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Research article

# A large-scale assessment of eastern whip-poor-will (*Antrostomus vociferus*) occupancy across a gradient of forest management intensity using autonomous recording units

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## ABSTRACT

Conservationists spend considerable resources to create and enhance wildlife habitat. Monitoring how species respond to these efforts helps managers allocate limited resources. However, monitoring efforts often encounter logistical challenges that are exacerbated as geographic extent increases. We used autonomous recording units (ARUs) and automated acoustic classification to mitigate the challenges of assessing Eastern Whip-poor-will (*Antrostomus vociferus*) response to forest management across the eastern USA. We deployed 1263 ARUs in forests with varying degrees of management intensity. Recordings were processed using an automated classifier and the resulting detection data were used to assess occupancy. Whip-poor-wills were detected at 401 survey locations. Across our study region, whip-poor-will occupancy decreased with latitude and elevation. At the landscape scale, occupancy decreased with the amount of impervious cover, increased with herbaceous cover and oak and evergreen forests, and exhibited a quadratic relationship with the amount of shrub-scrub cover. At the site-level, occupancy was negatively associated with basal area and brambles (*Rubus* spp.) and exhibited a quadratic relationship with woody stem density. Implementation of practices that create and sustain a mosaic of forest age classes and a diverse range of canopy closure within oak (*Quercus* spp.) dominated landscapes will have the highest probability of hosting whip-poor-wills. The use of ARUs and a machine learning classifier helped overcome challenges associated with monitoring a nocturnal species with a short survey window across a large spatial extent. Future monitoring efforts that combine ARU-based protocols and mappable fine-resolution structural vegetation data would likely further advance our understanding of whip-poor-will response to forest management.

## 1. Introduction

Forests of the eastern United States are largely dominated by uniformly aged, closed canopy forests (80–110 years old; Shifley et al., 2014). As such, many wildlife species that require forests with diverse structural conditions are in decline (Anders et al., 1998; Litvaitis, 2001; Boves et al., 2013; Fiss et al., 2020). Numerous conservation efforts are underway on public and private lands to increase the availability of

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diverse forest conditions to recover declining wildlife (Bauer, 2018; Shaffer, 2022). Monitoring programs associated with these efforts are essential for identifying factors that affect species responses to management and, thus, for facilitating adaptive management (Westgate et al., 2013). Indeed, ongoing efforts to enhance structural diversity in eastern forests have been accompanied by monitoring that assessed focal (Bauer, 2018; McNeil et al., 2020; Nareff et al., 2019) and non-focal species (Mathis et al., 2021; McNeil et al., 2023a) responses. Additional monitoring is needed to elucidate the degree to which other declining species benefit from various forest management practices, which form the basis for more holistic multi-species conservation strategies (Di Stefano et al., 2013).

The Eastern Whip-poor-will (*Antrostomus vociferus*; hereafter whip-poor-will) is a forest-dwelling species that benefits from structural diversity (Wilson and Watts, 2008; Akresh and King, 2016), but monitoring is needed to measure the effects of specific forest management actions. This nocturnal aerial insectivore inhabits forests of eastern North America (Cink et al., 2020; COSEWIC, 2022) and experienced an estimated 64% population decline (−1.9%, annually) from 1966 to 2019 (Pardieck et al., 2020). Factors thought to be contributing to whip-poor-will population declines include habitat loss and degradation due to human development, as well as the disruption of natural disturbance regimes (Spiller and Dettmers, 2019; COSEWIC, 2022).

Whip-poor-wills require early successional forest for foraging, and also use this successional stage and mature stands for nesting and roosting (Akresh and King, 2016; Spiller et al., 2022). Correspondingly, forest management has been recognized as an important tool for creating and maintaining stand- and landscape-scale conditions that encompass the range of habitat features attractive to whip-poor-wills (Wilson and Watts, 2008; Tozer et al., 2014; Farrell et al., 2017; Spiller and King, 2021). The whip-poor-will's breeding distribution falls within geographies heavily dominated by eastern deciduous forests (Cink et al., 2020). However, no studies have investigated factors that influence broad scale patterns of whip-poor-will occupancy among this forest type and associated management practices and landscape contexts. Given that forest management is a key influence on forest structure and composition in eastern forests (Shifley et al., 2014), it is imperative to understand the extent to which stand-level forest management practices satisfy the habitat needs of whip-poor-wills and to identify landscape contexts associated with high occupancy. Otherwise, conservation efforts that target breeding whip-poor-wills (*e.g.*, forest management) could be ineffective if conducted in inappropriate landscape contexts.

Although monitoring protocols have been created to standardize whip-poor-will population surveys over broad spatial extents, extensive monitoring regimes remain challenging for several reasons. For example, most whip-poor-will surveys are conducted from roads (*i.e.*, Nightjar Survey Network and Canadian Nightjar Survey) to avoid the challenges of navigating through off-road areas at night. However, road-based surveys greatly limit insights about the species' response to stand-level forest management, which often occurs away from public roads (Betts et al., 2007). Monitoring efforts are also limited by the brief temporal window for surveying whip-poor-wills, which sing predominantly on nights with the moon at least 50% illuminated (Wilson and Watts, 2006), a period less than a month in duration under ideal weather conditions. To overcome these challenges, low-cost 'autonomous recording units' (ARUs) can be deployed prior to the onset of a survey window and left *in situ* for the duration of a breeding season (Knight et al., 2022; Larkin, 2023; Markova-Nenova et al., 2023). Thus, the widespread deployment of ARUs across managed landscapes has significant potential to increase our understanding of habitat associations, population trends, behavior, response to forest management, and detectability of nocturnal birds, in ways traditional monitoring methods cannot.

In this study, we developed and implemented an ARU-based monitoring protocol to assess whip-poor-will occupancy across various silvicultural treatments, landscape contexts, and forest types in the eastern US. The objective of this study was twofold; 1) to assess territorial whip-poor-will occupancy across a gradient of canopy disturbance intensity resulting from forest management, and 2) to identify site- and landscape-level factors at various spatial scales that influence territorial whip-poor-will occupancy, in an understudied portion of the species breeding range. Based on past research, we hypothesized that whip-poor-wills would be positively associated with forest cover (English et al., 2017; Vala et al., 2020), shrub-scrub cover and understory woody stem density but negatively associated with urban development (i.e., impervious cover) and basal area (Spiller and King, 2021; Souza- Cole et al., 2022). We discuss our findings in the context of assessing whip-poor-will ecology and its response to conservation efforts that target other wildlife species, in addition to implications for implementing ARU-based surveys across large spatial extents.

## 2. Methods

### 2.1. Study area

We studied whip-poor-will occupancy in forests ranging from western North Carolina to southern Maine (Fig. 1). This geography encompasses a diversity of forest types dominated by oak-hickory and northern hardwoods. Stands monitored were between 0 and 110 years post-disturbance. Tree species composition varied across survey locations; however, most sites were dominated by deciduous species (*e.g.*, *Acer* spp., *Betula* spp., *Carya* spp., and *Quercus* spp.), with few (<8%, n = 103) locations having a significant evergreen component (>10% within 250 m; *Pinus* spp., *Picea* spp., and *Tsuga canadensis*). Understory vegetation composition and heights ranged from low (<2 m) herbaceous vegetation, shrubs, saplings, and brambles to tall (>2 m), dense, regenerating closed-canopy sapling stands. Elevations ranged between 6 and 1199 m above sea level.

### 2.2. Forest management treatments

Survey locations occurred on public and private lands and represented a continuum of forest management intensities ranging from recent clearcuts and partial timber harvest to closed-canopy forest. Closed-canopy forest (Fig. 2) included stands that were 21–110 years old. Basal area, tree size/spacing, and under-/mid-story structure varied among closed canopy stands depending on human and natural disturbance history and site conditions. Stands that had been recently treated (*i.e.*, <20 years) were either shelterwood or overstory removal harvests. Shelterwoods in our study were <10 year-old commercial harvests and non-commercial treatments that resulted in stand basal areas between 9 and 21 $m^2$/ha (40–90 $ft^2$/ac). Overstory removals (Fig. 2) in our study were <20 years old and included commercial harvests and non-commercial treatments that resulted in stands with basal areas between 0 and 7 $m^2$/ha (0–30 $ft^2$/ac). Stands within this treatment category were either in 1) the stand initiation stage (i.e., <10 years post-treatment) with a mix of herbaceous, shrub, saplings, and scattered residual trees, or 2) the early stem exclusion phase (i.e., 10–20 years post-treatment) with a mostly intact canopy of saplings and shrubs (<5 m tall) and a minimal herbaceous component.

### 2.3. Whip-poor-will survey locations

Study sites were associated with three forest bird monitoring programs: NRCS's Conservation Effects Assessment Project and National Fish and Wildlife Foundation's Delaware River Watershed and Central Appalachians Programs. These included 504 locations on private forests enrolled in Natural Resource Conservation Service's (NRCS) conservation programs that target other at-risk forest species (Working Lands for Wildlife [WLFW] Golden-winged Warbler [*Vermivora chrysoptera*; GWWA] and New England Cottontail [*Sylvilagus transitionalis*; NEC] and Regional Conservation Partnership Program [RCPP] Cerulean Warbler

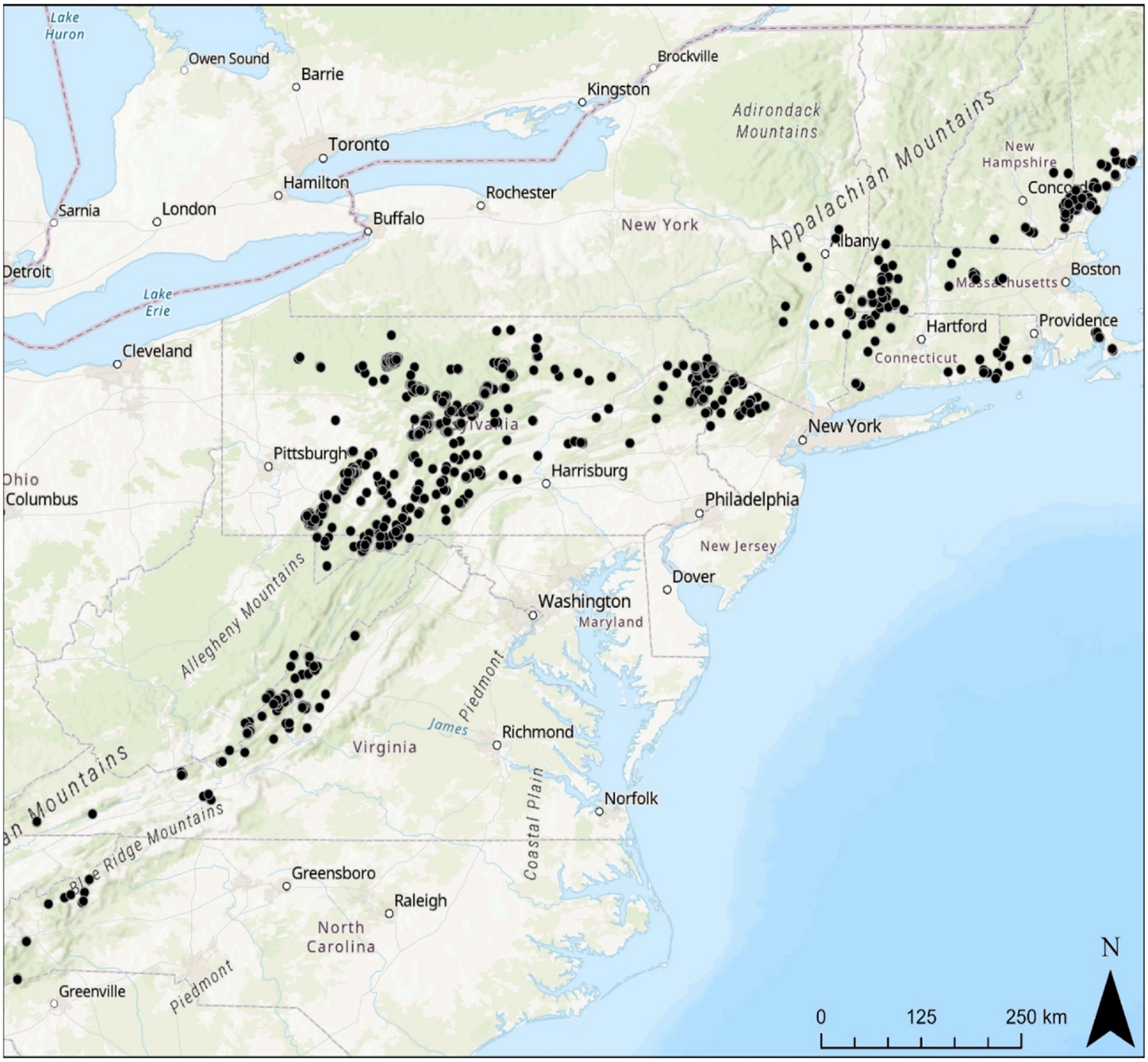

**Fig. 1.** Locations of autonomous recording units (n = 1263) deployed to monitor Eastern Whip-poor-wills within managed and unmanaged forest communities ranging from western North Carolina to southern Maine from April–July 2020 and 2021. Note: Each private land survey location was shifted in a random direction 0–25 km to preserve landowner privacy.

[*Setophaga cerulea*; CERW]) and 759 locations on public forests managed by various state/federal agencies and private forests managed by non-government organizations (Pennsylvania = 640; Virginia = 70; New Jersey = 8; Massachusetts = 17; NH = 18; and Maine = 6). Further details regarding the selection of survey locations are provided as supplemental material. At each site, random survey locations were generated using ArcMap 10.8.1 (Environmental System Research Institute, Redlands, CA) with the "Create Random Points" tool. We ensured that all survey locations used in our study were spaced a minimum of 500 m apart to maintain spatial independence of points (Bibby et al., 2000); past studies have reported whip-poor-will home range size to average 5 ha (~128 m radius circle; Cink et al., 2020; Hunt, 2013). Adhering to the above criteria, we generated 1263 unique survey locations that we included in our study (Fig. 1).

### 2.4. *Autonomous recording units and Acoustical processing*

We used ARUs (AudioMoths, Open Acoustic Devices) to collect audio recordings at each survey location during allowable nightjar survey windows which occurred between late April–July 2020 or 2021 (one season per location; nightjars.org, Hill et al., 2019; Larkin, 2023). ARUs were configured with AudioMoth firmware version 1.5.0, to have a 32 kHz sample rate, medium gain, and produce 16-bit WAV files. Units were programmed to record for 2 h after sunset (2100–2300 EST) onto a 64 gigabyte micro- Secure Digital (SD) card. We attached an ARU to a woody stem at each survey location at a height of 1.5–2m (see Larkin, 2023 for additional deployment details). After recovering ARUs from the field, we downloaded recordings and split recordings into 5-s clips using the Python package, OpenSoundscape version 0.6.1 (Van Rossum and Drake, 1995; Lapp et al., 2023). Clips were then processed through a binary, single target automated classifier (see supplemental materials for information on classifier development; Fig. A1) developed using whip-poor-will song recordings we collected and from Xeno-Canto (xeno-canto.org). The classifier assessed each clip for the presence of whip-poor-will songs and then assigned a score to the clip, with higher scores indicating increased likelihood that the clip contained a whip-poor-will song.

To assess the accuracy of our classifier, we listened to top scoring 5-sec clips from each survey location (3465 clips; Fig. A2). This process enabled us to determine a threshold score above which we detected no false positives. After determining the threshold score of 4.3 (Fig. A2), we randomly selected and listened to an additional 1500 clips with scores

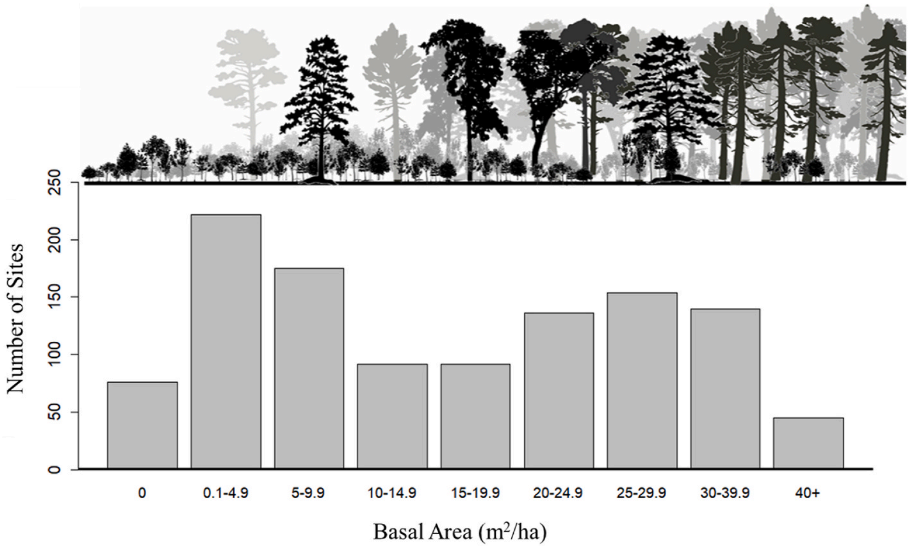

**Fig. 2.** Graphic displaying the gradient of canopy disturbance conditions that were monitored for Eastern Whip-poor-wills (top) and a barplot that displays the number of sites within each basal area range (bottom). Sites with these conditions ranged from western North Carolina to southern Maine and were monitored from April–July 2020 and 2021.

$\geq$4.3 to further ensure no false positives. We assessed site occupancy by referring to the daily top scoring clip for each survey location. If the clip score was $\geq$4.3 threshold, we considered the site to be occupied and if the clip score was <4.3, unoccupied. Using these data, we were able to create a daily occurrence history for each survey location whereby “1″ denoted a whip-poor-will detection and “0″ denoted a non-detection.

### 2.5. Vegetation sampling

We conducted bi-radial vegetation surveys centered on each ARU, after leaf out in late June and early July, to quantify several vegetation metrics. The vegetation survey had three components: 1) basal area prism sweeps, 2) 1 $m^2$ ground cover plots, and 3) 10 $m^2$ woody regeneration belt transects. Specifically, 35-m transects were oriented in 2 of 3 randomly selected bearings (0°, 120°, and 240°) radiating from plot center. At the end of each transect and at plot center we used a 2.3 $m^2$/ha factor wedge prism to estimate tree basal area and averaged the three estimates for a site-wide basal area value. We sampled ground cover within three 1 $m^2$ plots located at the end of each transect and at plot center. Within each 1 $m^2$ plot, we recorded the presence of the following: woody seedlings (<0.5m tall), herbaceous vegetation, leaf litter, bare ground/rock, brambles (*Rubus* spp.), and ferns. Lastly, along both 35 m transects we counted all woody stems >0.5 m in height and <10 cm diameter breast height (DBH) within a 1 × 10 m belt transect that ran from 15 to 25 m from plot center. Of the 1263 survey locations considered in our analyses, 127 did not have associated vegetation data.

### 2.6. Landscape assessment

We used the *extract* function in the “raster” package in program R (Hijmans et al., 2015, R Core Team, 2020), to characterize the local landscapes surrounding each survey location at the following spatial extents: 250, 500, 750, 1000, 1250, 1500, and 1750 m. These spatial extents were found by previous research to characterize whip-poor-will habitat associations (Hunt, 2013; Tozer et al., 2014; Vala et al., 2020). We used the 2019 National Land Cover Dataset (Dewitz, 2021) raster to quantify the percent composition of barren land, cultivated crops, hay/pasture, shrub-scrub, herbaceous, evergreen forest, mixed forest, wetland (emergent and woody combined). We used the 2019 NLCD “Urban Imperviousness” layer to quantify human development surrounding each survey location (Dewitz, 2021). We used the US Forest Service’s Forest Inventory and Analysis dataset (USDA Forest Service, 2008) to quantify forest community types (Oak [Oak-Hickory and Oak-Pine combined], Maple-Beech-Birch, White-Red-Jack pine, Spruce-Fir, Loblolly-Shortleaf pine, and Elm-Ash-Cottonwood), and the 2010 United States Geological Survey’s Global Multi-resolution Terrain Elevation Data (Danielson and Gesch, 2011) to quantify elevation at each survey location.

### 2.7. Data analysis

We considered a site ‘occupied’ by a territorial whip-poor-will if two detections (scores $\geq$4.3) were $\geq$10 days apart (Bibby et al., 2000) and excluded all survey locations with <10 days of data from our analyses. This criterion was determined by Bibby et al. (2000), who suggested a site be considered occupied by a territorial nocturnal/crepuscular species only if it is detected on at least two counts spaced at least ten days apart. This is a standard approach used by other studies to classify territoriality (e.g., Akresh et al., 2015; Broughton et al., 2018). To reduce the potential for false negatives in our dataset, we manually reviewed the daily detection scores between 3.0 and 4.3 for all the sites that we considered unoccupied based on our above criteria ($\geq$2 detections at least 10 days apart). This step resulted in changes to the occupancy designation of only two sites. We modeled whip-poor-will occupancy using Generalized Linear Models (GLM) fit to a binomial distribution in R (R Core Team, 2020). We chose to use GLMs instead of occupancy models because preliminary single-season occupancy analyses revealed that cumulative detection probability approached 1.0 after only four nights of recording (daily detection probability = 0.54; cumulative detection probability ($\hat{p}$): $1\text{-}(1\text{-}0.54)^4 = 0.96$), thus eliminating the need to account for imperfect detection in our analyses (MacKenzie et al., 2002). Further, we assessed whether occupancy was positively correlated with days of recording using a Wilcoxon test and found that this was not the case (the opposite was true; W = 137,714, p = 0.004248), an unexpected coincidence driven by the order in which we recovered ARUs from the field with units at higher quality, managed sites being recovered first.

We created a separate model set for three decreasing spatial scales: regional, landscape, and site-level; and compared models within each of these sets using an information-theoretic framework (Burnham and Anderson, 2002). Regional and landscape variables were modeled separately because we expected them to influence one another, and we were interested in the broad patterns described by variables in each set. This approach was useful for examining ecological variables associated with potentially different ecological processes (McGarigal et al., 2016; Hingee et al., 2022). We considered three predictor variables for inclusion in our "regional" model set (Tables A1 and A2). Prior to constructing our "landscape" model set we first removed from further consideration any cover type that occurred at <10% of our survey locations. Then, we ran univariate models for each of the remaining landscape variables to determine the spatial extent that best predicted whip-poor-will occupancy. Univariate models were ranked using Akaike's Information Criterion adjusted for small sample size ($AIC_c$, Burnham and Anderson, 2002), and the spatial extent contained in the top model for each landscape variable was used in our "landscape" model set (Table A3; Willey et al., 2022).

We considered 18 and 10 predictor variables for inclusion in our "landscape" and "site-level" model sets, respectively (Tables A1 and A2). We included quadratic terms for four variables in our landscape model set (shrub-scrub [Akresh and King, 2016], wetland [Vala et al., 2020], forest [Vala et al., 2020], and barren land [Grahame et al., 2021]) and two in the site-level model set (basal area and woody stem density), because published literature suggests that these variables may be optimized for whip-poor-wills at intermediate values or have non-linear relationships (Spiller et al., 2022). As such, we examined all subsets of variables in our global model in such a way that linear and quadratic versions were both tested and that a quadratic term never appeared without a linear term (but linear could appear without quadratic). Before creating the final regional, landscape, and site-level model sets, we tested for correlation among all variables within each model set by calculating pairwise Pearson's Correlation Coefficients. Variables that had correlation coefficients ≥±0.6 were considered correlated (Sokal and Rohlf, 1969). If two variables were correlated, we excluded from further analyses the variable with the least potential influence on whip-poor-will ecology based on published literature. The following terms were included in our final model sets: Regional ($n = 2$; latitude, and elevation); Landscape ($n = 13$; % barren land [1500 m], % barren land$^2$ [1500 m], % cultivated crops [1750 m], % hay/pasture [1250 m], % shrub-scrub [1500 m], % shrub-scrub$^2$ [1500 m], % herbaceous [750 m], % evergreen forest [1750 m], % mixed forest [250 m], % forest [250 m], % forest$^2$ [250 m], % imperviousness [500 m], and % Oak [1500 m]); and Site-level ($n = 10$; leaf litter, woody seedlings, herbaceous, fern, brambles, bare ground, basal area [$m^{2/}ha$], basal area$^2$ [$m^{2/}ha$], woody stem density [stems/10 $m^2$], and woody stem density$^2$ [stems/10 $m^2$]). We did not include a variable for treatment type (overstory removal, shelterwood, closed-canopy) in our analyses because there is considerable variation in vegetation structure across sites within a given treatment type. This variation can be driven by differences in many site-level factors (*i.e.*, soil quality, time since treatment, site history, browse pressure, and amount of residual canopy cover). Moreover, the vegetation metrics we collected and included in our site-level model set are those that forest managers desire from studies that examine wildlife species-vegetation relationships (Lott et al., 2021).

We created all possible combinations of five or fewer variables in each model set using the function *dredge* in the package "MuMIn" (Bartoń, 2022). We restricted the number of variables to a maximum of five to identify the best models that predicted whip-poor-will occupancy while keeping models relatively simple (Burnham and Anderson, 2002). In doing so, we only considered models with the most influential variables rather than constructing more parameterized models with many variables. We did not employ model averaging to ensure that model estimates and predictions were easily interpretable (Cade, 2015). We considered variables that were included in models within two $\Delta AIC_c$ of the top model of each set, and those with β 95% confidence intervals not including zero to have meaningful biological effects (Chandler et al., 2009; Arnold, 2010). Our model-building procedure resulted in 4 regional, 1727 landscape, 466 site-level models (Tables A4, A5, and A6).

We predicted whip-poor-will occupancy using coefficients from variables that had meaningful biological effects in our highest ranked landscape model across portions of Bird Conservation Regions 13, 14, 28, 29, and 30 (nabci-us.org) clipped to HUC 8 watershed boundaries within our study area. Lastly, to assess model fit we calculated Area Under the Curve (receiver operating characteristic; AUC) and Brier score using 10-fold cross validation for top model of each model set (Hijmans et al., 2017; Kuhn, 2015; McNeil et al., 2023b). A model was initially fit with the full dataset, and then fit using 75% of the data (with random sampling), testing the remaining 25% with AUC and Brier Scores. Lastly, scores were averaged over 10 runs (McNeil et al., 2023b).

## 3. Results

Of the 1263 locations surveyed, 100 had fewer than 10 days of recording due to ARU failure caused by bear (*Ursus americanus*) or water damage. Thus, data from 1163 survey locations were included in our regional and landscape analyses (days of recording $x = 22.61$, $SD = 6.75$, range = 10.00–30.00). Our site-level analysis incorporated data from 1094 (94%) survey locations for which associated vegetation data were collected. Based on the criteria of a) detection threshold score of >4.3 and b) at least two detections >10 days apart, 399 survey locations were considered occupied by territorial whip-poor-wills. Only two additional sites were considered occupied after we manually verified scores between 3.0 and 4.3 that were >10 days apart. Thus, our final dataset included 401 sites classified as occupied (naïve occupancy of territorial males = 34%). The 762 unoccupied points included 64 sites (8%) that had at least two whip-poor-will detections (score >3.0), but not >10 days apart. Of the survey locations on private lands enrolled in NRCS conservation programs that had ≥10 days of ARU recordings and were surveyed post-treatment, we detected whip-poor-wills at 33 of 129 (26%) WLFW – NEC sites, 139 of 244 (57%) WLFW –GWWA sites, and 37 of 66 (56%) RCPP – CERW sites.

Our top regional model included elevation and latitude (mean AUC = 0.59, mean Brier score = 0.22; Table 1). Whip-poor-will occupancy probability decreased with elevation ($\beta = -0.31$ [95% CI: −0.46 to −0.16]; Fig. 3A) and latitude ($\beta = -0.32$ [95% CI: −0.44 to −0.22]; Fig. 3B). Given that this pattern was relatively weak (based on Brier score and AUC), we did not use it to extrapolate broadscale patterns of occupancy across our study area. Our top landscape model contained impervious cover, oak forest, evergreen forest, herbaceous, and shrub-scrub (mean AUC = 0.74, mean Brier score = 0.18; Table 1). Occupancy decreased with the amount of imperviousness cover within 500 m of the survey location ($\beta = -0.43$ [95% CI: −0.76 to −0.18]; Fig. 3C), increased with the amount of oak forest within 1500 m ($\beta = 0.65$ [95% CI: 0.49–0.81]; Fig. 3D), evergreen forest cover within 1750 m ($\beta = 0.28$ [95% CI: 0.13–0.44]; Fig. 3E), and herbaceous cover within 750 m ($\beta = 0.27$ [95% CI: 0.11–0.45]; Fig. 3F), and exhibited a quadratic relationship with the amount of shrub-scrub cover within 1500 m, which was maximized at 9.3% ($\beta_1 = 1.04$ [95% CI: 0.81–1.27], $\beta_2$ [quadratic parameter estimate] = −0.11 [95% CI: −0.15 to −0.07]; Fig. 3G). When predicted across the study region, this model indicated that whip-poor-will occupancy was highest in the southern Appalachians (Fig. 4).

Our top site-level model contained basal area, a quadratic effect of woody stem density, and bramble presence (mean AUC = 0.70, mean Brier score = 0.20; Table 1). Occupancy decreased with increasing basal area ($\beta = -0.71$ [95% CI: −0.88 to −0.55]; Fig. 3H), exhibited a quadratic relationship with woody stem density that was maximized at 8.1 stems/$m^2$ (81,000 stems/ha; $\beta_1 = 0.36$ [95% CI: 0.17–0.56]), $\beta_2 = -0.06$ [95% CI: −0.11 to −0.02]; Fig. 3I), and had a negative association with bramble presence ($\beta = -0.17$ [95% CI: −0.31 to −0.03]). There were 15 competing models within two $AIC_c$ of the best site-level model, however none contained supported variables not already reported in the top model (Table 1).

**Table 1**
AIC tables displaying top and competing models (within 2 $\Delta AIC_c$) from generalized linear models within three separate model-sets. This analysis investigated Eastern Whip-poor-will occupancy in relation to regional-, site-, and landscape-level variables at locations which ranged from western North Carolina to southern Maine in 2020 and 2021.

| Model set | Model | K | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|
| Regional | Latitude + Elevation | 3 | 1469.4 | 0.00 | 1.00 |
| Landscape | Evergreen Forest + Imperviousness + Herbaceous + Oak Forest + Shrub Scrub$^2$ | 7 | 1309.2 | 0.00 | 0.76 |
| Site-level | BA + Brambles + Woody Stem Density$^2$ | 5 | 1294.8 | 0.00 | 0.06 |
| | BA + Herbaceous + Brambles + Woody Stem Density$^2$ | 6 | 1294.8 | 0.00 | 0.06 |
| | BA + Herbaceous + Leaf Litter + Brambles + Woody Stem Density$^2$ | 7 | 1295.1 | 0.28 | 0.05 |
| | BA + Leaf Litter + Brambles + Woody Stem Density$^2$ | 6 | 1295.2 | 0.39 | 0.05 |
| | BA + Fern + Brambles + Woody Stem Density$^2$ | 6 | 1295.7 | 0.93 | 0.05 |
| | BA + Fern + Herbaceous + Brambles + Woody Stem Density$^2$ | 5 | 1295.8 | 0.97 | 0.04 |
| | BA$^2$ + Brambles + Woody Stem Density$^2$ | 6 | 1295.9 | 1.08 | 0.04 |
| | BA$^2$ + Herbaceous + Brambles + Woody Stem Density$^2$ | 6 | 1295.9 | 1.08 | 0.04 |
| | BA + Fern + Leaf Litter + Brambles + Woody Stem Density$^2$ | 7 | 1296.0 | 1.17 | 0.03 |
| | BA + Bare Ground + Brambles + Woody Stem Density$^2$ | 6 | 1296.0 | 1.18 | 0.03 |
| | BA$^2$ + Leaf Litter + Brambles + Woody Stem Density$^2$ | 7 | 1296.0 | 1.20 | 0.03 |
| | BA + Bare Ground + Herbaceous + Brambles + Woody Stem Density$^2$ | 7 | 1296.0 | 1.25 | 0.03 |
| | BA + Bare Ground + Leaf Litter + Brambles + Woody Stem Density$^2$ | 6 | 1296.4 | 1.58 | 0.03 |
| | BA + Brambles + Woody Seedlings + Woody Stem Density$^2$ | 6 | 1296.7 | 1.90 | 0.02 |
| | BA + Brambles + Herbaceous + Woody Seedlings + Woody Stem Density$^2$ | 7 | 1296.7 | 1.92 | 0.02 |
| | BA$^2$ + Fern + Brambles + Woody Stem Density$^2$ | 7 | 1296.8 | 1.98 | 0.02 |

## 4. Discussion

Monitoring is key to conserving declining species since it provides information on habitat associations, which in turn guides habitat management. However, conducting standardized field surveys for species with large geographic ranges is expensive and logistically challenging. As a result, our understanding of habitat associations for species with large geographic ranges, such as the Eastern Whip-poor-will, is often based on the findings of comparatively small-scale studies (e.g., Akresh and King, 2016; Spiller and King, 2021; Souza-Cole et al., 2022) with very few studies assessing factors at broad spatial scales (e.g., English et al., 2017). Herein, we employed new field and analytical approaches to monitor over one thousand sites, an effort that simply would have been impossible to carry out using human observers conducting standard aural surveys. To our knowledge, this work constitutes one of the largest concerted efforts to monitor a single species using ARUs (Yip et al., 2021; Johnson and Bayne, 2022; Caouette et al., 2023). Our findings provide important insights regarding expected response of territorial whip-poor-will to conservation programs that target other at-risk forest species, provide actionable targets for land managers wishing to create whip-poor-will breeding season habitat, and offer guidance for future applications of automated acoustic monitoring for informing conservation.

We examined the influence of several landscape variables at multiple spatial scales on whip-poor-will occupancy, which is important for scale- and landscape-dependent conservation (Willey et al., 2022). Consistent with prior research, we found an association between whip-poor-will occupancy and evergreen forest (Wilson and Watts, 2008; Hunt, 2013; Tozer et al., 2014; Akresh and King, 2016). However, our findings also revealed a strong association with oak forests. Moreover, a post-hoc exploratory analysis where oak forest was replaced with a northern hardwood variable (maple-beech-birch forest), revealed a negative relationship between whip-poor-will occupancy and northern hardwoods. Thus, future management efforts for whip-poor-wills in the eastern portion of the species' range should also include landscapes dominated by at least 62% oak forest within 1.5 km of a site (with minimal northern hardwood cover) to maximize conservation outcomes (Hunt, 2013). The positive association with whip-poor-will occupancy and oak forest could be the result of more abundant and diverse prey in oak forests compared to other forest types. Moths (Lepidoptera) comprise the majority of whip-poor-will diets (Souza-Cole et al., 2022), and oaks are known to support among the highest densities of this taxa (Summerville and Crist, 2008; Narango et al., 2020). Moreover, other plant species that commonly co-occur within oak-dominated forests (such as *Prunus* spp. and *Vaccinium* spp.) also support a high diversity of moth species (Wagner et al., 1995; Summerville and Crist, 2008). Unfortunately, oak forests of the eastern US are experiencing unprecedented challenges that are leading to degradation and mesophication (*e.g.*, insect pests, intense ungulate browsing, high-grading, and fire suppression leading to compositional shifts; Knoot et al., 2010; Dey, 2014). Conservation of whip-poor-will populations across our study regions will be undoubtedly linked to management and policy decisions that promote the resilience and recovery of oak-dominated communities.

Our finding that whip-poor-will occupancy was greatest in landscapes with an intermediate amount of shrub-scrub cover reflects the ecology of this species, which requires early successional habitat but is also known to use shelterwood establishment harvests, adjacent mature forests, and ecotones (Tozer et al., 2014; Spiller et al., 2022). Given that whip-poor-wills are known to use older forest ecotones, in addition to early successional conditions (Akresh and King, 2016; Grahame et al., 2021), landscapes with a mosaic of diverse structural and forest age class conditions likely best meet the foraging and nesting habitat needs of this species (Wilson and Watts, 2008). Indeed, whip-poor-will dependence on young forest and associated ecotones is attributed to its foraging technique whereby birds sally upward from a stationary position to capture backlit aerial insects (Mills, 1986, Cink et al., 2020). Our analyses identified a value of young forest habitat (9.3%) in a landscape that would best promote whip-poor-will occupancy, which is generally consistent with targets for early successional birds presented by others (e.g., Dettmers, 2003). However, it is important to note that our estimated value is likely lower than the true value at which whip-poor-will occupancy is maximized because the NLCD data layer we used is known to underestimate shrub-scrub cover (Bulluck et al., 2022). Therefore, landscapes with greater than 9.3% early successional forest may be optimal for whip-poor-wills (Tozer et al., 2014).

The negative relationship between whip-poor-will occupancy and impervious cover is generally consistent with previous studies (Vala et al., 2020; Souza-Cole et al., 2022). However, whip-poor-will populations across the eastern portion of their range appear to be less sensitive to impervious cover (declining to nearly zero at 10% imperviousness in our study) than in the American Midwest, where whip-poor-will occupancy approached zero when only 1% of the landscape consisted of medium/high intensity development (Souza-Cole et al., 2022). A study of the European Nightjar (*Caprimulgus europaeus;* Sierro and Erhardt, 2019) demonstrated that light pollution, which is most prominent near impervious surfaces (Sutton, 2003; Bennie et al., 2014), may be driving the species' decline. Whip-poor-wills could be affected in a similar way by light pollution and impervious cover.

At the site-level, whip-poor-will occupancy in our study were associated with reduced basal area (<15.6 $m^2$/ha) and intermediate densities of shrubs/saplings (~8.1 stems/$m^2$). Such conditions are characteristics typical of forest management practices that leave varying

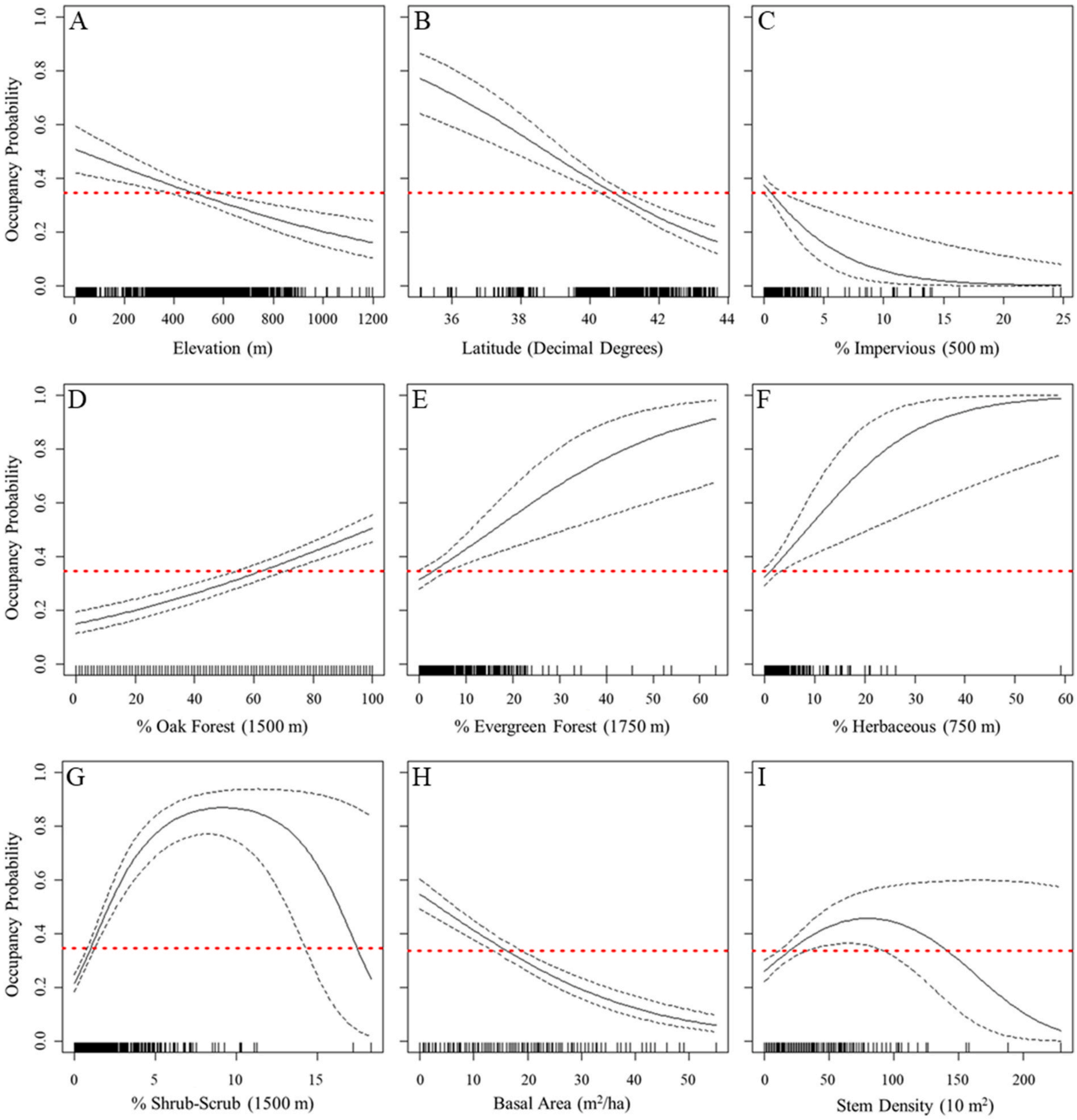

**Fig. 3.** Plots of functional relationships between Eastern Whip-poor-will occupancy and biologically meaningful variables from the regional (A & B), landscape (C–G), and site-level (H–I) model sets. Occupancy probability is on the y-axis and the predictor variable is on the x-axis in all plots. Occupancy was defined as two whip-poor-will detections at least 10 days apart. Solid black lines represent fitted regression curves and dotted black lines represent 95% confidence intervals (CI). Additionally, in all plots the red dashed line represents the mean occupancy probability (A–G: 0.34; H–I: 0.33) and rugs along each x-axis shows the distribution of data points. Areas where confidence intervals are particularly wide are typically data-sparse regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

amounts of residual canopy trees to promote the establishment and growth of woody regeneration, especially shelterwood, seed-tree, and clearcutting methods. While our analysis indicates a negative linear relationship between occupancy and basal area, a study in New York reported a quadratic relationship for which whip-poor-will occupancy peaked at 13.8 $m^2$/ha (Spiller and King, 2021). Regardless, the basal area values associated with high whip-poor-will occupancy in both studies are much lower than those of typical mature eastern deciduous forests (*i.e.*, 27 ± 1 [SE] $m^2$/ha; Boves et al., 2013). These findings demonstrate that, within oak-dominated landscapes, whip-poor-wills are more likely to occupy forests with complex, young forest conditions historically generated by natural disturbances and indigenous burning practices (Lorimer and White, 2003; Abrams et al., 2021).

Key to the success of our study was the implementation of ARUs and a machine learning classifier (Knight et al., 2022; Stowell, 2022). Specifically, we demonstrate how ARUs can be used to survey hundreds of sampling locations nightly across a large spatial extent in a single breeding season with limited personnel. This same effort using conventional human observer surveys would require supporting a considerably larger field crew. Furthermore, the performance of our machine learning classifier coupled with the high detectability of whip-poor-wills ($p = 0.999$ after 10 nights) enabled us to use an analytical approach that did not explicitly model detection probability, thus saving statistical power for inferences regarding the state variable of interest. When using

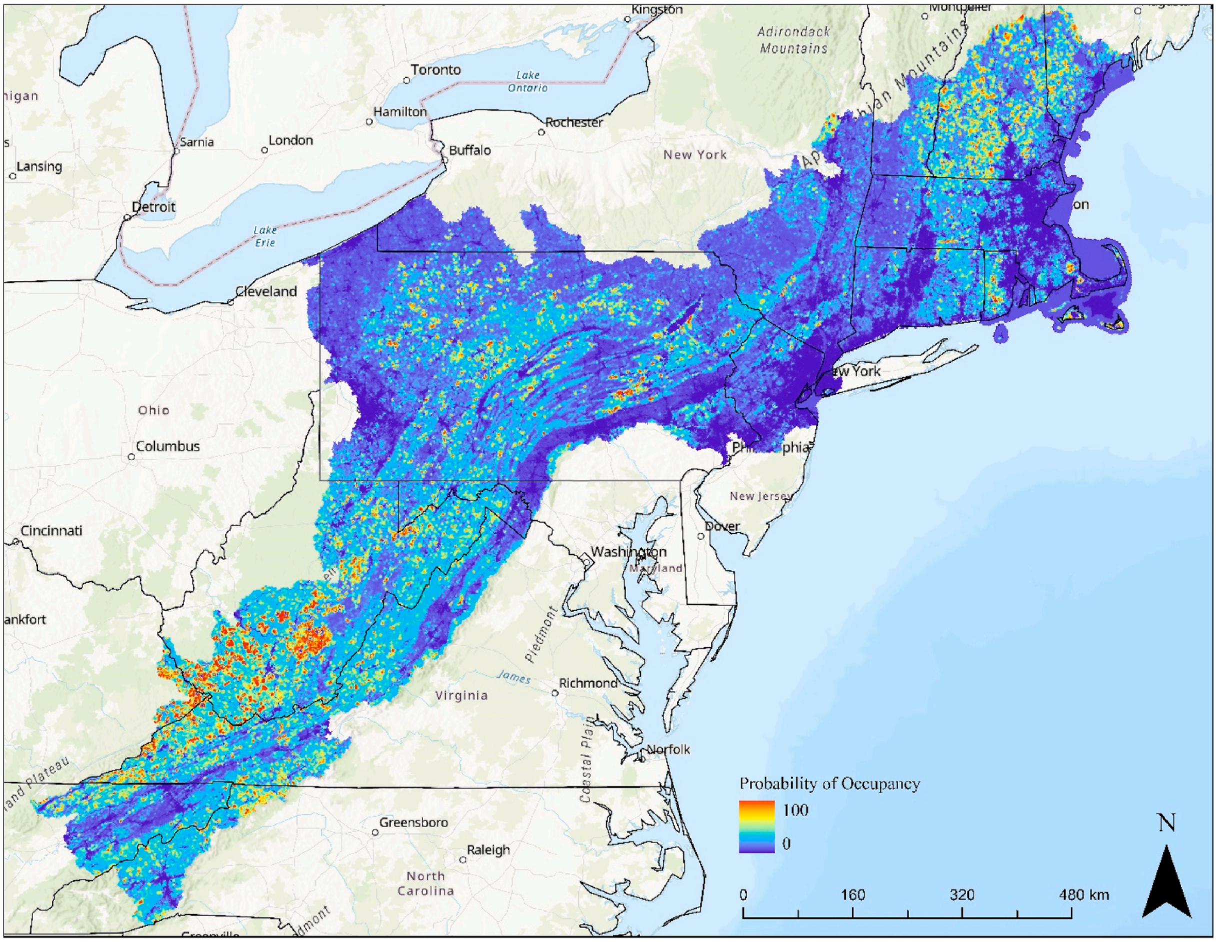

**Fig. 4.** Predictive map of Eastern Whip-poor-will occupancy created using parameter estimates from the top landscape model. Data used to model whip-poor-will occupancy was collected at 1163 sites ranging from western North Carolina to southern Maine from April–July 2020 and 2021.

ARUs, researchers should carefully assess whether any survey detection biases can be completely accounted for by study design alone, or if accounting for detection probability via analyses is also required (MacKenzie et al., 2002). Nevertheless, while there are certainly many benefits associated with ARU-based monitoring, as demonstrated here, there are also many challenges for which prospective users need to be prepared (*e.g.*, data processing and analysis, development of rigorously tested species-specific classifiers, etc.; Shonfield and Bayne, 2017; Kitzes and Schricker, 2019). Lastly, while a threshold approach to identify whip-poor-will presence appeared to work extremely well, authors examining bird species that sing less loudly and/or often need to carefully consider if a threshold method is appropriate.

When considered together, our results suggest whip-poor-wills in the eastern portion of their breeding range thrive in disturbance-driven, oak-dominated ecosystems. Here, we monitored whip-poor-will occupancy of individual stands managed for multiple objectives (e.g., WLFW-GWWA, WLFW- NEC, and RCPP-CERW). Future work examining how whip-poor-wills respond to landscapes managed in a more ‘dynamic’ fashion whereby forest age classes are more equally distributed through a series of shelterwood establishment and overstory removal harvests, along with mature forest reserves would be valuable (Loftis, 1990; Ashton and Kelty, 2018). Early successional forests like those we found to most likely host whip-poor-wills, are ephemeral, only remaining suitable for the species for 10–20 years without further disturbance. Restoration and maintenance of woodland systems (*e.g.*, open oak woodlands), an open-forest community commonly dominated by oak and pine species that once covered more than 100 million ha of eastern North America (Hanberry et al., 2020), may be the most viable and impactful conservation strategy for creating whip-poor-will breeding habitat. Regardless of the specific conservation practices implemented, site and landscape conditions important to whip-poor-will occupancy that we identified are attainable through conservation actions grounded in robust, science-informed forest management.

Recognizing that our models performed only moderately well, it is likely that our analyses were missing important predictors that could be used to better model site- and landscape-level characteristics. Still, even without the use of such datasets, the analyses presented here provide a critical overview of the factors driving site occupancy by this declining nightjar across a portion of the eastern United States. In fact, the predictive map we present shares many similarities with those predicted by the citizen science platform eBird (Fink et al., 2023) whereby both maps predict “hot spots” in southwestern Virginia, southern West Virginia, central Massachusetts, western Rhode Island, and eastern New Hampshire, to name a few. Further, both maps predict urban centers as low-quality habitat (Fink et al., 2023). Thus, despite only modest model performance, our approach yields a predictive map with many similarities to maps produced with much larger sample sizes. Future work that leverages emerging technologies such as mappable structural vegetation data (*e.g.*, Light Detection and Ranging; McNeil et al., 2023b) may also prove helpful in further advancing our understanding of whip-poor-will habitat associations and future conservation efforts.

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## CRediT authorship contribution statement

**Jeffery T. Larkin:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Darin J. McNeil:** Writing – review & editing, Writing – original draft, Formal analysis. **Lauren Chronister:** Writing – review & editing, Writing – original draft, Data curation. **Michael E. Akresh:** Writing – review & editing, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Emily B. Cohen:** Writing – review & editing, Investigation. **Anthony W. D'Amato:** Writing – review & editing. **Cameron J. Fiss:** Writing – review & editing, Investigation, Formal analysis. **Justin Kitzes:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Jeffery L. Larkin:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Halie A. Parker:** Writing – review & editing, Investigation. **David I. King:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The data that has been used is confidential.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.121786.

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