feller, R. Geboy, T. Hemberger, C. Herzog, A. C. Hicks, S. Houghton, J. Humber, J. A. Kath, R. A. King, S. C. Loeb, A. Massé, K. M. Morris, H. Niederriter, G. Nordquist, R. W. Perry, R. J. Reynolds, D. B. Sasse, M. R. Scafani, R. C. Stark, C. W. Stihler, S. C. Thomas, G. G. Turner, S. Webb, B. J. Westrich, and W. F. Frick. 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology* 35:1586–1597.
- Coulston, J. W., D. M. Jacobs, C. R. King, and I. C. Elmore. 2013. The influence of multi-season imagery on models of canopy cover: a case study. *Photogrammetric Engineering & Remote Sensing* 79:469–477.
- _____, G. G. Moisen, B. T. Wilson, M. V. Finco, W. B. Cohen, and C. K. Brewer. 2012. Modeling percent tree canopy cover: a pilot study. *Photogrammetric Engineering & Remote Sensing* 78:715–727.
- Cox, J. H. 2019. Using species distribution models and connectivity analyses to predict habitat suitability for three bat species. Master's thesis, Indiana State University, Terre Haute.
- Cryan, P. M., C. U. Meteyer, J. G. Boyles, and D. S. Blehert. 2010. Wing pathology of white-nose syndrome in bats suggests life-threatening disruption of physiology. *BMC Biology* 8:135.
- Cutler, D. R., T. C. Edwards, K. H. Beard Jr., A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. *Ecology* 88:2783–2792.
- De La Cruz, J. L., W. M. Ford, S. Jones, J. B. Johnson, and A. Silvis. 2023. Distribution of northern long-eared bat summer habitat on the Monongahela National Forest, West Virginia. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 10:114–124.
- Earth Resources Observation and Science (EROS) Center. 2020. Landsat 8-9 Operational Land Imager / Thermal Infrared Sensor Level-1, Collection 2 [dataset]. U.S. Geological Survey. <<https://doi.org/10.5066/P975CC9B>>. Accessed 1 January 2023.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudik, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43–57.
- Evans, J. S. and M. A. Murphy. 2023. spatialEco. R package version 2.0-2. Environmental Research Systems Institute (ESRI). 2021. ArcGIS Desktop Version 10.8.2. Redlands, California.
- _____. 2023. ArcGIS Pro Version 3.1.2. Redlands, California.
- Fick, S. E. and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatol-*
- Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian Forest. *Biological Conservation* 126:528–539.
- Francl, K. E., W. M. Ford, D. W. Sparks, and V. Brack Jr. 2012. Capture and reproductive trends in summer bat communities in West Virginia: assessing the impact of white-nose syndrome. *Journal of Fish and Wildlife Management* 3:33–42.
- Frick, W. F., Y. A. Dzal, K. A. Jonasson, M. D. Whitby, A. M. Adams, C. Long, J. E. Depue, C. M. Newman, C. K. R. Willis, and T. L. Cheng. 2023. Bats increased foraging activity at experimental prey patches near hibernacula. *Ecological Solutions and Evidence* 4:e12217.
- Friedman, J. H. 2001. Greedy function approximation: a gradient boosting machine. *Annals of Statistics* 29:1189–1232.
- Gao, B. C. 1996. NDWI - A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment* 58:257–266.

- Gaulke, S. M., A. B. Cable, T. C. Hohoff, B. A. Rogness, and M. A. Davis. 2023. One model to rule them all: identifying priority bat habitats from multi-species habitat suitability models. *Journal of Wildlife Management* 87:e22351.
- Geiser, F. 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Review of Physiology* 66:239–274.
- Glacken, I. and P. Blackney. 1998. A practitioner's implementation of indicator kriging. Pages 26–39 in *Proceedings of a One Day symposium: Beyond Ordinary Kriging*. Geostatistical Association of Australasia. Perth, Australia.
- Guyon, I., J. Weston, S. Barnhill, and V. Vapni. 2002. Gene selection for cancer classification using Support Vector Machines. *Machine Learning* 46:389–422.
- Haase, C. G., N. W. Fuller, Y. A. Dzal, C. R. Hranac, D. T. Hayman, C. L. Lausen, K. A. Silas, S. H. Olson, and R. K. Plowright. 2021. Body mass and hibernation microclimate may predict bat susceptibility to white-nose syndrome. *Ecology and Evolution* 11:506–515.
- Hammesfahr, A., C. C. Rega-Brotsky, K. Womack-Bulliner, and J. Whitney. 2022. Roost characteristics of a tricolored bat *Perimyotis subflavus* in the Missouri Ozarks. *Transactions of the Kansas Academy of Science* 125:159–164.
- Harris, M. T. 2018. Potential benefits of restored riparian zones in an agricultural matrix for bat communities. Master's thesis, James Madison University, Harrisonburg, Virginia.
- Hoyt, J. R., A. M. Kilpatrick, and K. E. Langwig. 2021. Ecology and impacts of white-nose syndrome on bats. *Nature Reviews* 19:196–210.
- Ingersoll, T. E., B. J. Sewall, and S. K. Amelon. 2016. Effects of white-nose syndrome on regional population patterns of 3 hibernating bat species. *Conservation Biology* 30:1048–1059.
- Iturbide, M., J. Bedia, S. Herrera, O. del Hierro, M. Pinto, and J. M. Gutiérrez. 2015. A framework for species distribution modelling with improved pseudo-absence generation. *Ecological Modelling* 312:166–174.
- Iverson, L. R. and A. M. Prasad. 2003. A GIS-derived integrated moisture index. U.S. Forest Service General Technical Report NE-299. Newton Square, Pennsylvania.
- Jarnevich, C. S., T. R. Holcombe, B. A. Grisham, J. Timmer, C. W. Boal, M. J. Butler, J. Pitman, S. C. Kyle, D. Klute, G. M. Beauprez, A. Janus, and W. E. Van Pelt. 2016. Assessing range-wide habitat suitability for the lesser prairie-chicken. *Avian Conservation and Ecology* 11:2.
- Johnson, C., D. J. Brown, C. Sanders, and C. W. Stihler. 2021. Long-term changes in occurrence, relative abundance, and reproductive fitness of bat species in relation to arrival of White-nose Syndrome in West Virginia, USA. *Ecology and Evolution* 11:12453–12467.
- Johnston, K., J. M. Ver Hoef, K. Krivoruchko, and N. Lucas. 2001. Using ArcGIS geostatistical analyst. Environmental Systems Research Institute, Redlands, California.
- LANDFIRE. 2020a. Digital Elevation Model layer. LANDFIRE 2.2.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. <<https://www.landfire.gov/data>>. Accessed 1 January 2023.
- _____. 2020b. Existing Vegetation Cover layer. LANDFIRE 2.2.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. <<https://www.landfire.gov/data>>. Accessed 1 January 2023.
- _____. 2020c. Existing Vegetation Height layer. LANDFIRE 2.2.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. <<https://www.landfire.gov/data>>. Accessed 1 January 2023.
- Loeb, S. C. and E. A. Winters. 2022. Changes in hibernating tricolored bat (*Perimyotis subflavus*) roosting behavior in response to white-nose syndrome. *Ecology and Evolution* 12:e9045.
- Lorch, J. M., C. U. Meteyer, M. J. Behr, J. G. Boyles, P. M. Cryan, A. C. Hicks, A. E. Ballmann, J. T. Coleman, D. N. Redell, D. M. Reeder, and D. S. Blehert. 2011. Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. *Nature* 480:376–378.
- McCune, B. and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13:603–606.
- Meierhofer, M. B., S. J. Leivers, R. R. Fern, L. K. Wolf, J. H. Young Jr., B. L. Pierce, J. W. Evans, and M. L. Morrison. 2019. Structural and environmental predictors of presence and abundance of tri-colored bats in Texas culverts. *Journal of Mammalogy* 100:1274–1281.
- Menzel, J. M., A. M. Menzel, J. C. Kilgo, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005. Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *Journal of Wildlife Management* 69:235–245.
- O'Keefe, J. M. 2009. Roosting and foraging ecology of forest bats in the southern Appalachian Mountains. Doctoral dissertation, Clemson University, South Carolina.
- _____, S. C. Loeb, P. D. Gerard, and J. D. Lanham. 2013. Effects of riparian buffer width on activity and detection of common bats in the southern Appalachian Mountains. *Wildlife Society Bulletin* 37:319–326.
- _____, J. L. Pettit, S. C. Loeb, and W. H. Stiver. 2019. White-nose syndrome dramatically altered the summer bat assemblage in a temperate southern Appalachian Forest. *Mammalian Biology* 98:146–153.
- Perea, S., J. A. Yearout, E. A. Ferrall, K. M. Morris, J. T. Pynne, and S. B. Castleberry. 2022. Seven-year impact of white-nose syndrome on tri-colored bat (*Perimyotis subflavus*) populations in Georgia, USA. *Endangered Species Research* 48:99–106.
- Perry, R. W. and P. N. Jordan. 2022. Changes in the forest bat community after arrival of white-nose syndrome in the Ouachita Mountains of Arkansas. *Southeastern Naturalist* 21:107–115.
- _____, and R. E. Thill. 2007. Tree roosting by male and female eastern pipistrelles in a forested landscape. *Journal of Mammalogy* 88:974–981.
- Poissant, J. A., H. G. Broders, and G. M. Quinn. 2010. Use of lichen as a roosting substrate by *Perimyotis subflavus*, the tricolored bat, in Nova Scotia. *Ecoscience* 17:372–378.
- Powers, K. E., R. J. Reynolds, W. Orndorff, W. M. Ford, and C. S. Hobson. 2015. Post-white-nose syndrome trends in Virginia's cave bats, 2008–2013. *Journal of Ecology and the Natural Environment* 7:113–123.
- Quinn, G. M. and H. G. Broders. 2007. Roosting and foraging ecology of eastern pipistrelle (*Perimyotis subflavus*) bats in SW Nova Scotia. Report to Nova Scotia Habitat Conservation Fund, Nova Scotia Department of Natural Resources and Renewables, Kentville.
- R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reeder, D. M., C. L. Frank, G. G. Turner, C. U. Meteyer, A. Kurta, E. R. Britzke, M. E. Vodzak, S. R. Darling, C. W. Stihler, A. C. Hicks, R. Jacob, L. E. Grieneisen, S. A. Brownlee, L. K. Muller, and D. S. Blehert. 2012. Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *PLoS ONE* 7:e38920.
- Rosales, E. 2024. Tri-colored bat habitat use and selection in northwestern South Carolina. Master's thesis, Clemson University, South Carolina.
- Ruefenacht, B., M. V. Finco, M. D. Nelson, R. Czaplowski, E. H. Helmer, J. A. Blackard, J. R. Holden, A. J. Lister, D. Salajanu, D. Weyermann, and K. Winterberger. 2008. Conterminous U.S. and Alaska forest type mapping using Forest Inventory and Analysis. *Photogrammetric Engineering & Remote Sensing* 74:1379–1388.
- Scherrer, D., P. Christe, and A. Guisan. 2019. Modeling bat distributions and diversity in a mountain landscape using focal predictors in ensemble of small models. *Diversity and Distributions* 25:770–782.
- Sewall, B. J., G. G. Turner, M. R. Scafani, M. F. Gagnon, J. S. Johnson, M. K. Keel, E. Anis, T. M. Lilley, J. P. White, C. L. Hauer, and B. E. Overton. 2023. Environmental control reduces white-nose syndrome infection in hibernating bats. *Animal Conservation* 26:642–653.

- Shute, K. E., S. C. Loeb, and D. S. Jachowski. 2021. Summer roosting ecology of the northern yellow bat and tri-colored bat in coastal South Carolina. *Southeastern Naturalist* 20:459–476.
- Silvis, A., R. Perry, and W. M. Ford. 2016. Relationships of three species of bats impacted by white-nose syndrome to forest condition and management. U.S. Forest Service General Technical Report SRS-214. Asheville, North Carolina.
- Sørensen, R., U. Zinko, and J. Seibert. 2006. On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth System Sciences* 10:101–112.
- Stevens, R. D., C. J. Garcia, E. E. Bohlender, and B. B. Gregory. 2017. Distributional updates and conservation status of bats from Louisiana. *Museum of Texas Tech University* 348:1–12.
- Strager, M. P. and A. E. Maxwell. 2020. Forest fragmentation of WV (2020). Natural Resource Analysis Center, West Virginia University, Morgantown. <<https://wvgis.wvu.edu/data/dataset.php?ID=453>>. Accessed 1 October 2025.
- Thames, D. B. 2020. Summer foraging range and diurnal roost selection of tri-colored bats, *Perimyotis subflavus*. Master's thesis. University of Tennessee, Knoxville.
- Turner, G. G., B. J. Sewall, M. R. Scafani, T. M. Lilley, D. Bitz, and J. S. Johnson. 2022. Cooling of bat hibernacula to mitigate white-nose syndrome. *Conservation Biology* 36:e13803.
- U.S. Fish and Wildlife Service (USFWS). 2021. Species status assessment report for the tricolored bat (*Perimyotis subflavus*), Version 1.1. Hadley, Massachusetts.
- _____. 2022. Endangered and threatened wildlife and plants; endangered species status for tricolored bat. *Federal Register* 87:56381–56393.
- U.S. Forest Service (USFS). 2011. Monongahela National Forest: land and resource management plan. Newtown Square, Pennsylvania.
- _____. 2023. Forest Inventory and Analysis National Core Field Guide, version 9.3. Volume I: Field data collection procedures for Phase 2 plots. Washington, D.C.
- U.S. Geological Survey (USGS). 2023. National Hydrography Dataset. <<http://nhd.usgs.gov>>. Accessed 24 March 2026.
- Valavi, R., J. Elith, J. J. Lahoz-Monfort, and G. Guillera-Arroita. 2021. Modeling species presence-only data with random forests. *Ecography* 44:1731–1742.
- _____, G. Guillera-Arroita, J. J. Lahoz-Monfort, and J. Elith. 2022. Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs* 92:e01486.
- Veilleux, J. P., J. O. Whitaker, S. L. Veilleux. 2003. Tree-roosting ecology of reproductive female eastern pipistrelles, *Perimyotis subflavus*, in Indiana. *Journal of Mammalogy* 84:1068–1075.
- Verant, M. L., C. U. Meteyer, J. R. Speakman, P. M. Cryan, J. M. Lorch, and D. S. Blehert. 2014. White-nose syndrome initiates a cascade of physiological disturbances in the hibernating bat host. *BMC Physiology* 14:10.
- Wilcox, A. and C. K. R. Willis. 2016. Energetic benefits of enhanced summer roosting habitat for little brown bats (*Myotis lucifugus*) recovering from white-nose syndrome. *Conservation Physiology* 4:cov070.
- Yates, M. D. and R. M. Muzika. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management* 70:1238–1248.

Appendix A

Table A1. Candidate environmental variables for explaining variability in summer habitat suitability for tricolored bats (*Perimyotis subflavus*) in the Monongahela National Forest (MNF), West Virginia. Variables were selected based on a literature review of tricolored bat habitat preferences. DEM = digital elevation model; NHD = National Hydrography Dataset; USFS = U.S. Forest Service; USGS = U.S. Geological Survey. An asterisk (*) following the variable name indicates that this variable was included in the final random forest model based on recursive feature elimination.

Variable	Description (Resolution)	Data Source (Author)	Year(s)	Literature Support
Annual mean temperature*	Annual mean temperature for 1970–2000 (30 arc-seconds [$\sim 1 \times 1$ km])	WorldClim database (Fick and Hijmans 2017)	1970–2000	Yates and Muzika 2006, Meierhofer et al. 2019, Scherrer et al. 2019, Gaulke et al. 2023
Annual precipitation	Annual precipitation for 1970–2000 (30 arc-seconds [$\sim 1 \times 1$ km])	WorldClim database (Fick and Hijmans 2017)	1970–2000	Shute et al. 2021
Canopy cover*	Percent tree canopy estimates (30 $\times$ 30 m)	National Land Cover Database (USGS)	1985–2021	Ford et al. 2005, Menzel et al. 2005, Yates and Muzika 2006, Scherrer et al. 2019, Shute et al. 2021, Hammesfahr et al. 2022, Gaulke et al. 2023
Distance to lentic waterbody*	Distance (m) from survey sites to nearest lentic water body polygon (1:24,000)	National Hydrography Dataset (USGS)	2023	Ford et al. 2005, Menzel et al. 2005, O'Keefe et al. 2009, Poissant et al. 2010, Bellamy et al. 2013, Bellamy and Altringham 2015, Scherrer et al. 2019
Distance to stream*	Distance (m) from survey sites to nearest stream polyline (1:24,000)	National Hydrography Dataset (USGS)	2023	Ford et al. 2005, Menzel et al. 2005, O'Keefe et al. 2009, Poissant et al. 2010, Bellamy et al. 2013, Bellamy and Altringham 2015, Scherrer et al. 2019
Elevation*	Raster created using DEM tiles (1 arc-second [$\sim 30 \times 30$ m])	LANDFIRE (USGS)	2020	Ford et al. 2005, O'Keefe et al. 2009, Meierhofer et al. 2019,
Existing vegetation cover	Raster of vertically projected canopy cover (30 $\times$ 30 m)	LANDFIRE (USGS)	2020	Yates and Muzika 2006, O'Keefe et al. 2009, Bellamy et al. 2013, Shute et al. 2021, Gaulke et al. 2023
Existing vegetation height	Raster representing average height of dominant vegetation (30 $\times$ 30 m)	LANDFIRE (USGS)	2020	Ford et al. 2005, Menzel et al. 2005, Yates and Muzika 2006, Perry and Thill 2007, O'Keefe et al. 2009, Bellamy et al. 2013, Gaulke et al. 2023
Forest fragmentation*	Forest fragmentation classified as patch, edge, perforated, small core (<101 ha), medium-sized core (101–202 ha), large core (>202 ha), and non-forested (9 $\times$ 9 m)	National Agricultural Imagery Program Forest Fragmentation of West Virginia (Strager and Maxwell 2020)	2020	Ford et al. 2005, O'Keefe et al. 2009, Bellamy et al. 2013, Bellamy and Altringham 2015, Scherrer et al. 2019, Hammesfahr et al. 2022
Heat load index	Heat accumulation in a specific area estimated using slope, aspect, and latitude. Calculated using DEM (1 arc-second [$\sim 30 \times 30$ m])	LANDFIRE (USGS)	2020	Veilleux et al. 2003, Meierhofer et al. 2019
Integrated moisture index (IMI)	Relative rating of moisture derived from hillshade, curvature, flow accumulation, and soil water capacity. Calculated using DEM (1 arc-second [$\sim 30 \times 30$ m]) and soil water capacity layer (resolution = 150 $\times$ 150 m)	LANDFIRE (USGS) and Soil properties dataset in the United States: U.S. Geological Survey data release (Boiko et al. 2021)	2020	Gaulke et al. 2023
Normalized difference moisture index	Moisture content in vegetation and soil calculated by quantifying the difference in near infrared and shortwave infrared reflectance. Calculated with satellite or aerial imagery (30 $\times$ 30 m)	Landsat data (USGS)	2020	Amorim et al. 2015
Normalized difference vegetation index	Quantification of vegetation greenness and therefore, vegetation health. Calculated with satellite or aerial imagery (30 $\times$ 30 m)	Landsat data (USGS)	2020	Meierhofer et al. 2019
Slope degree	Change in elevation over an area; calculated using DEM (resolution = 1 arc-second [$\sim 30 \times 30$ m])	LANDFIRE (USGS)	2020	Veilleux et al. 2003, Scherrer et al. 2019
Topographic Wetness Index (TWI)*	Metric of relative wetness of a point on a landscape; calculated from upslope contributing area and local slope. Calculated using DEM (resolution = 1 arc-second [$\sim 30 \times 30$ m])	LANDFIRE (USGS)	2020	Allagas 2020
Total basal area	Metric of density of a stand of trees (resolution $\sim 250 \times 250$ m)	Forest Inventory and Analysis Program (USFS)	2023	O'Keefe et al. 2009, Shute et al. 2021, Gaulke et al. 2023
Total quadratic mean diameter	Metric of average tree diameter (resolution $\sim 250 \times 250$ m)	Forest Inventory and Analysis Program (USFS)	2023	Perry and Thill 2007, O'Keefe et al. 2009, Shute et al. 2021, Gaulke et al. 2023
Total stand density index	Metric of density of a stand of trees (resolution $\sim 250 \times 250$ m)	Forest Inventory and Analysis Program (USFS)	2023	Perry and Thill 2007, O'Keefe et al. 2009, Gaulke et al. 2023
Tree frequency	Metric of frequency of occurrence of trees in an area (resolution $\sim 250 \times 250$ m)	Forest Inventory and Analysis Program (USFS)	2023	Menzel et al. 2005, Gaulke et al. 2023
Trees per acre	Metric of tree density per acre (resolution $\sim 250 \times 250$ m)	Forest Inventory and Analysis Program (USFS)	2023	Menzel et al. 2005, Gaulke et al. 2023
USFS forest type*	Forest type composition (resolution = 250 $\times$ 250 m)	National Forest Type Dataset (USFS Geospatial Technology and Applications Center)	2014–2018	Veilleux et al. 2003, Ford et al. 2005, Menzel et al. 2005, Perry and Thill 2007, O'Keefe et al. 2009, Poissant et al. 2010, Scherrer et al. 2019, Shute et al. 2021, Gaulke et al. 2023