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Bats of the Monongahela National Forest

by

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Thesis

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Ecology and Organismal Biology

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Ypsilanti, Michigan

APPROVAL

BATS OF THE MONONGAHELA NATIONAL FOREST

By

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APPROVED

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DEDICATION

This thesis is dedicated to my wife, Kristi, who provides me with continuous love and support. Thank you.

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My thesis would not have been possible without the enduring support of my thesis advisor, Dr. Allen Kurta; I thank you for all your knowledge, wisdom, and advice. I am also grateful to my thesis committee members, Dr. Katherine Greenwald and Dr. Steve Francoeur, for their time and assistance. I am indebted to Chris Sanders, for piquing my interest in bats and whose company, Sanders Environmental, Inc., was responsible for collecting the mist-netting data. I thank Cathy Johnson and other personnel of the Monongahela National Forest, for their commitment to the protection of bats and for allowing me to use the netting and spatial data, as well as the West Virginia Department of Natural Resources, for providing information on caves in that state. Finally, I express my gratitude to my family, for love and guidance throughout my life.

ABSTRACT

Populations of bats across the eastern United States have experienced significant declines in recent years. Insight into their distributions and habitat associations, as well as understanding population trends, will aid in conservation efforts. In this study, the geographic distributions of the 10 species of bats found in the Monongahela National Forest of West Virginia were analyzed, using maximum entropy modeling and mist-netting data from 1997 through 2012. Forest type, hydrologic features, elevation, land-cover type, and distance to caves were typically the most important explanatory variables within these models, although results varied among species. By understanding these foraging habitat associations and locations of bats, forest personnel will be able to use these localized data to guide their management decisions. Trends in species diversity and abundance also were examined. Species diversity remained mostly stable and although not significant, a decline in abundance over time indicated decreases in some populations of bats, particularly by those species affected by white-nose syndrome.

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INTRODUCTION

Ecosystem management and the National Forest System.—The decline of biodiversity across the globe has become a central concern in the field of conservation biology (Caughley, 1994). To combat this loss of biodiversity, many scientists and public land managers have implemented “ecosystem management” as a new approach to the management of natural resources (Butler and Koontz, 2005). Although many definitions exist, Grumbine (1994:31) defined the main goal of ecosystem management as the integration of “scientific knowledge of ecological relationships within a complex sociopolitical and values framework toward the general goal of protecting native ecosystem integrity over the long term.” Grumbine (1994:31) also listed 10 objectives of ecosystem management, including interagency cooperation, data collection, ecological integrity, adaptive management, and monitoring.

In June 1992, the U.S. Forest Service (USFS) became the first federal agency officially to adopt an ecosystem approach for the management of national lands (Robertson, 1992). The National Forest System includes over 93 million hectares throughout the United States and its territories; these lands represent a significant refuge for wildlife and are vital for maintaining biodiversity in the United States. Under this ecosystem approach, the U.S. Forest Service has the responsibility of managing healthy ecosystems, including conservation of threatened and endangered species and their habitats, and maintaining biodiversity throughout the National Forest System. Because the integration of scientific knowledge is at the core of ecosystem management, these goals are impossible to meet without sound science-based field work.

Current status of and threats to bats.—The order Chiroptera (meaning “hand-wing”) contains about one quarter of all known species of mammals. Worldwide, bats provide valuable ecosystem services for humans by pollinating plants, dispersing seeds, and controlling populations of insects (Kunz et al., 2011). In the United States, insectivorous bats are vitally important to the ecological and economic health of the nation, because they consume large quantities of nocturnal insects, many of which are forest and agricultural pests. The economic value of bats to American agriculture, for example, is estimated at $23 billion annually (Boyles et al., 2011). Until recently, the ecological and economic importance of bats has been largely ignored, and management activities typically have been lacking at the state and federal level.

Of the estimated 1,200 species of bats, almost half are considered threatened or near-threatened by the International Union for the Conservation of Nature and Natural Resources (Hutson et al., 2001). Globally, populations of bats are thought to have declined markedly over the past 50–100 years (Stebbings, 1988). Bats in North America have likely followed a similar path, with many species of bats in the United States experiencing range reductions and declines in populations (Hutson et al., 2001; Oshea and Bogan, 2003). For instance, range contractions have been noted for the Ozark big-eared bat (*Corynorhinus townsendii ingens*—Hensley and Scott, 1995), and populations of Indiana bats (*Myotis sodalis*) have decreased by 57% since the 1960s (Clawson, 2002), with the gray bat (*M. grisescens*) showing similar declines (Rabinowitz and Tuttle, 1980).

Until recently, destruction of habitat was likely the largest threat to North American bats. Bats use wooded areas for roosting and feeding, and disturbances to the forest can have serious impacts (Barclay and Kurta, 2007; Lacki et al., 2007). Furthermore, modification of openings to caves that offer commercial tours have prevented entry by bats to historic roosting sites or have changed internal thermal regimes so that ambient conditions are no longer acceptable (Currie, 2002). Many bats have adopted abandoned mines as maternity roosts in warm climates and as hibernation sites over much of North America, but permanent sealing of these sites or even the resumption of mining activity can also cause significant mortality (Tuttle and Taylor, 1998).

The newest threats to bats—white-nose syndrome and wind power—transcend the traditional hazards to bats and pose significant difficulties for conservation. White-nose syndrome is caused by a fungus, *Pseudogymnoascus destructans*, that affects cave-obligate species during hibernation (Verant et al., 2014). White-nose syndrome (WNS) was first reported in upstate New York during winter 2006–2007 and has since spread to 28 U.S. states and five Canadian provinces (Heffernan, 2016). Confirmed instances of white-nose syndrome are currently concentrated in the Appalachian Mountains; however, an environmental and climatic model indicates that WNS will spread to coastal areas in the Northeast, the Mississippi basin, and the Rocky Mountains (Alves et al., 2014). Another model indicates greater spread and impacts to more species than predicted by Alves et al. (2014), forecasting that most caves within the contiguous United States will be infested by early next century (Maher et al., 2012). Estimates of mortality of hibernating bats, 2 years after infection by the fungus, vary from 69 to 98%, depending on state and species (Turner et al., 2011).

Mortality of bats at wind turbines, through collisions or barotrauma (Baerwald et al., 2008), is also a recently noticed phenomenon. These deaths received little attention until 2003 when Kerns and Kerlinger (2003) reported an estimated 1,400–4,000 fatalities of bats at the Mountaineer Wind Energy Center in West Virginia. Estimates of annual mortality in the eastern United States currently range from 20.8 to 69.6 bats per turbine, with migratory species such as the hoary bat (*Lasiurus cinereus*), eastern red bat (*L. borealis*), and silver-haired bat (*Lasionycteris noctivagans*) being killed most often (Arnett et al., 2008). In the contiguous United States, an estimated 600,000 bats per year die at wind-energy developments (Hayes, 2013), and turbines in the Mid-Atlantic Highlands alone will kill an estimated 33,000–111,000 bats annually by the year 2020 (Kunz et al., 2007). Habitat destruction, modification of caves, sealing of mines, white-nose syndrome, and the ever-increasing construction of wind-power facilities have put bats in serious jeopardy, and conservation action is necessary if populations are to survive and ultimately recover.

The Monongahela National Forest.—West Virginia has some of the most extensive oak-hickory forests in the eastern United States, with an estimated 5 million ha of potential bat habitat (Johnson and Strickland, 2003). The Monongahela National Forest is located in the eastern highlands of West Virginia, in the central Appalachian Mountains, and consists of over 371,000 ha of land that is considered by the Nature Conservancy to be in an area of global ecological importance (U.S. Forest Service, 2006). The forest is a significant refuge for bats due to its concentration of suitable summer habitat and proximity to hibernacula. Nevertheless, most of the Monongahela National Forest occurs in areas now infected with white-nose syndrome (Heffernan, 2016). In addition, ridge tops in the central Appalachian Mountains are sites of consistently strong winds; consequently, bats in the Monongahela National Forest are potentially threatened by wind farms that are being constructed in many nearby areas of West Virginia.

Species of bat known to occur on the Monongahela National Forest include the big brown bat (*Eptesicus fuscus*), eastern red bat, eastern small-footed bat (*M. leibii*), hoary bat, Indiana bat, little brown bat (*M. lucifugus*), northern long-eared bat (*M. septentrionalis*), silver-haired bat, tricolored bat (*Perimyotis subflavus*), and Virginia big-eared bat (*Corynorhinus townsendii virginianus*). The Indiana bat and the Virginia big-eared bat are listed as endangered under the Federal Endangered Species Act of 1973, and the northern long-eared bat is considered threatened (U.S. Fish and Wildlife Service, 2007, 2008, 2015). Furthermore, the little brown bat, eastern small-footed bat, and tricolored bat are classified as Regional Forester Sensitive Species, which are species identified by wildlife biologists as having questionable long-term viability within a particular national forest (U.S. Forest Service, 2006).

The presence of endangered species and the threats posed by white-nose syndrome and wind turbines have increased interest in conservation of bats by the U.S. Forest Service (Szymanski et al., 2009). For conservation action to succeed, it is important to determine the current diversity and abundance of bats and understand past population fluctuations to establish base-line data for managers.

Continued declines of some bats, such as the Indiana bat, despite protection of hibernacula, suggest that preservation of summer habitat may be critical for the protection of many species (Clawson, 2002; O'Shea and Clark, 2002; O'Shea and Bogan, 2003). Of the various types of summer habitat, roosting habitats have been analyzed in more detail and in more areas (e.g., Butchkoski and Hassinger, 2002; Foster and Kurta, 1999; Johnson et al., 2009; Sherwin et al., 2000) than foraging habitat.

Protection of habitat for bats is the primary conservation action undertaken by the U.S. Forest Service. However, optimization of management strategies requires localized knowledge of ecological variables associated with utilization of landscape features by bats. Although a few, isolated studies addressing the ecology of bats in the Northeast have been conducted (e.g., Butchkoski and Hassinger, 2002; Carter et al., 2003; Ford et al., 2005; Johnson et al., 2009, 2012; Timpone et al., 2011), many unanswered questions remain.

Previous research on bats in the central Appalachian Mountains.—Previous research on bats, specifically in the central Appalachian Mountains, is limited and has focused primarily on rare and endangered species. For example, roosting studies have been conducted on northern bats

(Menzel et al., 2002; Ford et al., 2006; J. B Johnson et al., 2012), small-footed bats (Johnson et al., 2011), and Indiana bats (Ford et al., 2002; Johnson et al., 2010). Food habits of Virginia big-eared bats in West Virginia were analyzed, and intraspecific variation was found between colonies in frequency and volume of prey consumed, which was correlated with density of available prey in the interior of the forest (Sample and Whitmore, 1993). Dietary analyses in Pennsylvania and western Maryland found that temporal and spatial factors influence intraspecific variation in diet of big brown bats (Agosta and Morton, 2003). Analysis of feces from small-footed bats in West Virginia revealed a diverse diet, with Lepidoptera being most common (Johnson and Gates, 2007; Johnson et al., 2012). The distribution of reproductive females along an elevational gradient was inversely related to elevation for the tricolored bat and red bat in West Virginia and big brown bat in Pennsylvania (Brack et al., 2002).

Foraging studies in West Virginia have attempted to relate simple measures of habitat, including proximity to riparian areas, canopy cover, width of canopy gaps, and height of the canopy, to presence of various species and were moderately successful. Ford et al. (2005), for example, found that the little brown bat, Indiana bat, silver-haired bat, and tricolored bat were associated more often with wetland and riparian areas than upland areas in the central Appalachians; other studies have found similar results (Castleberry et al., 2004; Owens et al., 2004). Owens et al. (2004) concluded that, although foraging activity is often segregated by species and includes various types of habitat, special emphasis should be placed on riparian sites to maintain maximum species diversity.

Foraging ecology of bats.—Many techniques have been applied to analyzing foraging habitats of bats, including radio telemetry (e.g., Adam et al., 1994), acoustic monitoring (e.g., Burford et al., 1995), mist-netting (e.g., Perkins and Cross, 1988), and others (Lacki et al., 2007).

Each technique has drawbacks and is often combined with other methods to provide insight into foraging activity (Menzel et al., 2002; Tibbles and Kurta, 2003). Acoustic monitoring is the most common method for analyzing foraging activity; nevertheless, this technique is severely limited because acoustic activity cannot be related to population size nor does it provide information on the sex, age, or reproductive status of individuals (Lacki et al., 2007). Studies collecting data on species richness and diversity have long used mist-netting (Lacki et al., 2007), although investigations based solely on mist-netting data to evaluate habitat associations are few (e.g., Baker and Lacki, 2004; Perkins and Cross, 1988). This is likely because mist-netting is labor-intensive and requires a large data set to draw meaningful conclusions regarding habitat associations.

Studies have evaluated various components of foraging ecology of bats including size and shape of area used, distance traveled, effects of climate and elevation, role of patch size, habitat structure, habitat stratification, and importance of various features of the landscape (Lacki et al., 2007). Biologists generally classify foraging habitats with either categorical (e.g., upland or lowland) or continuous variables (e.g., distance to water), depending on the specific hypothesis, and apply appropriate statistical techniques (e.g., Ford et al., 2005; Menzel et al., 2002, 2005; Perkins and Cross, 1988). For example, Ford et al. (2005) evaluated predictions of habitat affinities, including proximity to riparian areas, canopy cover, width of canopy gap in forests, and height of canopy, using acoustic data as a measure of bat presence, and results of the study conformed moderately well to the predictions. Despite these studies, the geographic distribution and preferred foraging niche of bats remain poorly understood for many species (Lacki et al., 2007).

Ecological niche modeling.—Predictions of species occurrence have practical and diverse applications in ecology, evolution, and conservation biology (Elith et al., 2006). Ecological niche modeling predicts distribution of a species over a geographic area by combining data on presence and/or absence of the species with environmental variables to approximate the preferred habitat (Phillips and Dudík, 2008; Phillips et al., 2006; Warren and Seifert, 2011). Many traditional ecological niche models (ENMs) require systematic biological surveys to approximate presence, absence, and abundance, which can make post-hoc analyses difficult, if the assumptions of the model are not met during sampling. Modeling techniques familiar to ecologists often have such restrictions, including linear regression that requires random spatial sampling and occupancy modeling that requires sampling of sites two or more times (Elith et al., 2011). Although most ENMs require both presence and absence data (Guisan and Zimmerman, 2000), absence data are often lacking or unreliable (Anderson, 2003). This is particularly true of mist-net sampling of bats, which provides definitive presence data but is an unreliable source of absence data given the extreme sampling effort that is required to capture rare species in a given area (Weller and Lee, 2007). Without reliable absence data, using an ENM that relies on presence-only data is more appropriate than presence-absence models, such as logistic regression (Flory et al., 2012), when applied to mist-netting data.

The software program MAXENT (V.3.3.3k) uses a maximum entropy modeling technique to create an environmental niche model that predicts the probability of presence of a species over a geographic area (Phillips et al., 2006). MAXENT uses presence information and geographic data, such as elevation, land-cover, and mean temperature, as predictor variables or "features," to approximate the niche and potential geographic distribution of a species (Phillips and Dudík, 2008; Phillips et al., 2006; Warren and Seifert, 2011). MAXENT determines the probable density of covariates (features) across an entire region where a species may occur, $f(z)$, by sampling random “background points” of the area, as well as only in locations where species are known to be present, $f_1(z)$. Many values of $f_1(z)$ are possible, and the model chooses the one that minimizes relative entropy, i.e., the distance between $f(z)$ and $f_1(z)$, with constraints in place so that the solution reflects covariates that are close to the mean of presence locations. The null model equals z, meaning that a species has no preference for environmental variables and that it occupies features in proportion to their availability, which indicates a highly entropic distribution. MAXENT automatically accounts for nonlinearities among predictor variables by including potential interactions and limits overfitting of the model with a built-in regularization function (Phillips et al., 2006). This regularization function, which equals β x standard deviation/(sample size)$^{1/2}$, or β x standard error; β is 1 by default, but can be altered to adjust fit of the model. When sample sizes are large, β should be adjusted to prevent overfitting, which is a result of dividing the standard deviation by a large number (sample size), resulting in a low regularization multiplier (Anderson and Gonzalez, 2011).

The software MAXENT produces maps of the area of interest, with cells that contain a value from 0 to 1. Zero indicates the least suitable habitat for that species, and 1 indicates the most suitable habitat. MAXENT produces several output statistics, including a receiver operating characteristics (ROC) curve, which is most commonly used to evaluate model performance. ROC evaluates the probability of a false positive (1 minus specificity), which is equal to the fraction predicted area (FPA) divided by the probability of a true positive (sensitivity), which is equal to 1 minus omission rate, over a range of thresholds. A true positive means that the model correctly ranked a random point with presence data higher than a random point without presence data, and this cumulative probability gives the area-under-the-curve (AUC) score, which varies from 0 to 1 (Elith et al., 2011; Phillips and Dudík, 2008; Phillips et al., 2006;).

Purpose of study.—The Monongahela National Forest has been conducting a long-term bat-monitoring project, with emphasis on maternity colonies of the Indiana bat. Using data collected between 1997 and 2012, I will answer key ecological questions about bats in the Monongahela National Forest, especially questions concerning foraging ecology. Use of summer habitat by bats is likely influenced by many factors at the local level, including abundance and quality of prey, vegetative composition, proximity to water, and availability of roosting sites (Brack et al., 2002; Foster and Kurta, 1999; Johnson, 2008; Menzel et al., 2005). However, interspecific and intraspecific variability exists over various spatial scales (Lacki et al., 2007), and lack of localized studies has likely resulted in incomplete knowledge of the summer ecology of bats in the Monongahela National Forest, making science-based conservation difficult. My study examines current and historical abundance and richness of species, habitat associations, and spatial and temporal distribution of bats in the Monongahela National Forest. By determining the current state of populations and foraging habitat associations of bats in the Monongahela National Forest, this study will provide the Forest Service with localized data to guide their management decisions, as they deal with the critical threats posed by white-nose syndrome and wind-turbines.

There are four major goals for my study. I will evaluate spatial distribution of bats in the Monongahela National Forest, based on mist-netting captures and maximum entropy modeling, and examine habitat preferences of each species, using the results of maximum entropy modeling. Third, I will use mist-netting data and the Shannon-Wiener Index (Magurran, 2004) to assess diversity of present-day communities of bats on the forest and determine how they have changed over time. Finally, I will examine catch per unit effort for species, over years, to determine trends in abundance of bats in the Monongahela National Forest.

METHODS

Mist-netting.—Collection of data began in 1997, with consistent monitoring starting in 2001, under a contract between the Monongahela National Forest and Sanders Environmental, Inc. Biologists sampled populations of bats at 50 sites per year, on average, with many sites visited in multiple years. Monitoring occurred on over 1,300 net-nights at 458 locations during 2001–2012, resulting in the capture of more than 11,000 individuals from 10 species.

Locations for mist-netting were selected by biologists of the Monongahela National Forest, based partly on land-type association rankings developed for the purpose of locating Indiana bats on the forest (deMeo, 2001), as well as on-site investigations and results of past mist-netting surveys. Locations that yielded Indiana bats, Virginia big-eared bats, or a high diversity or abundance of bats were often resampled in subsequent years. New locations, not previously sampled were periodically added throughout the project.

Biologists collected bats following the mist-netting guidelines of the U. S. Fish and Wildlife Service for Indiana bats (U.S. Fish and Wildlife Service, 1999). Bats were captured in mist nets that varied from 2.6 to 18 m in width and 2.6 to 10.4 m in height. Nets were placed across intermittent or perennial streams, small rivers, small ponds, unimproved roads, fields, forested trails, and along forest edges (Kunz and Kurta, 1988). A minimum of two nets were placed at each site. Net sets were stationed at least 30 m apart, with an individual net or multiple adjacent nets < 30 m apart being considered a “net set.” Net placement was determined by an experienced biologist, and the location of nets was usually consistent if the site was monitored in consecutive years. Bats were surveyed for 5 h after dusk, on 2 nights, which usually were consecutive. Netting ceased and was repeated on a later date if ambient temperature fell below 10°C or if rain persisted for greater than 1 h. Nets were checked every 10 min.

Bats were identified to species, and morphometric and reproductive data were recorded. Bats were categorized as adult or juvenile by the degree of ossification of the phalangeal epiphyses (Anthony, 1988). Male bats were classified as non-reproductive or scrotal, based on size of testes and degree of testicular descent, and females were classified as non-reproductive, pregnant, lactating, or post-lactating, based on abdominal palpation, condition of nipples, and ability to express milk (Racey, 1988).

Spatial analyses.—Spatial data were obtained from various sources, including the Monongahela National Forest, U.S. Forest Service, U.S. Fish and Wildlife Service (USFWS) U.S. Geological Survey (USGS), Multi-resolution Land Characteristics Consortium (MRLC), and West Virginia Department of Natural Resources (WVDNR). These data included information on aspect and elevation (Gesch et al., 2007), hydrologic features (Roth and Dewald, 1999), geology, wetlands (U.S. Fish and Wildlife Service, 1996), forest type, forest-age class, relative forest density (Riitters, 2000), distance to caves, land-cover (Fry et al., 2011), landscape pattern (Riitters et al., 2000), and land-cover diversity (Riitters, 1999). Most data were publicly available. However, locations of caves were obtained under contract with the WVDNR, and the geology, forest type, forest-age class, and relative forest density were obtained directly from the Monongahela National Forest. All data were transformed into the same geographic coordinate system (NAD 1983), and point and polygonal data (shape files) were transformed into rasters, with a grid size of 30 by 30 m. Rasters were sampled using the nearest-neighbor technique that determines a cell's value based on the feature that is closest to the center of that cell (ESRI, 2011). These data were clipped to the declared property boundary of the Monongahela National Forest.

The layer for aspect was created using the Spatial Analyst tool in ArcMap 10 (ESRI, 2011) from a digital-elevation model (DEM) obtained from the USGS National Elevation Database (Gesch et al., 2007), which was re-classified as one of the four cardinal directions (north, south, east, west). This DEM was also used as the source for the elevation layer. Geologic data were obtained directly from the Monongahela National Forest and were reclassified into the categories sandstone, limestone, shale, alluvium, shale/sandstone, and sandstone/ limestone.

Hydrologic data came from the USGS National Hydrologic Features Dataset and reclassified; these data include streams, small rivers, and large rivers, as defined by Roth and Dewald (1999). Areas without hydrologic data receive a no-data value. Ponds, lakes, and wetlands were not included in hydrologic features, because they were represented in the wetlands feature. Data for wetlands were attained from the USFWS National Wetlands Inventory (U.S. Fish and Wildlife Service, 1996) and were reclassified as unconsolidated bottom, emergent, scrub-shrub, forested, open water, unconsolidated shore, stream bed, rock bottom, aquatic bed, rocky shore, and no data (Cowardin et al., 1979).

Forest type was obtained from the Monongahela National Forest and is based on existing vegetation codes from the Forest Service Handbook for Region 9 (U.S. Department of Agriculture, 1974). Forest age was acquired from the Monongahela National Forest and was reclassified as early successional (1), mid-early successional (2), mid-successional (3), late successional (4), and no data (0). Relative forest density was created from data of MRLC and is presented as the proportion of forest in an area relative to the proportion of forest in the surrounding 30 by 30 m analysis window. These data are relative values that are most applicable when compared to other pixels of the same map; cell values range from 0 to 255 (Riitters, 2000).

Land-cover data were also obtained from MRLC and included the following classifications: open water, developed open space, developed low intensity, developed medium intensity, developed high intensity, barren land, deciduous forest, evergreen forest, mixed forest, shrub/scrub, grassland/herbaceous, pasture/hay, cultivated crops, woody wetlands, and emergent herbaceous wetlands (Riitters, 1999). Landscape pattern was derived from MRLC data and represents the amount of agriculture to urban to forest in a given area and is separated into 19 categories based on these proportions (Riitters et al., 2000). Land-cover diversity represents the proportion of different land-cover types in the surrounding area and was calculated from MRLC data (Riitters, 1999). Distance to nearest cave in the state of West Virginia was derived using ArcMap10. Although distance to nearest road was initially included, this parameter was removed from the analysis because most netting sites were located on or close to a road, leading to probable sampling bias.

Correlations between spatial variables were examined using ENMtools (Warren et al., 2008). Although MAXENT is fairly robust to correlated variables, highly correlated features can be confounding (Phillips et al., 2006). Consequently, highly correlated features (> 0.5, or < - 0.5) were removed and not included in the final analyses. Some areas within the proclamation boundary of the national forest were not included in the model maps, because of missing feature data.

MAXENT.—Default model settings were used in most cases because these settings typically performed the best (Elith et al., 2006); however, some were adjusted based on preliminary evaluations of data (Collins, 2012). A regularization multiplier of 10 was set for each model to prevent overfitting, which is recommended for large datasets (Anderson and Gonzalez, 2011). The default regularization multiplier of 1 constrained probabilities with a resolution that was narrower than desired, and likely over fit the model at the desired scale. Duplicates were not removed, because preliminary testing determined that when multiple presence records at the same locations were included test and training AUC scores became closer in value to each other, indicating better model performance. Eighty percent of these data were used to "train" the model, a process during which the model samples the background points of each feature of the study area, thus producing "training points." Similarly, the model is then tested using the remaining 20 percent of data, and background points are sampled giving "test points"; all other model parameters were left at default values (MAXENT v.3.3.3k; Phillips et al., 2006). Evaluations of model performance, such as AUC, are performed on both training and test points.

Model performance was evaluated using the area-under-the-curve (AUC) score for the training and the testing data. Fractional predicted area (FPA) is reported as an estimate of the proportion of the project area with presence of a particular species. FPA was used to evaluate the extent of the predicted distribution for each model, with a higher FPA indicating that the model predicted a high proportion of the area as suitable habitat. FPA is measured in multiple ways by the model; however, the balance FPA is likely the most meaningful (Elith et al., 2011). A one-sided *P*-value is associated with the FPA value, and the null hypothesis is that test points are no better than a random prediction with the same FPA.

Permutation of importance (PI) was determined for each environmental variable. To determine this, the values of the variables on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is calculated and normalized to percentages, giving an idea of which variables were important to the model. This index is used because it relies only on the final model and not the pathway selected by the algorithm, which can be misleading when predictor variables are correlated. Finally, probability of presence (POP) is reported as an indication of the likelihood of presence with indicated values for that location. Probability of presence (POP) is calculated by MAXENT from the logistic output response curves and is used to estimate the probability of finding that species in an area with a given feature value (Elith et al., 2011; Phillips and Dudík, 2008; Phillips et al., 2006).

Diversity and abundance.—The Shannon-Wiener index of diversity (Magurran, 2004) was used to estimate the diversity of the bat community in the Monongahela National Forest. The Shannon-Wiener Index has been widely used in conservation biology and combines two aspects of community composition—richness and abundance. The Shannon-Wiener Index was calculated for each year that sampling was conducted on the forest and plotted over time to determine trends in diversity. The number of bats by species captured per night was divided by the number of sites sampled for each year to determine catch-per-unit effort for each species. These data were then graphed by year to analyze visually trends in abundance.

RESULTS

MAXENT.—A total of 11,149 captures of bats were used to create maximum entropy models for 10 species of bats in the Monongahela National Forest. Location of suitable habitat for each species on the forest, as determined by modeling with MAXENT, is graphically depicted in Figures 1–10. Model performance is evaluated by the training area under the curve score ($\mathrm{AUC}_{\mathrm{training}}$) and test area under the curve score ($\mathrm{AUC}_{\mathrm{test}}$) ± *SD* (Table 1). Features that exceed 10% permutation of importance are presented in the text, with all other variables reported in Tables 2–10 and Figures 11–14. Other information on the models and indices of model performance, including number of presence points used for training and testing, regularized training gain, unregularized training gain, number of test samples, and test gain are reported in Appendix A. Most models performed well, with only silver-haired bats and hoary bats failing to perform significantly better than random.

Virginia big-eared bat.—Using 98 presence records for training and 24 for testing, a maximum entropy model was created for the Virginia big-eared bat. The model performed well with $AUC_{training} = 0.969$ and $AUC_{testing} = 0.966 \pm 0.021$ (Table 1), indicating that the northeast portion of the forest provides the primary habitat for the species with the rest of the forest having a low probability of presence (Fig. 1). The predicted distribution area was calculated using the balance fractional predicted area (FPA); for the Virginia big-eared bat, FPA = 0.268 ($P < 0.0001$; Table 1). Distance to caves was identified as the highest contributing feature to the model (Table 2; Fig. 11). The permutation of importance (PI) for distance to caves was 63.6, along with elevation (PI = 11.8) and relative forest density (PI = 11.1; Table 2). When only distance to caves was considered (Fig. 11), the probability of presence from the response curve (POP) decreased sharply as distance increased from 5 km (POP = 0.22) to 10 km (0.05). Elevation was inversely correlated with POP; when elevation was 200 m, POP = 0.80, and when elevation exceeded 1,500 m, POP < 0.05 (Fig. 12). The Virginia big-eared bat showed an exponential relationship with relative forest density, with probability of presence peaking (POP = 68) at 250 (Fig.13).

Big brown bat.—The model created for the big brown bat used 937 presence records for training and 234 for testing with a resulting $AUC_{training} = 0.858$ and $AUC_{test} = 0.844 \pm 0.011$ (Table 1). The model indicated that the southwestern corner of the forest provides the most suitable habitat for the species, although many regions of the forest have high-to-moderate probability of presence (FPA = 0.704; $P < 0.0001$; Fig. 2). Forest type (PI = 27.7), elevation (PI = 20.5), land-cover type (PI = 18.5), hydrologic features (PI = 10.8), and land-cover diversity (PI = 10.2) were identified as the important variables (Table 2). Important forest types identified include northern red oak (*Quercus rubra*; POP = 75), yellow poplar (*Liriodendron tulipifera*)-white oak (*Q. alba*)-northern red oak (POP = 58), and eastern white pine (*Pinus strobus*; POP = 69; Table 5). Elevation was inversely correlated with probability of presence, with POP = 68 at 200 m, but POP < 28 when elevation exceeded 1,400 m (Fig. 12). Only one land-cover type, developed open space (POP = 80), increased the probability of presence, with all other types being equal (POP = 48; Table 8). Large rivers greatly increased the probability of presence (POP = 83) over other types of hydrologic features, including small rivers (0.55), streams (0.55), and no hydrologic features (0.49; Table 7). Land-cover diversity was inversely correlated with probability of presence that ranged from POP = 0.63 when land-cover diversity index was zero, and POP = 0.32 when the land-cover diversity index equaled 200 (Fig. 14).

Silver-haired bat.—Seventy-six presence points were used for training and 18 for testing the model created for the silver-haired bat. The model resulted in $AUC_{training} = 0.821$ and $AUC_{test} = 0.735 \pm 0.064$, and indicated that distribution across the forest is ubiquitous, with only a few regions having a low probability of presence (FPA = 0.902; $P = 0.16$; Table 1; Fig. 3). Hydrologic features was the most important feature (PI = 40.8), with relative forest density (PI = 19.6) and land-cover type (PI = 10.5) also contributing to the model (Table 2). Small rivers (POP = 0.71), large rivers (POP = 0.88), and streams (POP = 0.71) each had a higher probability of presence than areas without hydrologic features (POP = 0.38; Table 7). Relative forest density produced a linear relationship with POP for silver-haired bats, with POP < 0.10 when relative forest density was zero, and a POP = 0.38 when relative forest density equaled 250 (Fig 13). Developed open space, which included roads, had the highest POP of land-cover types at 0.55, with all other categories having POP < 0.35 (Table 8).

Eastern red bat.—The model for the eastern red bat was created using 1,080 records from training and 269 for testing, and performed well with $\mathrm{AUC}_{\mathrm{training}} = 0.864$ and $\mathrm{AUC}_{\mathrm{test}} = 0.849 \pm 0.012$ (Table 1). Many areas on the Monongahela National Forest were distinguished by the model as having a high probability of presence (FPA = 0.818; $P < 0.0001$; Fig. 4). Forest type (PI = 33.8), hydrologic features (PI = 20.7), land-cover type (PI = 18.6), and elevation (PI = 12.3) were all important (Table 2). Open areas were established as having the highest POP (0.48) in the forest type feature, with mixed oaks (POP = 0.38) and eastern white pine (POP = 0.41) also salient; all other forest types had low POP (< 0.35; Table 5). For hydrologic features, large rivers had the highest probability of presence (POP = 0.79), with small rivers (0.55) and streams (0.55) having a higher POP than no hydrologic features present (0.38; Table 7). Developed open space had a higher probability of presence (0.69) than all other categories of land-cover types (POP < 0.53; Table 8). Probability of presence was inversely related with elevation, with POP = 0.60 at 200 m and POP = 0.17 at 1,400 m (Fig. 12).

Hoary bat.—For the hoary bat, 156 presence records were used to build the model and 38 to test. The model resulted in an $\mathrm{AUC}_{\mathrm{training}}$ of 0.874, and $\mathrm{AUC}_{\mathrm{test}}$ of 0.803 ± 0.046 (Table 1). The POP was medium to high across most of the Monongahela National Forest, but some small areas received higher scores (FPA = 0.952; $P = 0.08$; Fig. 5). Features with the highest contribution to the model were hydrologic features (PI = 34.3), forest type (PI = 23.6), land-cover type (PI = 18.6), and land-cover diversity index (PI = 17.5; Table 2). Large rivers yielded the highest POP (0.75), and all other classes had a POP of less than 0.35 (Table 7). Open forest type produced the highest POP of 0.87, with yellow poplar-white oak-northern red oak second at 0.59; all other forest types were less than 0.40 (Table 5). Developed open space had the highest POP (0.50) for land-cover type; and all other classes were less than 0.23 (Table 8). Land-cover diversity index was inversely related to POP when considered alone (Fig. 14), but when considered with other variables, POP was exponentially related to land-cover diversity index, with POP = 0.46 when land-cover diversity index equaled 0 and POP = 0.58 when land-cover diversity index was 200.

Eastern small-footed bat.—The model for the small-footed bat used 130 presence records to train the model and 32 to test. The $AUC_{training} = 0.926$, and $AUC_{test} = 0.949 \pm 0.011$ (Table 1). The model showed significant contrast between areas of the forest, with the highest POP in the eastern part of the Monongahela National Forest (FPA = 0.677; $P < 0.0001$; Fig. 6). Forest type had the highest PI (43.2), with elevation (15.7), hydrologic features (13.7), and land-cover diversity index (10.5) also highly ranked (Table 2). Northern red oak yielded the highest POP (0.87), and all other forest types had a POP of less than 0.50 (Table 5). Elevation showed an inverse relationship with habitat preference; when elevation increased, probability of presence decreased (e.g., at 200 m, POP = 0.65, and at 1,400 m, POP = 0.08; Fig. 12). Large rivers had the highest probability of presence (POP = 0.93), with all other classes less than 0.60 (Table 7). Land-cover diversity index (LCDI) was inversely proportional to POP; POP = 0.65 when LCDI = 0, and POP = 0.27 when LCDI = 200 (Fig. 14).

Little brown bat.—This model was created using 1,985 presence records for training ($AUC_{training} = 0.839$), and 496 for testing ($AUC_{test} = 0.854 \pm 0.008$; Table 1). The model determined several areas of the forest as important to little brown bats (FPA = 0.757; $P < 0.0001$; Fig. 7). The features with the highest permutation of importance include hydrologic features (PI = 39.5), forest type (27.5), and land-cover type (12.5; Table 2). Large rivers had the highest probability of presence (POP = 0.80), with small rivers (0.58) and streams (0.48) ranking higher than no hydrologic features (0.35; Table 7). Probability of presence was approximately even across forest types with most POP equal to about 0.35 (Table 5). Open spaces (0.48) and eastern white pine (0.42) had the highest POP. Developed open spaces (POP = 0.56), and open water (POP = 0.42) were the highest among land-cover types, whereas mixed forest was among the lowest (POP = 0.23; Table 8).

Northern long-eared bat.—The model for the northern long-eared bat used the most presence points of all models—3,877 for training ($AUC_{training}$ = 0.773) and 969 for testing (AUC_{test} = 0.771 ± 0.006; Table 1). The model had a high degree of discrimination, with both high and low POP being found throughout the forest (FPA = 0.844; $P < 0.0001$; Fig. 8). Forest type was the principle feature (PI = 50.5), with land-cover diversity index (22.3) and hydrologic features (10.5) also contributing to the model (Table 2). Open space was the highest-ranking category (POP = 0.62), with mixed oaks (0.58) and white oak (0.48) forest also being important. All other forest types yielded a relatively low POP (ca. 0.40), and no forest had the lowest POP (0.23; Table 5). Land-cover diversity index was inversely proportional to POP; when LCDI = 0, POP = 0.69, and when LCDI = 200, POP = 0.33 (Fig. 14). Large rivers (POP = 0.88), streams (0.68), and small rivers (0.68) had high probability of presence (Table 7).

Indiana bat.—The model for the Indiana bat used the least number of presence points for training (40) and for testing (10). Both the training and test AUC were high for the model ($AUC_{training}$ = 0.952, and AUC_{test} = 0.944 ± 0.037;Table 1). The model pinpointed the northeastern corner of the Monongahela National Forest as having the highest POP (FPA = 0.411; $P < 0.0001$; Fig. 9). Elevation (PI = 29.8), geology (23.6), and relative forest density (22.1) were the most significant features in this model (Table 2). Elevation was inversely proportional to probability of presence; for example, POP equaled 0.81 when elevation was 200 m, and 0.30 when elevation was 1,000 m (Fig. 12). All geologic features had a high POP = 0.65, with the exception of shale (0.25; Table 6). Relative forest density was linearly related to probability of presence; when relative forest density was zero, POP equaled 0.35, and when relative forest density was maximum (250), POP equaled 0.65 (Fig. 13).

Tricolored bat.—This model used 538 presence points to train and 134 to test and resulted in an $\mathrm{AUC}_{\mathrm{training}}$ of 0.889 and $\mathrm{AUC}_{\mathrm{test}}$ of 0.859 ± 0.015 (Table 1). The most eastern and western parts of the Monongahela National Forest had the highest POP (FPA = 0.760; $P <$ 0.0001; Fig. 10). Hydrologic features (PI = 30.2), elevation (20.2), forest type (20.1), land-cover type (12.4), and land-cover diversity index (11.4) were all central to the model (Table 2). Large rivers (POP = 0.84), small rivers (0.64), and streams (0.64) had a higher POP than no hydrologic features (0.35; Table 7). Elevation was inversely proportional to probability of presence so that when elevation was 200 m, POP was at its highest (0.60), but when elevation was 1,400 m, POP was at its lowest (0.08; Fig. 12). The most important forest type was open space (POP = 0.43), along with eastern white pine (POP = 0.40) and mixed oaks (POP = 0.35; Table 5). Low intensive developed space was the only category of land-cover type to contribute more to the model than any other land-cover type (POP = 0.60; Table 8). Land-cover diversity index did not react linearly; POP was highest when land-cover diversity was zero (POP = 0.68) and lowest when land-cover diversity equaled 100 (POP = 0.43; Fig. 14).

Diversity and abundance.—A total of 11,149 bats from 10 species were captured at 458 mist-netting sites over 1,361 nights. Species diversity ranged between 3.2 in 2003 to 5.6 in 2010 (Fig. 15). Diversity remained mostly stable from the beginning to the end of the survey period with no significant increase or decrease ($r^2 = 0.11$; $t_{13} = 1.35$, $P = 0.2$). An apparent dip in diversity in 2003 apparently was caused by a failure to capture the three rarest species on the forest; a slight jump in diversity occurred in 2010 and continued in subsequent years.

The most abundant species on the forest was the northern long-eared bat, which was captured 4,846 times at a capture rate (CR) of 3.3 bats/night/site (Fig. 16). The little brown bat was the second most common bat with 2,481 captures and a capture rate of 1.8 bats/night/site, followed by the eastern red bat (*n* = 1,352 captures; CR = 1.1 bats/night/site), big brown bat (1,173; 0.9), tricolored bat (673; 0.5), and hoary bat (194; 0.2). The least abundant species were the Virginia big-eared bat (123; 0.1), silver-haired bat (95; < 0.1), and Indiana bat, which was only captured 50 times during the project (CR < 0.1). Capture rates varied greatly throughout the project, with the eastern small-footed bat, Indiana bat, northern long-eared bat, and tricolored bat all trending toward slight declines in catch per unit effort after the introduction of white-nose syndrome to the region (Fig. 17).

DISCUSSION

Niche modeling offers environmental managers a unique tool that estimates the geographic distribution of species and simultaneously allows determination of preferred habitat characteristics. Maximum entropy modeling is an emerging technique that has demonstrated an ability to make strong predictions of distribution, based on species presence data and environmental variables (Elith et al., 2006; Phillips et al., 2006; Phillips and Dudik, 2008; Elith et al., 2011). Although its previous application to research on bats is limited, maximum entropy modeling increasingly is considered as a reliable tool for predicting occurrence of species of bats (Buckman-Sewald et al., 2014; Wordley et al., 2015).

Mist-netting data collected in the Monongahela National Forest between 1997 and 2012 provides a robust data set from which accounts of species presence can be drawn. Sampling occurred with standard protocols, with many sites surveyed in multiple years. These data were combined with various environmental variables to create models in MAXENT for the 10 species of bats living in the Monongahela National Forest. Most models performed well, with only the models of the silver-haired bat and the hoary bat failing to perform significantly better than a random model with the same fraction predicted area (FPA). These are likely still good models, and the failed significance test is an unfortunate result of the high FPA, because it is more difficult for a model to perform better than random if probability of presence is high throughout the study area, as indicated by the FPA (Elith et al., 2011). AUC scores were consistently high, with all models exceeding the 0.70 threshold typically considered the minimum AUC for a viable model (Elith et al., 2011). Although caution should be exercised when interpreting these data, particularly for the silver-haired bat and hoary bat, these models offers a clear picture of the distribution of bats on the Monongahela National Forest and their habitat preferences.

Broad trends across species.—The overall results describe broad trends in use of habitat by bats in the Monongahela National Forest. Forest type and hydrologic features were the features most commonly indicated as important. Forest type was influential for all species, except the Virginia big-eared bat, silver-haired bat, and Indiana bat. Northern red oak and eastern white pine had the highest average POP of the forest classifications (Table 5). The category of hydrologic features was important for some species, including silver-haired bat, hoary bat, little brown bat, and tricolored bat, with streams, small rivers, and large rivers having a higher POP than upland areas for all species tested (Table 7). Riparian areas are considered good habitat for bats, which is likely related to a high density of prey (Brigham and Fenton, 1991; Grndal et al., 1999; Hayes and Loeb, 2007; Law and Chidel, 2002).

Elevation, land-cover type, distance to caves, land-cover diversity, and relative forest density were also high ranking in most models. Elevation was important to big brown bats, Indiana bats, and tricolored bats, and POP was inversely correlated with elevation for all 10 species (Fig. 12). This altitudinal relationship has been documented for many species of bats, especially reproductive females and juveniles that are more sensitive to thermal constraints than adult males (Brack et al., 2002; Cryan et al., 2000; Grindal et al., 1999). Furthermore, activity of bats is lower at cooler temperatures, and this effect is greater at higher elevations (Wolbert et al., 2014).

Land-cover type was an important factor for the POP of big brown bats, hoary bats, and eastern red bats. Developed open space had the highest POP of any land-cover type for all species (Table 8), but this relationship is likely a result of sampling bias; developed open space is the classification given to roads, and most netting sites were located on or near a road. Roads offer natural foraging and travel corridors that funnel bats toward waiting mist nets (Hobson and Holland, 1995; Russell et al., 2009).

Land-cover diversity was most important to the hoary bat, for which POP increased with land-cover diversity, and to the northern long-eared bat, which had the opposite response. The response curves for land-cover diversity indicated that other species were not influenced by this measure (Fig. 14). POP was correlated with relative forest density for most species and was most influential to the silver-haired bat and Indiana bat (Fig. 13).

Geology, landscape pattern, aspect, wetlands, and forest age were the least important features to models for all species (Table 6). Geology was key only for the Indiana bat, for which shale had a lower POP than other classifications of sedimentary rock. Landscape pattern was not important to any model, and there was no change in probability of presence between classifications (Table 9). Probability of presence varied little with wetland classification, and wetlands were not salient to any models (Table 10). This may be because mist-netting sites were not often located in wetland areas, and although wetlands typically are considered good habitat for bats (e.g., Lookingbill et al., 2010; Menzel et al., 2005), wetlands tend to be open and not conducive to mist-netting. Aspect also showed little change in the probability of presence and was not influential to any species (Table 3). Distance to caves was important to only the Virginia big-eared bat, with POP being inversely correlated with distance to caves (Fig. 11).

Forest age was likely not significant because of missing data and a lack of specificity in the age classes that were used. Small portions of the forest had missing data on forest age, and forest age class likely changed throughout this multi-year project, although this change was not represented in the data. In addition, the classifications for forest age included only four categories (ages), and this may have been too coarse of a filter for the model to discern patterns in usage by bats.

A few broad conclusions can be drawn from the results of these models. Lowland river valleys are likely important to all species of bats, and forest type may be more essential than age of the forest. Corridors, such as roadways, likely provide foraging opportunities and travel pathways for bats that fly below the canopy. Despite these generalities, the models of each species were varied, indicating substantial interspecific variation in habitat preferences.

Virginia big-eared bat.—The model for the Virginia big-eared bat had high AUC scores, performed significantly better than random, and provided useful habitat information for this endangered species (Table 1; Fig. 1). The model predicted that only a small portion of the

Monongahela National Forest was suitable for the Virginia big-eared bat, and these areas had a strong association with distance to caves. This was not surprising because the Virginia big-eared bat was the only cave-obligate species on the Monongahela National Forest during summer, and distance to caves was not identified as important for any other species. These data were also consistent with past foraging studies using radio telemetry, which reported that the Virginia big-eared bat never foraged farther than 8.4 km from its roost (Adam et al., 1994). My study found that probability of presence (POP) decreased precipitously as distance from nearest cave increased; POP = 0.70 at zero km from a cave and decreased to zero at 10 km from the nearest cave.

Elevation was also important, with POP decreasing as elevation increased, for the six species for which elevation was considered key. This was likely a result of thermal constraints imposed at higher elevations, particularly for females, or due to lower insect density at higher elevations (Brack et al., 2002; Cryan et al., 2000). However, some studies have found that Virginia big-eared bats preferred to forage along cliff bases (Adam et al., 1994), which could also account for this relationship; future studies may consider using slope to determine the impact of cliffs (i.e., 100% slope) on the presence of the species. As relative forest density increased, so did the POP. This result was not surprising, because Virginia big-eared bats in previous studies also relied greatly on wooded areas for foraging and tended to avoid open habitats (Adam et al., 1994).

Big brown bat.—Previous studies were largely unable to identify habitat associations for the big brown bat, so the species was considered a habitat generalist (Agosta, 2002; Furlonger et al., 1987; Krusic and Neefus, 1996). The model created in this study performed significantly better than random and predicted that a large portion of the forest was suitable habitat, indicating that the big brown bats was indeed a generalist species (Table 1; Fig. 2). Developed open space was the only land-cover type that increased the POP for big brown bats. However, this was the category assigned to primary and secondary roads, and past studies indicated that roadways and riparian areas were probably important foraging and/or commuting features for big brown bats (A. Kurta, pers. comm.; Krusic and Neefus, 1996). Presence of big brown bats likely increased in the presence of roads (excluding smaller roads, such as forest service “roads,” which were not categorized as roads) because they are important foraging and travel corridors.

High values in the land-cover diversity index were assigned to edge habitat, whereas low values were given to homogeneous landscapes. POP was inversely correlated with land-cover diversity for this species, suggesting that big brown bats preferred homogeneous environments (Table 14). This conclusion contrasted with other studies that indicated that edge, especially between forest and agricultural fields, was important to many species of bats, including big brown bats (Wolcott and Vulinec, 2012). Land-cover diversity was not indicated as important to the model probably because the Monongahela National Forest had few openings in the forest, resulting in little edge habitat and inhibiting the model from perceiving importance.

Silver-haired bat.—The model for the silver-haired bat did not perform significantly better than random, and AUC scores were lower than models for other species (Table 1). The FPA was high for silver-haired bats but not significantly different from that of a random model. A high FPA could mean that the bat was a generalist and not constrained by landscape features, as were other species, or that the model failed to find these relationships. It is more difficult for a model to perform significantly better than random when FPA is high because a large portion of the area is predicted to have a high POP; therefore, it is difficult to tell how well the model is actually performing for silver-haired bats.

Probability of presence increased linearly with relative forest density—a trend that was similar among species. Developed open space had a higher POP than other land-cover types; however, this was likely due to the sampling bias associated with roadways. Silver-haired bats also had a higher POP along all hydrological features than terrestrial features, suggesting some preference for these habitats.

Little is known about the preferred habitat of the silver-haired bat. One study in Ontario found forest age to be a primary factor in the distribution of silver-haired bats, particularly in old-growth white-pine forest, and that uncut forest provided the best habitat (Jung et al., 1999). In contrast, my results, showed that, although presence increased with relative forest density, it was not influenced by forest age. Silver-haired bats migrate long distances (McGuire et al., 2012), so it was not surprising that they tolerated an array of habitat types.

Eastern red bat.—The model for the eastern red bat performed very well, having high AUC scores, despite a high FPA (Table 1). The high FPA indicated that eastern red bats were generalists or that their preferred habitat was located throughout the forest. Open areas (not forested) were higher-ranking than any single forest type, although POP did not differ greatly among habitats. These results were similar to a study conducted in South Carolina that found red bats associated with sparse vegetation (Loeb and O’Keefe, 2006). Wing morphology may explain this correlation because long-distance migrants (Fleming and Eby, 2003) tend to have high aspect ratio (long, narrow wings) and low wing loading, which provide maximum energy savings during long flights (Norberg and Rayner, 1987). Although some studies showed that red bats had an affinity for wetlands (Johnson et al., 2008; Lookingbill et al., 2010; Menzel et al., 2005), the model did not distinguish wetlands as influential, potentially because wetlands were not often sampled. Large rivers had a higher POP than other hydrologic features that were all higher than terrestrial areas. As with other species, developed open space was slightly more important than other land types, but again, this association probably was a result of sampling bias. Probability of presence was inversely correlated with elevation, which was likely a result of thermal constraints (Cryan et al., 2000).

Hoary bat.—The model for the hoary bat did not perform as well as models for most other species, which probably resulted from the low number of captures for hoary bats. Although AUC scores were high, the model failed to perform significantly better than random (Table 1). This may still be a good model, and the failed significance test may be an unfortunate result of the high FPA because it is more difficult for a model to perform better than random if probability of presence is high throughout the study area, which is what FPA indicates (Elith et al., 2011). Large rivers were important, and this was likely because hoary bats have high aspect ratios and low wing loading, which increase flight efficiency, but decrease maneuverability, making flight in cluttered environments more difficult (Norberg and Rayner, 1987).

Land-cover diversity index was inversely and linearly related to POP when considered alone; however, when the index was considered with other variables, the relationship became exponential, with POP higher in areas with high land-cover diversity, which may reflect edge habitat (Fig. 14). The change in response between POP when considered alone and POP when considering other variable indicates the presence of correlated variables, although these correlations are not identified within the model. Because land-cover diversity index was created from land-cover type, correlation between these variables is not surprising. However, this relationship was not seen in the models of other species, indicating that the specific response of hoary bats to land-cover diversity and the correlated variable was such that it increased POP when considered together. As a hypothetical example, hoary bats may prefer edge habitats at lower elevations but not at higher elevations, thus causing this type of response; this particular explanation may or may not be true, but it illustrates one potential reason that the results look like they do. Although the model can account for confounding variables, it does not identify the specific interactions.

As with the other migratory tree bats (i.e., eastern red and silver-haired bats), the FPA of this model was high, indicating that the hoary bat was somewhat of a habitat generalist. Previous reports from Canada indicated that old growth forest was key to the presence of hoary bats in aspen and mixed pine forest (Crampton and Barclay, 1998; Jung et al., 1999); however, these types of forest were not representative of the Monongahela National Forest, and likely not an important factor in predicting presence of hoary bats in the Appalachians. Alternatively, poor performance of the model may be related to poor classification and limited extent of the data set for forest age.

Eastern small-footed bat.—The model for the small-footed bat performed very well, with high AUC scores, and was significantly better than random (Table 1). The low FPA was expected given the habitat limitations of the species. Small-footed bats have been found roosting almost exclusively in exposed rock piles, such as talus slopes (Johnson et al., 2011), and such habitat limitations could explain the low FPA; unfortunately, data on location of rock outcroppings or talus piles were not available for input into the model. Detection rates of small-footed bats have also been directly linked to distance from suitable roosting habitat (Johnson et al., 2009). Nevertheless, elevation was established as important, with POP decreasing as elevation increased. Although information regarding the foraging preferences of the small-footed bat was limited, my results were dissimilar to those found in a radio-telemetry study in Maryland that showed small-footed bats foraging along forested ridge tops (Johnson et al., 2009). Although relative forest density was not important to the model, the low wing loading and high-frequency echolocation calls of small-footed bats indicated that they were capable of foraging in dense forest (Johnson et al., 2009). Furthermore, dietary analysis suggested that these bats use gleaning behavior, which also was indicative of foraging in the forest interior (Moosman et al., 2007)

Little brown bat.—The model for the little brown bat performed significantly better than random and had relatively high AUC scores (Table 1). FPA was high because little brown bats were the second most commonly captured bat on the forest. Dietary analyses indicated that little brown bats foraged in a variety of habitat types, although insects with aquatic larval stages were typically important (Clare et al., 2011, 2014). Hydrologic features was influential to the model, with large rivers particularly important. Important land-cover types included developed open spaces and open water, which probably increased prey availability, particularly insects with aquatic larval stages (Clare et al., 2014). In the Northeast, little browns were more prevalent in riparian forest and forested sites than other habitats at the landscape scale, including open water and developed spaces (Coleman et al., 2014).

Northern long-eared bat.—The northern long-eared bat had the highest number of presence records and, therefore, should theoretically have the best performing model. Although the model did perform well, the AUC scores were not as high as other species (Table 1). This demonstrates why AUC should be used with caution, because a lower number of presence records can increase AUC scores, although model performance is likely less accurate (Elith et al., 2011). Fewer records of presence can result in overfitting, causing the model to appear to perform better than reality. To account for this concern, the regularization multiplier was increased to 10 for all species, limiting overfitting and producing more realistic AUC scores. Model performance has been shown to vary greatly depending on the regularization multiplier, with intermediate regularization leading to the best performing models (Anderson and Gonzalez, 2011). The FPA was relatively high, because this species was frequently captured on the Monongahela National Forest. All forest types had a higher POP than non-forested areas for the northern long-eared bat, and POP was highest when land-cover diversity was low. Surprisingly, permutation of importance was less than 3% for relative forest density, although POP was correlated with relative forest density, especially when considered with other variables.

Hydrologic features were vital to the species, with large rivers having the highest POP of any hydrologic category. These results were somewhat consistent with observations of northern long-eared bat using cluttered interior forests, streams, and vernal pools as their primary foraging areas (Brack and Whitaker, 2001; Carroll et al., 2002; Lookingbill et al., 2010; Owen et al., 2002, 2004). The northern long-eared bat was recorded more often than other species at ephemeral pools in West Virginia and at constructed woodland ponds in Kentucky (Francl, 2008; Huie, 2002; Owen et al., 2002).

Indiana bat.—Despite having the fewest number of presence records, the model for the Indiana bat performed significantly better than a random model (Table 1). FPA was very low, as expected, because of the difficulty of capturing the species and its limited distribution across the forest. Elevation was inversely correlated to POP, as with other species. Interestingly, geology was high-ranking, with all sedimentary rocks having a high POP except shale. Limestone had a higher POP than other rock types; however, this relationship was only found when the model considered correlated variables but not when variables were considered individually. This could be an association with caves; nevertheless, distance to caves was not influential to the model, although POP did have an inverse relationship with distance to caves. This relationship could also be coincidence because of the broad classification used for this feature and the limited distribution of Indiana bat, or could be the result of another feature association.

Hydrologic features were somewhat important, with streams and rivers having a much higher POP than upland areas, regardless of size. This was consistent with typical Indiana bat habitat—woody vegetation < 30 m of a stream bank (Cope et al., 1978) and associated floodplain forest (U.S. Fish and Wildlife Service, 2007). In the Midwest, maternity colonies were commonly located in bottomland riparian areas, which likely represented the preferred habitat of the species (Carter, 2006). Areas with hydrologic features may have been important because of the abundance of snags and aquatic insects (Kurta and Whitaker, 1998; Murray and Kurta, 2002), although one study in the Midwest did not identify hydrologic features as important to Indiana bats (Farmer et al., 2002). Bottomland riparian forest and wetlands were limited on the Monongahela National Forest, which likely explained why the association with hydrologic features was not stronger. Although hydrological features likely are the preferred habitat for Indiana bats, other factors, such as competition and availability, may force the species to occupy other habitats.

Tricolored bat.—The model for the tricolored bat performed significantly better than random, with high AUC scores (Table 1). Hydrologic features all had higher POP than terrestrial features. Open space was identified as the most salient forest type, with developed open space as the most important land-cover type. Few studies have focused on the foraging ecology of tricolored bats specifically; however, the species was thought to be present at wetland areas more often than other species on the Monongahela National Forest (Johnson et al., 2008; Lookingbill et al., 2010; Menzel et al., 2005). As with other species, this attraction to riparian locations was likely a function of prey density (Bringham and Fenton, 1991).

Model building.—Features input into these models were created using the best available spatial data. Despite efforts to maintain the highest possible resolution and use the most current, geographic data, errors inevitably are present in these data. Size of the grid, for example, is limited by the largest raster input into a model, and for the models considered in this study, 30-by-30 m was the greatest resolution and that of most rasters; therefore, a 30-by-30 m grid was chosen for the model. Caparisons of MAXENT models at various spatial scales have indicated that using the finest possible resolutions provide the strongest models for foraging bats (Bellamy et al., 2013).

Models of all species performed robustly, except those for silver-haired and hoary bats. Maps were created for each species identifying locations on the Monongahela National Forest with highest habitat suitability. Although this habitat suitability is the probability of capturing an individual bat in a mist-net, these results can be extrapolated to approximate habitat suitability across the forest. These data, however, should be considered with caution, because correlated variables can alter response curves when each variable is considered in isolation. Although this makes it difficult to interpret the response of individual features, the model accounts for these non-linearities, and the overall model is not affected.

As a new technique, maximum entropy is not without pitfalls. Critics of MAXENT cite incorrect interpretation of maximum entropy models and lack of random sampling as common flaws in studies using MAXENT (Royle et al., 2012; Yackulic et al., 2013). Reliance on solely the maps or the logistic response curves can lead to misinterpretations, particularly when features are correlated (Elith et al., 2011; Phillips et al., 2006). Although these mist-netting data are not without correlation (particularly with roads), they represent a large sampling effort over a broad range of habitat types and are a good candidate for use with MAXENT. Geospatial errors in feature data and errors related to resampling of rasters are likely, but if limited in extent, the influence to the model is not significant (Elith et al., 2011; Phillips et al., 2006). Validation of these models based on mist-netting data using an alternative sampling method, such as acoustic monitoring, would allow errors due to sampling bias to be determined and provide more robust models. Models should be updated as new geospatial information becomes available. Although these models could be extended beyond the Monongahela National Forest, doing so would assume niche preference is consistent across the distribution of the species, which is unlikely.

Diversity and abundance.—Diversity did not vary significantly although there were changes likely due to decreases in abundance of species impacted by white-nose syndrome. Little brown bats have experienced the sharpest declines (Turner et al., 2011). Some species not affected by white-nose syndrome, namely the Virginia big-eared bat and silver-haired bat have experienced increases in catch per unit effort that are simultaneous with declines of species of *Myotis*. These declines are almost certainly due to white-nose syndrome and have been well documented across the eastern United States, with estimates of population decline ranging from 12% for the tricolored bat to 98% for the northern long-eared bat (Turner et al., 2011). A recent study that used the mist-netting data from the Monongahela National Forest as a large portion of their overall data found that capture rates were 10–37% lower in post-WNS years for the little brown bat, northern long-eared bat, small-footed bat, Indiana bat, and tricolored bat (Francl et al., 2012). These data are consistent with mathematical models that predict little brown bats, Indiana bats, northern long-eared bats, and tricolored bats have the potential to go extinct or to be extirpated from a large portion of their range in the coming years (Dzal et al., 2011; Ford et al., 2011; Frick et al., 2010; Thogmartin et al., 2013).

Management implications.—The results of this study indicate that populations of some species of bats are declining within the Monongahela National Forest. Although this trend is likely associated with the deadly white-nose syndrome, understanding habitat associations of each species that occupies the forest will allow biologists to protect and manage these bats. By understanding habitat associations of the bats of the Monongahela National Forest, forest managers will be able to locate rare species and to identify and protect quality summer habitat. Ultimately, the models constructed in this study will provide a strong tool for managers seeking to locate species on the forest or rank habitat quality.

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Table 1.—AUC score for training model and testing model ± standard deviation (*SD*), fraction predicted area (FPA), and associated probability (*P*) for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012.

Species[a]	$AUC_{training}$	AUC_{test}	test *SD*	FPA	*P*
COTO	0.969	0.966	0.021	0.268	<0.0001
EPFU	0.858	0.844	0.011	0.704	<0.0001
LANO	0.821	0.735	0.064	0.902	0.16
LABO	0.864	0.849	0.012	0.818	<0.0001
LACI	0.874	0.803	0.046	0.952	0.084
MYLE	0.926	0.949	0.011	0.677	<0.0001
MYLU	0.839	0.854	0.008	0.757	<0.0001
MYSE	0.773	0.771	0.006	0.844	<0.0001
MYSO	0.952	0.944	0.037	0.411	<0.0001
PESU	0.889	0.859	0.015	0.76	<0.0001

[a] COTO, Virginia big-eared bat (*Corynorhinus townsendii virginianus*); EPFU, big brown bat (*Eptesicus fuscus*); LANO, silver-haired bat (*Lasionycteris noctivagans*); LABO, eastern red bat (*Lasiurus borealis*); LACI, hoary bat (*L. cinereus*); MYLE, eastern small-footed bat (*Myotis leibii*); MYLU, little brown bat (*M. lucifugus*); MYSE, northern long-eared bat (*M. septentrionalis*); MYSO, Indiana bat (*M. sodalis*); and PESU, tricolored bat (*Perimyotis subflavus*). Cells are lumped when values are the same in adjacent columns.

Table 2.—Permutation of importance of different features for the MAXENT models that were created for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Species abbreviations are defined in Table 1.

Feature	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
Aspect	0.1	1	1.1	0.1	0	1.3	0.7	0.4	1.3	0
Distance to caves	63.6	9.4	0	1.4	3.7	5.7	7.1	2.5	5.2	1.2
Elevation	11.8	20.5	6.9	12.3	1.5	15.7	7.3	0	29.8	20.2
Forest age	0.1	0	0	0	0	0	0.6	0	0	0.3
Relative forest density	11.1	0.7	19.6	1.8	0.8	0.3	1.4	2.5	22.1	1.9
Forest type	3.8	27.7	9.9	33.8	23.6	43.2	27.5	50.5	0	20.1
Geology	7.1	1.1	0	1.5	0	1.1	0	0.9	23.6	2.3
Hydrologic features	1.3	10.8	40.8	20.7	34.3	13.7	39.2	10.5	11	30.2
Land-cover diversity	0	10.2	1.7	8.8	17.5	10.5	3.5	22.3	0	11.4
Land-cover type	1.1	18.5	10.5	18.6	18.6	6.9	12.5	10	6.9	12.4
Landscape pattern	0	0	9.6	0.7	0	0	0.2	0.3	0	0
Wetlands	0	0.1	0	0.4	0	1.5	0.1	0.1	0	0

Table 3.—Logistic output (probability of presence) of cardinal direction of aspect for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Direction	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
North	0.63	0.49	0.37	0.38	0.17	0.45	0.36	0.57	0.59	0.35
East		0.43			0.15		0.33			
South	0.57		0.36	0.37	0.17		0.36	0.55		
West	0.63		0.37	0.38		0.29		0.57	0.63	

Table 4.—Logistic output (probability of presence) of forest age by successional stage for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Stage	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
Early	0.63	0.485	0.37	0.38	0.16	0.45	0.32	0.57	0.63	0.35
Mid-early							0.46			0.38
Mid	0.58						0.36			0.35
Late	0.63									

Table 5.—Logistic output (probability of presence) of forest type (U.S. Forest Service, 1974) for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Forest type	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
Sugar maple-northern red oak	0.63	0.36	0.41	0.1	0.2	0.45	0.2	0.36	0.63	0.23
Mixed oaks		0.48	0.37	0.58			0.35	0.57		0.35
Mixed upland hardwoods				0.45		0.28	0.36	0.46		0.27
Beech						0.45	0.35			
Sugar maple-beech-yellow birch-red spruce				0.38						
Virginia pine-hardwoods				0.3			0.07	0.36		0.19
Northern red oak		0.73		0.45		0.88	0.37	0.46		0.27
Oak-eastern white pine		0.48				0.45	0.35			
unkwn/no data	0.45	0.03		0.35	0.15	0.2	0.2	0.22		0.17
Pitch pine	0.63	0.48	0.37	0.45	0.2	0.45	0.35	0.46	0.63	0.27
Black cherry-white ash-yellow poplar										
Chestnut oak										
Yellow poplar-white oak-northern red oak		0.58			0.23					
Red spruce-balsam fir		0.35		0.19	0.2		0.23	0.44		
Open		0.51		0.81	0.57		0.48	0.63		0.44
Red maple (dry site)		0.48		0.45	0.2		0.35	0.37		0.27
Birch								0.46		
Sugar maple-basswood										
Black oak-scarlet oak-hickory										
Red pine										
Eastern white pine		0.69		0.6			0.41	0.47		0.4
Upland shrubs		0.48		0.45			0.35	0.44		0.27
Black locust								0.46		
Lowland shrubs										

Forest type	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
Sugar maple	0.63	0.48	0.37	0.45	0.2	0.45	0.35	0.46	0.63	0.27
Hemlock										
White oak								0.48		
Tamarack								0.46		
Virginia pine										
River birch-sycamore										
Red maple (wet site)										
Eastern white pine-northern red oak-white ash										
Norway spruce										
Eastern white pine-hemlock										
Quaking aspen										

Table 6.—Logistic output (probability of presence) of geology by type of sedimentary rock for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Rock	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
Sandstone	0.63	0.49	0.37	0.45	0.17	0.48	0.36	0.57	0.65	0.4
Limestone				0.44		0.45				0.36
Shale	0.28			0.38					0.25	0.35
Alluvium	0.63			0.44					0.65	0.36
Shale/sandstone		0.30						0.41		
sandstone/ limestone		0.49						0.57		

Table 7.—Logistic output (probability of presence) of hydrologic feature by size of stream/river for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Feature	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
Upland	0.63	0.5	0.37	0.43	0.17	0.45	0.35	0.54	0.63	0.35
Small stream	0.8	0.55	0.7	0.55	0.34	0.57	0.48	0.67	0.84	0.64
Small river							0.57			0.84
Large river		0.84	0.87	0.8	0.75	0.93	0.8	0.87		

Table 8.—Logistic output (probability of presence) of land-cover types (National Land-cover Database, 2007) for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Land-cover	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
Open water	0.63	0.49	0.37	0.42	0.22	0.45	0.44	0.57	0.63	0.35
Developed, open space	0.85	0.8	0.56	0.69	0.5	0.74	0.56	0.73	0.82	0.6
Developed, low intensity	0.63	0.49	0.37	0.42	0.22	0.45	0.37	0.57	0.63	0.35
Developed, medium intensity										
Developed, high intensity										
Barren land										
Deciduous forest				0.38	0.17		0.36			
Evergreen forest		0.42		0.42	0.22	0.36	0.37	0.34		
Mixed forest		0.3		0.36		0.45	0.22	0.57		0.24
Shrub/scrub		0.49		0.42			0.37			0.35
Grassland/herbaceous										
Pasture/hay				0.53						
Cultivated crops				0.42						
Woody wetlands										
Emergent herbaceous wetlands										

Table 9.—Logistic output (probability of presence) of landscape pattern (proportion of forest, agriculture, and urban environments) for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Landscape	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
No data	0.6	0.49	0.29	0.36	0.17	0.45	0.41	0.53	0.63	0.35
Forest	0.63		0.37	0.38			0.36	0.57		
Agriculture	0.6		0.29	0.36				0.53		
Forest/ Developed										
Forest/ Agriculture										
Forest/ Developed/ Agriculture										
Agriculture – Developed										
Agriculture – Developed – Forest										

Table 10.—Logistic output (probability of presence) of wetland classification for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

Wetland	COTO	EPFU	LANO	LABO	LACI	MYLE	MYLU	MYSE	MYSO	PESU
No data (upland)	0.63	0.49	0.37	0.39	0.17	0.44	0.36	0.57	0.63	0.35
Unconsolidated bottom		0.42				0.11	0.32	0.47	0.56	
Emergent		0.48					0.36	0.55		
Scrub-shrub		0.6		0.5						
Forested		0.49		0.39						
Unconsolidated shore										
Rock bottom										

Figure 1.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Corynorhinus townsendii* on the Monongahela National Forest.

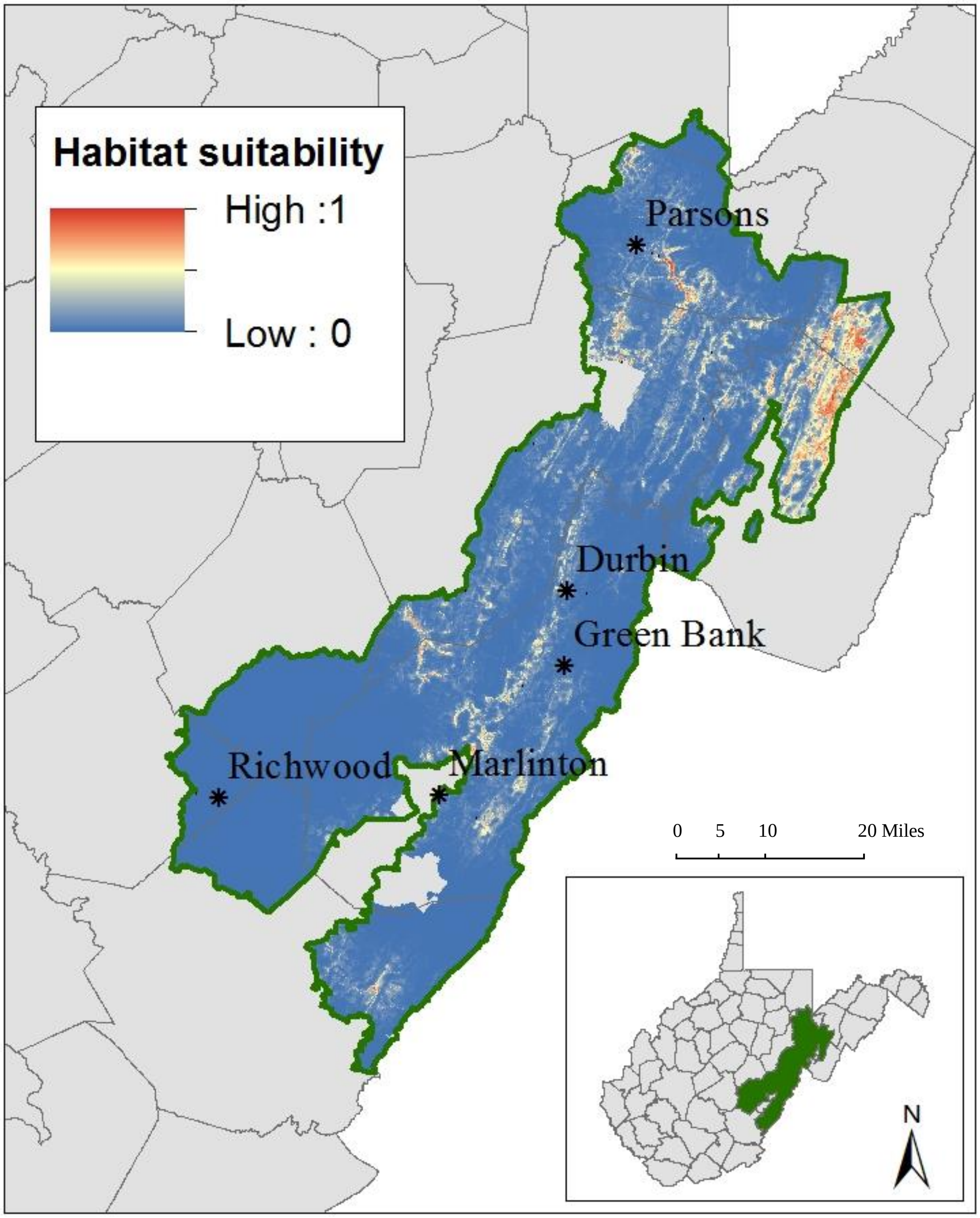


Figure 2.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Eptesicus fuscus* on the Monongahela National Forest.

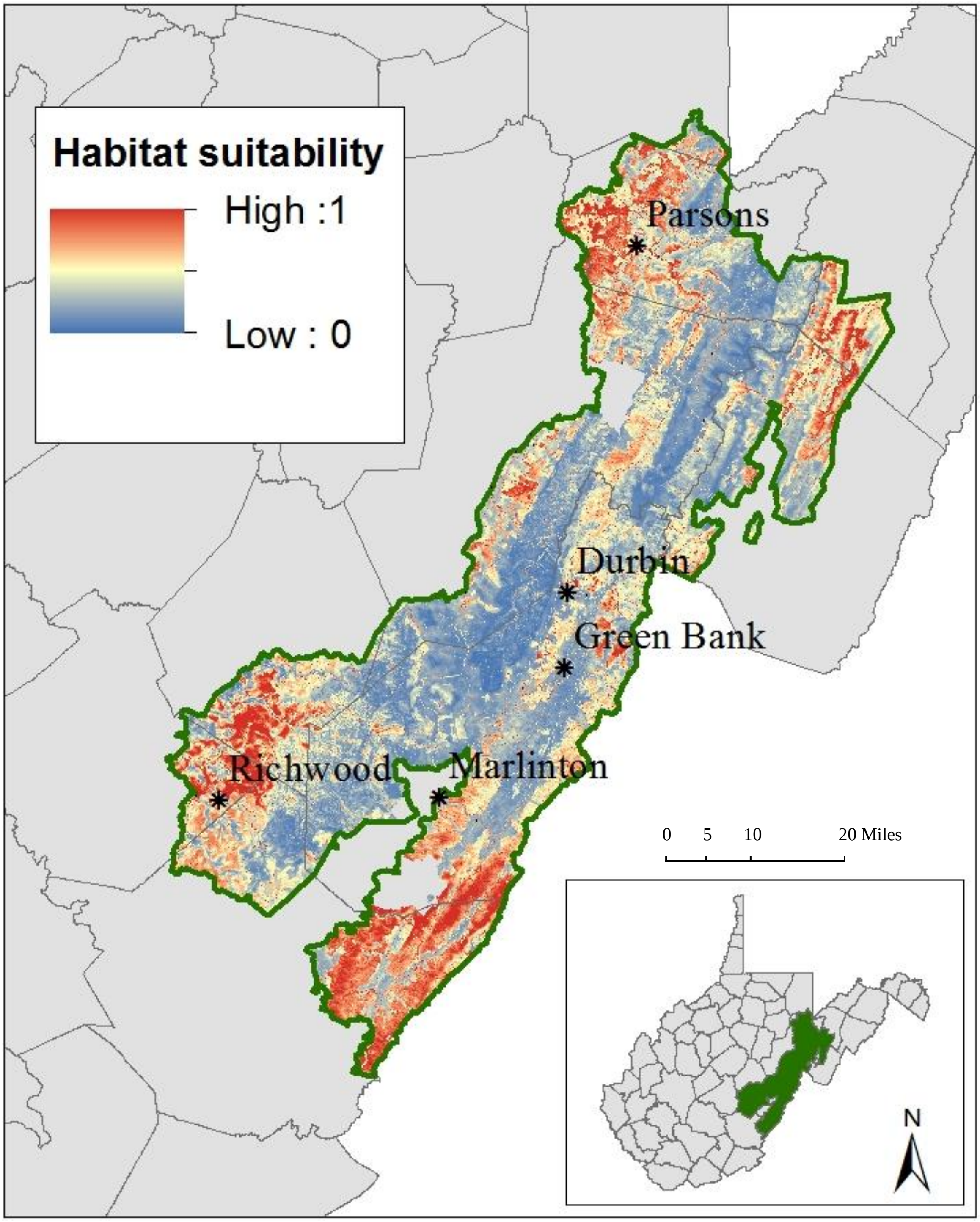


Figure 3.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Lasionycteris noctivagans* on the Monongahela National Forest

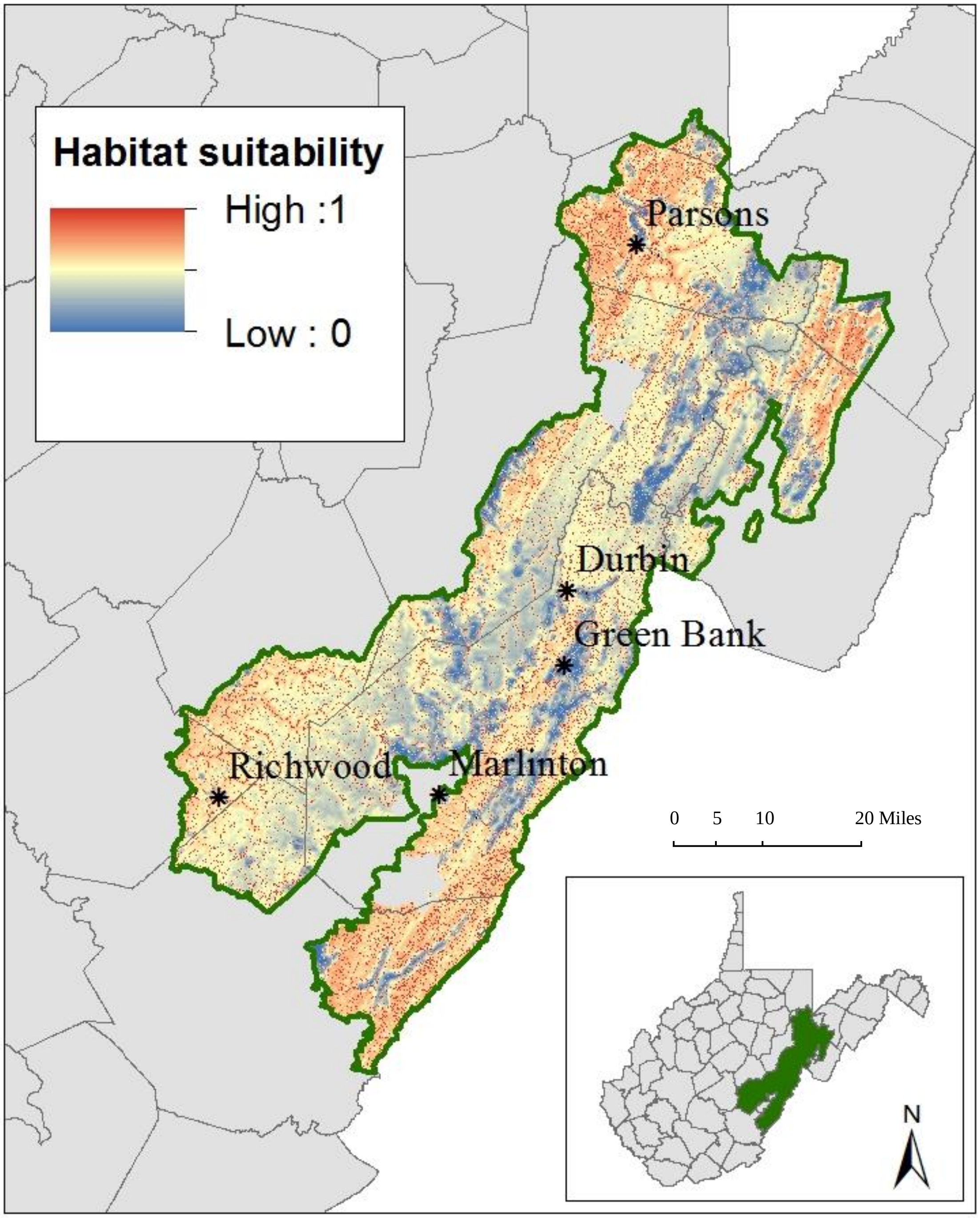


Figure 4.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Lasiurus borealis* on the Monongahela National Forest

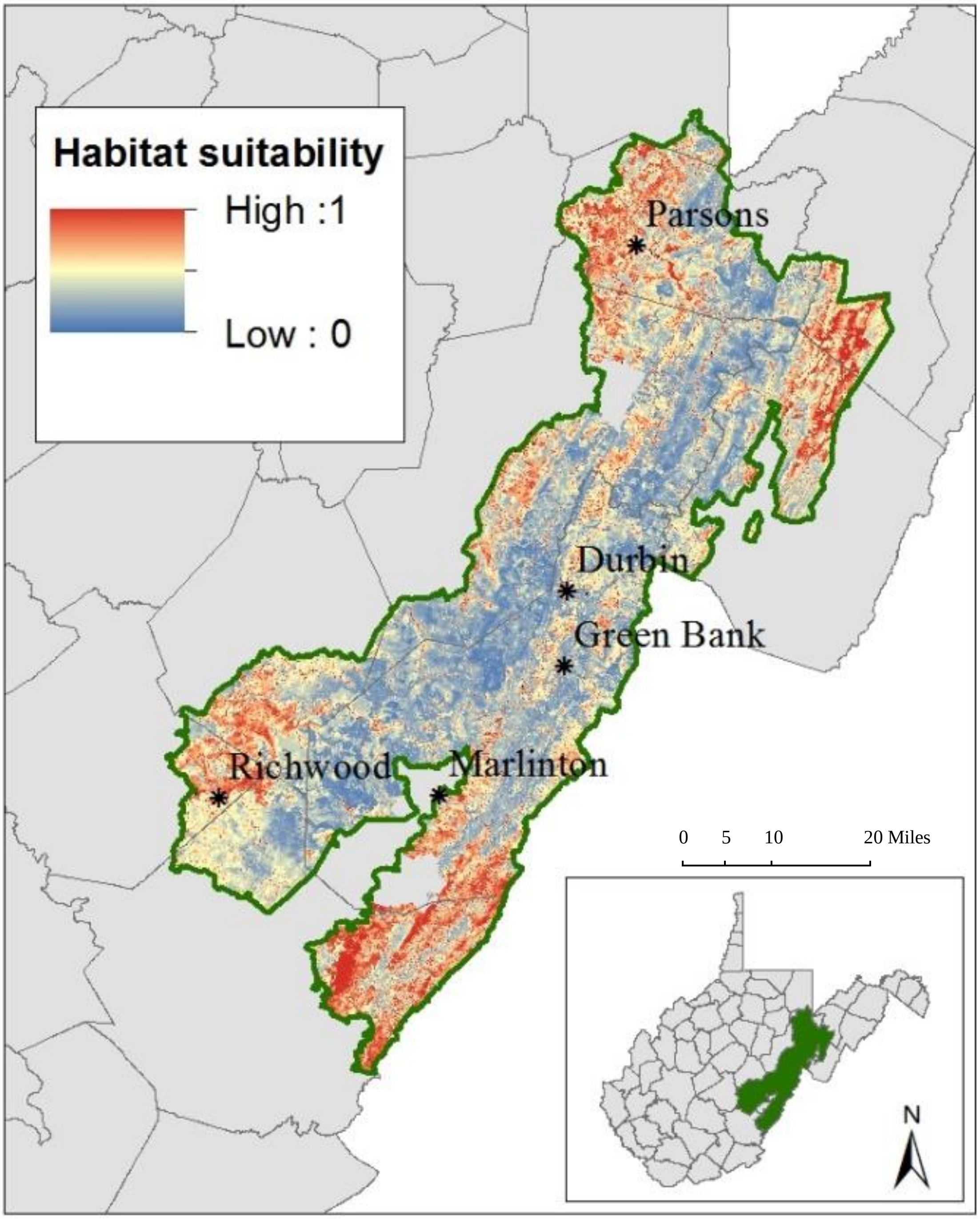


Figure 5.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Lasiurus cinereus* on the Monongahela National Forest

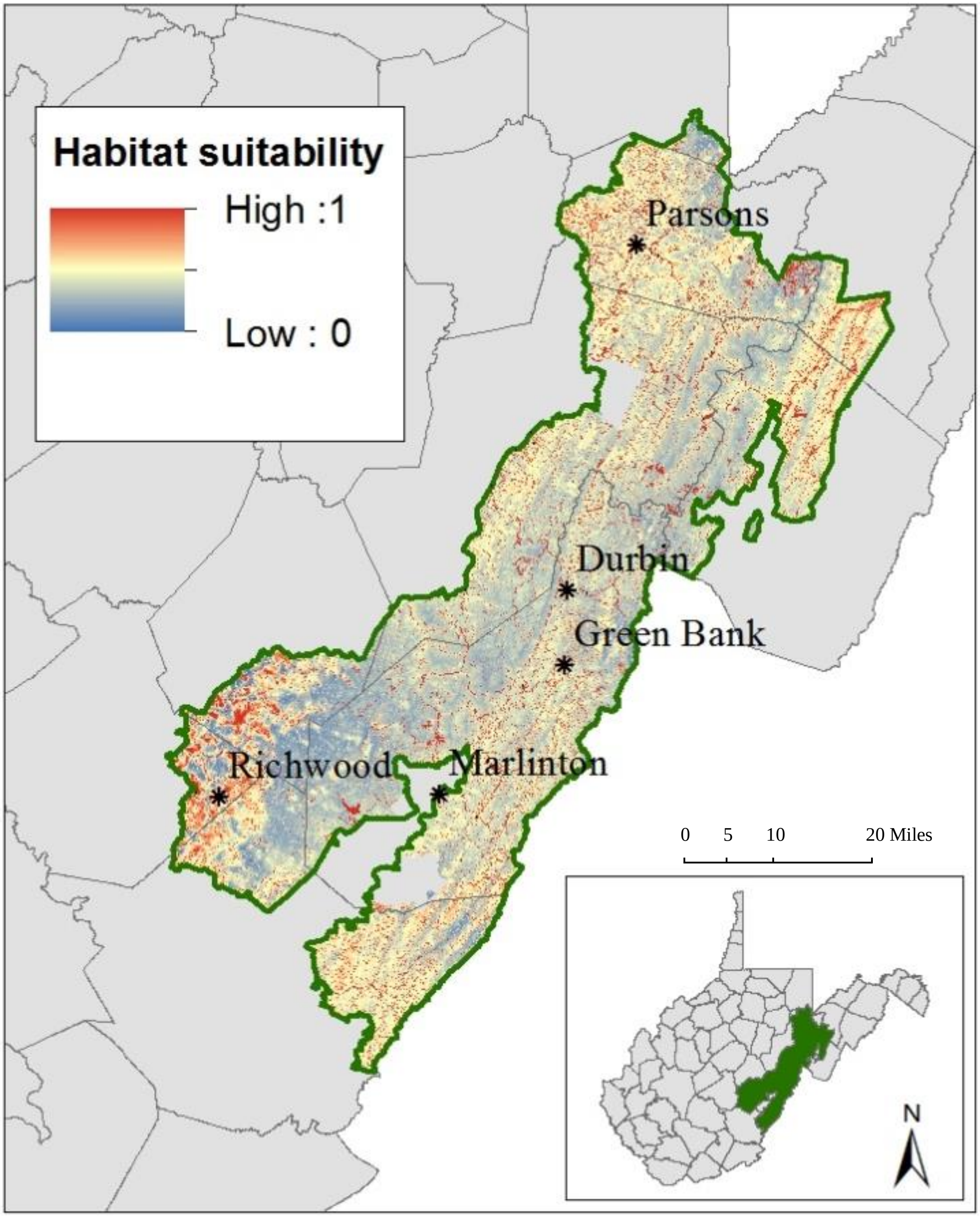


Figure 6.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Myotis leibii* on the Monongahela National Forest

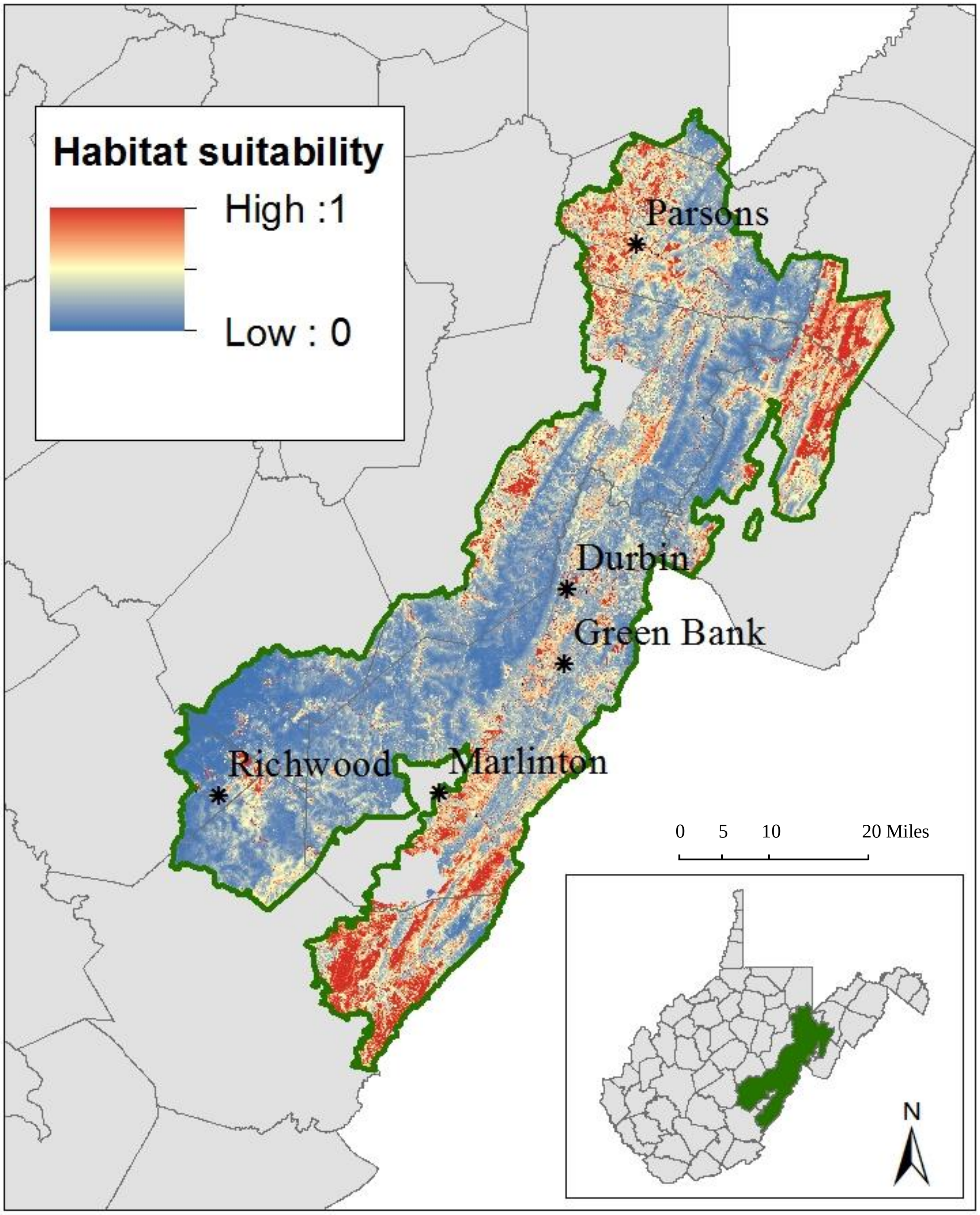


Figure 7.―Results of a MAXENT model predicting the distribution of (habitat suitability for) *Myotis lucifugus* on the Monongahela National Forest

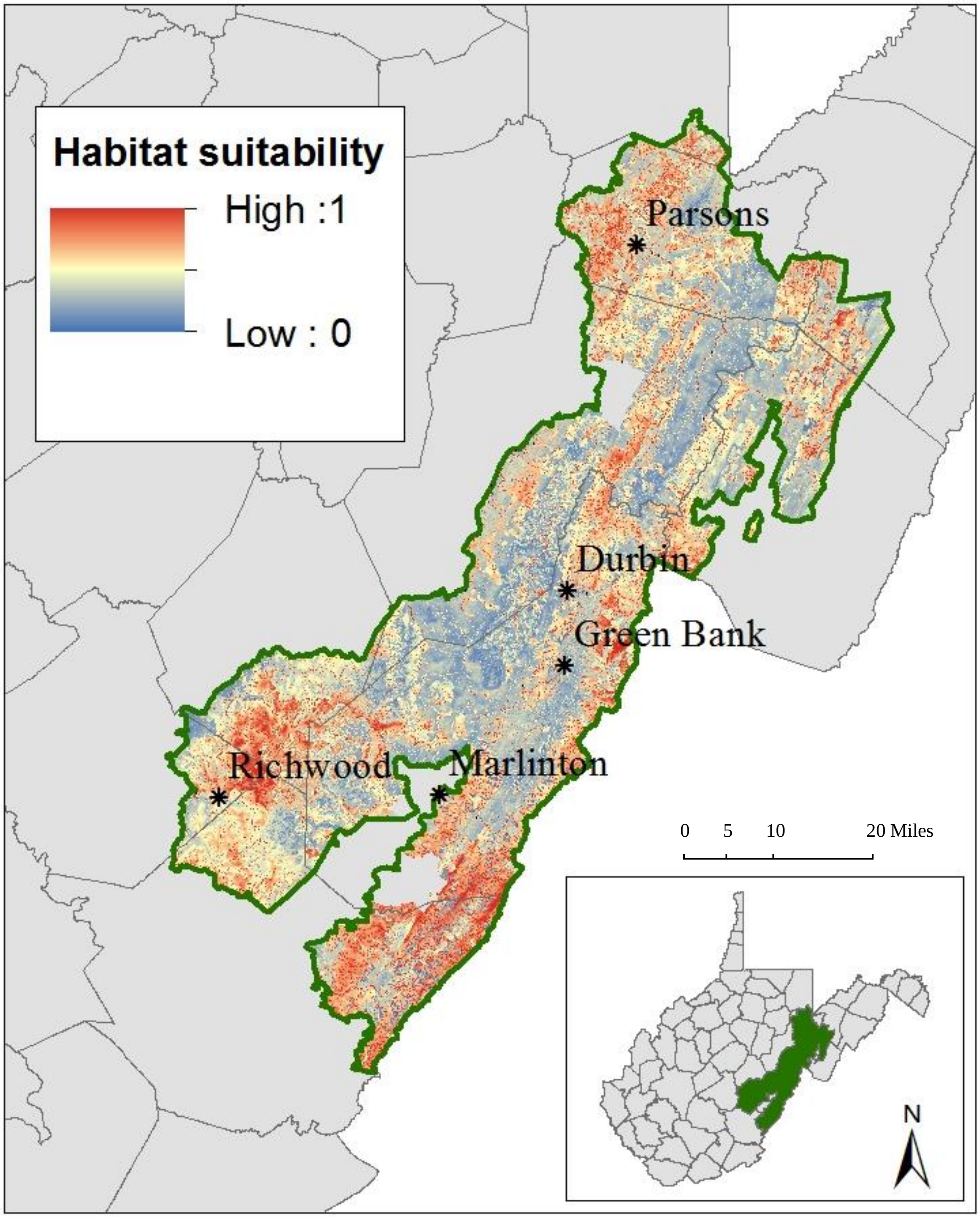


Figure 8.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Myotis septentrionalis* on the Monongahela National Forest

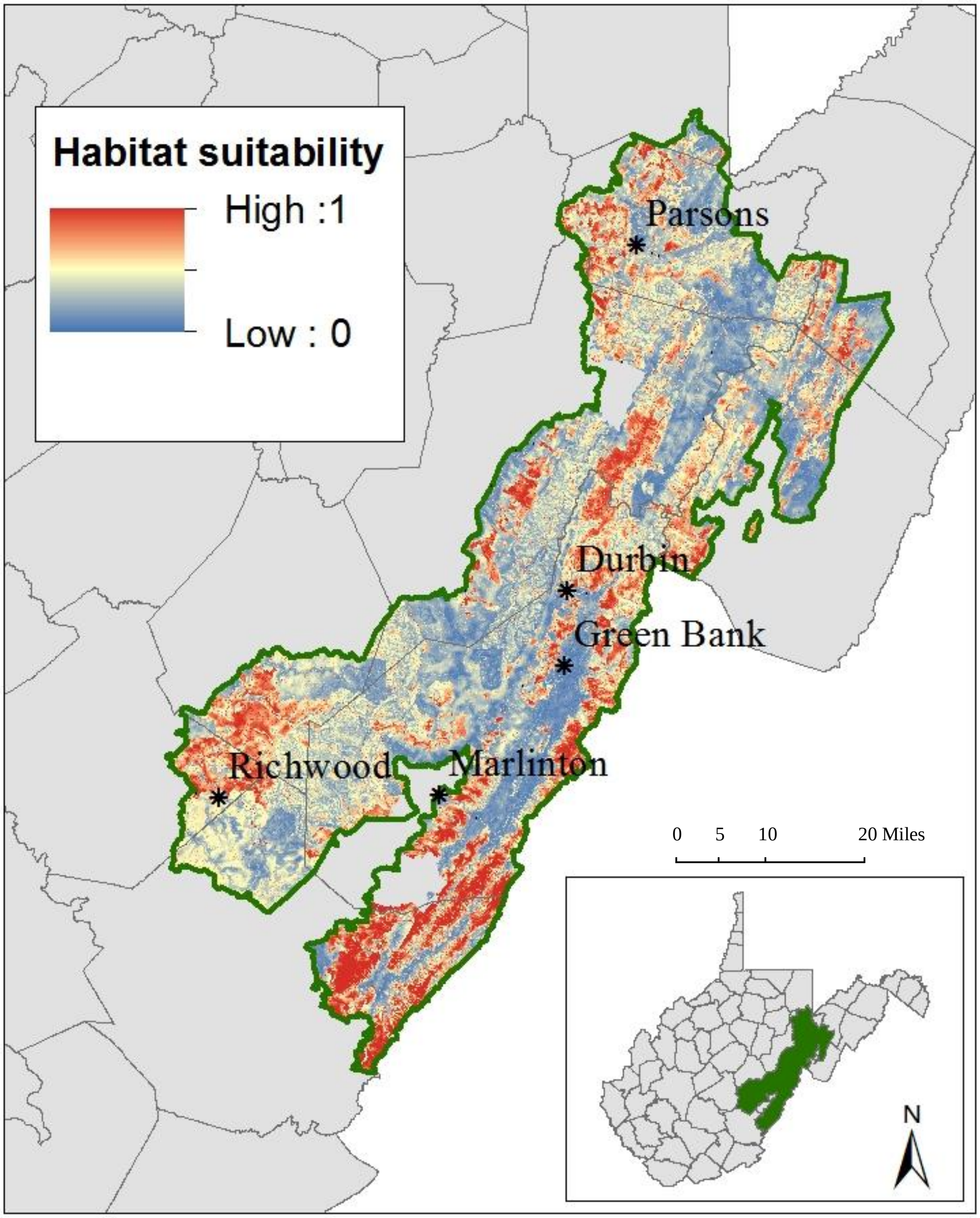


Figure 9.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Myotis sodalis* on the Monongahela National Forest

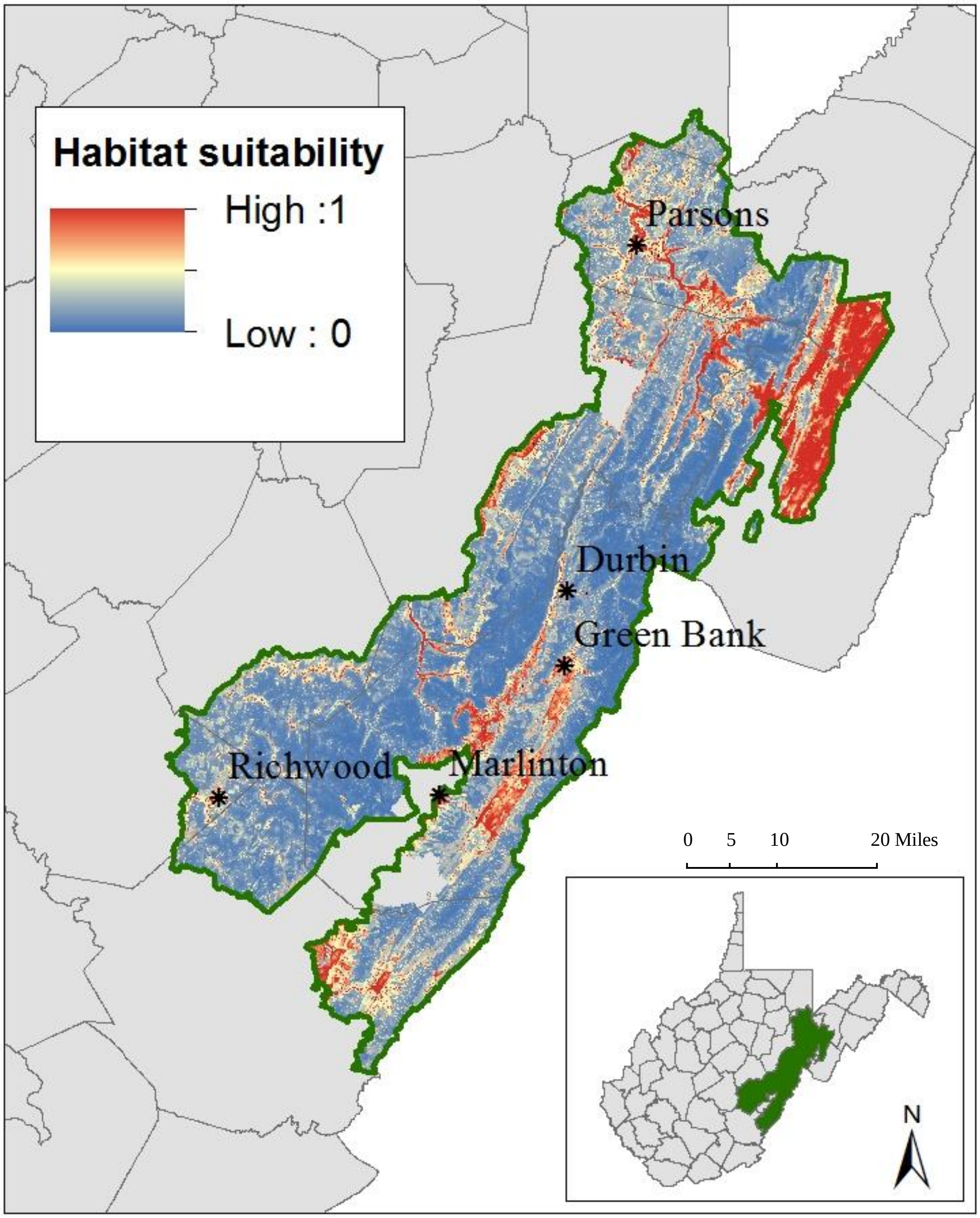


Figure 10.—Results of a MAXENT model predicting the distribution of (habitat suitability for) *Perimyotis subflavus* on the Monongahela National Forest

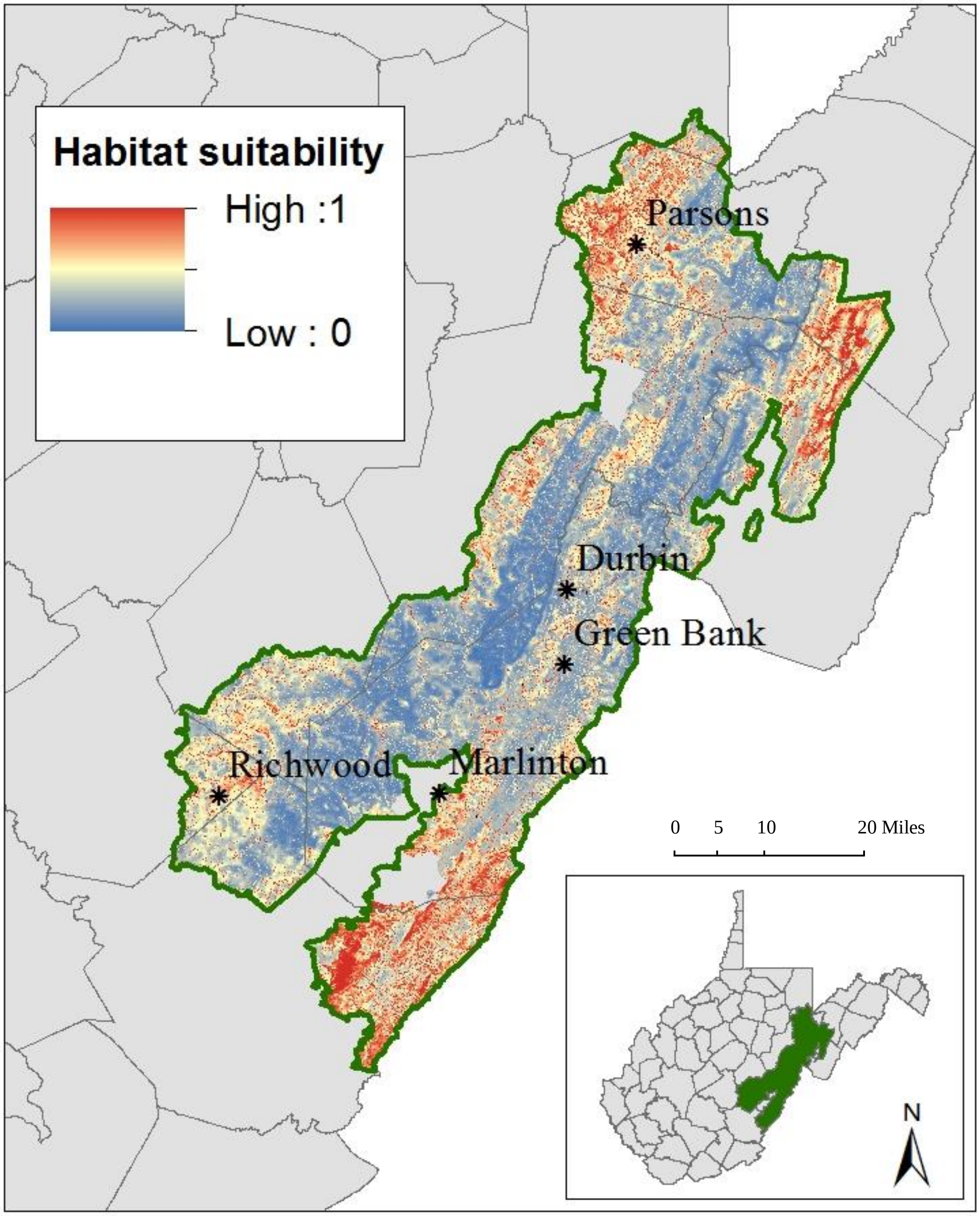


Figure 11.—Response curve relating probability of presence to distance from nearest cave, for the 10 species captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

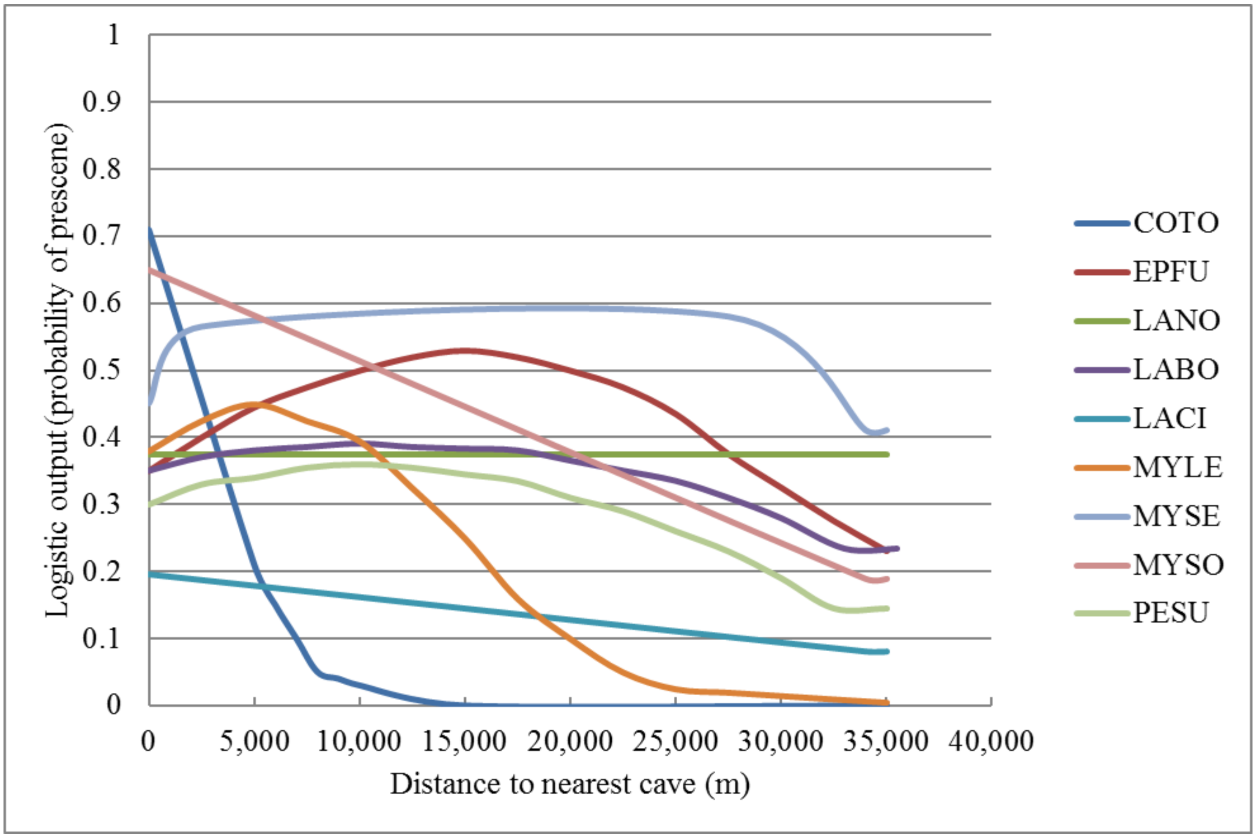


Figure 12.—Response curve relating probability of presence to elevation above sea level, for the 10 species captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

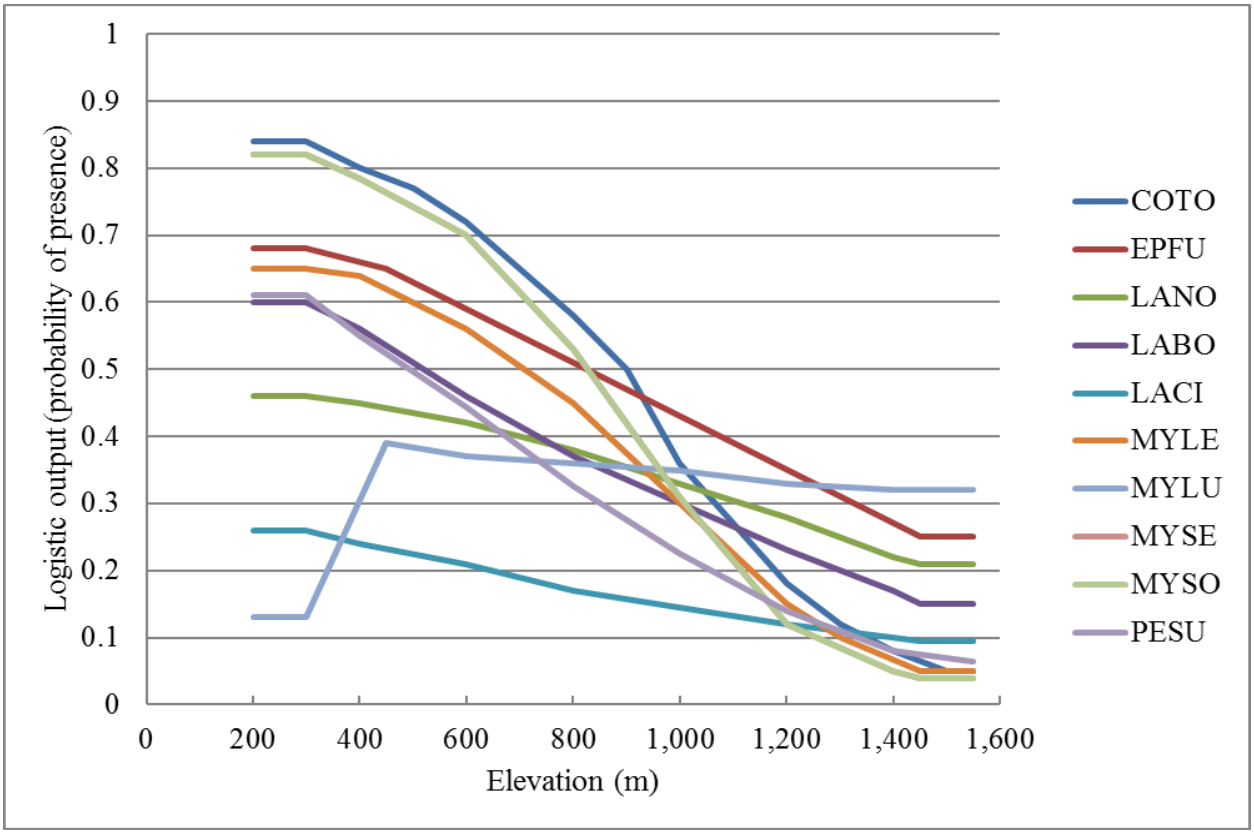


Figure 13.—Response curve relating probability of presence to relative forest density, for the 10 species captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

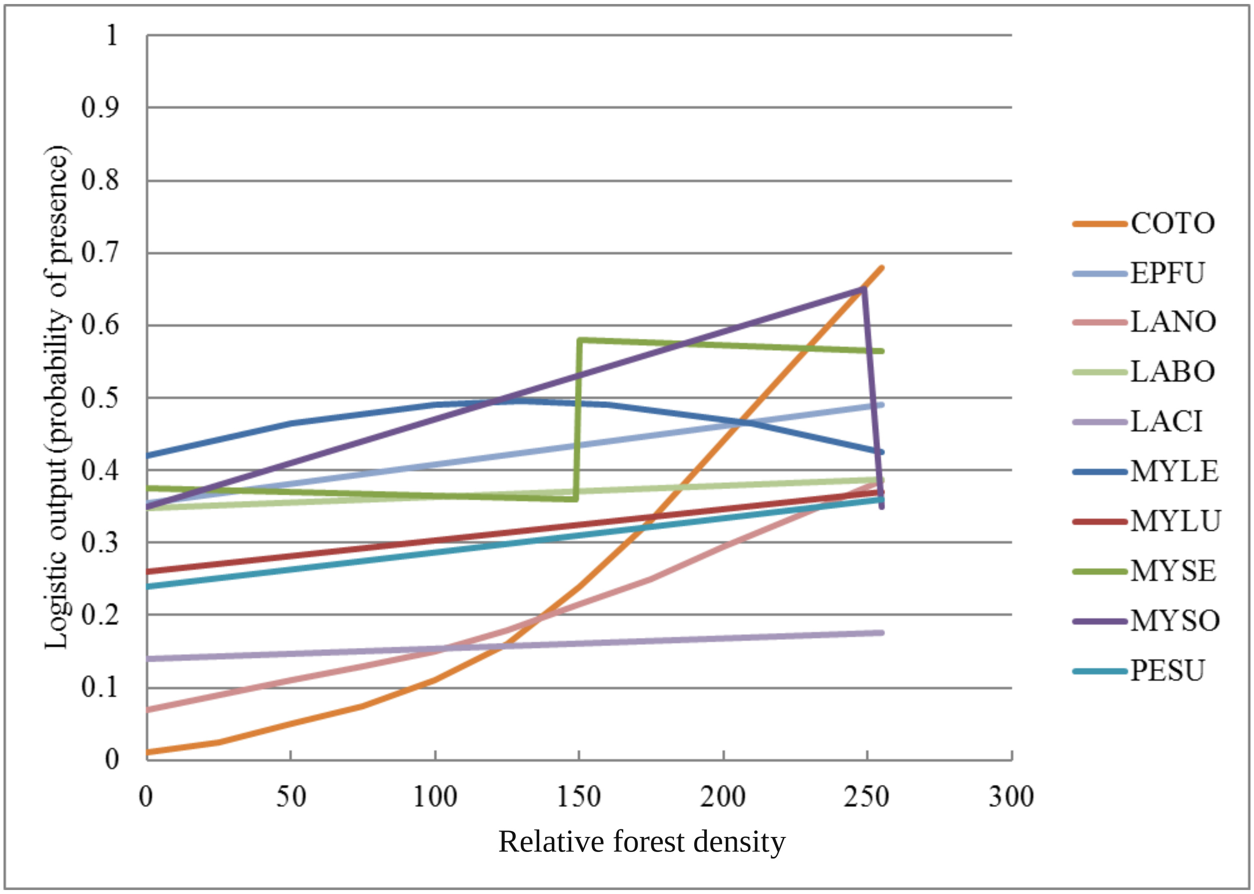


Figure 14.—Response curve relating probability of presence to diversity of land-cover based on Simpson's (1949) index of diversity, for the 10 species captured on the Monongahela National Forest between 1997 and 2012. Abbreviations for species are as in Table 1.

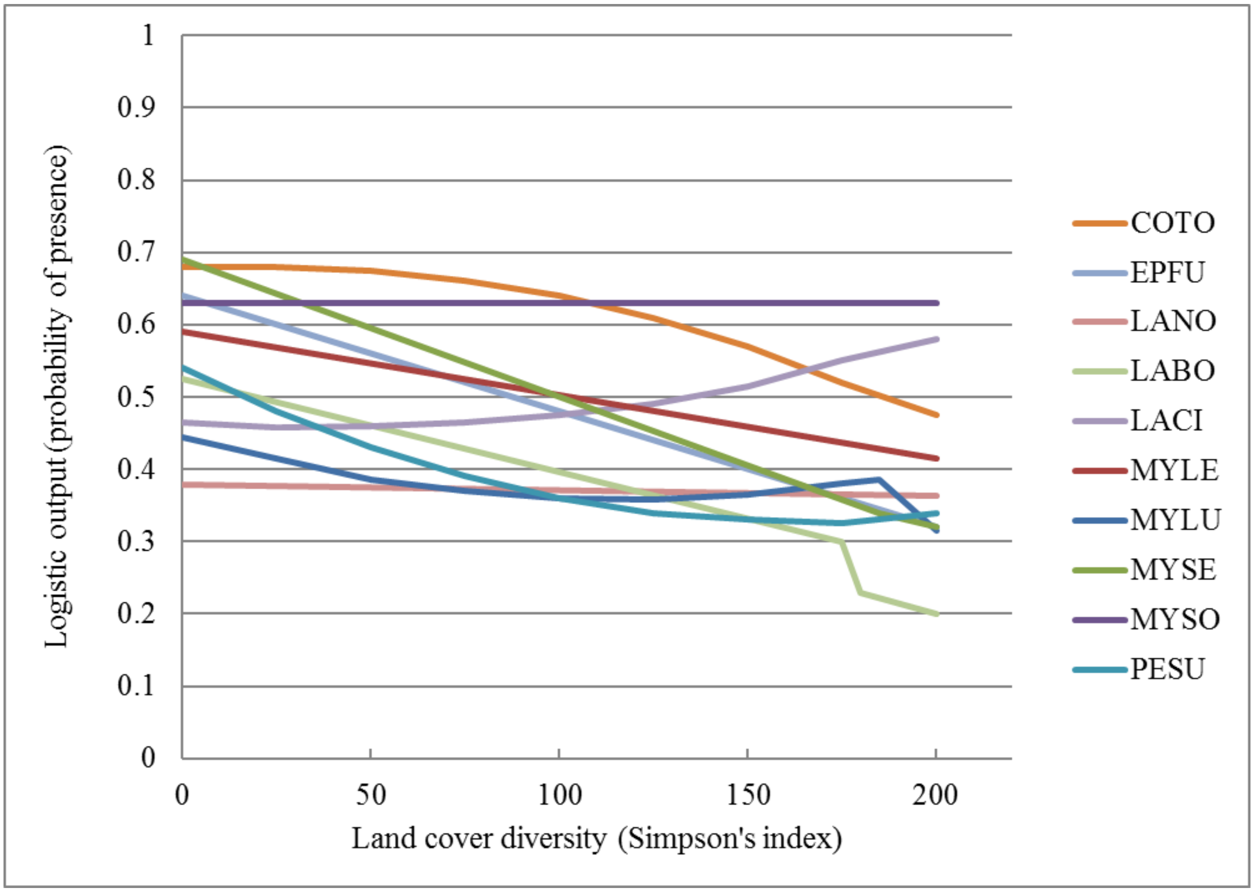


Figure 15.—Shannon-Wiener Index of Diversity of the bats of the Monongahela National Forest captured in mist-nets between 1997 and 2012.

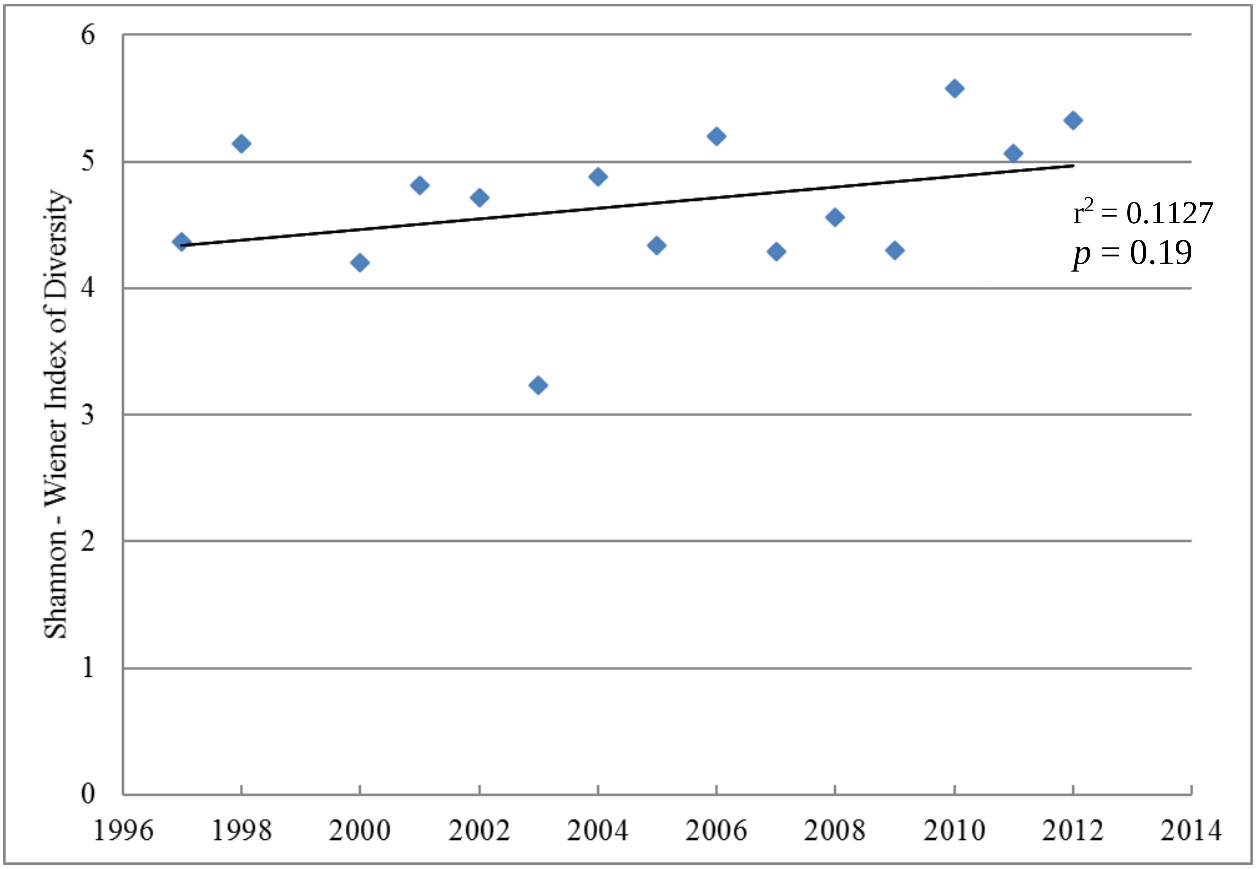
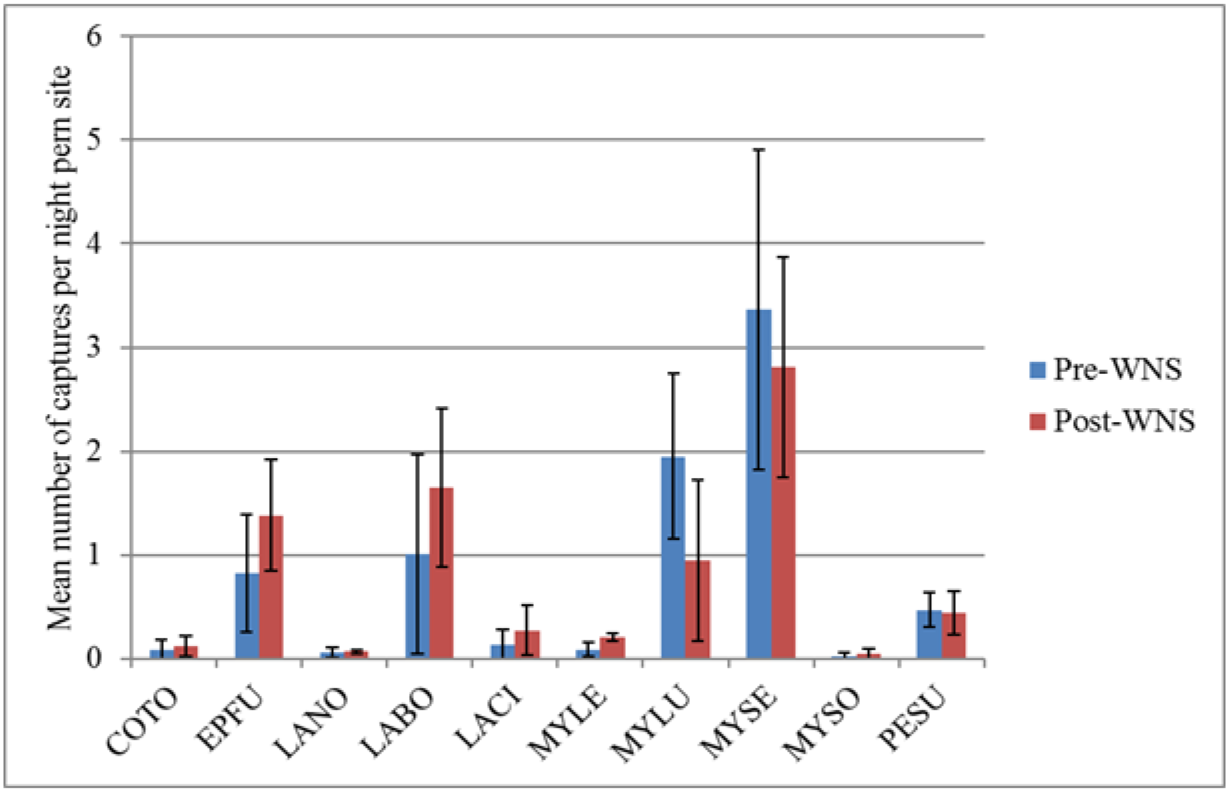


Figure 16.—Average number of bats of each species captured on the Monongahela National Forest per night per site between 1997 and 2012. Note logarithmic scale for y-axis. Abbreviations for species are as in Table 1.

Figure 17.—Number of bats (mean ± SD) captured at mist-netting sites per night at each site for 1997–2009 (pre-WNS) and 2010–2012 (post-WNS) on the Monongahela National Forest. Abbreviations for species are as in Table 1.



Appendix A

Accessory data on performance of the MAXENT models created for the 10 species of bats captured on the Monongahela National Forest between 1997 and 2012.

Species	Number of training samples	Regularized training gain	Unregularized training gain	Number of Test samples	Test gain	Number of Background points
COTO	98	1.91	2.58	24	2.80	10,098
EPFU	937	0.61	0.86	234	0.80	10,937
LANO	76	0.37	0.89	18	0.61	10,076
LABO	1080	0.64	0.88	269	0.87	11,080
LACI	156	0.89	1.52	38	0.97	10,156
MYLE	130	1.00	1.92	32	1.84	10,130
MYLU	1985	0.51	0.69	496	0.81	11,985
MYSE	3877	0.39	0.47	969	0.47	13,877
MYSO	40	1.11	2.16	10	2.20	10,040
PESU	538	0.82	1.14	134	0.94	10,538