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Searching for gold: Using a novel land cover classification to identify multiscale drivers of site occupancy by a flagship species for early-successional habitat conservation

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
in Biology at Virginia Commonwealth University

By

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Abstract

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Understanding habitat selection at multiple scales is an important step in guiding conservation programs and reversing species declines. This, however, is difficult for species that occupy early-successional habitats (ESH) due to a lack of accurate representation of shrub cover in publicly available land cover data. The Golden-winged Warbler (*Vermivora chrysoptera*; GWWA) is a threatened species of conservation concern and a flagship for ESH conservation. We used a novel, LIDAR-derived land cover classification that accurately identifies shrubs at a fine resolution (1m) to investigate how habitat composition and configuration influence GWWA site occupancy. We aggregated this same land cover data to 30m resolution to compare with models using commonly used spatial data. Our results confirm that elevation, forest and shrub cover are important habitat features for GWWA and suggest specific extents and optimum amounts that these cover types should be maintained: elevation 900-1000m, 10-15% shrub cover at 500m, and 50-60% forest cover at 1km. Models using coarse resolution data identified the same cover types and extents as important for GWWA. Our results can improve communication and implementation of GWWA conservation efforts. Widely available land cover data that includes an accurate representation of shrub cover are needed to extend these results across the

Appalachian region. We projected GWWA occupancy probability across a five-county region to plan future surveys and recruitment for ESH management. Our study highlights the importance of understanding habitat selection at multiple scales and integrating freely available spatial data to guide conservation programs.

Introduction

Habitat loss is a primary cause of species declines. A major driver of habitat loss is land use change associated with human use such as agriculture, industry, and suburban/exurban development (King and Schlossberg 2014). Understanding habitat requirements for species with declining populations is therefore an important step in conservation planning. However, this is complicated in species that alter their preference during different life history stages. For example, Wood Thrush (*Hylocichla mustelina*) and other forest songbirds frequently move from breeding areas in mature forest to post-fledging areas in early- to mid-successional habitats because of shifts in seasonal requirements (i.e. from nest-site and mate selection to caring for offspring) and resource prioritization (Vitz and Rodewald 2011). Simultaneously, selection of habitat may be scale-dependent with some features being important at small spatial scales and other features being important at larger scales (Mayor et al. 2009), and this is likely true for species that seasonally shift their habitat use like the Wood Thrush. Habitat heterogeneity may also influence the scale of habitat selection; muskoxen (*Ovibos moschatus*) consistently select the same habitat features across multiple scales in the relatively homogeneous environment of the arctic tundra (Schaefer and Messier 1995), whereas elk (*Cervus canadensis*) habitat selection is scale-dependent in the more structured landscape of the Rocky Mountains (Boyce et al. 2003). It is therefore important to consider whether and how habitat use varies across spatial scales to manage declining species in heterogeneous landscapes.

Studies of cross-scale habitat require accurate, multi-scale land cover data, yet these data are not always readily available. For example, shrubs in the eastern United States are not well represented in available land cover datasets. Shrubs are an essential cover type for early successional habitats (ESH), which are characterized by persistent grasses, forbs, and shrubs/saplings within a predominantly forested landscape. ESH typically occur following natural or anthropogenic disturbances (Brooks 2003; King and Schlossberg 2014). Natural disturbances that historically promoted ESH include grazing by large herbivores, wildfire, dam construction by beavers, and severe weather events such as high winds and ice; however, these are less common today due to land use change and fragmentation (King and Schlossberg 2014). As a result, the species that depend on these habitats are in decline across much of the eastern United States (Askins 1993, Brawn et al. 2001; Hunter et al., 2001). Shrubs are often underrepresented in land cover classifications because they are spectrally similar to mature forest and pasture (i.e. shrubs appear similar to mature forest and pasture in aerial imagery used for land cover classifications) (Laliberte and Rango 2009). Furthermore, there is likely insufficient training data for this less common cover type. Global- or national-scale land cover classifications typically prioritize common land cover types to improve accessibility and use. For example, the National Landcover Dataset (NLCD) provides land cover data across the continental United States at a 30m resolution. These data are best used for assessing habitat selection and vegetation composition (amount of cover types) and configuration (arrangement of cover types) at broad scales (i.e., regional, national). The coarse resolution of NLCD limits its ability to accurately represent uncommon cover types that may be important to focal species or communities of concern. Efforts to manage for high quality ESH and the species that depend on them would benefit from habitat models based on spatial data that includes an accurate and high-resolution representation of shrub cover.

Another challenge of managing for many rare species is that they can be difficult to survey, yet conservation efforts must be informed by precise estimates of species occurrence. Bird population trends are commonly estimated using Breeding Bird Survey (BBS) data. These data are collected by citizen scientists, primarily from roadsides and on publicly owned lands (Pardieck et al. 2019). Therefore, BBS data do not effectively capture occurrences and species that occur primarily on privately owned lands, resulting in imprecise estimates. Sixty-six percent of the United States is privately owned (Benson 2001), and there is increasing awareness that private lands support many priority species, provide essential ecosystem services (Knight 1999, Bennett et al. 2018, Burger et al. 2019), and must be a part of effective conservation plans. Local conservation efforts that attempt to engage landowners must rely on occurrence data within their focal region because management within close proximity of rare species occurrences are more likely to have an impact than management at isolated sites far from known/likely occurrences (Margules and Pressey 2000, Stephens et al. 2019). Though we have recognized the importance of protecting biodiversity on private lands, recommended conservation practices must be guided by consistent biodiversity monitoring across public and private lands to ensure appropriate conservation actions are implemented.

Golden-winged Warblers (*Vermivora chrysoptera*; hereafter, GWWA) are a species of conservation concern that require ESH and adjacent mature forest during the breeding season, and often occur on private lands, especially in the Appalachian portion of their range (Bakermans et al. 2015, Rohrbaugh et al. 2016). They nest in areas with a mix of shrubs and herbaceous cover while foraging and feeding fledglings in adjacent forests (Bulluck and Buehler 2008, Frantz et al. 2016; Klaus and Buehler 2001). They are recognized as a species of high conservation concern by Partners in Flight (Rosenberg et al. 2016), the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2008), and across many Bird Conservation Regions (BCRs) in which they occur. Other breeding birds dependent on ESH in the Appalachian Mountains BCR are also in decline (Pardieck et al. 2019). Conservation efforts focused on the

GWWA will therefore benefit a suite of species of conservation concern (Streby et al. 2016, Aldinger et al. 2017). GWWA populations have declined at an average annual rate of -2.6% (95% CI: -1.8, -3.3) globally and -7.8% (95% CI: -6.6, -8.9) in the Appalachian Mountains BCR (Pardieck et al. 2019). Causes of these declines include habitat loss on the breeding and non-breeding grounds, as well as competition and hybridization with the closely related Blue-winged Warbler (*Vermivora cyanoptera*; hereafter, BWWA) (Buehler et al. 2007, Rosenberg et al. 2016). BWWA populations in the Appalachian Mountains BCR are more stable at -0.8% annually (95% CI: -2.6, 0.9; Pardieck et al. 2019). GWWA and BWWA occupy similar habitats, but GWWA are more common at higher elevations and latitudes (Crawford et al. 2016, Rohrbaugh et al. 2016). Nevertheless, our understanding of interactions between both species are incomplete and there are no current research efforts to monitor BWWA (Rohrbaugh et al. 2016). Yet, current GWWA conservation efforts and management recommendations are guided by research focused on GWWA habitat use (Roth et al. 2012) and sometimes aim to prevent hybridization with BWWA (Roth et al. 2012, Wood et al. 2016). We have learned much from the research and conservation attention given to GWWA over the last decade, including spatial scales relevant to their life history (Streby et al. 2016, Aldinger et al. 2017, Kramer et al. 2018); however, because accurate maps of shrub cover do not exist, models of habitat use to date have been based on coarse resolution data that lack a shrub component (Crawford et al. 2016, Wood et al. 2017, McNeil et al. 2020) and/or hand digitized data within individual habitat patches that cannot be projected across the landscape (Aldinger et al. 2017). Effective conservation action for this declining species requires a complete understanding of ideal habitat conditions, including the composition and configuration of important cover types in the Appalachian Mountains BCR at multiple spatial scales.

In this study, we developed multi-scale occupancy models for *Vermivora* warblers (GWWA, BWWA, and their hybrids) in western Virginia within a priority area for conservation established by the USDA Natural Resources Conservation Service's Working Lands for Wildlife (WLFW) program. The GWWA is a focal species for this program that aims to create and maintain high quality ESH. We used a recently developed land cover classification (Bulluck et al., in prep) that accurately represents shrub cover and *Vermivora* survey data from private lands in this same region to build occupancy models. Specifically, we assessed how probability of site occupancy varies as a function of land cover composition (i.e., percent forest, shrub, and pasture cover) and configuration (i.e., degree of shrub aggregation) at varying spatial scales. Spatial scale is a combination of extent and grain; we developed occupancy models using habitat features calculated within small (100m radius), medium (500m), and large (1km) circular buffers around each survey location, and used rasters with fine (1m) and coarse (30m) spatial resolution. We compared our models to recently-developed occupancy models for GWWA based on 30m resolution NLCD (Crawford et al. 2016, Wood et al. 2017, McNeil et al. 2020), which does not accurately represent shrubs in the Appalachian Mountains BCR. We also compared our model results with current recommendations for best management practices (BMPs) (GWWA Working Group 2013) used to guide management for the WLFW program. We expect that our models will corroborate recent findings for the amount of forest cover required for GWWA breeding sites and add important details regarding the amount and configuration of shrub cover required for this priority species. Because our focal region is within the hybrid zone for GWWA and BWWA, we developed these models for *Vermivora* (occupancy for either GWWA, BWWA, or hybrids) as well for each species separately (GWWA-only or BWWA-only). The degree to which model outputs differ for the species modelled separately or combined will inform whether management recommendations should also differ. We expect that models will be similar with regard to land cover, but differ in elevation. Such similarities are expected considering these two species are genetically very similar (Toews et al. 2016). These *Vermivora* models may also provide insight about habitat features where hybridization is most likely to occur.

Methods

Study area

From 2019 to 2020, we studied GWWA habitat in the Valley and Ridge portions of the Central Appalachian Mountains region in southwest Virginia, specifically in Smyth, Tazewell, Bland, and Russell Counties. This landscape is predominantly composed of forested ridges (60-70%), many of which are owned by the US Forest Service. Along the forested ridges are Appalachian hardwood and mixed pine-hardwood stands that typically include oak (*Quercus* sp.), cherry (*Prunus* sp.), maple (*Acer* sp.), poplar (*Populus* sp.), pine (*Pinus* sp.), and hickory (*Carya* sp.). Several tree species are managed for timber using a variety of harvest techniques. The valleys tend to be privately owned and used for agriculture, primarily cattle and hay production. Abandoned and active pastures often contain patches of saplings and shrubs; the most common species are blackberry (*Rubus* sp.), multiflora rose (*Rosa multiflora*), blueberry (*Vaccinium* sect.), barberry (*Berberis* sp.), hawthorn (*Crataegus* sp.), autumn olive, and black locust (*Robinia pseudoacacia*).

Site selection

Before the 2019 breeding season (May 1 to June 15), we selected survey sites by manually delineating suitable area polygons from Google Earth aerial imagery in QGIS (version 3.10) where there was a combination of forest and open areas with varying amounts of shrub cover or regenerating saplings in open pastures or following timber harvest. The polygons were intersected with publicly available parcel data to identify landowners. We worked with local partners (The Nature Conservancy, United States Department of Agriculture's Natural Resources Conservation Service, and Department of Conservation and Recreation's Soil and Water Conservation District) to solicit landowners for access to their properties to conduct bird surveys. Survey points were regularly placed 300m apart from each other within these polygons using the regular points function in QGIS. A few additional points were added to small patches where only 1-2 points were placed by QGIS, but we maintained a minimum of 250m distance in all cases. Due to COVID travel restrictions in 2020, we prioritized surveying points that were only visited once or late in the 2019 breeding season.

Point count surveys

In 2019 and 2020, three observers conducted point count surveys across 201 survey points (Figure 1) during the breeding season (May 1 - June 14 in 2019; May 4 - May 8 in 2020) following a shortened version of the Cornell Lab of Ornithology's Golden-winged Warbler Atlas Protocol (GOWAP 2009). During each breeding season, observers conducted two surveys at each survey point to estimate detection probability. Observers visited the same survey point at least 15 minutes or at most 1 week after the first survey to maintain independence across surveys and meet survey site closure assumptions (Lele et al. 2012). Point counts began at sunrise and ended by 11am through May 15, 10:30am through May 31, and 10am through June 1. Surveys lasted 8 minutes and were divided into four two-minute periods. The first three periods were silent, followed by a two-minute playback period when GWWA Type I song was played using a bluetooth speaker. Broadcasting male GWWA songs during surveys is warranted because it increases their already low likelihood of detection (Aldinger and Wood 2015, Wood et al. 2017), and all *Vermivora* will respond to GWWA songs (Confer 1992). For each *Vermivora* detected, observers recorded detection type (auditory, visual, or flyover), time detected (1-2 min, 3-4 min, 5-6 min, 7-8 min), distance from survey point (<25m, 25m-50m, 50-100m, >100m). Species detections were based on the typical Type I song phenotype for each *Vermivora* species (Ficken and Ficken 1967), but visual confirmation of species ID was always attempted. Observers spent no more than 5 minutes after each survey to visually confirm auditory detections as GWWA, BWWA, or hybrid species. We recorded whether each detection was visually confirmed during the survey, after the survey or not at all.

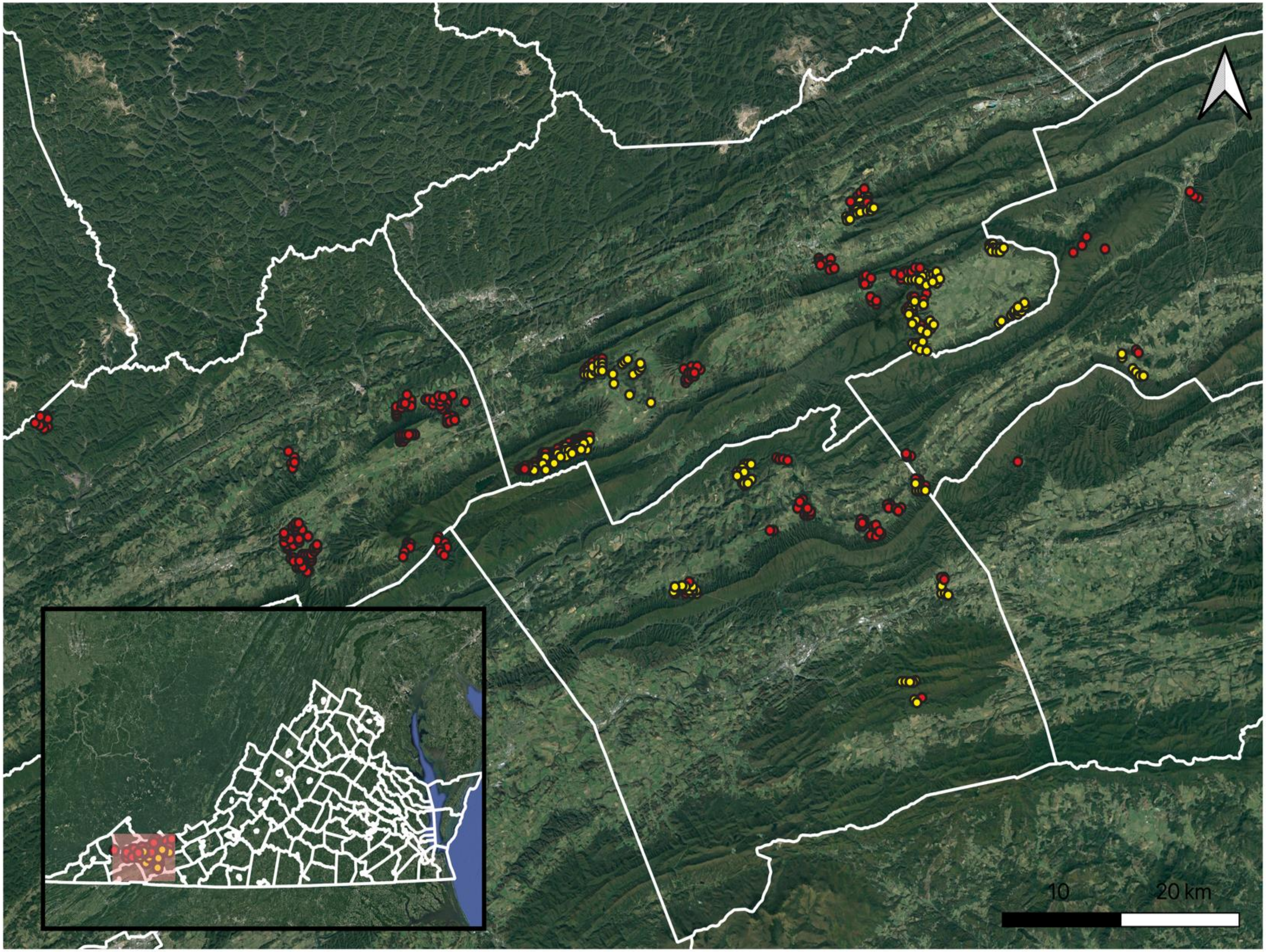

Figure 1*: Map of focal region and survey points. Red points were surveyed once in a breeding season and yellow points were surveyed at least twice in a breeding season. Only yellow points were used for occupancy models*.

Habitat characteristics/landscape metrics

We calculated landscape metrics using a custom land cover classification for our focal region and the landscapemetrics package in R (Hesselbarth et al. 2019). This land cover map accurately identifies shrubs and other cover types at a high resolution (1m) (Bulluck et al. in prep). To assess how spatial grain influences occupancy, we used the aggregation function in the sp package in R (Bivand et al. 2013) to decrease the spatial resolution of this land cover classification to a coarser, 30m resolution raster. We calculated landscape composition and configuration metrics using both rasters separately. Landscape composition metrics consisted of percent cover of shrub, pasture (herbaceous cover) and forest (deciduous and mixed forest types), all of which are required cover types for *Vermivora* during the breeding season (Crawford et al. 2016, Frantz et al. 2016). We also assessed the importance of habitat configuration, specifically, the degree of shrub or aggregation or dispersion (shrub clumpiness index). Metrics were also calculated at varying extents around each survey point (radius of circular buffers = 100m, 500m, and 1km; Figure 2). Spatial extents were selected and modified from Aldinger et al. (2017) to represent extraterritorial and/or within-season movements (1km radius), fledgling dispersal distance (500m radius), and the size of defended local territories (100m radius). Table 1 summarizes descriptions, notations, and justifications for the extents at which landscape metrics were calculated and habitat characteristics were used to model detection probability and site occupancy.

In addition to composition and configuration metrics, we calculated the standard deviation of the LIDAR-derived canopy height model within the 100m radius extent to represent vegetation structural diversity thought to be an important habitat component for *Vermivora* (Bellush et al. 2016). Lastly, we extracted the elevation at each survey point from USGS

National Elevation Dataset (USGS) because GWWA are known to occur at higher elevation than BWWA (Crawford et al. 2016, Rosenberg et al. 2016).

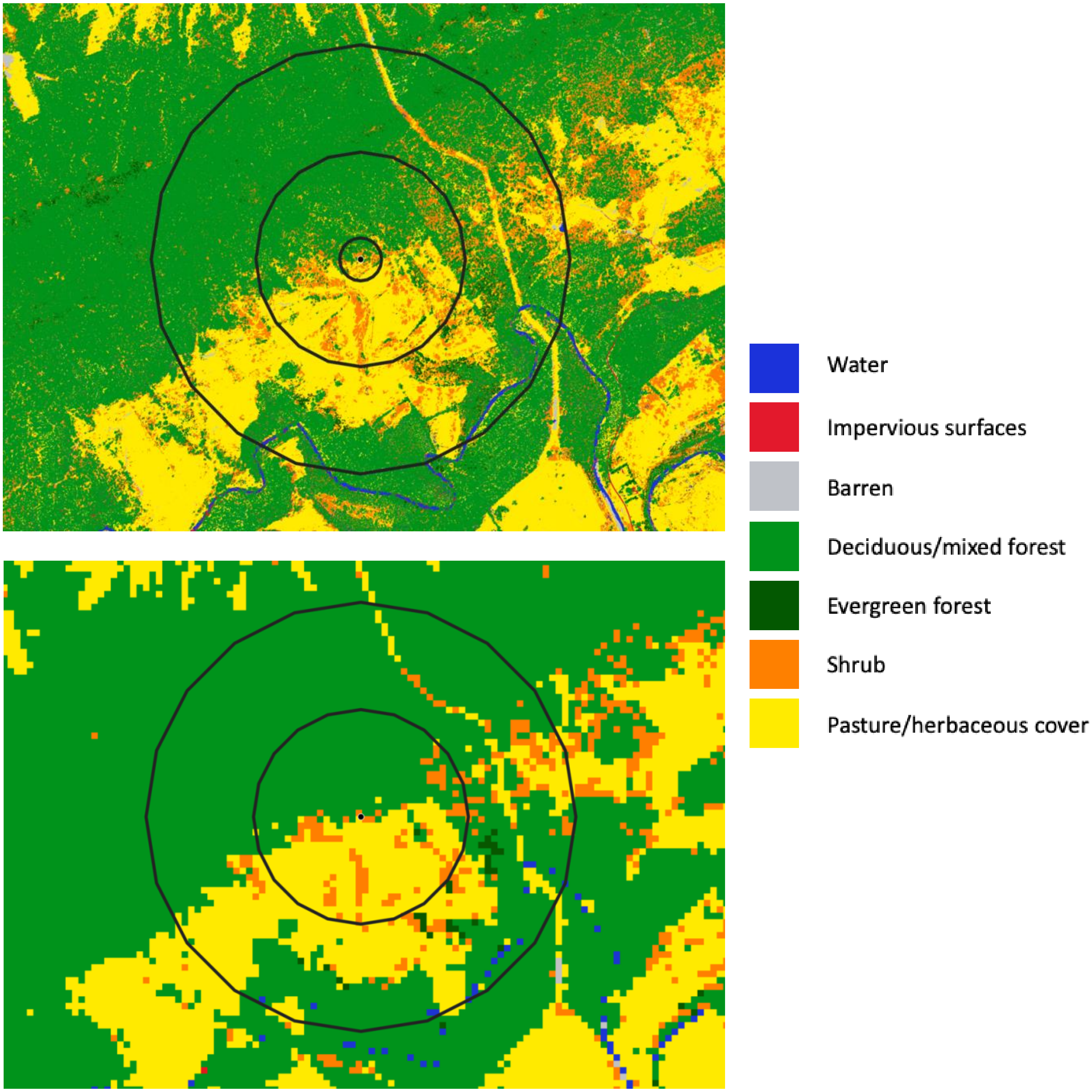

Figure 2*: Three extents at which landscape metrics were calculated using fine resolution (1m; top) and two extents for coarse resolution (30m; bottom). Landscape metrics were calculated from the land cover data shown here. Black concentric rings represent 100m, 500m, and 1km radial buffers around a survey point.*

Table 1*: Descriptions, notations, and justifications for the habitat covariates and extents used to model detection probability and Vermivora site occupancy.*

Covariate [abbreviation]	Justification
Ordinal date [date]	Birds sing less later in the breeding season (citation)
Time of survey [time]	Birds sing less later in the day (citation)
Observer	Differences in experience and expertise are accounted for in pre-season training, but observer ability to detect species can still vary (citation)
Elevation (meters)	Elevation predicts occurrence of GWWA and likely limits contact with BWWA in Appalachian Mountains region (Crawford et al. 2016)
Composition [%]	
Deciduous/mixed forest [forest]	GWWA and BWWA are commonly found in landscapes >60% deciduous and mixed forest types (Crawford et al. 2016). GWWA forage and feed fledglings in forests (Klaus and Buehler 2001, Frantz et al. 2016).
Pasture/herbaceous cover [pasture]	GWWA nest in dense herbaceous cover (Confer et al. 2020). GWWA occupancy is positively associated with fallow pasture (Crawford et al. 2016).
Shrub	GWWA forage and nest in shrub patches (Frantz et al. 2016, Terhune II et al. 2016). GWWA populations have declined due in part to the decline of shrubland cover types (Yahner 2003). Creating shrubland is a conservation priority for GWWA (Roth et al. 2016).
Configuration	
Shrub clumpiness index	GWWA typically found in woodland and grassland mosaics that consist of patchily distributed shrubs (Crawford et al. 2016).
Canopy height heterogeneity	
Standard deviation [CHM STD]	Vegetation structure influences GWWA prey availability and is a focus of ESH habitat management (Bellush et al. 2016, Roth et al. 2016).
Extents/radial buffers	
100m	Approximate size of spot-mapped GWWA territories (Frantz et al. 2016) and size of point count radius.
500m	Mesoscale where adults move fledglings (Peterson et al. 2016).
1km	Approximate scale of within-season movements of radio-tagged GWWA (Frantz et al. 2016).

Statistical analysis/occupancy modeling

We separately modeled *Vermivora*, GWWA-only, and BWWA-only occupancy probability as a function of the above habitat/landscape covariates and spatial scales using single-season occupancy models in the R package *unmarked* (Fiske and Chandler 2011). Elevation and landscape composition metrics were standardized using the scale function in R to facilitate model convergence. When modeling *Vermivora* occupancy, we used auditory (either Type I or II song) and/or visual detections of GWWA, BWWA, and hybrid males within 100m of survey points. When modeling GWWA-only and BWWA-only occupancy respectively, we included auditory (Type I song) and/or visual detections of only GWWA or only BWWA within 100m of survey points. We adopted a sequential approach to create our final occupancy model for *Vermivora*, GWWA, and BWWA (Figure 3). We first modeled factors that influence detection probability using three survey covariates: (1) ordinal date, (2) time of day, and (3) observer. Estimates of detection probability are conditional on both the presence of a species at the point and the availability of that species during a survey period (i.e., whether or not an individual vocalized). We considered covariates to be informative if they had ΔAICc <2.0 and had β () 95% confidence intervals that did not include zero (Burnham and Anderson 2002).

Informative survey covariates of detection probability were then incorporated in occupancy models. We first assessed whether a linear or quadratic elevation term for occupancy improved model performance (ΔAICc <2.0) over the best performing detection model. We carried the best performing elevation term over when comparing composition and configuration metrics. We compared linear and quadratic relationships for landscape composition metrics because we expected predicted occupancy to peak at optimal amounts of these cover types. We were interested in identifying whether composition or configuration metrics were more important and at which extent these metrics were most predictive of occupancy, as well as differences in model performance when using high or coarse resolution spatial data. So, we separately compared univariate models using landscape metrics calculated with fine or coarse resolution. Then, we built additive models including landscape metrics from top performing univariate models at extents that were not highly correlated with one another (-0.6 < r < 0.6; Figure S1) or if β 95% confidence intervals did not include zero. For example, if shrub cover at 100m, forest cover at 500m, and shrub clumpiness index at 100m all performed better than the null occupancy model, we would create a new model set with all combinations of these variables. We assessed model goodness of fit using the mb.gof.test function. We also used the crossVal function to perform a model-based statistical validation of our top models for each taxon.

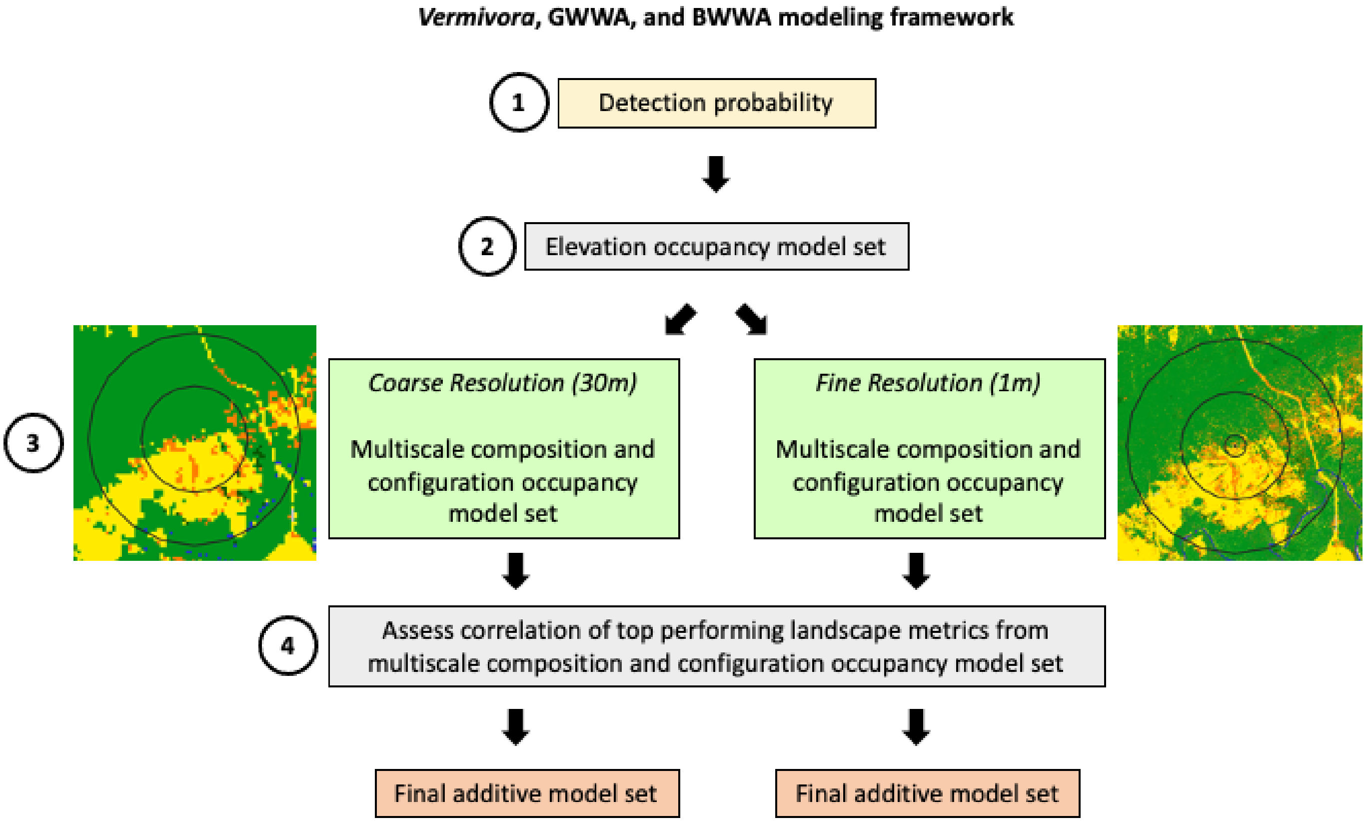

Figure 3: *Stepwise framework for modeling detection probability and occupancy using coarse and fine resolution spatial data.*

Projection of occupancy across focal region

We projected the top performing occupancy models for GWWA to identify potential areas for future survey and management efforts (Figure 3). We used the FocalStatistics function in ArcGIS Pro (version 2.7) to create percent cover rasters at each of the extents from the top performing models that used high resolution data (500m shrub, 1km forest). Prediction rasters were scaled using the mean and standard deviation from the survey data used to create the occupancy models because the β estimates need to be applied to scaled rasters to create accurate maps (Chandler 2020). They were then aggregated to have a 5m resolution for ease of processing. This coarser resolution is sufficient for prediction of bird occupancy whereas a finer resolution was preferred during land cover classification and identification of shrubs. We applied β estimates from our top performing models to create our logit and psi (predicted occupancy) output rasters following the sample code developed by Chandler (2020). Lastly, we performed an informal validation of model performance by extracting predicted *Vermivora* occupancy to points that were only surveyed once and compared mean predicted occupancy across occupied and unoccupied points with a t-test. This informal procedure was executed as a simple attempt to incorporate *Vermivora* presences that were independent of survey data used for occupancy models.

Results

Detection probability and occupancy modeling

We recorded detections of male *Vermivora* at 88 of 201 survey points (Table 2). Not all GWWA vocalizations were confirmed visually; 57% of the observations in GWWA-only models were visually confirmed (Table S1). Date emerged as the most important detection covariate when modeling *Vermivora*, GWWA-only, and BWWA-only. Detection probability was highest in early May when breeding activity was at its peak and decreased linearly through June (Figure 4). After accounting for detection probability, including a quadratic term for elevation greatly improved model performance over the null model across *Vermivora*, GWWA-only, and BWWA-only models (Table S2) and was therefore carried over to all other occupancy models. As expected, GWWA-only occupancy was associated with higher elevation sites than BWWA-only (Figure 5).

Univariate models with composition metrics calculated using high resolution data consistently ranked higher than models with configuration metrics for *Vermivora* and GWWA, and shrub clumpiness ranked high for BWWA. Quadratic composition models performed better than linear composition terms across all three taxa. *Vermivora*, GWWA, and BWWA occupancy was associated with percent forest cover at 1km and percent shrub cover at 500m. Shrub clumpiness at 1km was also significantly associated with BWWA occupancy (Table S3).

For *Vermivora* and GWWA, models that included quadratic terms for elevation, forest cover at 1km, and shrub cover at 500m outperformed other additive models (Table S4). Specifically, occupancy was highest at intermediate amounts of shrub and forest cover, and BWWA occupancy was associated with slightly higher percent shrub cover at 500m than GWWA (Figure 6). Forest cover at 1km and shrub cover at 500m remained important for predicting BWWA, but the best performing model also included shrub clumpiness at 1km (Table S5; Figure 7). All covariates used in final models, except for the quadratic term for elevation, had 95% confidence bounds that did not include 0 (Table S5).

Our final additive models for each taxon exhibited good fit (c-hat = 0.97 for *Vermivora*, 1.17 for GWWA, and 0.88 for BWWA). K-fold cross validation (5-fold) suggests that the accuracy of psi is lower for *Vermivora* models compared with GWWA and BWWA only models (*Vermivora* RMSE = 0.418 and MAE = 0.343; GWWA 0.380, 0.283; BWWA 0.327, 0.287) (Peterson et al. 2016). A RMSE or MAE value of 0.3 can be interpreted as the psi value calculated through validation is within 0.3 of the actual psi value produced by our model.

Models that incorporated landscape metrics calculated with coarse resolution data performed similar to the above models. Composition metrics typically ranked higher than configuration metrics for *Vermivora* and GWWA, and shrub clumpiness ranked high for BWWA, but 95% confidence intervals included 0. For all taxa, forest cover at 1km remained important for predicting occupancy. Shrub cover at 500m remained important for *Vermivora* and GWWA, but shrub cover at 1km became more important for BWWA. Final additive models for BWWA did not fit as well as *Vermivora* and GWWA models (c-hat = 1.11 for *Vermivora*, 0.92 for GWWA, and 1.46 for BWWA). K-fold cross validations (5-fold) also suggested that model accuracy is lower for *Vermivora* models than GWWA and BWWA models (*Vermivora* RMSE = 0.4216 and MAE = 0.351, GWWA 0.419, 0.3502; BWWA 0.3342, 0.2215).

Table 2*:Summary of Vermivora detections from point count surveys used to develop occupancy models. The total detection column represents the data used to develop models, and the audio-only and visual detections columns show the portion of the total detections of the total detections of each type. Audio-only detections were identified by Type I song which differs between Vermivora species. Visual confirmations were made before, during, or after surveys.*

Vermivora detections						
Species	Points occupied	% of points occupied	Total detections	Audio-only detections	Visual confirmations	% visually confirmed
Vermivora	88	43.78	231	120	111	48.05
GWWA	61	30.35	136	55	81	59.56
BWWA	49	24.38	91	65	26	28.57

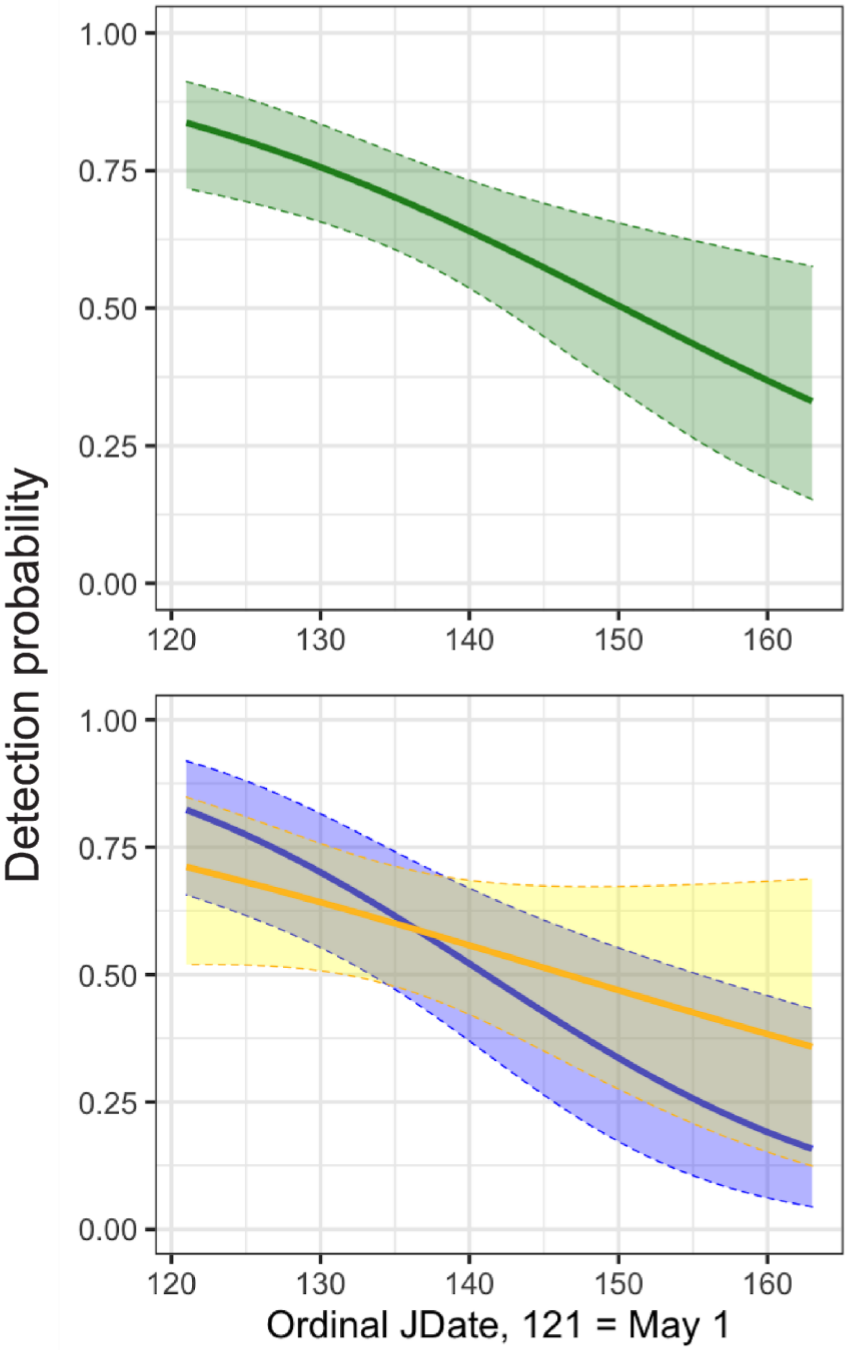

Figure 4*: Model predicted detection probability as a function of ordinal date of surveys for all Vermivora (top) and GWWA-only (bottom, yellow) and BWWA-only (bottom, blue). Detection probability declines throughout the season for all taxa.*

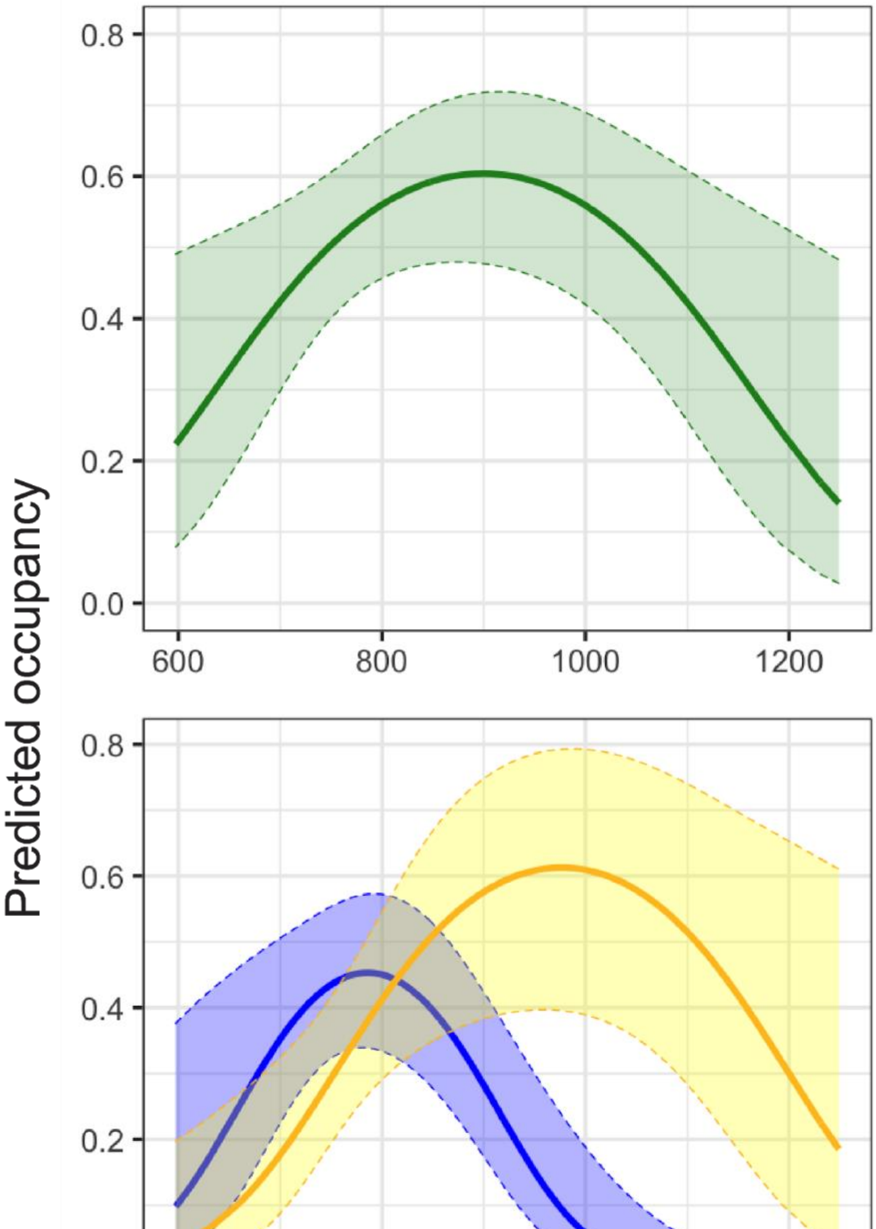

***Figure 5**: Model predicted occupancy for all Vermivora (top panel, green), GWWA-only (bottom panel, yellow), and BWWA-only (bottom panel, blue) as a function of elevation. Occupancy probability is highest at intermediate elevations that differ for each taxa.*

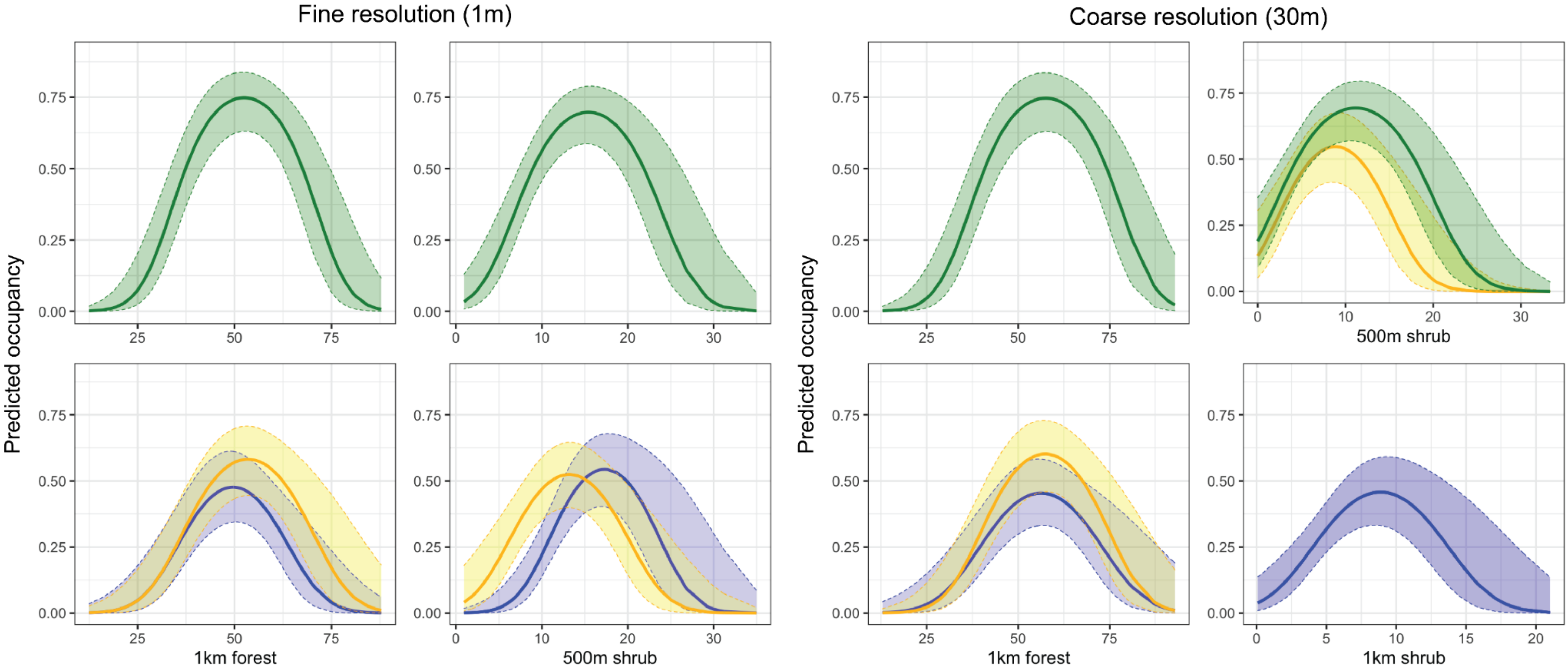

Figure 6: *Model predicted occupancy for all Vermivora (green), GWWA-only (yellow), and BWWA-only (blue) as a function of the most important habitat characteristics and extents, calculated using fine (left panels) and coarse (right panels) resolution land cover data. Forest cover at 1km and shrub cover at 500m from fine resolution spatial data were most important for all taxa. Forest cover at 1km calculated using coarse resolution spatial data was important for all taxa. Shrub cover at 500m remained important for Vermivora and GWWA when using coarse resolution spatial data, but shrub cover at 1km was most important for BWWA.*

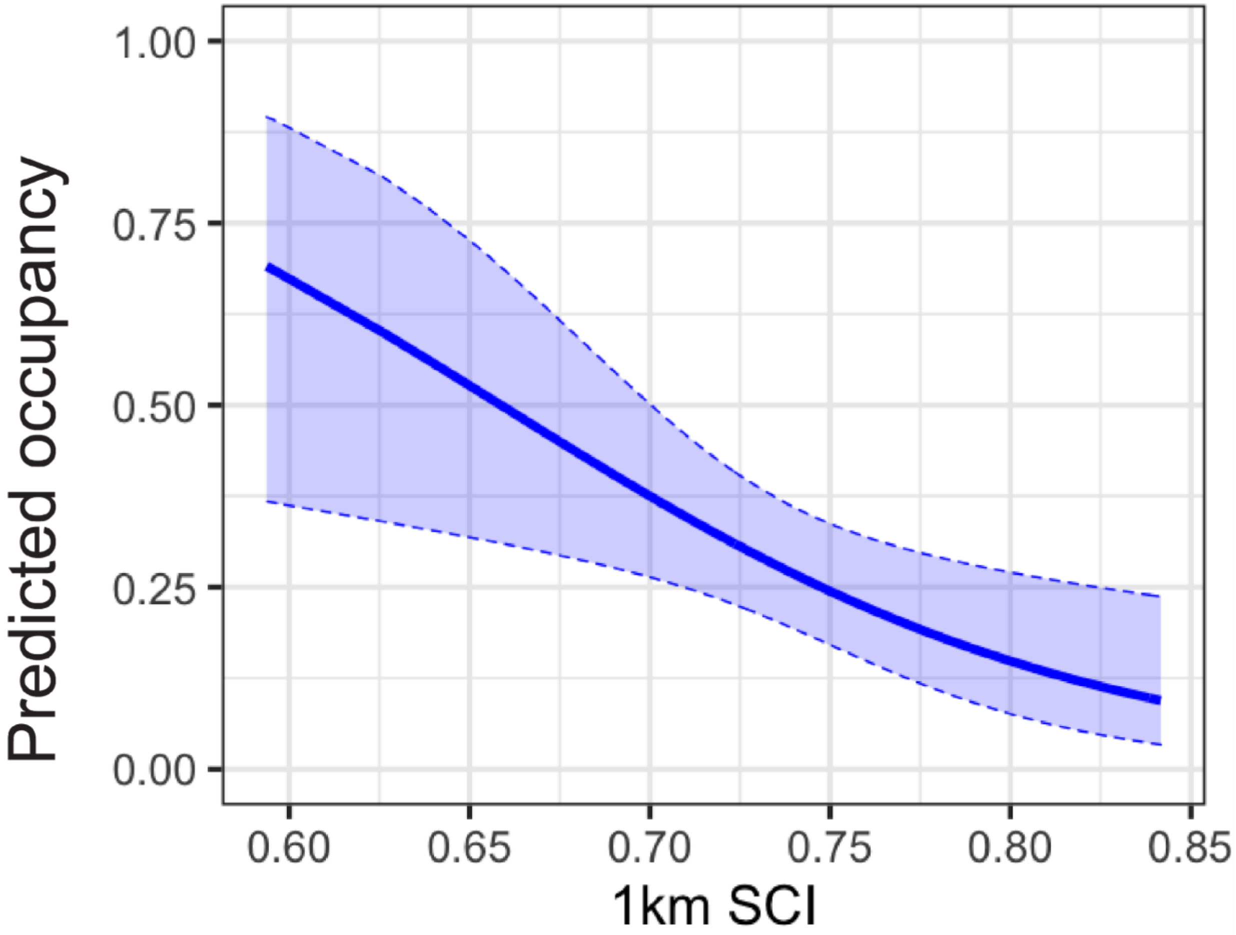

Figure 7: *Model predicted BWWA occupancy as a function of shrub clumpiness index (SCI) at 1km using fine resolution (1m) spatial data.*

Projection of occupancy across focal region

The projected occupancy maps extrapolate model results across the five-county focal region, and highlight ~17,000ha with probability of GWWA-only occupancy >0.5 (Figure 8) and ~60,000ha with probability of *Vermivora* occupancy >0.5. The GWWA-only predicted occupancy is a higher elevation subset of the *Vermivora* occupancy predictions. Occupied sites not included in occupancy models had a greater mean predicted occupancy (0.46) than unoccupied sites (0.38).

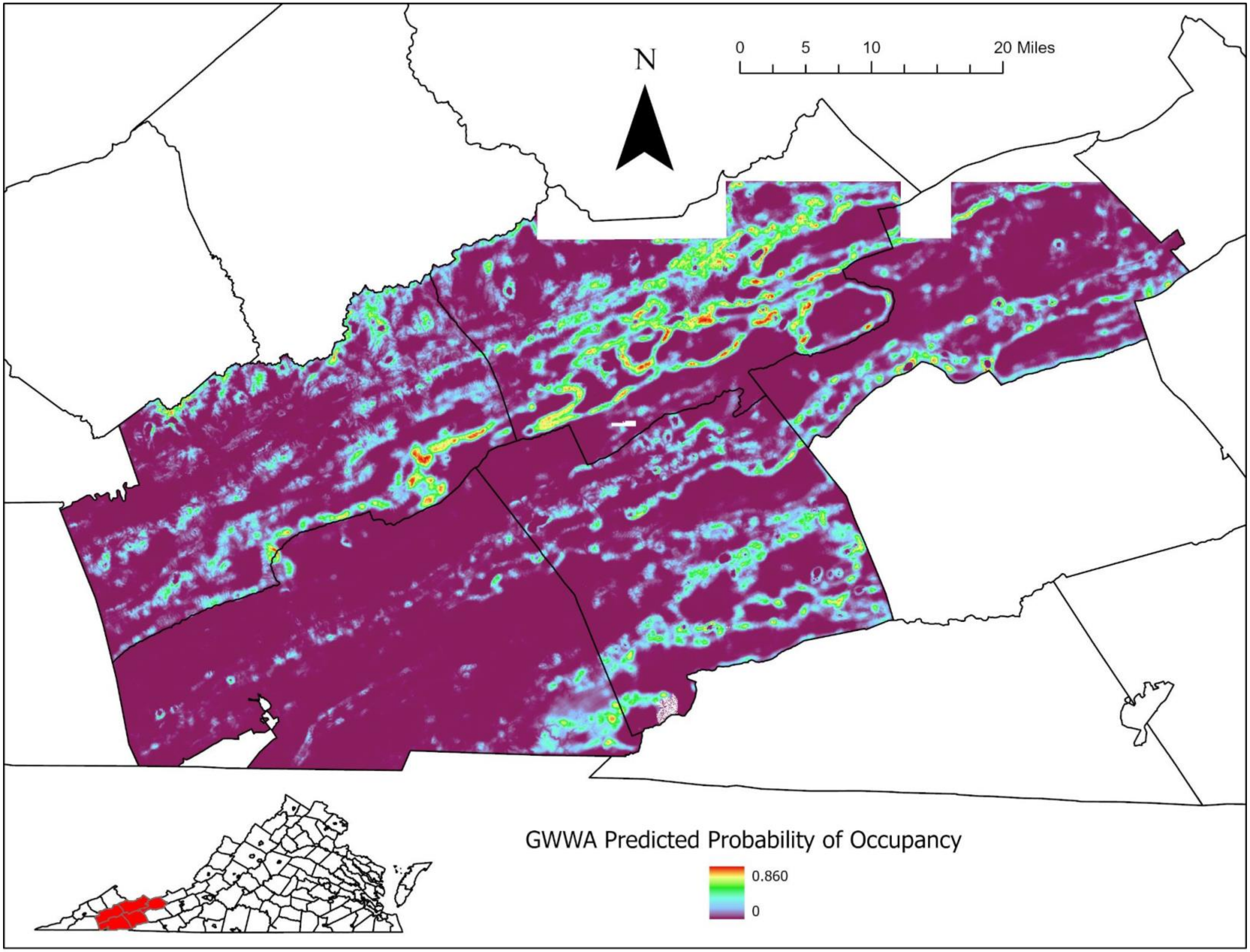

Figure 8*: Map of predicted probability of GWWA occupancy across the five county region in southwestern Virginia, USA. Regions with occupancy >0.5 (green to red) are being targeted for model validation surveys in 2021.*

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Discussion

Our study is the first to utilize a custom LIDAR-derived land cover classification that accurately identifies shrubs at a fine resolution to model *Vermivora* warbler occupancy, highlighting the use of freely available spatial data to better understand habitat selection and refine conservation strategies. Our best performing occupancy models confirm that elevation, as well as forest and shrub cover, are important habitat features for *Vermivora* and specify at what extent these cover types should be maintained. All final models identified similar habitat composition metrics and extents important for predicting site occupancy, but predicted site occupancy for GWWA-only peaked at higher elevations than BWWA-only. Habitat composition (amount of cover types) was generally more important than habitat configuration (arrangement of cover types) for predicting *Vermivora* occupancy. Occupancy models using habitat metrics calculated with fine resolution (1m) land cover data performed similarly to models calculated with coarse resolution (30m) land cover data; this is because shrubs were well represented at both grain sizes. Widely available land cover data that includes an accurate representation of shrub cover are needed to extend these results to the entire Appalachian region or the breeding ranges of *Vermivora* warblers. Predictive maps created from our occupancy models can be used to identify sites for future surveys and recruitment for ESH management programs like WLFW in a critical region for this species of conservation concern.

Elevation

Our results provide supporting evidence of GWWA occupying higher elevation sites than BWWA (Buehler et al. 2007, Crawford et al. 2016), but also indicate that the ideal elevational range for GWWA in this region may be shifting upward. GWWA-only occupancy in this study peaked at 900-1000m elevation and BWWA-only occupancy peaked at 750-800m. WLFW currently prioritizes sites for ESH management at >600m elevation to limit co-occurrence with BWWA (GWWA Working Group 2013), but our results suggest that this would not be effective. BMPs in our focal region were based on studies and observations from over 10 years ago (e.g., Wilson et al. 2007) and our results indicate that GWWA have moved to higher elevations since then. These upslope movements could be induced by competition and hybridization with BWWA and/or climate change. Regardless of the cause, elevation recommendations for GWWA-focused management should be updated to >800m in this region, especially if limiting co-occurrence with BWWAs is a management goal. However, it is likely that BWWA are also moving up in elevation and that such efforts to limit co-occurrence are futile (Gill et al. 2020). Though informative for the Virginia region of the Appalachian Mountains, ideal elevations for *Vermivora* in this region may not be suitable for *Vermivora* further north or south within the Appalachians because of the latitude-elevation relationship of -100m/1° C (Cogbill and White 1991). We detected GWWA at high elevations, but our models indicate a reduction in the probability of GWWA occupancy at elevations higher than 1000m and that there may be other factors influencing occupancy at these elevations. These findings highlight the importance of elevation for *Vermivora* warblers, as well as a need for better understanding of GWWA and BWWA behavioral dynamics (i.e., competition and hybridization) in the Appalachian Mountains BCR.

Habitat composition

Though elevation was the primary differentiating habitat feature for GWWA-only and BWWA-only occupancy, other studies have found additional habitat features to differ between these two taxa. Specifically, they found that BWWA are more tolerant of human land uses such as development and agriculture (Crawford et al. 2016) compared with GWWA, but these tend to occur at lower elevations in the Appalachian region making their independent effects difficult to disentangle.

Our models predict occupancy by GWWA-only to peak at intermediate amounts of forest and shrub cover, providing much-needed detail that can be used to update and improve existing best management practices for the rapidly declining Appalachian GWWA population. GWWA occupancy peaked when forest cover within a 1km radius (314 ha) was ~50-60%, and shrub cover within a 500m radius (78.5 ha) was ~10-15%. Current BMPs for GWWA management in the Appalachian Mountains BCR recommend maintaining 30-70% shrub and sapling cover and 10-30% canopy cover (20-40 ft^2 basal area) within a landscape with >60% deciduous forest cover (GWWA Working Group 2013). Our results corroborate the recommendation for intermediate amounts of shrub cover but differ in the amount due to the extent at which shrub cover is found to be most predictive of GWWA occupancy. Patches of habitat, however, are notoriously difficult to define and may not be meaningful for organisms that rely on a mix of cover types within a habitat patch (Johnson et al. 2005). In landscape ecology a patch is defined as a group of contiguous pixels of the same value (With 2019); however, a habitat patch for *Vermivora* contains a mix of shrub, forest and herbaceous cover. BMPs indicate the amount of shrubs needed “within habitat patches,” rather than detailing a specific extent that is more informative of GWWA habitat selection like we have found in this study. The lack of a specific extent where the recommended amount of shrub cover is to be maintained in current BMPs makes communication and implementation of these recommendations on any given property/landscape challenging.

Previous studies have modeled GWWA nest site selection as a function of on-the-ground vegetation measurements and typically suggest that a mix of herbaceous, woody, and grass cover are important for nesting (Bulluck and Buehler 2008, Terhune II et al. 2016). Aldinger et al. (2017) found that predicted GWWA density was greatest when shrub cover within 100m radius circle of a survey point was 100% and suggested maintaining a minimum of 9-10ha of continuous shrub patches to promote GWWA nesting. These findings are informative and have guided conservation practices in regard to maintaining shrub cover for GWWA, but acquiring fine-scale vegetation data via rigorous field surveys is not always feasible or efficient. Our results also suggest that shrub cover at the 100m extent is correlated with GWWA occupancy when using a fine resolution land cover classification that accurately identifies shrubs, with occupancy peaking at 10-30% shrub cover within 100m. However, our best performing models did not include shrub cover at the 100m extent; shrub cover at the 500m extent was a better predictor of GWWA occupancy. Because our models are based on maps that accurately represent shrub cover, we can specify the amount of shrub cover within 500m (78.5ha) that should be maintained to support breeding GWWA. Likewise, current BMPs recommend managing for >60% deciduous forest cover in the landscape ("within 1.5mi of a habitat patch") and 60-80% forest cover "within 800ft of a habitat patch" (GWWA Working Group 2013). These recommendations were based on expert input and knowledge of the conditions at occupied sites throughout the Appalachian region and not on modeling of occupancy from randomly sampled survey locations. Our models indicate a lower optimum amount of deciduous forest cover in the landscape (specifically 50-60% within 314 ha), but corroborates the BMPs recommendation that GWWA require a predominantly forested landscape. Our study area has a significant amount of pasture and likely represents the lower threshold of forest cover required for *Vermivora* warblers.

These specific recommendations about land cover composition will lead to improved communication and implementation of habitat management for Appalachian GWWA.

Habitat configuration

In addition to land cover composition, current GWWA BMPs also make recommendations about shrub configuration because GWWA are known to occupy a complex mosaic with clumps of shrubs amidst forest and herbaceous cover (Confer et al. 2010, Crawford et al. 2016, Aldinger et al. 2017). Habitat configuration, specifically the degree of clumping or clustering of shrub cover, was effectively captured with our fine resolution land cover data. We found that BWWA-only occupancy models were the only models to show a negative association with shrub clumpiness index at the 1km (314ha) extent. Larger shrub clumpiness index values indicate that shrubs are more clustered whereas smaller values indicate that shrubs are more dispersed. Therefore, scattered shrub clumps are more ideal than large, continuous patches of shrub for BWWA at the 314 ha extent. The range of shrub clumpiness index values at this extent across all survey points was small (0.59 – 0.84) such that there may not be enough variation in shrub clumpiness index values in our dataset to understand the importance of habitat configuration for *Vermivora* warblers; our occupancy models primarily indicated that habitat composition was more important than configuration.

Several studies have documented how habitat selection is influenced by habitat composition and configuration (Radford and Bennett 2007, Hins et al. 2009, Gillies and St. Clair 2010), especially in ephemeral ecosystems like ESH or agriculture-dominated landscapes (Fahrig 1998). Furthermore, previous studies that collected on-the-ground vegetation measurements indicate that GWWA nest site selection is influenced by a mix of cover types (Bulluck and Buehler 2008, Terhune II et al. 2016), but they do not compare the effects of fine scale habitat characteristics across larger extents like we have in this study. Future studies could stratify survey sites across a larger range of shrub configuration, integrate on-the-ground vegetation measurements, and consider other configuration metrics (e.g. forest-shrub adjacency) to further explore whether habitat configuration influences *Vermivora* site occupancy.

Spatial grain or resolution

The grain or resolution of land cover maps can have significant impacts on models of species-habitat relationships. Finer resolution maps generally perform better than coarser resolution maps, especially for bird species that are sensitive to small-scale habitat features (Gottschalk et al. 2011). Despite this general understanding, our model performance and predictions were similar among the continuum of resolutions. When comparing model outputs based on fine and coarse resolution data, the extents at which forest and shrub cover were predictive did not change for *Vermivora* and GWWA-only, but did change slightly for the extent at which shrub cover predicted BWWA-only (from 500m to 1km). Such consistency between models using coarse and fine resolution data may partly be because habitat composition at the smallest extent assessed (100m) did not emerge as predictive for *Vermivora* occupancy when using fine-grained maps. Differences in percent cover caused by changes in grain are more likely at smaller extents than at larger extents (Connor et al. 2019); at small extents, fine resolution data are more likely to capture unique habitat patches and spatial heterogeneity than coarse resolution data (Wiens 1989). Further, we did not calculate percent cover within a 100m radius for the coarse grained data because so few 30m grid cells (~35 cells within 100m) would be present within this small extent. NLCD has been used to estimate GWWA occupancy in the Appalachian

Mountains BCR because it is freely available and due to its coarse resolution (30m) making it easy to process across large regions. Previous studies (Crawford et al. 2016, Wood et al. 2016, McNeil et al. 2020) identified significant associations between GWWA occupancy and forest cover calculated with NLCD, but associations were small and nonlinear effects were not considered; thus they did not identify optimum amounts of forest cover for GWWA as we have done in this study.

Forest cover is one of the most common cover types across our focal region and is overrepresented by ~5% in the resampled coarse resolution data compared to the fine resolution data (Bulluck et al. in prep). Likewise, shrub cover is consistently underestimated by ~5% in the coarse resolution data (Bulluck et al. in prep). Therefore, it is not surprising that the optimal percent cover identified in our models for *Vermivora* warblers shifted up for forest cover and down for shrub cover by ~5-10%. Implementing management recommendations based on coarse resolution data could result in slightly more forest and fewer shrubs than when based on fine resolution data, but these differences are minor and would still result in suitable GWWA habitat. Managers could broaden the range of suggested amounts of forest and shrub cover identified by occupancy models that incorporate coarse and fine resolution data. Slight differences in model predictions between the two spatial grains indicate that either resolution may be suitable for modeling species occurrences as a function of habitat composition metrics. Gottschalk et al. (2011) suggest using fine resolution data (1-3m) when building habitat-suitability models of bird species because fine resolution data have higher thematic resolution (i.e. more cover types are identified) and can identify specific features such as hedgerows and individual bushes. Though fine-grained spatial data can be difficult and time-consuming to process, it is essential for species that rely on such small scale habitat features. However, we have shown here that aggregating fine-grained data that accurately identifies shrubs to a coarser spatial grain (e.g. 30m) may be appropriate to assess and map *Vermivora* occupancy across larger portions of their range.

Projection of occupancy across the focal region and broad-scale management implications

Our projections of GWWA occupancy across the focal region identifies many new potential breeding areas for a rare and threatened species where only a few breeding records were known until recently, and nearly all predicted occupancy are on private lands. Anecdotally, the predicted map of GWWA occupancy based on our models appears to primarily identify regions with ideal GWWA habitat; however, there are some areas of mature forest that are included where GWWA are not expected to breed. Such inclusion of unsuitable GWWA habitat may be the result of two factors. First, the predictors in our top performing models did not include habitat features at the 100m extent, such that any given pixel may have suitable habitat at the 500m and 1km extents, but lack features at smaller spatial extents. Because shrub cover at 100m and 500m were significantly correlated, we did not include both in the same model. Second, our survey sites were randomly sampled within ESH rather than across the entire landscape. It would not have been efficient to survey all potential habitats on the landscape for a species that we know requires ESH; however, by omitting interior forests from our original surveys, our models were not informed by landscape features in interior forests at smaller extents around the survey point (e.g. near 100% forest cover within 100m). We are confident that updating our occupancy models with survey data collected in areas predicted to have high GWWA occupancy from our original models will result in more accurate predictions.

It is notoriously difficult to extrapolate model predictions outside of the bounds of the data used to develop them (Miller et al. 2004, Yates et al. 2018) and spatial extrapolation of species distributions is no exception (Buckley et al. 2010, Bulluck et al. 2006). Despite these challenges, spatial extrapolation is common and increasingly useful as we aim to predict species range shifts due to climate change (Peterson et al. 2019, Sinclair et al. 2010). Areas with high predicted GWWA occupancy are currently being targeted for additional surveys in 2021 which will be used to validate and improve our occupancy models. Statistical validation of our occupancy models suggests that there is room for improvement (RMSE and RME >0.25), though these values are similar to what is reported for other species distribution models when attempting to transfer model output to new locations (Wenger and Olden 2012). Though not a formal field-validation, mean predicted *Vermivora* occupancy at sites not included in model development and was greater at occupied points than unoccupied points, which justifies further field validation. Species distribution models are used to guide conservation actions but rarely validated with independent field-collected data due to the time and expense of collecting these data (Araújo et al. 2005, Araújo and Guisan 2006). However, field validation can provide valuable data to assess model performance (Johnson and Gillingham 2005, Haughiana et al. 2019) and improve understanding of what constitutes habitat quality (Westwood et al. 2020). Therefore, model refinement via field validation is warranted for GWWA and other threatened species.

Implementing conservation practices that support the exact habitat features identified in our models to other regions across GWWA distributions should be done with caution. Although GWWA requires a mix of shrubs, forest and herbaceous cover throughout its breeding range, research about whether the exact proportion of each varies by region and climate interactions is warranted. We recommend that such efforts be based on up-to-date, fine resolution spatial data that accurately identifies shrubs. Unfortunately, these data are not currently widely available, but the imagery and LIDAR data necessary to develop them are freely available (Bulluck et al. in prep). Due to its ephemeral nature, acquiring the most current spatial data is important when quantifying habitat characteristics to guide conservation actions for ESH. Furthermore, efforts to quantify complex habitat characteristics like ESH must consider rare and uncommon cover types that are not effectively captured in commonly used land cover data. However, fine resolution data are becoming increasingly accessible because of the proliferation of unmanned aerial vehicles and advancements in airborne sensors (Morgan et al. 2021). These data may help managers identify rare and important habitat characteristics that are essential for declining species, as well as implement and translate detailed conservation actions focused on complex ecosystems.

Frequent monitoring of threatened and endangered species distributions on private lands is essential; these efforts can help concentrate management efforts and improve decision-making processes. For example, the location of known occupied GWWA sites factor into the ranking and prioritization of funding for WLFW projects because birds are more likely to colonize new habitat when it is within dispersal distance of occupied sites. Sometimes, distribution data from basic monitoring programs are more valuable and effective than elucidating all possible ecological relationships (Lyons et al. 2008). For example, consistent monitoring of Kirtland’s Warblers revealed temporal and spatial shifts in their habitat use, informed managers about how they responded to habitat restoration efforts, and eventually led to their removal from the Endangered Species List (Donner et al. 2008). Our study also showcases the importance of including privately owned lands when surveying for species of conservation concern; monitoring efforts that rely solely on public lands in Virginia would miss the majority of GWWA occurrences. We recommend continued monitoring of *Vermivora* on public and private lands to accurately estimate local populations, establish relationships with private land stewards, and increase outreach for conservation programs.

It is well known that consideration of the multiple scales at which habitat selection occurs is essential for modeling species distributions (Johnson 1980), and our study corroborates this. Conservation practices that only consider one scale (typically vegetation data collected within small extents, around a nest for example) may be missing features that promote fitness outcomes in other life stages (forest cover at larger extents that support fledgling survival and dispersal). However, without data on habitat features at these larger scales, this is not possible. Understanding habitat selection processes at multiple scales can help managers identify priority areas for conservation and contribute to efforts to reverse species declines and habitat loss.

Implications for practice in Virginia

We recommend that conservation programs update their BMPs for GWWA to prioritize sites with elevation >800m, 50-60% forest cover at 1km, and 10-15% shrub cover at 500m. If limiting co-occurrence by GWWA and BWWA is a conservation goal, managers should identify areas of overlapping high probability of occupancy by comparing projections of *Vermivora* and GWWA-only models. Our models suggest that elevation is the primary differentiating factor for these species; the optimal forest and shrub composition was nearly identical for GWWA-only and BWWA-only.

If limiting co-occurrence with BWWA is less of a conservation priority, a broader approach that focuses management efforts on both *Vermivora* species is possible. A broader taxonomic approach would mean a broader range of suitable conditions; predicted *Vermivora* occupancy peaked at broader ranges of forest cover at 1km and shrub cover at 500m compared with either species model. Justifications for taking this approach in the Appalachians are that our models for each taxon were very similar, the two species are genetically similar (Toews et al. 2016), and efforts to limit co-occurrence by GWWA and BWWA may be futile if BWWA continue to move up in elevation. We recommend taking a broad taxonomic approach to forest and shrub cover recommendations from our models, but prioritizing management in higher elevation sites (i.e., ranking projects at or above 800m ahead of those at lower elevations). This approach will prioritize GWWA management while not completely neglecting BWWA and other shrub dependent species. In this study, we highlight the importance of understanding habitat selection at multiple scales, considering private and public lands for conservation, and integrating freely available spatial data to guide conservation programs.

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Supplementary materials

***Table S1**: Models of detection probability (p) for Vermivora (GWWA, BWWA, and/or hybrids), GWWA-only, and BWWA-only with associated detection covariates: Julian date ("date"), time of survey ("time"), and observer. Also shown are the number of model parameters (k), model weight (w), and ΔAkaike's Information Criterion adjusted for small sample size (ΔAIC_c).*

Detection probability				
	Model	k	ΔAIC_c	w
Vermivora	p(date)	3	0.00	0.97
	p(null)	2	7.10	0.03
	p(obs)	4	10.09	0.01
	p(time)	3	29.12	0.00
GWWA	p(date)	3	0.00	0.40
	p(obs)	4	0.21	0.36
	p(null)	2	1.09	0.23
	p(time)	3	9.87	0.00
BWWA	p(date)	3	0.00	0.98
	p(null)	2	8.48	0.01
	p(obs)	4	11.52	0.00
	p(time)	3	13.35	0.00

***Table S2**: Univariate models of occupancy (Ψ) for Vermivora, GWWA-only, and BWWA-only with associated linear and quadratic elevation terms (elevation and elevation^2, respectively). All occupancy models include date as a detection covariate. Also shown are the number of model parameters (k), model weight (w), and ΔAkaike's Information Criterion adjusted for small sample size (ΔAIC_c).*

Occupancy models - elevation				
	Model	k	ΔAIC_c	w
Vermivora	Ψ(elevation^2)	5	0.00	0.76
	Ψ(null)	3	2.87	0.18
	Ψ(elevation)	4	4.94	0.06
GWWA	Ψ(elevation^2)	5	0.00	0.96
	Ψ(elevation)	4	6.96	0.03
	Ψ(null)	3	9.27	0.01
BWWA	Ψ(elevation^2)	5	0.00	1.00
	Ψ(elevation)	4	14.34	0.00
	Ψ(null)	3	25.88	0.00

***Table S3**: Univariate occupancy (Ψ) models for Vermivora, GWWA-only, and BWWA-only with associated linear and quadratic habitat composition and configuration metrics calculated using fine resolution (1m) land cover data. Also shown are the number of model parameters (k), model weight (w), and ΔAkaike's Information Criterion adjusted for small sample size (ΔAIC$_c$). SCI is a shrub clumpiness index and represents the configuration of shrub cover.*

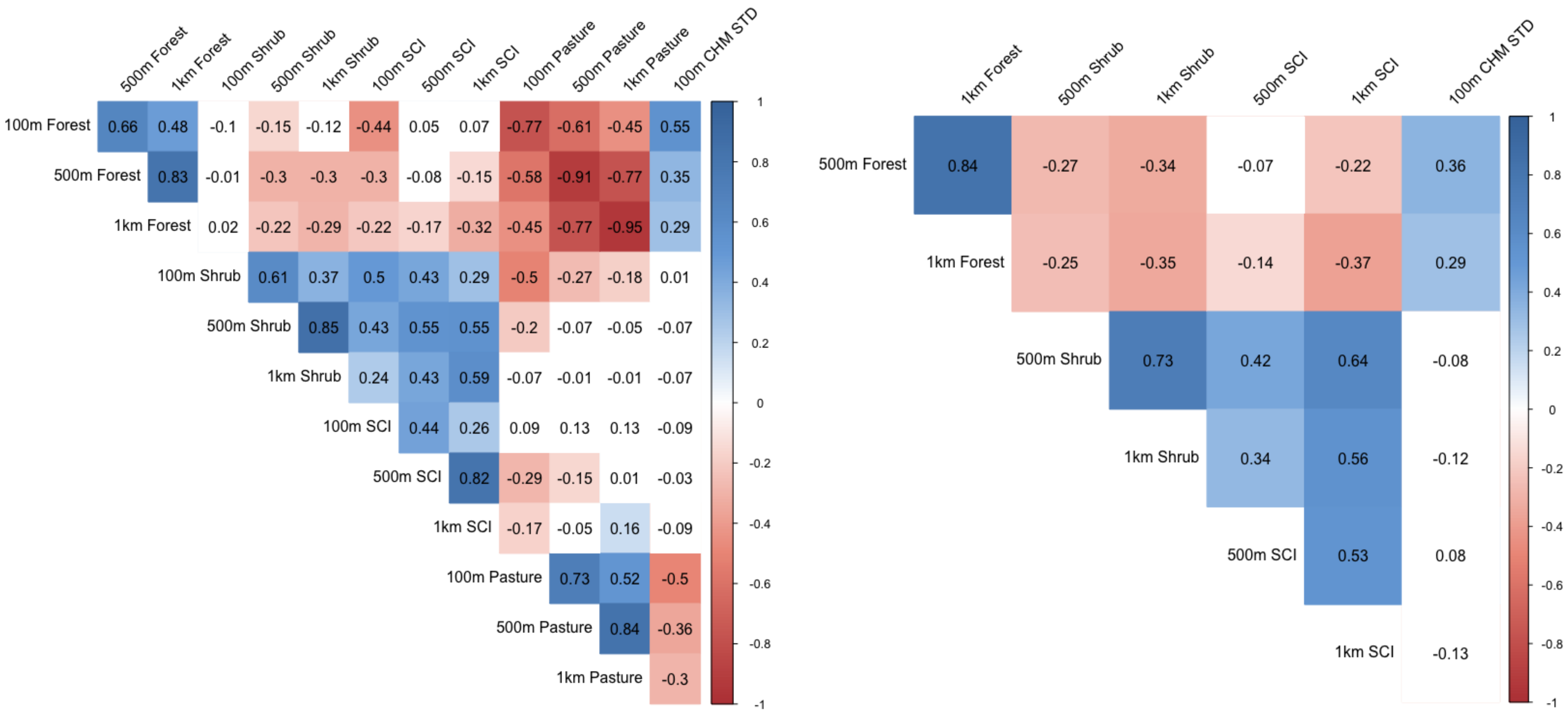
Occupancy models – composition and configuration metrics				
	Model	k	ΔAIC$_c$	w
Vermivora	Ψ(1km forest^2)	7	0.00	1.00
	Ψ(500m shrub^2)	7	15.51	0.00
	Ψ(1km shrub^2)	7	20.43	0.00
	Ψ(500m forest^2)	7	29.08	0.00
	Ψ(100m shrub^2)	7	37.81	0.00
	Ψ(1km forest)	6	38.03	0.00
	Ψ(1km shrub)	6	40.79	0.00
	Ψ(100m pasture^2)	7	42.26	0.00
	Ψ(500m forest^2)	6	44.45	0.00
	Ψ(500m SCI)	6	46.11	0.00
	Ψ(500m shrub)	6	46.38	0.00
	Ψ(null)	5	46.40	0.00
GWWA	Ψ(1km forest^2)	7	0.00	0.75
	Ψ(500m shrub^2)	7	2.60	0.20
	Ψ(1km shrub^2)	7	5.73	0.04
	Ψ(500m forest^2)	7	15.99	0.00
	Ψ(100m shrub^2)	7	18.06	0.00
	Ψ(100m pasture^2)	7	20.47	0.00
	Ψ(1km forest)	6	21.49	0.00
	Ψ(1km shrub)	6	21.96	0.00
	Ψ(null)	5	22.63	0.00
BWWA	Ψ(1km forest^2)	7	0.00	0.96
	Ψ(1km SCI)	6	7.43	0.02
	Ψ(500m shrub^2)	7	8.71	0.01
	Ψ(500m SCI)	6	11.16	0.00
	Ψ(1km forest)	6	12.65	0.00
	Ψ(500m forest^2)	7	13.26	0.00
	Ψ(1km shrub^2)	7	15.40	0.00
	Ψ(100m shrub^2)	7	21.35	0.00
	Ψ(null)	5	22.39	0.00

***Table S4**: Comparison of additive occupancy (Ψ) models for Vermivora, GWWA-only, and BWWA-only that include covariates from the best performing univariate composition/configuration models (Table 5) using fine resolution (1m) land cover spatial data. Also shown are the number of model parameters (k), model weight (w), and ΔAkaike's Information Criterion adjusted for small sample size (ΔAIC_c).*

Occupancy models – additive model sets				
	Model	k	ΔAIC_c	w
Vermivora	Ψ(1km forest^2 + 500m shrub^2)	9	0.00	0.76
	Ψ(1km forest^2 + 500m shrub^2 + 100m pasture^2)	11	2.35	0.24
	Ψ(1km forest^2 + 100m pasture^2)	9	17.56	0.00
	Ψ(500m shrub^2 + 100m pasture^2)	9	27.37	0.00
	Ψ(null)	5	62.67	0.00
GWWA	Ψ(1km forest^2 + 500m shrub^2)	9	0.00	0.88
	Ψ(1km forest^2 + 500m shrub^2 + 100m pasture^2)	11	3.96	0.12
	Ψ(500m shrub^2 + 100m pasture^2)	9	14.62	0.00
	Ψ(1km forest^2 + 100m pasture^2)	9	16.53	0.00
	Ψ(null)	5	36.32	0.00
BWWA	Ψ(1km forest^2 + 500m shrub^2 + 1km SCI)	10	0.00	0.89
	Ψ(500m shrub^2 + 1km SCI)	8	4.13	0.11
	Ψ(1km forest^2 + 500m shrub^2)	9	12.84	0.00
	Ψ(1km forest^2 + 1km SCI)	8	14.74	0.00
	Ψ(null)	5	41.26	0.00

Table S5: β *estimates and confidence intervals from the final occupancy (Ψ) models for Vermivora, GWWA-only, and BWWA-only including the most important landscape metrics and extents at which they were calculated using fine (1m) and coarse (30m) resolution land cover data.*

	Model	β	CI
Vermivora	Fine resolution		
	Ψ(elevation^2)	-0.159	-0.502 – 0.611
	Ψ(1km forest^2)	-1.118	-1.646 – -0.591
	Ψ(500m shrub^2)	-0.831	-1.318 – -0.344
	Coarse resolution		
	Ψ(elevation^2)	-0.200	-0.546 – 0.146
	Ψ(1km forest^2)	-1.166	-1.651 – - 0.681
	Ψ(500m shrub^2)	-0.946	-1.497 – -0.396
GWWA	Fine resolution		
	Ψ(elevation^2)	-0.468	-0.919 – 0.0156
	Ψ(1km forest^2)	-1.064	-1.718 – -0.411
	Ψ(500m shrub^2)	-1.167	-1.852 – -0.481
	Coarse resolution		
	Ψ(elevation^2)	-0.477	-0.918 – -0.0364
	Ψ(1km forest^2)	-1.103	-1.720 – -0.487
	Ψ(500m shrub^2)	- 1.446	-2.283– -0.609
BWWA	Fine resolution		
	Ψ(elevation^2)	-0.121	-0.855 – 0.612
	Ψ(1km forest^2)	-0.955	-1.849 – -0.0605
	Ψ(500m shrub^2)	-0.894	-1.640 – -0.148
	Ψ(1km SCI)	-31.093	-51.197 – -10.988
	Coarse resolution		
	Ψ(elevation^2)	-0.519	- 1.225 – 0.186
	Ψ(1km forest^2)	-0.868	-1.497 – -0.239
	Ψ(1km shrub^2)	-0.446	-0.903 – 0.0107



	500m Forest	1km Forest	100m Shrub	500m Shrub	1km Shrub	100m SCI	500m SCI	1km SCI	100m Pasture	500m Pasture	1km Pasture	100m CHM STD
100m Forest	0.66	0.48	-0.1	-0.15	-0.12	-0.44	0.05	0.07	-0.77	-0.61	-0.45	0.55
500m Forest		0.83	-0.01	-0.3	-0.3	-0.3	-0.08	-0.15	-0.58	-0.91	-0.77	0.35
1km Forest			0.02	-0.22	-0.29	-0.22	-0.17	-0.32	-0.45	-0.77	-0.95	0.29
100m Shrub				0.61	0.37	0.5	0.43	0.29	-0.5	-0.27	-0.18	0.01
500m Shrub					0.85	0.43	0.55	0.55	-0.2	-0.07	-0.05	-0.07
1km Shrub						0.24	0.43	0.59	-0.07	-0.01	-0.01	-0.07
100m SCI							0.44	0.26	0.09	0.13	0.13	-0.09
500m SCI								0.82	-0.29	-0.15	0.01	-0.03
1km SCI									-0.17	-0.05	0.16	-0.09
100m Pasture										0.73	0.52	-0.5
500m Pasture											0.84	-0.36
1km Pasture												-0.3

	1km Forest	500m Shrub	1km Shrub	500m SCI	1km SCI	100m CHM STD
500m Forest	0.84	-0.27	-0.34	-0.07	-0.22	0.36
1km Forest		-0.25	-0.35	-0.14	-0.37	0.29
500m Shrub			0.73	0.42	0.64	-0.08
1km Shrub				0.34	0.56	-0.12
500m SCI					0.53	0.08
1km SCI						-0.13

***Figure S1**: Correlation matrices for landscape metrics calculated with fine resolution (1m; left) and coarse resolution (30m; right) used in occupancy models. Composition metrics focused on shrub, forest, and pasture cover, whereas shrub clumpiness index (SCI) and the standard deviation of the canopy height model within 100m (CHM STD) represented habitat configuration and structure, respectively. Landscape metrics were not calculated within 100m radii for models that incorporated the coarse resolution data.*

Vita

Baron H. Lin was born on August 10th, 1992 in St. Louis, MO. He graduated in 2015 from Virginia Tech with a Bachelor of Science in Wildlife Conservation. He discovered a passion for birds while working as a research technician on a variety of projects focused on waterbirds in Washington and Snail Kites in Florida. However, Baron was eager to return to Virginia, participate in applied ecological research, and contribute to local conservation efforts. Prior to joining the Bulluck Avian Ecology Lab, he solidified his interests in avian ecology, science communication, and land management as a research intern at Virginia Working Landscapes.