Bird-habitat relationships in southern Iowa forests

by

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ABSTRACT

Recent avian population declines emphasize the need to quantify populations of at-risk species, assess bird community diversity, and better understand the habitat characteristics associated with bird population densities and community diversity. In response to bird declines, the Iowa Department of Natural Resources has established Bird Conservation Areas (BCAs) and has listed many at-risk bird species as Species of Greatest Conservation Need (SGCN). This study focuses primarily on Iowa forest birds, one of many groups of birds with declining populations. The goals of this study were to 1) estimate densities of breeding avian SGCNs and other species of management interest, 2) determine relationships between breeding bird densities and habitat metrics, and 3) quantify bird diversity and determine relationships between bird diversity and habitat metrics. Our study took place in three primarily forested Bird Conservation Areas in south-central Iowa. To estimate density, we used point counts over a grid of 493 points visited twice each breeding season from 2016 to 2019 and hierarchical distance sampling (HDS) models. To estimate relationships between bird density and habitat, we incorporated 13 habitat covariates over a range of spatial scales into HDS models for 10 species of conservation and management concern. To estimate bird diversity and determine bird diversity-habitat relationships, we estimated species richness by summing occupancy probabilities from HDS models for 77 total species and 24 SGCN and used multiple regression to compare estimates with 13 habitat metrics over a range of spatial scales. The five SGCN with the greatest estimated densities (in descending order) were Eastern Wood-Pewee (*Contopus virens*), Ovenbird (*Seiurus aurocapilla*), Common Yellowthroat (*Geothlypis trichas*), Acadian Flycatcher (*Empidonax virescens*), and Scarlet Tanager (*Piranga olivacea*), with mean estimated densities ranging from 0.195 – 0.698 birds/ha. Median estimated overall species richness within a 100-m point count radius was 20.4, and median estimated SGCN species richness was 4.0. Densities of Red-headed Woodpecker (*Melanerpes erythrocephalus*), Acadian Flycatcher, Wood Thrush (*Hylochichla mustelina*), Ovenbird (*Seiurus aurocapilla*), Common Yellowthroat, and Scarlet Tanager (*Piranga olivacea*) were positively associated with landscape scale forest cover at either a 1 km or 10 km scale, while Field Sparrow densities were negatively associated with landscape-scale forest cover. Landscape-scale forest cover within 10 km was also positively associated with overall species richness and SGCN species richness. Densities of forest birds such as Eastern Wood-Pewee, Acadian Flycatcher, Wood Thrush, Ovenbird, and Scarlet Tanager were positively associated with distance to forest edge, while densities of Field Sparrow and Common Yellowthroat, two species of edges and open areas, had a negative association with distance to forest edge. Edges and forest interiors (~800 m from edge) both had relatively high species richness overall and for SGCN; SGCN species richness was greatest in the forest interior. Bird-habitat relationships at smaller spatial scales were less consistent. For example, leaf litter ground cover was positively associated with densities for five of ten individual species analyzed, but negatively associated with Common Yellowthroat densities, overall species richness, and SGCN species richness. Our results suggest that intact interior forest away from edges is especially beneficial to SGCN and the bird community as a whole, but that the maintenance of some edge and open habitat is also needed for some species.

CHAPTER 1. GENERAL INTRODUCTION

Background

At both continental and regional scales in North America, vegetation and primary productivity explain much of the patterns of avian diversity and distributions; more productive environments tend to have greater avian species richness (Hawkins and Porter 2003; Rowhani et al. 2008). Deciduous forests are one of the most productive ecosystems in temperate North America (Turner et al. 2003), and in the Midwestern United States alone, more than 120 bird species breed in forests and woodlands (Niemi et al. 2016). Despite the plethora of bird species in the eastern deciduous forest biome, which spans the Atlantic Coast of the United States and extends as far northwest as Minnesota and as far southwest as northeastern Texas (Dyer 2006), more than 60% of species which breed primarily in this biome are in decline (Rosenberg et al. 2019). These declines of avian populations and biodiversity make their assessments a high priority.

On local landscape scale, disturbance by agriculture and suburban development within 1-2 km negatively impacts bird diversity and the densities of forest species in eastern deciduous and mixed forests (Askins and Philbrick 1987; Rodewald and Yahner 2001), although landscape-scale reforestation efforts in the wake of disturbance can allow bird communities to recover (Askins and Philbrick 1987). Habitat fragmentation and increasing edge habitat can also negatively impact bird diversity because some species require a minimum area and interior forest species often avoid forest edges (Kroodsma 1982; Ambuel and Temple 1983). At a stand scale, vegetation structure is the primary driver of bird diversity and densities in eastern deciduous forest. More structurally complex stands usually host a higher species diversity (MacArthur and MacArthur 1961), and characteristics such as tree density, shrub density, and ground cover type affect density of a variety of species at a stand scale (Anderson and Shugart 1974; Reidy et al. 2014). Conversion of structurally diverse mixed species forest to even-age, single species silvicultural plantations can negatively impact bird diversity and densities (Twedt et al. 1999) Thinning forests to increase regeneration of oak trees can positively impact bird diversity and density by leaving ample canopy habitat while increasing habitat structure below the canopy (Newell and Rodewald 2012).

In response to the decline of bird diversity and bird habitat in Iowa and the Midwest, the Iowa Department of Natural Resources (DNR), in cooperation with the Partners in Flight Midwest Working Group, established the Bird Conservation Areas (BCA) program with goals of reducing habitat fragmentation and improving private land management (Iowa DNR 2010; Ehresman 2015). In 2015, BCAs as a whole harbored 83 out of the 85 bird species designated by the Iowa DNR as Species of Greatest Conservation Need (SGCN; Ehresman 2015; Iowa Department of Natural Resources 2015).

Objectives

The goals of this study were to quantify bird populations and the overall bird community in the public cores of three primarily forested Bird Conservation Areas in south-central Iowa, and to determine bird-habitat relationships in these areas. We had three primary objectives to reach these goals:

1) Estimate densities of breeding avian SGCNs and other species of management interest using hierarchical distance sampling.
2) Determine relationships between breeding bird densities and habitat metrics using hierarchical distance sampling.

3) Quantify bird diversity while accounting for imperfect detection probability using hierarchical distance sampling, and determine relationships between bird diversity and habitat metrics.

The findings of this study have several intended uses. First, they provide important baseline data about the distribution and abundance of conservation priority species in these areas. Second, an understanding of bird-habitat relationships will be useful to forest managers who seek to manage the forest resource in a manner that is consistent with bird conservation. Third, there is local interest to develop a birding trail, and information about the distribution and abundance of conservation priority breeding birds will provide the basis for identifying key hotspots for breeding birds.

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CHAPTER 2. DENSITY ESTIMATES OF CONSERVATION PRIORITY BIRDS IN SOUTH-CENTRAL IOWA

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Abstract

With recent declines in avian populations, it is important to obtain accurate estimates of bird populations. Our study focused on 26 species of breeding birds of management concern, in three primarily forested Bird Conservation Areas (BCAs) in south-central Iowa. We used point counts with distance sampling to account for imperfect detection when estimating density, visiting a grid of 493 points twice each breeding season from 2016 to 2019 for a total of 3944 surveys. We produced hierarchal distance sampling models with a variety of covariates on detection probability, as well as a binary forest cover covariate on abundance. For species with <60 observations, we lumped data for similar species and used a species-specific covariate on abundance. We combined survey-scale empirical Bayesian abundance distributions to estimate an overall density, BCA-specific densities, and annual densities for each species. Overall density estimates varied considerably between species. The five species with the greatest estimated estimated densities (in descending order) were Eastern Wood-Pewee (*Contopus virens*), Ovenbird (*Seiurus aurocapilla*), Common Yellowthroat (*Geothlypis trichas*), Acadian Flycatcher (*Empidonax virescens*), and Scarlet Tanager (*Piranga olivacea*), with mean estimated densities ranging from 0.195 – 0.698 birds/ha . The five species with the lowest estimated densities (in ascending order) were Veery (*Catharus fuscescens*), Cerulean Warbler (*Setophaga cerulea*),

Broad-winged Hawk (*Buteo platypterus*), Northern Bobwhite (*Colinus virginianus*), and Eastern Meadowlark (*Sturnella magna*), with mean estimated densities ranging from 0.003 – 0.008 birds/ha. Eastern Wood-Pewee densities were exceptionally high compared to similar studies, while grassland species (e.g., Eastern Meadowlark) and species on the periphery of their breeding range (e.g., Cerulean Warbler) generally had low densities. This study provides current population density estimates that have potential to serve as a baseline for future studies estimating trends over time. In addition, these data will be useful to local forest managers as they consider forest management practices and their impacts to local breeding birds. We recommend maintaining interior forest habitat at the two most heavily forested BCAs for the benefit of species such as Acadian Flycatcher while also some open habitat to benefit species such as Field Sparrow.

Introduction

North American bird abundance has declined by almost 30% in recent decades (Rosenberg et al. 2019), making accurate population estimates of declining and at-risk breeding birds a high priority. Declines in some species have been severe enough that their current breeding ranges have contracted to a fraction of their original extent (Rodriguez 2002). Forest birds are one of many threatened groups of North American birds; more than 60% of species that breed primarily in forests in the Eastern and Midwestern United States are in decline (Rosenberg et al. 2019). On their breeding grounds, disturbance by suburban development, agriculture, and forest fragmentation can all lead to forest bird population declines (Ambuel and Temple 1983; Askins and Philbrick 1987; Rodewald and Yahner 2001). Although the effects of these types of disturbance are often negative, the creation of edge habitat by removing forest benefits some bird species (Kroodsma 1982). In addition to long-term declines in bird populations, bird populations can fluctuate between years due to factors such as food availability, making multi-year studies essential to accurately assess population sizes and trends (Holmes and Sherry 1988; Holmes and Sherry 2001). Additionally, bird population trends on a local scale do not always match those on a regional or continental scale (Holmes and Sherry 1988), making population assessments at various sites within a region essential.

A basic and well understood challenge in bird studies is that not all birds present are detected during surveys. Accounting for this imperfect detection when estimating bird abundances is therefore critical to avoid biased estimates (Norvell et al. 2003). A variety of methods exist to estimate detection probability of birds, including distance sampling (Buckland et al. 2001), time removal methods (Farnsworth et al. 2002), double observer methods (Nichols et al. 2000), and N-mixture models based on multiple visits (Royle 2004). Of these methods, distance sampling is particularly common (Buckland et al. 2001). Detection probabilities from distance sampling can be incorporated into models of abundance, thus allowing for modeled bird density to vary between sampling locations based on habitat in a hierarchical distance sampling model (Royle et al. 2004; Chandler et al. 2011).

While it is straightforward to estimate overall abundance for the entire study region from a distance sampling model, or to estimate abundance at the scale of a single survey when using hierarchical distance sampling (Royle et al. 2004; Fiske and Chandler 2011), obtaining estimates with precision for areas representing larger subsets of surveys using maximum likelihood-based methods is less straightforward. R package ‘unmarked’ estimates survey-scale abundance using empirical Bayes methods; these survey scale estimates can be summed to create area-specific estimates (Morris 1983; Fiske and Chandler 2011; Furnas et al. 2019). Obtaining precision for these estimates is somewhat challenging, given that empirical Bayes methods do not incorporate uncertainty in detection probability and abundance coefficients (Laird and Louis 1987; Fiske and Chandler 2011). Parametric bootstrapping across the different levels of model hierarchy allows for calculation of confidence intervals that capture uncertainty in hyperparameters, but this can take considerable computation time with large datasets and multiple subsets (Furnas et al. 2019). In spite of issues with biased and narrow confidence intervals as a result of not incorporating hyperparameter uncertainty, using quantiles of empirical Bayesian posterior distributions remains the fastest way to produce a precision estimate for empirical Bayesian estimates (Laird and Louis 1987).

In this study we focus on 24 Iowa Species of Greatest Conservation Need (SGCN), as well as two additional bird species of management concern. Our goal for each study species was to use hierarchical distance sampling to 1) estimate a single overall density across all BCAs and years, 2) estimate density for each of the 3 BCAs across year, and 3) estimate an annual density for each of the four years across all BCAs, eight estimates per species and 408 estimates in total. We used hierarchical distance sampling with empirical Bayes methods to estimate densities for each survey, and we combined posterior distributions from each survey to estimate a mean density and quantile-based 95% confidence interval for the subsets of surveys listed above, acknowledging the tradeoff between computational ease and bias when using quantile-based empirical Bayes confidence intervals. We predicted a wide range of densities between species, that forest species would occur in higher densities in more forested BCAs, and that some species' populations would vary between years.

Methods

Study Area

Our study area comprised six units of Stephens State Forest and Sand Creek Wildlife Management Area, spanning Clarke, Decatur, Lucas, Monroe, and Ringgold counties in south-central Iowa, USA. These properties are the "cores" of three primarily forested Bird Conservation Areas (BCA), areas designated as containing habitat important to Iowa bird populations (Ehresman 2015). The Woodburn, Whitebreast, and Lucas Units of Stephens State Forest are almost entirely contiguous and are located within the Stephens Forest BCA; these units combined are 2,767 ha and will hereafter be collectively called "Stephens" (Figure 3.1A). The Cedar Creek, Chariton, and Thousand Acres Units of Stephens State Forest are separated from each other by a distance of 1-4 km and are located within Stephens Forest -Thousand Acres BCA; these units combined are 2,361 ha and will hereafter be collectively called "Thousand Acres" (Figure 3.1B). Sand Creek Wildlife Management Area (hereafter "Sand Creek"), is 1,457 ha and is located within the Sand Creek Woodland Savanna BCA (Figure 3.1C).

These areas are comprised primarily of deciduous forest and woodlands, especially upland oak (*Quercus* spp.)-hickory (*Carya* spp.) forest, but also bottomland cottonwood (*Populus deltoides*)-silver maple (*Acer saccharinum*) woodlands. Small portions of these forests are actively managed; activities include girdling to create standing dead wood and selective harvesting of trees to create a more open canopy. The topography of these forests is characterized primarily by ridges and ravines; many ravines have seasonal streams. Some larger perennial streams and rivers are also present; bottomland forests tend to occur along these waterways. Other habitats present in smaller patches are pine plantations, wetlands, grassland, pasture, and crop fields; grasslands were more prevalent at Sand Creek compared to the other two study areas, and wetlands were largely confined to a small corner of Stephens (Figure 3.1). Dominant tree species were white, northern red, and bur oaks (*Quercus alba*, *Q. rubra*, and *Q. velutina*), shagbark hickory (*Carya ovata*), and American elm (*Ulmus americana*). Three species of ash (*Fraxinus* spp.) were also present, but most individuals were standing deadwood killed by emerald ash borer (*Agrilus planipennis*). Common woody plants in the understory and in clearings included ironwood (*Ostrya virginiana*), coralberry (*Symphoricarpos orbiculatus*), multiflora rose (*Rosa multiflora*), black raspberry (*Rubus occidentalis*), blackberry (*Rubus allegheniensis*), and eastern redcedar (*Juniperus virginiana*).

Study Species and Species Groups

We modeled densities for 26 breeding bird species, 24 of which were listed as Species of Greatest Conservation Need (SGCN) in Iowa (Iowa Department of Natural Resources 2015). We excluded other SGCN for which there were <5 detections. In addition to SGCN, we also chose to include Ovenbird (*Seiurus aurocapilla*) and Scarlet Tanager (*Piranga olivacea*). Ovenbirds are only locally abundant in Iowa (pers. obs.) and Scarlet Tanagers are considered an indicator species for forest habitat quality (Rosenberg et al. 1999; Urban et al. 2012).

The general cutoff for number of detections in distance sampling analyses is ~60 (Buckland et al. 2001), but species with similar song volume, quality, and frequency can be modeled with shared detection functions to improve sample size (Alldredge, Pollock, et al. 2007). We grouped SGCN with <60 detection into six different groups containing species with similar song quality and habitat preferences; seven species in these groups were not one of the 26 species of interest; we do not report densities for these species. Northern Bobwhite (*Colinus virginianus*), a SGCN, was grouped with Ring-necked Pheasant (*Phasianus colchicus*), a non-

SGCN, on account of both being gallinaceous birds of open habitats with loud vocalizations; this grouping will be called the "gallinaceous group" (Brennan et al. 2020; Giudice and Ratti 2020). Yellow-billed Cuckoo (*Coccyzus americanus*) and Black-billed Cuckoo (*Coccyzus erythropthalmus*), both SGCN, were grouped due to similar vocalizations and a shared preference for shrubby habitat away from deep forest; this group will be called the "cuckoo group" (Hughes 2020a; Hughes 2020b). We grouped Red-shouldered Hawk (*Buteo lineatus*) and Broad-winged Hawk (*Buteo platypterus*), two SGCN, with Cooper's Hawk (*Accipiter cooperii*) and Red-tailed Hawk (*Buteo jamaicensis*), two non-SGCN; this group will collectively be called the "hawk group". Although vocalizations and habitat preferences differ between these hawk species, all are members of the family *Accipitridae* and have at least moderately loud vocalizations (Dykstra et al. 2020; Goodrich et al. 2020; Preston and Beane 2020; Rosenfield et al. 2020). Eastern Kingbird (*Tyrannus tyrannus*), an SGCN, was grouped with Eastern Bluebird (*Sialia sialis*), a non-SGCN; both species prefer savanna-type habitat, engage in aggressive and vocal territory defense, and have a combination of soft and loud vocalizations; this group will be referred to as "the savanna group" (Gowaty and Plissner 2020; Murphy and Pyle 2020). We grouped Bell's Vireo (*Vireo bellii*) and Brown Thrasher (*Toxostoma rufum*), two SGCN, with two non-SGCN: White-eyed Vireo (*Vireo griseus*) and Yellow-breasted Chat (*Icteria virens*). Each of these four species is relatively secretive, prefers scrubland and thicket habitats, and has a moderately loud song; this group will be referred to the as "the scrubland grouping" (Cavitt and Haas 2020; Eckerle and Thompson 2020; Hopp et al. 2020; Kus et al. 2020). We grouped Sedge Wren (*Cistothorus platensis*), Grasshopper Sparrow (*Ammodramus savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*), three SGCN, into a "quiet grassland grouping." All are all secretive grassland species with quiet songs; previous research suggests that Grasshopper

Sparrows are somewhat harder to detect than the other two species, but Henslow's Sparrow and Sedge Wren generally have similar detection probabilities (Rigby and Johnson 2019). Given our low number of Grasshopper Sparrow detections we believed this grouping was our best option to estimate density that species' density. We grouped Veery (*Catharus fuscescens*) and Cerulean Warbler (*Setophaga cerulea*), two SGCN, along with the non-SGCN, Summer Tanager (*Piranga rubra*) and (*Piranga olivacea*) as "forest grouping." There is previous precedent for grouping Scarlet Tanager and Veery in distance sampling analyses (Alldredge, Pollock, et al. 2007), and all of these species are area-sensitive forest birds that have moderately loud songs (Buehler et al. 2020; Heckscher et al. 2020; Mowbray 2020; Robinson 2020). We grouped Eastern Meadowlark *(Sturnella magna)* and Bobolink *(Dolichonyx oryzivorus),* two SGCN, into a "loud grassland grouping" due to being loudly singing, easy-to-detect grassland species (Rigby and Johnson 2019). SGCN with single-species models included Red-headed Woodpecker (*Melanerpes erythrocephalus*), Northern Flicker (*Colaptes auratus*), Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher (*Empidonax virescens*), Wood Thrush (*Hylocichla mustelina*), Field Sparrow (*Spizella pusilla*), Baltimore Oriole (*Icterus galbula*), and Common Yellowthroat (*Geothlypis trichas*); Ovenbird also had a single species model.

Bird Surveys

We conducted bird point counts from mid-to-late May through early-to-mid August 2016-2019. We randomly placed a grid of points 300 m apart at each site, and we removed points within 150 m of a study area boundary, resulting in 503 total points (Figure 2.2). We conducted 10-min, 100-m radius multispecies bird point counts. Data were collected on all bird detections, but we excluded visual-only detections and detections of known females and juveniles. For consistency with other studies, we would have ideally used only singing males for most species but due to slight changes in data collection protocol between years, we were unable to reliably determine singing males versus other types of detections. Our survey condition parameters were to conduct surveys between 0.7 hours before and 4.5 hours after sunrise with wind speeds <20 km/h and no precipitation. Both wind speed and time since sunrise were considered as covariates in models to account for deviations from our protocol (see Bird Survey Covariates below). Of 503 original points, 493 were surveyed twice each year for an early and late season visit; the cutoff between the seasons was approximately 1 July, and 10 of the original points were missed at least one of four years due logistical issues such as flooding. There were five total observers and two observers per season; when possible (85% of cases), each observer visited each point once during a season to minimize observer bias. Two relatively inexperienced observers surveyed in 2016 only, one experienced observer surveyed 2017-2019, one moderately experienced observer surveyed in 2017 and 2018, and a separate experienced observer surveyed in 2019 only.

Bird Survey Covariates

We obtained precipitation data and average wind speed data from climate stations at municipal airports in Chariton, Iowa, USA (Station ID: WBAN:04913) and Osceola, Iowa, USA (Station ID: WBAN:54942), as these variables may affect an observer's ability to hear a bird vocalization. The Chariton station was ~21 km from the center of Thousand Acres, ~14 km from the center of Stephens, and ~57 km from the center of Sand Creek. The Osceola station was ~48 km from the center of Thousand Acres, ~16 km from the center of Stephens, and ~34 km from the center of Sand Creek. Despite the somewhat long distances, these were the closest weather stations to our study areas, and we lacked consistent weather data from the survey points. At both stations, weather data were recorded at 15 minutes, 35 minutes, and 55 minutes after each hour.

Precipitation was defined as at least one station having a present weather code indicating rain, fog, etc., and thus we likely overestimated the proportion of surveys with precipitation. Due to a low proportion of surveys with precipitation and lack of survey site-specific data, we did not ultimately include precipitation as a model covariate.

When both weather stations were functional, we averaged wind speeds for Chariton and Osceola for all sites. Occasionally, one of the two stations was offline; in these cases, we only used data from the functional station. We excluded one aberrant wind speed reading at the Chariton weather station (>1000 km/h) and used only the Osceola data. There were seven (7) instances out of 629 where neither station recorded data; in these cases; we found a time within 40 minutes of the missing value and used the averaged wind speed from that time. For each bird survey, we used the wind speed value that was closest in time to the start of the bird survey; e.g., if a bird survey started at 8:01 a.m., we would use the wind speed data from 7:55 a.m.

We obtained sunrise times for the Iowa municipalities of Grand River, Woodburn, Lucas, and Russell from the Astronomical Observations Department of the United States Naval Observatory (3450 Massachusetts Ave NW, Washington, DC 20392). We used Grand River sunrise times for Sand Creek, Woodburn for the Woodburn and Whitebreast Units in Stephens, Lucas for the Lucas Unit in Stephens, and Russell for all units of Thousand Acres.

Forest Delineation

In response to the combination of forest and grassland species in our study area, we assigned points to “forest” or “non-forest” categories. To determine if a point was in a forest, we digitized forest to polygons in ArcGIS Pro® using 2016-2018 Iowa Spring Color Infrared Orthophotos, which were taken prior to leaf-out (Iowa State University, 2018). We identified deciduous forest images as large, dark reddish-brown patches, and coniferous trees and shrubs as bright red, irregularly shaped patches, categorizations corroborated by our vegetation surveys. Forest only split by streams and narrow gravel roads was considered continuous and was digitized as a single patch, as narrow non-forest corridors do not seem to affect deciduous forest bird habitat use (Rich et al. 1994). Internal fields and lakes were not counted as forest. We did not categorize cedar groves with open canopy (i.e., visible spacing between trees) as forest. We selected "forest points" as bird survey points within forest patch polygons using the Intersect tool in ArcGIS Pro®.

Mapping

To create a mappable dataset of point-scale densities for each species, we used the arithmetic mean of point-year density estimates for each point. We used ArcGIS Pro® to create a 300 m x 300 m square buffer centered on each point and depicted point-scale density within each buffer using a discrete version of the 'viridis' color scale. For all but one species, we used a density interval of [0.00, 0.05) birds/ha to depict extremely low densities. Densities ≥0.05 birds/ha were generally depicted in either 0.10 birds/ha-wide intervals or 0.20 birds/ha-wide intervals; 0.10 was used for species with a maximum point scale density <0.80 birds/ha. If the hundredth's place of the maximum density was 6, maximum density was used as the upper bound of highest density interval instead of creating a new interval, e.g., an interval of [0.85, 1.06]. Common Yellowthroat densities were symbolized differently due to exceptionally high minimum and maximum densities; the first two intervals were [0.00, 0.10) and [0.10, 0.35), and subsequent intervals were 0.30 birds/ha in width.

Statistical Approach

We used hierarchical distance sampling (HDS) models using the 'distsamp' and 'gdistsamp' functions in R package 'unmarked' to estimate bird densities; these functions produced identical results within our analysis framework (Chandler et al. 2011; Fiske and Chandler 2011; R Core Team 2019). HDS models in ‘unmarked’ use a site-specific likelihood for data collected at each site. For this analysis, we defined “site” as the 100-m radius plot around a point on a single visit, meaning each point count station served as the location of eight separate “sites” from 2016 to 2019. We chose this definition so we could estimate separate densities for each year, and because preliminary analyses using both visits to a point within a year as a single site resulted in unreasonably small and imprecise detection probabilities.

In hierarchical distance sampling in ‘unmarked,’ site-level abundance is treated as a random effect, and analysis is based on the integrated likelihood or on a function of the parameters of the detection function, detectability covariates, abundance, and abundance covariates, with the number of model components varying based on the inclusion or exclusion of covariates at each stage of the hierarchy (Royle et al. 2004; Royle 2004; Chandler et al. 2011). Distance sampling assumes that (1) detection is perfect at distance 0 from the observer, (2) individuals are detected at their initial location, and (3) individuals are counted in the correct distance bins (Buckland et al. 2001).

We used a half-normal detection function for all hierarchical distance sampling models and a Poisson distribution for abundance (the default in ‘unmarked’). The distance bins matched those described in “Bird Surveys” for most species; the one exception was the hawk group, which used distance bins of 0-75 m and 75-100 m due to relatively few detections close to the sampling point. Possible detection covariates for models included time since sunrise (TSSR), the quadratic of TSSR, Julian date (JDAY), and the quadratic of JDAY, observer, and wind speed; each of these covariates has previously been demonstrated to affect detection probability (Alldredge, Simons, et al. 2007; Sólymos et al. 2013; Rigby and Johnson 2019). Possible abundance covariates depended on the species being modeled. For single species, we only considered binary forest versus non-forest. For all multispecies groups, we also considered species as a fixed effect on abundance. For the hawk group only, we also considered a species by forest interaction in combination with both species and forest as covariates due to the differing habitat preferences of the species in that group. Per guidelines for abundance models accounting for imperfect detection probability, we attempted to consider models with all combinations of both detectability and abundance covariates, and we selected the top model using AIC (Doherty et al. 2012). This modeling framework resulted in 128 possible models for single species, 256 possible models for most multispecies groups, and 320 possible models for the hawk group. However, due to some species with small sample size, not all combinations of covariates produced converging models; models which failed to converge were discarded from consideration. Due to the need for a single model per species or multispecies group to estimate year-specific and area-specific densities, we did not model average (Cade 2015).

To estimate detection probability, we first estimated the mean and 95% confidence intervals for σ of half normal detection functions for each survey and species using the 'predict' function in 'unmarked.' To convert σ to a detection probability, we integrated from 0 to 100 m using the circular half normal function 'grhn' in 'unmarked' (Fiske and Chandler 2011). For each species or multispecies grouping, we report an arithmetic mean of all survey-scale mean detection across all surveys, and a standard deviation of the distribution of survey-scale means. To provide an estimate of precision, we used lower quartile, median, and upper quartile of the survey-scale detection probabilities and report the 95% confidence intervals for each species or multispecies group. For coefficients of continuous variables, we report the signs (+ or -) and whether the 95% confidence intervals overlapped 0. For fixed effects, we report presence or absence in a top model.

We used multi-step process to convert visit-specific probability distributions from the ‘ranef’ function methods in ‘unmarked’ to area-wide density estimates. This function uses empirical Bayes methods to estimate site-scale densities. One previously mentioned caveat to this method is that it does not incorporate hyperparameter uncertainty, in this case uncertainty in detection probability and abundance parameters (Laird and Louis 1987; Fiske and Chandler 2011). When calculating a visit-specific density, ‘unmarked’ adds the observed count of individuals to a distribution of possible unobserved counts, ~Poisson in this case, calculated from detection and abundance coefficients. Because we visited each point twice within a year, each “point-year” had two observed counts and two distributions of unobserved counts. We subtracted the observed counts from the mean of each ‘ranef’ distribution to obtain the mean (λ) of the unobserved count Poisson distribution. For each point-year, we selected the higher observed count because we assumed a closed population within each year. We selected the unobserved count distribution with the lower λ because abundance covariates were constant between visits, so a lower λ estimate corresponded to the visit with a higher detection probability. To calculate an area-wide abundance, we first estimated λ for the unobserved counts (λ_{area}) by summing the selected λ values for all point-years within that area. We used λ_{area} as the mean estimate of unobserved individuals and to estimate credible intervals (see below). We summed the selected observed counts from the same point years, and added that sum to both λ_{area} and the credible interval bounds to get area-wide abundance with an estimate of precision. To convert abundances to birds/ha, we divided abundance by the number of point-years and the area of a point count circle (~3.14 ha).

To calculate the equivalent of 95% credible intervals, we used the ‘qpois’ function in R to calculate the 2.5% and 97.5% quantiles of a Possion distribution with $\lambda = \lambda_{area}$; these are equivalence to the methods used by ‘unmarked’ to calculate these estimates from empirical Bayes posterior distributions (Fiske and Chandler 2011). However, we note that empirical Bayes credible intervals derived from quantiles are easy to compute but tend to be overly narrow (Laird and Louis 1987); given our large dataset (n = 3944 surveys) and large number of desired estimates (n = 408), we decided to accept this tradeoff and continue with quantile-based credible intervals. Given the nature of the lower bounds of these intervals, we consider 95% credible intervals overlapping 0.001 birds/ha to indicate possible absence of a species from an area.

We calculated densities for three groupings of point-years: 1) across all BCAs and years for each species individually to produce an overall probability distribution, 2) across all years for each BCA for each species individually to produce BCA-specific probability distributions, and 3) across all BCAs for each year for each species individually to produce annual probability distributions. For the annual densities, we only report the two years with the maximum and minimum annual density estimates; when multiple years shared the same maximum or minimum density, we only report the most recent year. To compare HDS estimates to metric which assumes perfect detection, we also calculated a “naïve” density as the sum of the maximum number of birds at each point with a year across all years divided by the number of surveys and the area covered by all surveys (12,390 ha).

Results

Bird Survey and Covariate Summaries

Bird survey covariates had relatively wide and continuous ranges of values (Table 2.1). When delineating forest points, 407 points were classified as forest, and 86 were classified as non-forest; Sand Creek had proportionally fewer forest points compared to the other areas (Table 2.2). We detected 25 breeding SGCN from 2016 to 2019, only one of which had <10 detections (Table 2.3).

Detection Probabilities and Model Coefficients

Mean detection probabilities by species ranged from 0.202 to 0.861; 8 of 26 species had mean detection probability >0.50 (Table 2.4). Confidence interval widths on detection probability varied between species groups, with widths ranging in rare instances between 0.0 (hawk group) and 1.0 (gallinaceous group); most confidence interval widths were close to 0.1 or 0.2 (Table 2.5). All detectability covariates appeared in the top models for multiple species; wind speed was the only covariate with a consistent sign (negative; Table 2.6, Table 2.7). Forest appeared as an abundance coefficient in 15 of 18 species/multispecies groups. Only one species or multispecies group, the hawk group, had a forest coefficient with 95% CI overlapping 0 (Table 2.7).

Bird Densities

Overall density estimates varied considerably between species. The five species with the highest estimated densities (in descending order) were Eastern Wood-Pewee, Ovenbird, Common Yellowthroat, Acadian Flycatcher, and Scarlet Tanager, with mean estimated densities ranging from 0.195 – 0.698 birds/ha (Table 2.4). The five species with the lowest estimated densities (in ascending order) were Veery, Cerulean Warbler, Broad-winged Hawk, Northern Bobwhite, and Eastern Meadowlark, with mean estimated densities ranging from 0.003 – 0.008 birds/ha (Table 2.4). For 21 of 26 species, the lower 95% confidence interval bound of the estimated density was greater than naïve density estimate (Table 2.4). All species with densities

<0.012 birds/ha (n = 8) had very narrow 95% CI widths, ranging from 0.000-0.003 birds/ha (Table 2.4).

When comparing estimated densities between BCAs, the top three most common study species in each BCA were Eastern Wood-Pewee, Ovenbird, and Common Yellowthroat (Table 2.8). For both Stephens and Thousand Acres, Acadian Flycatcher and Scarlet Tanager were among the top five most common study species. Among all study areas, Stephens had the highest mean density of four of 26 study species: Broad-winged Hawk, Ovenbird, Kentucky Warbler, and Scarlet Tanager (Table 2.8). Thousand Acres had the highest mean densities of ten of 26 study species, including Eastern Wood-Pewee, Acadian Flycatcher, Yellow-billed Cuckoo, and Northern Flicker (Table 2.8). At Sand Creek, Yellow-billed Cuckoo and Field Sparrow were among the top five most common study species. Sand Creek had the highest mean densities of thirteen of 26 study species, including Eastern Kingbird, Field Sparrow, and Common Yellowthroat; Yellow-billed Cuckoo densities were equal in Thousand Acres and Sand Creek (Table 2.8). Only three species had estimated densities with a 95% credible overlapping 0.001 birds/ha in at least one BCA: Broad-winged Hawk and Veery in Sand Creek and Cerulean Warbler in both Stephens and Sand Creek (Table 2.8).

When comparing maximum and minimum mean annual densities between years, the highest ratio of maximum to minimum mean annual density was 3.0; Northern Bobwhite and Black-billed Cuckoo shared this ratio. An addition six of 26 species had a maximum annual density >2.0 times their minimum annual density: Broad-winged Hawk, Sedge Wren, Veery, Eastern Meadowlark, Baltimore Oriole, and Cerulean Warbler. The lowest ratio of maximum to minimum mean annual density was 1.2; Acadian Flycatcher, Field Sparrow, Kentucky Warbler, Common Yellowthroat, and Scarlet Tanager all shared this ratio (Table 2.9).

Spatial distributions of bird densities varied between species. In general, open area species were densest in areas with "grass" landcover, forest species were densest in areas with forest land cover, and rare species had spotty distributions, usually with small clusters (Figure 2.1, Figures A1-A26).

Discussion

The three BCAs in this study were home to at least 25 different breed bird SGCN from 2016 to 2019, as well as Ovenbird and Scarlet Tanager. More than 60% of forest bird species that breed primarily in the Eastern and Midwestern United States are in decline (Rosenberg 2019); this trend, along with the high number of SGCN in our study area, confirms these BCAs' importance for populations of at-risk and threatened breeding bird species. Below, we compare our density estimates to those in similar studies, offer likely biological and statistical reasons for our estimated densities, and posit guidelines for future studies and management practices within our study areas.

Eastern Wood-Pewee, our most numerous SGCN, had an estimated density in our study area of 0.698 birds/ha (mean territory size of ~1.4 ha/bird), higher than a recent study in Missouri Ozark habitats (0.22 to 0.40 birds/ha; Kendrick et al. 2013) and in other parts of Iowa 30 years earlier (territory size of 2.2 ha/bird, Best and Stauffer 1986), potentially making our study areas a hotspot of Eastern Wood-Pewee density. However, it should be noted that our detection probability for Eastern Wood-Pewee was lower than another study on density of this species (0.44 versus 0.65; Kendrick et al. 2013), and we were unable to exclude all non-singing male detections due to dataset limitations.

Other forest and woodland species that ranged from uncommon to relatively common (>0.040 birds/ha) in our study area were Red-headed Woodpecker, Northern Flicker, Wood

Thrush, Ovenbird, and Scarlet Tanager. Acadian Flycatcher, Ovenbird, and Scarlet Tanager are all area-sensitive (i.e., occur almost exclusively in large forest patches) and are indicators of relatively undisturbed forest habitat (Ambuel and Temple 1983; Gibbs and Faaborg 1990; Urban et al. 2012). In terms of BCA-specific density, each of these indicator species, along with almost all other forest and woodland birds in this study, had their highest density in either Stephens of Thousand Acres, indicating that these BCAs are especially important to breeding forest birds of conservation and management concern.

A Missouri Ozarks study in forest and restored woodland-savanna with many of the same species offered a nice comparison. Compared to the Missouri study, our Yellow-billed Cuckoo and Field Sparrow were slightly higher, and our Acadian Flycatcher and Kentucky Warbler densities were lower (Reidy et al. 2014). Given the mixture of grassland and forest within our study area, slightly higher densities of Yellow-billed Cuckoo and Field Sparrow compared to savanna restoration sites and forests elsewhere in the Midwest makes sense. Acadian Flycatcher densities are negatively associated with landscape-scale human disturbance elsewhere in the Midwestern United States (Bakermans and Rodewald 2006), so lower densities in the heavily-disturbed state such as Iowa is expected. The Kentucky Warbler is at the northwestern edge of its range in southern Iowa, a likely explanation for very low densities (0.024 birds/ha) in our study areas (McDonald 2020).

In addition to Kentucky Warbler, 14 of 25 other SGCN had very low density (<0.040 birds/ha), or too few detections to estimate density in the case of the Horned Lark. Southern Iowa is at or near the periphery of the normal breeding range for Broad-winged Hawk, Veery, and Cerulean Warbler (Buehler et al. 2020; Goodrich et al. 2020; Heckscher et al. 2020), explaining the very low densities of these species, and in the case of Cerulean Warbler, probable absence from multiple BCAs. The Veery in particular is declining on the edge of its range, causing it to disappear from some of its historical breeding grounds (Rodriguez 2002). Black-billed Cuckoos are generally uncommon and have declined throughout their range (Hughes 2020a), making very low densities unsurprising. Baltimore Oriole densities were unexpectedly low, although a study in Mississippi only recorded this species in cottonwood plantations as opposed to “natural” bottomland forest similar to the bottomland forests in our study (Twedt et al. 1999). Our study areas were primarily forested, and many of the SGCN with very low densities were grassland or scrubland species, including Northern Bobwhite, Eastern Kingbird, Bell’s Vireo, Sedge Wren, Horned Lark, Grasshopper Sparrow, Brown Thrasher, Henslow’s Sparrow, Eastern Meadowlark, and Bobolink. With the exception of Bell’s Vireo and Sedge Wren, all of these species were most abundant at Sand Creek, indicating that this site is relatively important to open area species.

Field Sparrow and Common Yellowthroat were the only two SGCN that live primarily in open areas that were relatively common in our study areas. Like other open area SGCN, these species were most abundant at Sand Creek. Field Sparrows have small territories (average of 0.76 ha in Illinois) and are known to pack tightly into suitable habitat (Best 1977), which could explain unexpectedly high densities of this open area species in a primarily forested area. Common Yellowthroats have even smaller territories, ranging in size from 0.16–0.60 ha elsewhere in the Midwest (Hofslund 1959), and they occur in very small patches of suitable shrubland-type habitat (Lehnen and Rodewald 2009). Management activities which open parts of the forest canopy, such as the activities in our study area, can benefit Common Yellowthroat densities if they lead to increased undergrowth (Burger et al. 1998; Twedt et al. 1999).

The multi-year nature of this study emphasizes that annual densities within the same area can vary for some species. For example, estimated densities of Northern Bobwhite and Black-billed Cuckoo varied three-fold between the year with the lowest density and the year with the highest density. Both of these species have well-documented boom-and-bust population cycles (Brennan et al. 2020; Hughes 2020a), meaning multi-year studies may be needed to detect areas that are important. Sand Creek on average had the highest densities of each of these species.

As predicted, confidence intervals were generally narrower than would be expected for this type of model, with 95% CI widths ≤0.003 for eight species, a likely result of using quantile-based empirical Bayes confidence intervals (Laird and Louis 1987). This issue was most prevalent for species with low densities. However, our modeling framework tended to produce density estimates close to naïve density estimates for rare species. At the very least, our estimates for rare species are either equal to or very close to naïve density, meaning our estimates are conservative despite unreasonably high estimated precision.

Detection probabilities seemed unrealistically high for the hawk group and Wood Thrush, especially the former, and the gallinaceous group had very wide confidence intervals for detection probability. All of these species have loud songs or calls, making fitting a declining half normal detection function difficult given our truncation distance of 100 m (Brennan et al. 2020; Dykstra et al. 2020; Evans et al. 2020; Goodrich et al. 2020). A previous study found an effective detection radius of Wood Thrush of 90-120 m using a 200 m truncation; the addition distance bins in their study likely allowed for a better detection probability estimates; their estimates were generally between 0.0 and 0.5 (Simons et al. 2000). Wider spacing of points and longer distance bins may have assisted in estimating detection probability of these specific species, but our goal was to maximize coverage for the greatest number of species possible without overlap between points. Another potential method of increasing precision of detection probability estimates, especially for rare species, would be a conditional replicates design where sites with rare species are visited more frequently to increase the number of detections (Specht et al. 2017).

The hawk group produced an additional challenge of territory size. Red-shouldered Hawks generally have territories of 90-200 ha (Dykstra et al. 2020), which would lead to densities between 0.02 birds/ha to 0.01 birds/ha, assuming non-overlapping territories, a saturated landscape, and detections of both members of a pair. However, our estimated and naïve densities were higher than this value at 0.029 birds/ha, suggesting detections of the same individual at multiple points. Roadside repeated visits with 0.8 km spacing using playback have previously been effective in estimating densities of Red-shouldered Hawk (Johnson and Chambers 1990); this method may be more appropriate than 100-m radius point counts for future studies of forest raptors in south-central Iowa.

Despite modeling issues for a few species and narrow confidence intervals on density, this study provided valuable population density estimates for the cores of three Bird Conservation Areas in south-central Iowa. We identified 25 Species of Greatest Conservation need in these areas, ranging in abundance from common to very rare. Aside from Field Sparrow and Common Yellowthroat, the most common SGCN were forest species. This study has the potential to serve as a baseline for future studies by providing density estimates that can be combined with future studies to estimate population trends. Although 100-m radius point counts were appropriate for many species, different survey protocols, such as roadside broadcast surveys, may be needed to better estimate densities for species such as Red-shouldered Hawk. We believe the very low estimated densities for Veery, Kentucky Warbler, and Cerulean Warbler are a result of these species being at the edge of their breeding range in southern Iowa, meaning management directly specifically at these species is unlikely to increase local populations. Due to higher densities of SGCN that use grassland, shrubland, and edge habitats at Sand Creek compared to the other BCAs, we suggest maintaining open habitats at this site. We recommend the maintenance of forest at Stephens and Thousand Acres, especially large patches, to continue to benefit species such as Acadian Flycatcher, Ovenbird, and Scarlet Tanager. We also recommend multi-year bird monitoring, especially for species with volatile populations such as Northern Bobwhite and Black-billed Cuckoo.

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Tables

Table 2.1. Descriptive statistics for bird survey variables collected in and near south-central Iowa forests, 2016-2019.

Variable	Variable Type	Min	Quartile (25%)	Median	Quartile (75%)	Max	Unique values
Julian day	Continuous	136	163	184	206	228	92
Time since sunrise (hrs)	Continuous	-0.7	0.7	1.6	2.6	6.0	333
Observer	Categorical	-	-	-	-	-	5
Average wind speed (km/hr)	Continuous	0	8	11	15	38	45

Table 2.2. Summary of survey points by Bird Conservation Area (BCA) used to survey breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. "Forest points" are points within a forest boundary derived from aerial imagery, and "proportion forested" refers to points, not the entire BCA. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA.

BCA	Total points	Forest Points	Proportion forested
Stephens	205	174	0.74
Thousand Acres	162	140	0.85
Sand Creek	126	93	0.86
Total	493	407	0.83

Table 2.3. Detections of breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Surveys were 10 minutes with a 100 m radius and were completed twice per breeding for four years, with a total of eight visits per point. * = not a Species of Greatest Conservation Need (SGCN) in Iowa; all other species have SGCN designation.

Common name	**Scientific name**	**No. Detections**
Northern Bobwhite	*Colinus virginianus*	39
Yellow-billed Cuckoo	*Coccyzus americanus*	841
Black-billed Cuckoo	*Coccyzus erythropthalmus*	48
Red-shouldered Hawk	*Buteo lineatus*	172
Broad-winged Hawk	*Buteo platypterus*	28
Red-headed Woodpecker	*Melanerpes erythrocephalus*	212
Northern Flicker	*Colaptes auratus*	692
Eastern Kingbird	*Tyrannus tyrannus*	77
Eastern Wood-Pewee	*Contopus virens*	3317
Acadian Flycatcher	*Empidonax virescens*	522
Bell's Vireo	*Vireo bellii*	32
Horned Lark	*Eremophila alpestris*	1
Sedge Wren	*Cistothorus platensis*	59
Veery	*Catharus fuscescens*	11
Wood Thrush	*Hylocichla mustelina*	574
Brown Thrasher	*Toxostoma rufum*	80
Field Sparrow	*Spizella pusilla*	1003
Grasshopper Sparrow	*Ammodramus savannarum*	45
Henslow's Sparrow	*Ammodramus henslowii*	65
Eastern Meadowlark	*Sturnella magna*	34
Bobolink	*Dolichonyx oryzivorus*	39
Baltimore Oriole	*Icterus galbula*	94
Ovenbird*	*Seiurus aurocapilla*	2061
Kentucky Warbler	*Geothlypis formosa*	112
Common Yellowthroat	*Geothlypis trichas*	1614
Cerulean Warbler	*Setophaga cerulea*	10
Scarlet Tanager*	*Piranga olivacea*	710

Table 2.4. Density estimates and detection probabilities for breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Naïve density is the sum of the maximum number of birds at each point with a year across all years divided by the number of surveys and the area covered by all surveys (12,390 ha). Data used for all other estimates were derived from hierarchical distance sampling models. Density estimates and 95% credible intervals are derived from combining survey-scale empirical Bayesian posterior distributions of abundance and dividing by the area covered by all surveys. Standard deviation for detection probability is of the estimates of cumulative detection probability (one per survey per species) and does not account for the uncertainty of survey-scale cumulative detection probability estimates. A letter under the "Group" column signifies species with shared detection functions on account of low detections for at least one species in that group; these species use similar habitats and have similar vocalization habits; groups are detailed as a footnote. Species with the same letter share a detection function. Seven grouped species are excluded from this table due to not being target species of our analyses. All naïve densities are in italics.

Species	***Naïve density***	**Estimated density with 95% credible interval**		**Mean detection probability ± SD**	**Group**
Northern Bobwhite	*0.006*	0.007	(0.006, 0.008)	0.673 ± 0.360	a
Yellow-billed Cuckoo	*0.124*	0.181	(0.175, 0.187)	0.504 ± 0.124	b
Black-billed Cuckoo	*0.008*	0.011	(0.010, 0.012)	0.504 ± 0.124	b
Red-shouldered Hawk	*0.027*	0.029	(0.028, 0.031)	0.601 ± 0.274	c
Broad-winged Hawk	*0.005*	0.005	(0.005, 0.005)	0.601 ± 0.274	c
Red-headed Woodpecker	*0.033*	0.045	(0.042, 0.047)	0.487 ± 0.286	
Northern Flicker	*0.103*	0.126	(0.122, 0.130)	0.648 ± 0.167	
Eastern Kingbird	*0.012*	0.021	(0.019, 0.024)	0.334 ± 0.189	d
Eastern Wood-Pewee	*0.377*	0.698	(0.684, 0.712)	0.435 ± 0.065	
Acadian Flycatcher	*0.069*	0.199	(0.190, 0.208)	0.228 ± 0.102	
Bell's Vireo	*0.005*	0.010	(0.009, 0.012)	0.289 ± 0.161	e
Sedge Wren	*0.009*	0.027	(0.023, 0.030)	0.202 ± 0.095	f
Veery	*0.002*	0.003	(0.002, 0.004)	0.356 ± 0.085	g
Wood Thrush	*0.083*	0.084	(0.083, 0.084)	0.861 ± 0.235	
Brown Thrasher	*0.012*	0.027	(0.024, 0.030)	0.289 ± 0.161	e
Field Sparrow	*0.128*	0.154	(0.150, 0.158)	0.680 ± 0.143	
Grasshopper Sparrow	*0.007*	0.019	(0.017, 0.022)	0.202 ± 0.095	f
Henslow's Sparrow	*0.009*	0.028	(0.024, 0.031)	0.202 ± 0.095	f
Eastern Meadowlark	*0.006*	0.010	(0.008, 0.011)	0.407 ± 0.241	h
Bobolink	*0.005*	0.008	(0.007, 0.010)	0.407 ± 0.241	h
Baltimore Oriole	*0.015*	0.037	(0.033, 0.040)	0.225 ± 0.187	
Ovenbird	*0.281*	0.495	(0.484, 0.507)	0.358 ± 0.211	
Kentucky Warbler	*0.017*	0.024	(0.022, 0.026)	0.435 ± 0.268	
Common Yellowthroat	*0.204*	0.421	(0.409, 0.432)	0.346 ± 0.117	
Cerulean Warbler	*0.002*	0.003	(0.002, 0.004)	0.356 ± 0.085	g
Scarlet Tanager	*0.100*	0.195	(0.188, 0.203)	0.356 ± 0.085	g

a = Northern Bobwhite + Ring-necked Pheasant, b = both cuckoos, c = Cooper's Hawk + Red-shouldered Hawk + Broad-winged Hawk + Red-tailed Hawk, d = Eastern Kingbird + Eastern Bluebird, e = Bell's Vireo + White-eyed Vireo + Brown Thrasher + Yellow-breasted Chat, f = Sedge Wren + Grasshopper Sparrow + Henslow's Sparrow, g = Veery + Cerulean Warbler + Scarlet Tanager + Summer Tanager, h = Eastern Meadowlark + Bobolink

Table 2.5. Selected detection probability estimates with 95% confidence intervals for breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Estimates are for single visits to a point count station and represent the lower quartile, median, and upper quartile of all detection probabilities for a species or multispecies group. Multispecies groups contain species with shared detection functions on account of low detections for at least one species in that group; these species use similar habitats and have similar vocalization habits; groups are detailed as a footnote. See Table 2.4 the mean and standard deviation of the entire sample of detection probabilities for all visits.

	Lower quantile		**Median**		**Upper quantile**	
Species or group	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
Red-headed Woodpecker	0.245	(0.181, 0.325)	0.390	(0.277, 0.514)	0.765	(0.219, 0.966)
Northern Flicker	0.538	(0.400, 0.665)	0.670	(0.560, 0.761)	0.781	(0.657, 0.866)
Eastern Wood-Pewee	0.381	(0.337, 0.427)	0.430	(0.385, 0.475)	0.480	(0.448, 0.513)
Acadian Flycatcher	0.143	(0.114, 0.179)	0.230	(0.183, 0.285)	0.302	(0.260, 0.348)
Wood Thrush	0.872	(0.645, 0.960)	0.972	(0.801, 0.997)	0.988	(0.860, 0.999)
Field Sparrow	0.607	(0.509, 0.694)	0.691	(0.551, 0.799)	0.785	(0.622, 0.886)
Baltimore Oriole	0.090	(0.054, 0.150)	0.125	(0.090, 0.173)	0.299	(0.212, 0.402)
Ovenbird	0.140	(0.120, 0.163)	0.435	(0.391, 0.479)	0.549	(0.505, 0.590)
Kentucky Warbler	0.161	(0.084, 0.298)	0.412	(0.239, 0.603)	0.693	(0.311, 0.906)
Common Yellowthroat	0.244	(0.204, 0.291)	0.358	(0.319, 0.399)	0.438	(0.398, 0.479)
Gallinaceous group	0.296	(0.113, 0.583)	0.999	(0.000, 1.000)	1.000	(0.000, 1.000)
Cuckoo group	0.405	(0.345, 0.467)	0.510	(0.392, 0.624)	0.602	(0.495, 0.696)
Hawk group	0.353	(0.228, 0.499)	0.537	(0.340, 0.713)	1.000	(1.000, 1,000)
Savanna group	0.151	(0.084, 0.265)	0.315	(0.171, 0.506)	0.511	(0.354, 0.659)
Scrubland group	0.170	(0.113, 0.253)	0.275	(0.160, 0.432)	0.412	(0.263, 0.573)
Quiet grassland group	0.121	(0.077, 0.190)	0.187	(0.107, 0.315)	0.270	(0.211, 0.339)
Forest group	0.289	(0.244, 0.337)	0.355	(0.313, 0.399)	0.411	(0.360, 0.463)
Loud grassland group	0.236	(0.109, 0.450)	0.377	(0.226, 0.551)	0.554	(0.217, 0.830)

Gallinaceous group = Northern Bobwhite + Ring-necked Pheasant, Cuckoo group = Yellow-billed Cuckoo + Black-billed Cuckoo, Hawk group = Cooper's Hawk + Red-shouldered Hawk + Broad-winged Hawk + Red-tailed Hawk, Savanna group = Eastern Kingbird + Eastern Bluebird, Scrubland group = Bell's Vireo + White-eyed Vireo + Brown Thrasher + Yellow-breasted Chat, Quiet grassland group = Sedge Wren + Grasshopper Sparrow + Henslow's Sparrow, Forest group = Veery + Cerulean Warbler + Scarlet Tanager + Summer Tanager, Loud grassland group = Eastern Meadowlark + Bobolink

Table 2.6. Top covariate combinations for hierarchical distance sampling models for breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Multispecies groups contain species with shared detection functions on account of low detections for at least one species in that group; these species use similar habitats and have similar vocalization habits; groups are detailed as a footnote. "Species" as a categorical main effect was only used in multispecies group. "Species * forest" denotes an interaction between species and forest in addition to a main effect of each covariate; this interaction was only considered for the hawk group. We attempted to perform all combinations of models, but not all models converged. "No. mods." is the number of models that converged of one of the total possible models: 128 for single species, 256 for most multispecies groups, and 320 for the hawk group. OBS = categorical main effect of observer (df = 4), WIND = wind speed, JDAY = Julian date, TSSR = time since sunrise. "Forest" was a binary covariate denoting whether point surveys occurred in forest (1) or non-forest (0). Continuous covariates used in these analyses were center-scaled prior to analyses, and quadratic terms, denoted by "(variable)^2" were calculated from center-scaled covariates.

Species or group	**No. mods.**	**Detection covariates**	**Abundance covariates**
Red-headed Woodpecker	113	OBS + (JDAY)^2 + (TSSR)^2	(none)
Northern Flicker	123	OBS + WIND + JDAY + TSSR + (TSSR)^2	forest
Eastern Wood-Pewee	128	OBS + WIND + JDAY + (JDAY)^2 + TSSR + (TSSR)^2	forest
Acadian Flycatcher	123	OBS + WIND + JDAY + (JDAY)^2 + TSSR	forest
Wood Thrush	61	JDAY + (JDAY)^2 + TSSR	forest
Field Sparrow	127	OBS + JDAY + (JDAY)^2 + TSSR	forest
Baltimore Oriole	38	JDAY + (JDAY)^2	(none)
Ovenbird	99	OBS + JDAY + (JDAY)^2	forest
Kentucky Warbler	33	WIND + JDAY	forest
Common Yellowthroat	128	OBS + WIND + JDAY + (JDAY)^2 + TSSR	forest
Gallinaceous group	40	OBS + TSSR	forest
Cuckoo group	239	OBS + WIND + JDAY + TSSR + (TSSR)^2	species
Hawk group	320	OBS + WIND	species * forest
Savanna group	123	OBS + JDAY	species + forest
Scrubland group	177	OBS + WIND + JDAY + TSSR	species + forest
Quiet grassland group	251	OBS + WIND + JDAY + (TSSR)^2	species + forest
Forest group	230	OBS + (JDAY)^2 + TSSR	species + forest
Loud grassland group	103	OBS + TSSR + (TSSR)^2	forest

Gallinaceous group = Northern Bobwhite + Ring-necked Pheasant, Cuckoo group = Yellow-billed Cuckoo + Black-billed Cuckoo, Hawk group = Cooper's Hawk + Red-shouldered Hawk + Broad-winged Hawk + Red-tailed Hawk, Savanna group = Eastern Kingbird + Eastern Bluebird, Scrubland group = Bell's Vireo + White-eyed Vireo + Brown Thrasher + Yellow-breasted Chat, Quiet grassland group = Sedge Wren + Grasshopper Sparrow + Henslow's Sparrow, Forest group = Veery + Cerulean Warbler + Scarlet Tanager + Summer Tanager, Loud grassland group = Eastern Meadowlark + Bobolink

Table 2.7. Signs of coefficients for continuous detectability and abundance covariates from hierarchical distance sampling models for breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Multispecies groups contain species with shared detection functions on account of low detections for at least one species in that group; these species use similar habitats and have similar vocalization habits; groups are detailed as a footnote. “Forest” is the only abundance coefficient listed; all others are for detectability JDAY = Julian date, TSSR = time since sunrise, † = model has a species X forest interaction in addition to a main effect, * = 95% confidence interval overlapped zero; sign of the mean coefficient is reported. “Forest” was a binary covariate denoting whether point surveys occurred in forest (1) or non-forest (0). All continuous covariates used in these analyses were center-scaled prior to analyses, and quadratic terms, denoted by “(variable)^2” were calculated from center-scaled covariates.

Species or group	**Wind speed**	**JDAY**	**(JDAY)^2**	**TSSR**	**(TSSR)^2**	**Forest**
Red-headed Woodpecker			+		-	
Northern Flicker	-	+		+	-*	+
Eastern Wood-Pewee	-	+	+	-	+*	+
Acadian Flycatcher	-*	+*	-	-		+
Wood Thrush		-	-	-		+
Field Sparrow		+	-	-		-
Baltimore Oriole		-	+			
Ovenbird		-	-			+
Kentucky Warbler	+*	-				+
Common Yellowthroat	-	-	-	-		-
Gallinaceous group				+		-
Cuckoo group	-	-		-*	-	
Hawk group	-*		+*			+*†
Savanna group		+				-
Scrubland group	-*	-		-		-
Quiet grassland group	-	-			+	-
Forest group			-	-		+
Loud grassland group				+	+*	-

Gallinaceous group = Northern Bobwhite + Ring-necked Pheasant, Cuckoo group = Yellow-billed Cuckoo + Black-billed Cuckoo, Hawk group = Cooper’s Hawk + Red-shouldered Hawk + Broad-winged Hawk + Red-tailed Hawk, Savanna group = Eastern Kingbird + Eastern Bluebird, Scrubland group = Bell’s Vireo + White-eyed Vireo + Brown Thrasher + Yellow-breasted Chat, Quiet grassland group = Sedge Wren + Grasshopper Sparrow + Henslow’s Sparrow, Forest group = Veery + Cerulean Warbler + Scarlet Tanager + Summer Tanager, Loud grassland group = Eastern Meadowlark + Bobolink

Table 2.8. Density estimates (birds/ha) within three different Bird Conservation Areas (BCAs). for breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Density estimates and 95% credible intervals are derived from combining survey-scale empirical Bayesian posterior distributions of abundance and dividing by the area covered by all surveys within each BCA. Sand Creek has few forest points (74% of points) compared to the other BCAs (~85% for Stephens and Thousand Acres). Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. Densities with 95% credible intervals overlapping 0.001 birds/ha are in italics, the highest mean densities between all three BCAs are in bold.

	Stephens		**Thousand Acres**		**Sand Creek**	
Species	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
Northern Bobwhite	0.005	(0.005, 0.007)	0.004	(0.003, 0.005)	**0.014**	**(0.013, 0.016)**
Yellow-billed Cuckoo	0.166	(0.157, 0.175)	**0.191**	**(0.181, 0.202)**	**0.191**	**(0.179, 0.203)**
Black-billed Cuckoo	0.011	(0.009, 0.014)	0.009	(0.007, 0.012)	**0.012**	**(0.009, 0.015)**
Red-shouldered Hawk	0.031	(0.029, 0.033)	**0.032**	**(0.031, 0.034)**	0.023	(0.021, 0.025)
Broad-winged Hawk	**0.007**	**(0.006, 0.007)**	0.006	(0.005, 0.007)	*0.001*	*(0.001, 0.003)*
Red-headed Woodpecker	0.045	(0.041, 0.049)	**0.051**	**(0.046, 0.056)**	0.036	(0.032, 0.042)
Northern Flicker	0.123	(0.116, 0.129)	**0.137**	**(0.131, 0.143)**	0.117	(0.111, 0.124)
Eastern Kingbird	0.014	(0.010, 0.017)	0.022	(0.018, 0.026)	**0.034**	**(0.029, 0.040)**
Eastern Wood-Pewee	0.692	(0.670, 0.715)	**0.758**	**(0.733, 0.783)**	0.631	(0.604, 0.657)
Acadian Flycatcher	0.173	(0.160, 0.188)	**0.258**	**(0.243, 0.275)**	0.165	(0.148, 0.182)
Bell's Vireo	0.005	(0.003, 0.008)	**0.015**	**(0.012, 0.018)**	0.013	(0.009, 0.018)
Sedge Wren	0.029	(0.025, 0.035)	0.018	(0.013, 0.024)	**0.033**	**(0.025, 0.041)**
Veery	0.003	(0.002, 0.004)	**0.005**	**(0.003, 0.007)**	*0.002*	*(0.001, 0.004)*
Wood Thrush	0.080	(0.078, 0.081)	**0.115**	**(0.114, 0.116)**	0.051	(0.050, 0.052)
Brown Thrasher	0.028	(0.024, 0.033)	0.021	(0.016, 0.026)	**0.032**	**(0.026, 0.039)**
Field Sparrow	0.101	(0.095, 0.108)	0.132	(0.126, 0.139)	**0.267**	**(0.258, 0.275)**
Grasshopper Sparrow	0.016	(0.012, 0.021)	0.012	(0.008, 0.017)	**0.033**	**(0.027, 0.040)**
Henslow's Sparrow	0.022	(0.017, 0.028)	0.024	(0.019, 0.030)	**0.041**	**(0.033, 0.050)**
Eastern Meadowlark	0.009	(0.007, 0.011)	0.007	(0.005, 0.009)	**0.016**	**(0.013, 0.019)**
Bobolink	0.007	(0.005, 0.009)	0.007	(0.005, 0.009)	**0.014**	**(0.011, 0.017)**
Baltimore Oriole	0.034	(0.029, 0.039)	0.036	(0.029, 0.043)	**0.041**	**(0.033, 0.049)**
Ovenbird	**0.574**	**(0.556, 0.592)**	0.508	(0.488, 0.529)	0.350	(0.329, 0.373)
Kentucky Warbler	**0.030**	**(0.027, 0.033)**	0.021	(0.017, 0.025)	0.019	(0.016, 0.024)
Common Yellowthroat	0.415	(0.398, 0.433)	0.387	(0.368, 0.406)	**0.472**	**(0.447, 0.498)**
Cerulean Warbler	*0.002*	*(0.000, 0.003)*	**0.006**	**(0.004, 0.008)**	*0.001*	*(0.000, 0.003)*
Scarlet Tanager	**0.217**	**(0.205, 0.229)**	0.203	(0.189, 0.216)	0.151	(0.136, 0.165)

Table 2.9. Annual density estimates for breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Minimum and maximum annual densities are shown for each species, along with the percent change between the minimum and the maximum. Data used for estimates were derived from hierarchical distance sampling models. Density estimates and 95% credible intervals were calculated by combining survey-scale empirical Bayesian posterior distributions of abundance and dividing by the area covered by all surveys in a year. Densities with 95% credible intervals containing 0.001 birds/ha are in italics.

	Min. Annual Density			**Max. Annual Density**			**Max/ Min**
Species	**Year**	**Mean**	**95% CI**	**Year**	**Mean**	**95% CI**	
Northern Bobwhite	2017	0.004	(0.004, 0.005)	2016	0.012	(0.012, 0.012)	3.0
Yellow-billed Cuckoo	2017	0.135	(0.123, 0.148)	2019	0.243	(0.232, 0.255)	1.8
Black-billed Cuckoo	2019	0.006	(0.003, 0.009)	2018	0.018	(0.015, 0.021)	3.0
Red-shouldered Hawk	2019	0.020	(0.015, 0.024)	2018	0.038	(0.038, 0.039)	1.9
Broad-winged Hawk	2016	0.003	(0.003, 0.005)	2019	0.008	(0.006, 0.010)	2.7
Red-headed Woodpecker	2019	0.032	(0.025, 0.039)	2017	0.063	(0.061, 0.067)	2.0
Northern Flicker	2016	0.103	(0.094, 0.112)	2018	0.155	(0.150, 0.161)	1.5
Eastern Kingbird	2016	0.016	(0.011, 0.023)	2019	0.030	(0.026, 0.035)	1.9
Eastern Wood-Pewee	2016	0.582	(0.553, 0.612)	2017	0.810	(0.783, 0.838)	1.4
Acadian Flycatcher	2016	0.184	(0.167, 0.203)	2019	0.220	(0.203, 0.237)	1.2
Bell's Vireo	2017	0.009	(0.006, 0.012)	2018	0.012	(0.008, 0.015)	1.3
Sedge Wren	2018	0.019	(0.013, 0.026)	2017	0.040	(0.034, 0.046)	2.1
Veery	2018	*0.002*	*(0.000, 0.004)*	2019	0.005	(0.004, 0.007)	2.5
Wood Thrush	2016	0.070	(0.069, 0.072)	2017	0.101	(0.099, 0.103)	1.4
Brown Thrasher	2018	0.022	(0.016, 0.028)	2017	0.036	(0.031, 0.042)	1.6
Field Sparrow	2016	0.144	(0.136, 0.152)	2018	0.171	(0.165, 0.178)	1.2
Grasshopper Sparrow	2019	0.016	(0.011, 0.022)	2018	0.021	(0.016, 0.027)	1.3
Henslow's Sparrow	2016	0.023	(0.015, 0.030)	2019	0.031	(0.025, 0.039)	1.3
Eastern Meadowlark	2018	0.008	(0.005, 0.012)	2019	0.012	(0.010, 0.015)	1.5
Bobolink	2018	*0.005*	*(0.001, 0.008)*	2019	0.013	(0.010, 0.016)	2.6
Baltimore Oriole	2016	0.022	(0.015, 0.030)	2019	0.055	(0.048, 0.063)	2.5
Ovenbird	2016	0.429	(0.405, 0.455)	2017	0.576	(0.554, 0.599)	1.3
Kentucky Warbler	2017	0.021	(0.017, 0.025)	2019	0.026	(0.023, 0.030)	1.2
Common Yellowthroat	2016	0.374	(0.349, 0.400)	2017	0.455	(0.433, 0.478)	1.2
Cerulean Warbler	2019	*0.002*	*(0.001, 0.004)*	2017	0.005	(0.004, 0.008)	2.5
Scarlet Tanager	2016	0.181	(0.166, 0.198)	2019	0.219	(0.205, 0.233)	1.2

Figures

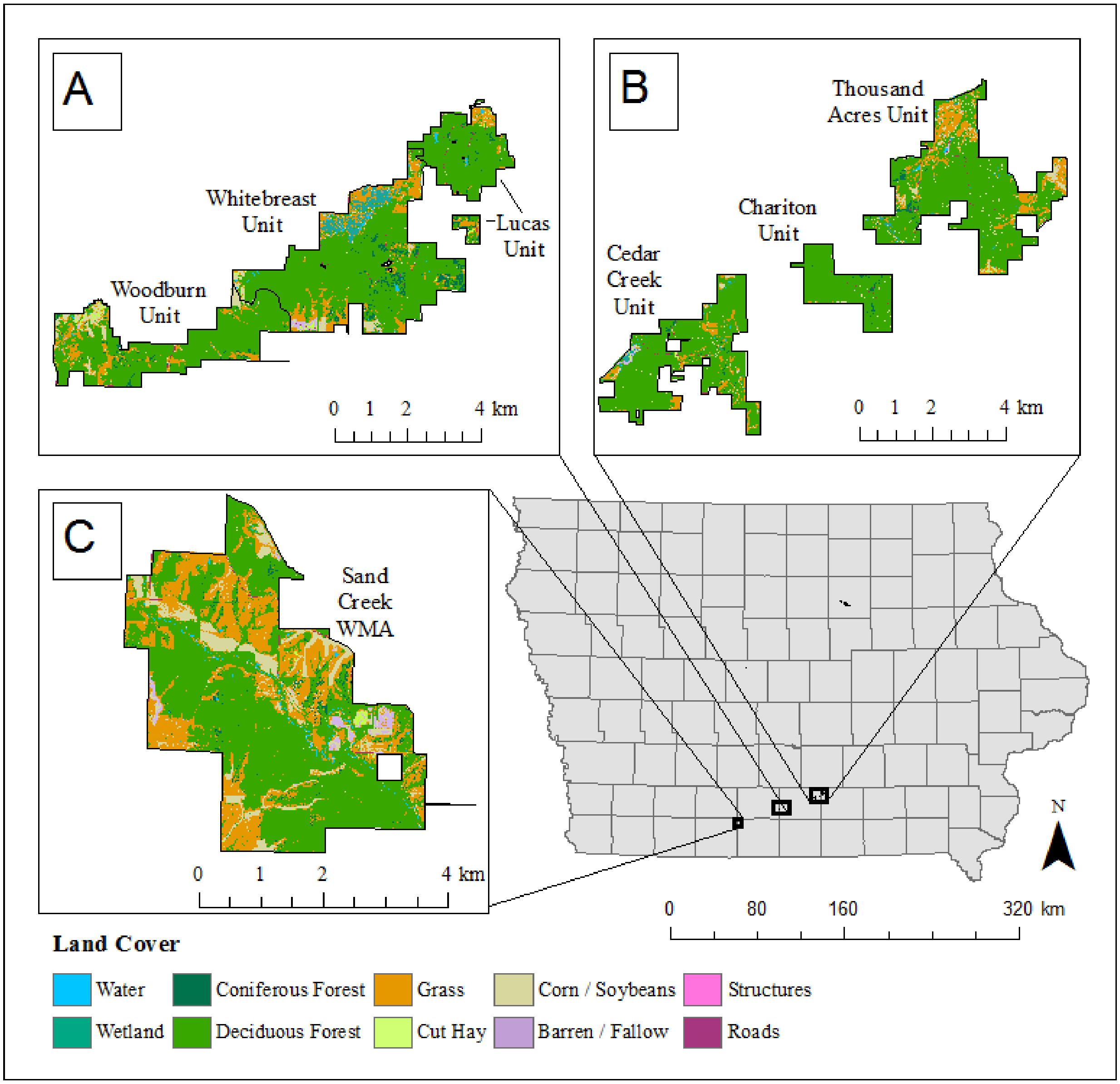

Figure 2.1. Land cover maps of the study areas used for breeding bird point counts in south-central Iowa, 2016-2019. Maps A and B represent the units of Stephen State Forest with the Stephens Forest and Stephens Forest – Thousand Acres Bird Conservation Areas (BCAs), respectively. Map C is of the Sand Creek Wildlife Management Area, located within the Sand Creek Woodland Savanna BCA. Land cover maps are modified from the Iowa Department of Natural Resource's 2009 High Resolution Land Cover of Iowa.

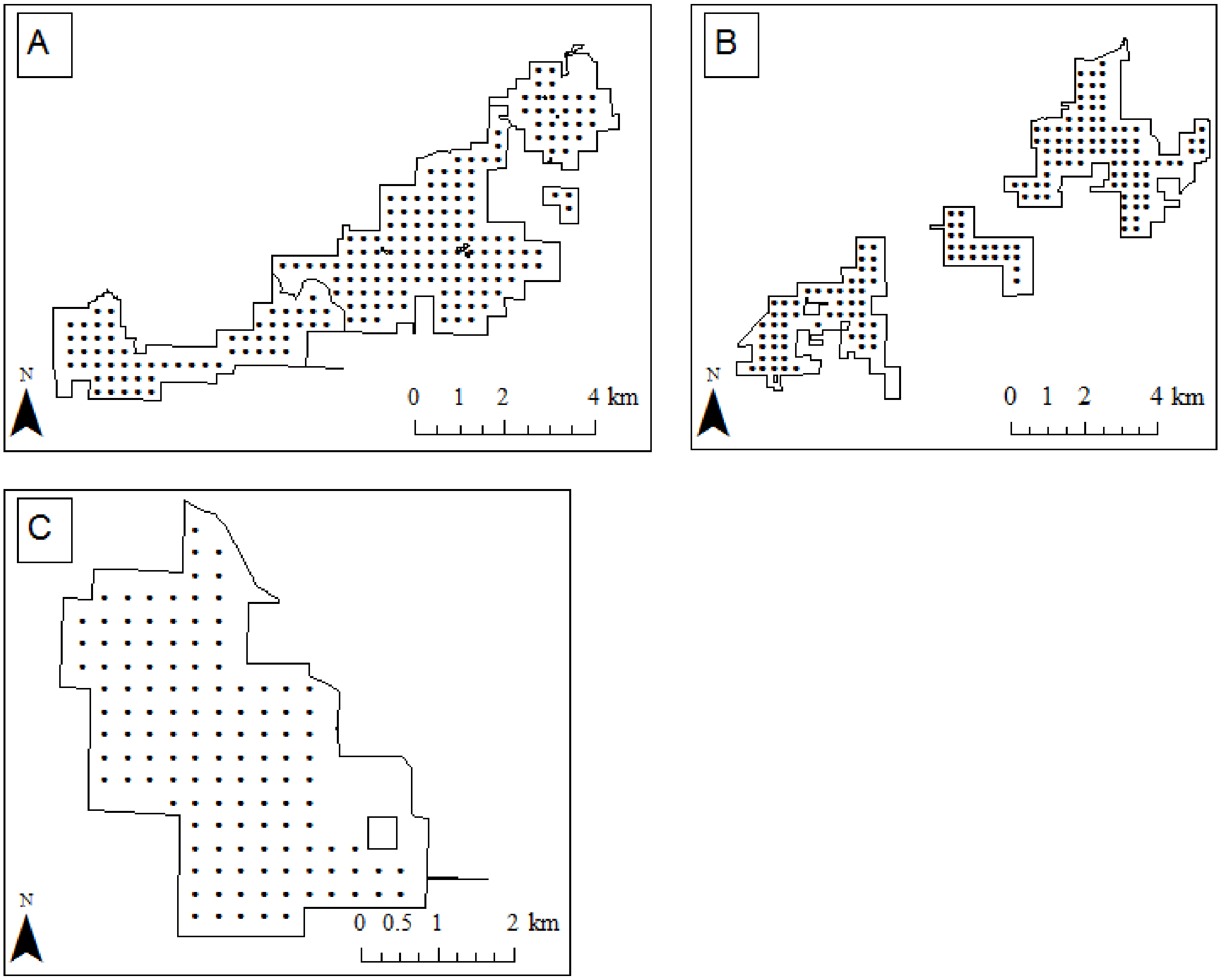

Figure 2.2. Point count locations used for surveys of breeding birds in south-central Iowa, 2016-2019, within the cores of three Iowa Bird Conservation Areas (BCAs): A) Stephens Forest BCA, B) Stephens Forest – Thousand Acres BCA, and C) Sand Creek Woodland Savanna BCA.

CHAPTER 3. HABITAT RELATIONSHIPS OF CONSERVATION PRIORITY BIRDS IN SOUTHERN IOWA FORESTS

A manuscript to be submitted to *Forest Ecology and Management*

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Abstract

Recent avian population declines emphasize the need to better understand the habitat characteristics associated with population densities of at-risk species. Our study focused on 10 species of forest and forest edge breeding birds of conservation and management concern in three primarily forested Bird Conservation Areas in south-central Iowa, each with >200 detections. We used distance sampling point counts over a grid of 493 points visited twice each breeding season from 2016 to 2019. We incorporated thirteen habitat covariates into hierarchical distance sampling models to assess relationships between bird densities and habitat, using AIC to select top habitat models for each species. Habitat characteristics ranged in scale from landscape to site-level. Mean cumulative detection probabilities by species ranged from 0.083 to 0.841. Landscape-scale forest cover and distance to forest edge were among the most prevalent habitat variables in top models. Densities of Red-headed Woodpecker (*Melanerpes erythrocephalus*), Acadian Flycatcher (*Empidonax virescens*), Wood Thrush (*Hylochichla mustelina*), Ovenbird (*Seiurus aurocapilla*), Common Yellowthroat (*Geothlypis trichas*), and Scarlet Tanager (*Piranga olivacea*) were positively associated with landscape scale forest cover, while Field Sparrow (*Spizella pusilla*) densities were negatively associated with landscape-scale forest cover. Densities of forest birds such as Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher,

Wood Thrush, Ovenbird, and Scarlet Tanager were positively associated with distance to edge, while densities of Field Sparrow and Common Yellowthroat, two species of edges and open areas, had a negative association. Site level covariates were less prevalent in models with the exception of leaf litter cover, which appeared in top models for six of ten study species, appearing as a positive coefficient for Eastern Wood-Pewee, Acadian Flycatcher, Wood Thrush, Field Sparrow and Ovenbird and as a negative coefficient for a single species, Common Yellowthroat. Overall, landscape scale forest cover, distance to edge, and leaf litter cover were generally positively associated with densities of our study species, although management activities designed to promote these characteristics may negatively affect some species, such as Common Yellowthroat and Field Sparrow.

Key words: Bird habitat, Distance-based models, Landscape forest cover, Edge effects, Leaf litter

Introduction

Populations of forest birds in North American have declined by nearly 20% in recent decades (Rosenberg et al., 2019), making conservation of forest birds and their habitats a high priority. Forest bird populations in North America are influenced by habitat characteristics at a variety of scales. Landscape-scale forest cover is an important factor for several species of forest bird, including species of conservation concern such as Acadian Flycatcher (*Empidonax virescens*) and Cerulean Warbler (*Setophaga cerulea*) (Bakermans and Rodewald, 2006; Reidy et al., 2014; Thompson et al., 2012). At a site scale, habitat structure is a primary factor influencing bird species' distributions and diversity, especially in highly-structured habitats such as forests (MacArthur and MacArthur 1961). There are also relationships between the tree species community (i.e., floristics) and the presence and densities of specific bird species (Sierzega

2016; Rodewald and Abrams 2002) However, differences between tree species that influence foraging, such as leaf petiole length (Holmes and Robinson 1981) and bark texture (Jackson 1970), are structural characteristics that may underlie the effect of floristics on breeding bird distributions. Many other site-level vegetation structure characteristics, including those related to tree characteristics, midstory traits, and ground cover, are associated with forest bird population densities (Burger et al., 1998; Kendrick et al., 2013; Reidy et al., 2014)

Human activities that alter habitat at a variety of spatial scales affect forest bird populations and communities. Both agricultural and urban disturbance within one kilometer of otherwise suitable forest habitat have a negative effect on forest bird abundance (Bakermans and Rodewald, 2006; Rodewald and Yahner, 2001). Forest bird populations for many species are lower in small, fragmented patches, than unfragmented patches, and species such as Wood Thrush have decreased nesting success in forest fragments (Ambuel and Temple, 1983; Robinson et al., 1995). Conversion of bottomland hardwood forests into monoculture cottonwood (*Populus deltoides*) stands results in decreased bird species richness and abundance (Twedt and Loesch 1999). Largely due to continued fire suppression dating back to European settlement, many ecosystems previously dominated by oak (*Quercus* spp.) are being converted to denser, closed-canopy forests dominated by maples (*Acer* spp.) and other fire intolerant species (Abrams 1992; Nowacki and Abrams 2008). This shift has resulted in potentially inferior habitat for many forest bird species. For example, Eastern Wood-Pewee abundance during the breeding season is lower in forests not dominated by oaks and hickories (*Carya* spp.; Sierzega 2016). The shorter petioles of oaks when compared to maples may make it easier for foraging birds to reach arthropods on oak leaves, and deeper furrowing on oak bark may provide more foraging opportunities for birds (Rodewald and Abrams 2002; Holmes and Robinson 1981; Jackson

1970). In contrast, certain management activities, such as landscape-scale reforestation and thinning of forest to promote regeneration, can have a positive impact on forest bird populations and communities (Askins and Philbrick, 1987; Newell and Rodewald, 2012; Twedt et al., 1999).

In Iowa, the Iowa Department of Natural Resources (DNR), in cooperation with the Partners in Flight Midwest Working Group, has responded to bird declines and habitat loss by establishing Bird Conservation Areas (BCAs). Bird Conservation Areas are at least 4,047 ha in size, are at least 35% native habitat by land area, and are based around a "core" of at least 809 ha of permanently protected lands (Ehresman, 2015). The goals of BCAs include reducing habitat fragmentation and improving private and public land management (Ehresman, 2015; Iowa DNR, 2010). This study focuses on three primarily forested BCAs in south-central Iowa. It uses hierarchical distance sampling models is to determine associations between habitat characteristics a variety of scales densities of bird species of conservation and management, with the goals of informing management practices and providing a basis for experimental management activities to establish causal relationships between habitat and bird densities.

Results

Bird Survey Covariates and Habitat Surveys

Most bird survey covariates and habitat metrics had relatively wide and continuous ranges of values (Table 3.2). Exceptions for variables included in models were zero inflation of dead tree basal and proportion oak, a narrow range of proportions of forest within 10 km of each point, and notably skewed distributions of both green and grassy ground cover. For broad habitat classifications, 407 points were classified as forest and 86 were classified as non-forest. We mea a total of 32 tree species in our prism samples with a mean live tree basal area of 14.9 m^2/ha at the 407 forest points; oak and hickory dominated the tree community (Table A1).

Bird Detection Summaries and Forest Obligates

The number of detections per species was >500 for all but one species (Red-headed Woodpecker) and ranged from 212 to 3317 (Table 3.3). Five species had at least one point count survey station with 7+ detections: Eastern Wood-Pewee, Acadian Flycatcher, Field Sparrow, Ovenbird, and Common Yellowthroat. Three species were detected on ≤5 visits at all points: Yellow-billed Cuckoo, Red-headed Woodpecker, and Northern Flicker. The remaining two species (Wood Thrush and Scarlet Tanager) each had three points where they were detected on six separate visits but no points with >6 visits with detections (Table 3.4). Of our ten study species, six were deemed forest obligates from the results of exact binomial tests: Northern Flicker, Eastern Wood-Pewee, Acadian Flycatcher, Wood Thrush, Ovenbird, and Scarlet Tanager (Table A3).

Detection Probabilities

Mean cumulative detection probabilities by species ranged from 0.083 to 0.841; 5 of 10 species had >0.690 mean cumulative detection probability (Table 3.5). Selected detectability estimates from individual visits for each species ranged from 0.367 (Common Yellowthroat) to 0.818 (Wood Thrush); selected availability estimates from individual visits ranged from 0.011 (Red-headed Woodpecker) to 0.472 (Acadian Flycatcher; Table 3.6). “Year” was the only availability covariate to appear in the top model for all species; all other availability and detectability covariates appeared in the top models of at least six of ten species (Table 3.7).

Bird Density-Habitat Relationships

Northern Flicker was the only species with no habitat covariates in its final model. All other species had multiple coefficients associated with population density, detailed below.

Landscape and Edge

Eight of ten species had at least one landscape scale forest cover metric in their top model. Red-headed Woodpecker, Acadian Wood Thrush, and Common Yellowthroat densities were positively associated with forest cover within 10 km. Field Sparrow density was negatively associated with forest cover within 10 km. Scarlet Tanager had forest cover within 10 km as a positive coefficient in its top model, but the 95% confidence interval overlapped 0 (Table 3.8). Wood Thrush, Ovenbird, and Scarlet Tanager densities were positively associated with forest cover within 1 km. Field Sparrow density was negatively associated with forest cover within 1 km. Yellow-billed Cuckoo had forest cover within 1 km as a positive coefficient in its top model, but the 95% confidence interval overlapped 0 (Table 3.8).

Seven of ten species had distance to forest edge in their top model. Eastern Wood-Pewee, Acadian Flycatcher, Wood Thrush, Ovenbird, and Scarlet Tanager densities were positively associated with distance to edge. Field Sparrow and Common Yellowthroat densities were negatively associated with distance to edge (Table 3.8).

Tree Attributes

Six of ten species had at least one basal area-related coefficient in their top model. Eastern Wood-Pewee, Ovenbird, and Scarlet Tanager densities were positively associated with live tree basal area. Red-headed Woodpecker and Common Yellowthroat had live tree basal area in their top models, but the 95% confidence intervals overlapped 0 (Table 3.9). Yellow-billed Cuckoo, Red-headed Woodpecker, and Eastern Wood-Pewee each had a negative quadratic live tree basal area term in their models with, but all 95% confidence intervals overlapped 0 (Table 3.9). Ovenbird density was positively associated with dead tree basal area while Yellow-billed Cuckoo density was negatively associated with dead tree basal area. Common Yellowthroat had dead tree basal area as a negative coefficient in its top model with a 95% confidence interval overlapping 0 (Table 3.9).

Only one species had tree species richness in its top model; Wood Thrush density was negatively associated with tree species richness (mean coef. = -0.141, 95% CI = [-0.26, -0.021]). Five species had proportion oak in their top model. Eastern Wood-Pewee density was positively associated with proportion oak. Yellow-billed Cuckoo and Red-headed Woodpecker densities were negatively associated with proportion oak. Scarlet Tanager had proportion oak as a positive coefficient in its top model, but the 95% confidence interval overlapped 0. Common Yellowthroat had proportion oak as a positive coefficient in its top model, but the 95% confidence interval overlapped 0 (Table 3.9).

Midstory Layer

Six of ten species had at least on midstory-related coefficient in its top model. Acadian Flycatcher and Field Sparrow densities were positively associated with midstory foliage density at 2.5 m in height. Red-headed Woodpecker density was negatively associated with midstory foliage density at 2.5 m in height. Ovenbird density was positively associated with midstory foliage density at 5 m in height. Wood Thrush density was negatively associated with midstory foliage density at 5 m in height (Table 3.10). Common Yellowthroat was the only species with midstory SD in its top model; the coefficient was negative, but the 95% confidence interval overlapped zero (mean coef. = -0.06, 95% CI = [-0.13, 0.01]).

Shrub and Ground Layer

Three of ten species had shrub stem density in their top model. Acadian Flycatcher density was negatively related to shrub density. Red-headed Woodpecker and Wood Thrush had shrub stem density as negatives coefficients in their top models, but the 95% confidence interval overlapped 0 (Table 3.11).

Nine of ten species had at least one ground cover-related coefficient in its top model. Field Sparrow density was positively associated with grassy ground cover. Wood Thrush and Ovenbird densities were negatively associated with grassy ground cover. Eastern Wood-Pewee, Acadian Flycatcher and Scarlet Tanager each had grassy ground cover as a negative coefficient in their top model, but the 95% confidence intervals for each overlapped 0. Yellow-billed Cuckoo, Red-headed Woodpecker, and Common Yellowthroat densities were positively associated with green ground cover. Wood Thrush had green ground cover as a negative coefficient in its top model, but the 95% confidence interval overlapped 0. Eastern Wood-Pewee, Acadian Flycatcher, Wood Thrush, Field Sparrow, and Ovenbird densities were all positively associated with leaf litter cover. Common Yellowthroat density was negatively associated with leaf litter cover (Table 3.11).

Methods

Study Area

Our study area comprised six units of Stephens State Forest and Sand Creek Wildlife Management Area, spanning Clarke, Decatur, Lucas, Monroe, and Ringgold counties in south-central Iowa, USA. The Woodburn, Whitebreast, and Lucas Units of Stephens State Forest are almost entirely contiguous and are located within the Stephens Forest BCA; these units combined are 2,767 ha and will hereafter be collectively called “Stephens” (Figure 3.1A). The Cedar Creek, Chariton, and Thousand Acres Units of Stephens State Forest are separated from each other by a distance of 1-4 km and are located within Stephens Forest -Thousand Acres BCA; these units combined are 2,361 ha and will hereafter be collectively called “Thousand

Acres” (Figure 3.1B). Sand Creek Wildlife Management Area (hereafter “Sand Creek”), is 1,457 ha and is located within the Sand Creek Woodland Savanna BCA (Figure 3.1C).

These areas are comprised primarily of deciduous forest and woodlands, especially upland oak (*Quercus* spp.)-hickory (*Carya* spp.) forest, but also bottomland cottonwood (*Populus deltoides*)-silver maple (*Acer saccharinum*) woodlands. Small portions of these forests are actively managed; activities include girdling to create standing dead wood and selective harvesting of trees to create a more open canopy. The topography of these forests is characterized primarily by ridges and ravines; many ravines have seasonal streams. Some larger perennial streams and rivers are also present; bottomland forests tend to occur along these waterways. Other habitats present in smaller patches are pine plantations, wetlands, grassland, pasture, and crop fields (Figure 3.1). Dominant tree species were white, northern red, and bur oaks (*Quercus alba*, *Q. rubra,* and *Q. velutina*), shagbark hickory (*Carya ovata*), and American elm (*Ulmus americana*). Three species of ash (*Fraxinus* spp.) were also present, but most individuals were standing deadwood killed by emerald ash borer (*Agrilus planipennis*). We documented a total of 33 tree species (Table A1). Common woody plants in the understory and in clearings included ironwood (*Ostrya virginiana*), coralberry (*Symphoricarpos orbiculatus*), multiflora rose (*Rosa multiflora*), black raspberry (*Rubus occidentalis*), blackberry (*Rubus allegheniensis*), and eastern redcedar (*Juniperus virginiana*).

Study Species

We modeled habitat relationships for eight breeding avian Species of Greatest Conservation Need (SGCN) in Iowa that were detected during our surveys (Iowa Department of Natural Resources, 2015), along with two other forest bird species of management interest. Preliminary analyses with fewer than 200 observations of a species resulted in poor precision for density estimates or unrealistically low detection probabilities (<1%), so we only analyzed species with >200 observations. The SGCN meeting these criteria were Yellow-billed Cuckoo (*Coccyzus americanus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), Northern Flicker (*Colaptes auratus*), Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher (*Empidonax virescens*), Wood Thrush (*Hylocichla mustelina*), Field Sparrow (*Spizella pusilla*), and Common Yellowthroat (*Geothlypis trichas*). We also chose to include Ovenbird (*Seiurus aurocapilla*) and Scarlet Tanager (*Piranga olivacea*). Ovenbirds are only locally abundant in Iowa (pers. obs.) and Scarlet Tanagers are considered an indicator species for forest habitat quality (Rosenberg et al., 1999; Urban et al., 2012).

Bird Surveys

We conducted point counts from mid-to-late May through early-to-mid August 2016-2019. We randomly placed a grid of points 300 m apart at each site, and we removed points within 150 m of a study area boundary, resulting in 503 total points (Figure 3.2). We conducted 10-min, 100-m radius multispecies bird point counts. Data were collected on all bird detections, but we excluded visual-only detections and detections of known females and juveniles. For consistency with other studies, we would have ideally used only singing males for most species but due to slight changes in data collection protocol between years, we were unable to reliably determine singing males versus other types of detections. Our survey condition parameters were to conduct surveys between 0.7 hours before and 4.5 hours after sunrise with wind speeds <20 km/h and no precipitation. Both wind speed and time since sunrise were considered as covariates in models to account for deviations from our protocol (see Hierarchical Models). Of 503 original points, 493 were surveyed twice each year for an early and late season visit; the cutoff between the seasons was approximately 1 July, and 10 of the original points were missed at least one of four years due logistical issues such as flooding. There were five total observers and two observers per season; when possible (85% of cases), each observer visited each point once during a season to minimize observer bias. Two relatively inexperienced observers surveyed in 2016 only, one experienced observer surveyed 2017-2019, one moderately experienced observer surveyed in 2017 and 2018, and a separate experienced observer surveyed in 2019 only.

Bird Survey Covariates

We obtained precipitation data and average wind speed data from climate stations at municipal airports in Chariton, Iowa, USA (Station ID: WBAN:04913) and Osceola, Iowa, USA (Station ID: WBAN:54942), as these variables may affect an observer's ability to hear a bird vocalization. The Chariton station was ~21 km from the center of Thousand Acres, ~14 km from the center of Stephens, and ~57 km from the center of Sand Creek. The Osceola station was ~48 km from the center of Thousand Acres, ~16 km from the center of Stephens, and ~34 km from the center of Sand Creek. Despite the somewhat long distances, these were the closest weather stations to our study areas, and we lacked consistent weather data from the survey points. At both stations, weather data were recorded at 15 minutes, 35 minutes, and 55 minutes after each hour. Precipitation was defined as at least one station having a present weather code indicating rain, fog, etc., and thus we likely overestimated the proportion of surveys with precipitation. Due to a low proportion of surveys with precipitation and lack of survey site-specific data, we did not ultimately include precipitation as a model covariate.

When both weather stations were functional, we averaged wind speeds for Chariton and Osceola for all sites. Occasionally, one of the two stations was offline; in these cases, we only used data from the functional station. We excluded one aberrant wind speed reading at the Chariton weather station (>1000 km/h) and used only the Osceola data. There were seven (7) instances out of 629 where neither station recorded data; in these cases; we found a time within 40 minutes of the missing value and used the averaged wind speed from that time. For each bird survey, we used the wind speed value that was closest in time to the start of the bird survey; e.g., if a bird survey started at 8:01 a.m., we would use the wind speed data from 7:55 a.m.

We obtained sunrise times for the Iowa municipalities of Grand River, Woodburn, Lucas, and Russell from the Astronomical Observations Department of the United States Naval Observatory (3450 Massachusetts Ave NW, Washington, DC 20392). We used Grand River sunrise times for Sand Creek, Woodburn for the Woodburn and Whitebreast Units in Stephens, Lucas for the Lucas Unit in Stephens, and Russell for all units of Thousand Acres.

Landscape and Forest Patch Metrics

To assess forest cover at a landscape scale, obtained landscape cover data for 2016-2019 at 30-m spatial resolution from the Cropland Data Layer (CDL; USDA NASS, 2019, 2018, 2017, 2016). Using Esri® ArcGIS Pro®, we clipped the CDL rasters for each year to 1 km and 10 km buffers around each bird survey point, saving each clipped raster as a separate image file. We imported image files for each combination of point, year, and buffer size into R using package ‘raster’ (R Core Team, 2019). We defined mature forest cover as CDL cells with values 141, 142, 143, and 190 (deciduous forest, mixed forest, coniferous forest, and woody wetland, respectively; USDA NASS, 2019). We note that “forest” in the CDL dataset can include as little as 25% canopy cover within a 300 m x 300 m cell (USDA NASS, 2019). Woody wetland was included as “forest” because aerial imagery and ground-truthing both suggested that the majority of “woody wetlands” in our study area were bottomland cottonwood-silver maple woodlands. To assess the relative abundance of mature forest within each buffer as a percentage (“percent forest cover”), we imported clipped image files into R using package ‘raster’, (Hijmans, 2019), used the ‘getValues’ function to find the number of raster cells matching the criteria for forest, and then divided the number of forest cells by the total number of cells in the clipped image file. We averaged percent forest cover at each scale (1 and 10 km) across all four years for each point to get single covariate values.

To calculate distance to edge and forest patch size, we digitized forest polygons in ArcGIS Pro® using 2016-2018 Iowa Spring Color Infrared Orthophotos (Iowa State University, 2018). We identified deciduous forest as large, dark reddish-brown patches, and coniferous trees and shrubs as bright red, irregularly shaped patches, categorizations corroborated by our vegetation surveys. Forest only split by streams and narrow gravel roads was considered continuous and was digitized as a single patch, as narrow non-forest corridors do not seem to affect deciduous forest bird habitat use (Rich et al., 1994). Internal fields and lakes were counted as edges and did not contribute to forest area. We did not categorize cedar groves with open canopy (i.e., visible spacing between trees) as forest. We calculated forest patch size as the area of each digitized forest polygon. We selected “forest points” as bird survey points within forest polygons using the Intersect tool in ArcGIS Pro®, setting distance to edge for all points outside of forest polygons to 0 m. To measure distance to forest edge for forest points, we converted forest polygons to polylines to create forest boundaries and measured distance from each forest point to the nearest forest boundary using the "Near" tool in ArcGIS Pro®; we used geodesic distance and a 1-km search radius.

Vegetation Surveys

Our vegetation survey protocols were derived from three standardized vegetation survey protocols for forest birds (Hamel, 1996; James and Shugart, 1970; Martin et al., 1997). Ultimately, we sought to avoid seasonal vegetation changes by using a short survey period while also meaningfully describing forest structure as it relates to avian habitat. We surveyed vegetation at each bird survey point between 16 July and 28 August 2019, with the assumption of minimal vegetation structure change from 2016 to 2019. Each vegetation metric we collected was justified by previous forest bird studies, primarily in the Midwestern United States (Table 3.1).

We used five metrics to assess tree community and structure: live tree basal area, dead tree basal area, relative amount live tree basal area comprised of oaks (genus *Quercus*) as a proportion ("proportion oak"), tree species richness, and canopy closure. Trees were defined as woody stems at 1.4 m with diameter >8 cm; stems meeting these criteria were counted separately even if they shared a base (James and Shugart, 1970; Martin et al., 1997). All tree metrics except canopy closure were calculated from a variable radius forestry prism sample centered on a bird survey point; we counted every other "borderline" tree in the prism sample (Figure A27; Hovind and Rieck, 1961). Prism-sampled basal area can be collected in a more time-efficient manner than fixed radius plots while covering a larger area. To maximize the number of trees in our sample and increase our average survey radius, we used a 1-m basal area factor cruising prism (Cruise-Master Prisms, Sublimity, Oregon). We identified each tree in our prism sample to species and counted all dead trees in a separate category. We separated live and dead trees because dead trees provide habitat for woodpeckers and secondary cavity nesters, while the foliage of live trees provides foraging opportunities for foliage gleaners and cover for tree-nesting birds. Proportion oak was calculated as the basal area of living oaks divided by total live BA. When basal area was equal to zero, we set proportion oak to 0. We calculated tree species richness as the number of tree species in a prism sample. Canopy closure was measured using a periscope-style densitometer (Geographic Resource Solutions, Arcata, California). There were

20 presence/absence observations of canopy closure recorded along two 20-m transects centered on the survey point and oriented in the cardinal directions. We made ten observations along each transect spaced every 2 m, excluding the survey point itself. Canopy was marked was “present” if, when the densitometer was oriented straight upward, there was vegetation in the densitometer’s crosshairs, and the proportion of canopy closed was calculated by multiplying the number of “present” observations by 0.05 (Hamel et al. 1996). Canopy closure was excluded from analyses due to multicollinearity (see Data Formatting).

We used three metrics to quantify horizontal midstory structure: foliage density at 2.5 m in height, foliage density at 5 m, and standard deviation of foliage density. Studies quantifying deciduous forest midstory in the Midwestern United States are lacking (though see Yahner, 1982 for work on shelterbelt midstory in Minnesota), but studies in the Southern United States have found relationships between midstory foliage density and breeding forest bird species (Burger et al., 1998; Twedt et al., 1999). We modified the midstory protocol from Hamel (1996). Instead of using a checker pattern, our board was a 50 cm x 50 cm piece of plexiglass painted with OSHA Safety Orange spray paint over a coat of white primer attached to a telescoping aluminum pole. With the observer at the survey point, we situated the board 10 m away in three different randomly-selected cardinal directions, with the board facing the observer at heights of 2.5 m and 5 m in each selected direction (Figure A27). We elected not to take photographs at 0 m in height because we felt our ground cover and shrub metrics (below) adequately captured that vegetation layer. To keep our vegetation survey period as short as possible, we excluded one of the four cardinal direction via a random number generator, although we deviated on rare occasions from this selection if there was an obstruction or obstacle in the selected direction, such as a steep ravine or recently downed tree that would have been upright during the breeding season. When a board was entirely exposed or entirely obstructed from the observer vantage point, we recorded proportion covered as 0 or 1, respectively. For intermediate levels of obstruction, we photographed the board at each position from observer eye level (~1.6 m) using a Fujifilm FinePix XP120 Digital Camera (Fujifilm, Tokyo, Japan; Figure A28). For consistency, we set camera ISO to 800 and white balance to fluorescent light setting #3. When necessary, we altered the exposure bias of the camera manually to avoid extremely dark photos, washed out (i.e., white) board pixels, and blurry photos. At two (2) survey points we were only able to take photographs in two directions. For each board, we estimated the proportion covered by vegetation using a novel image analysis technique (see Midstory Image Analysis below). We calculated mean foliage density at both 2.5 m and 5 m by averaging percent cover for all boards at a point at the specified height. Variability in midstory foliage density is associated with differences in bird communities in some North American forests (MacArthur and MacArthur, 1961; Young et al., 2013); we assessed midstory variability as the standard deviation of proportion covered of all boards at a point (“midstory SD”).

We assessed four different metrics for the shrub and ground layer of the forest: shrub stem density, and percentage of ground covered by “green” vegetation, “grassy” vegetation, and leaf litter cover. We counted shrub stems covered or intercepted by an observer’s outstretched arms along two perpendicular 1.8 m wide x 22.6 m long transects running north-south and east-west; both centered on the survey point (James and Shugart, 1970). Shrubs were defined as woody stems under 8 cm in diameter and >0.5 m in height. We did not count shrubs and saplings separately, but we did count stems that split at a height of 10 cm or lower separately (Martin et al. 1997). Density was calculated as number of stems divided by 78 m^2, the approximate transect area. All ground cover metrics were measured using a periscope-style densitometer. There were

20 presence/absence observations of three ground cover types recorded along two 20 m transects centered on the survey point and oriented in the cardinal directions. We made ten observations along each transect spaced every 2 m, excluding the survey point itself. A ground cover type was marked was "present" if, when the densitometer was oriented straight downward, that ground cover type was in the densitometer's crosshairs, and the proportion of ground covered was calculated by multiplying the number of "present" observations by 0.05 (Hamel et al. 1996). Multiple ground cover types could be contained in a sample due to vertical stratification, e.g., herbaceous plants growing over leaf litter. We defined green cover as the proportion of ground covered by herbaceous plant foliage or foliage from woody plants that were too small to be considered shrubs, e.g., seedling trees. We defined grassy cover as the proportion of ground covered by graminoids, including grasses (Family: Poaceae) and sedges (Family: Cyperaceae). We defined litter cover as the proportion of ground covered by leaf litter, brown coniferous needles, or dead woody vegetative matter.

Midstory Image Analysis

Our goal in analyzing midstory photos was to calculate the proportion of a 50 cm x 50 cm orange board covered by vegetation. The relative size of the orange board in the midstory photos varied due to factors such as tilt of the board, the slope of the ground, and error in the measurement between the board and the photographer, meaning we could not simply count orange pixels and divide by a constant number for the majority of the photos. When the location of the edges of a partially obscured orange board could be determined or estimated within a photograph (n = 1798), we traced a quadrilateral shape bounded by the edges of orange board using the Polygon Lasso in Adobe® Photoshop® CS6. We filled the background with blue (red = 0, green = 0, blue = 255); the resulting image was saved as a JPEG file (Figure A28). We counted the blue pixels using the ‘rectangularRange’ function in R package ‘countcolors,’ and subtracted that value from the total number of pixels to get the board size in that image (R Core Team, 2019; Weller, 2019). R generally uses values between 0 and 1 as opposed to standard 0 to 255 for RGB (red-green-blue) values, so we used an upper vector of (red = 0.092, green = 0.092, blue = 1) and a lower vector of (red = 0, green = 0, blue = 0.91); there is a range of values due to JPEG image compression. This range did not overlap any pixels in our photographs. When the board edges could not be determined (n = 211), we followed a similar protocol, except that photos were cropped to an arbitrary shape containing all exposed areas of the orange board as opposed to a quadrilateral, and for this small proportion of photos we assumed the total board size was equal to the median board size at a board height of either 2.5 m or 5 m in height (805,370 px or 741,480 px, respectively).

For our first attempt at quantifying the number of orange board pixels in each photo, we used the following broad definition of an “orange” pixel to account for a variety of lighting conditions: 1) hue value in the ranges of 0°-59° (red to warm yellow) or 300°-359° (magenta to red); 2) saturation of 14%-100%; and 3) luminance of 8% - 75%. We used package ‘imager’ to load JPEG images into R as 4-dimensional ‘cimg’ objects and convert them from RGB to HSL (hue-saturation-luminance; Barthelme, 2020). We reduced the 4D HSL cimg objects to three dimensional arrays by taking only the first “slice” of dimension 3 of the cimg object, converted all hue values >299° to 0, and divided all hue values by 360 to get a scale from 0-1. We then used the ‘rectangularRange’ function in R package ‘countcolors’ using an upper vector of (0.166, 1.00, 0.75) and a lower vector of (0.00, 0.14, 0.08) to do two things: 1) count the number of pixels meeting the criteria we set for orange, and 2) create a 3D array replacing the putative orange pixels with hue = 267°, saturation = 100%, and luminance = 62% (purple). The 3D arrays with replaced orange pixels were converted to cimg objects and then from HSL to RGB to create an initial set of indicator images (Figure A28). Indicator images were compared to the original images; orange pixel counts were deemed satisfactory if the corresponding indicator image had 1) the entire exposed board covered by purple, and 2) no leaves, clusters of twigs, or branches mostly covered by purple. Small, isolated twigs and small portions of branches covered by purple were deemed acceptable; 1812 of 2009 initial indicator images met these criteria.

For the remaining 197 images, we first tried an upper HSL vector (0.166, 1.00, 0.8) and a lower HSL vector (0.00, 0.25, 0.20), again setting all hue values >299° to zero and dividing hues by 360 prior to putting values in a vector. This set of values excludes more brown and dark plant material by upping lower limits for saturation and luminance at the cost of missing shaded parts of the orange board; it also includes some brighter board patches by increasing upper luminance. This second fixed set of criteria produced satisfactory indicator images for 114 of 197 remaining images. For the remaining 83 images, we manually set the upper and lower vector values for each individual image to include the orange board and exclude plant material. Hue generally stayed in the original range, but we occasionally included more bluish-gray values for very backlit and washed out photographs (250-299°). Both saturation and luminance limits varied anywhere from 0 to 1 based on the lighting of the photograph. After obtaining orange board pixel counts, we divided the orange pixel counts by the board size (calculated or median per above) to get proportion of the board covered; we used these proportions for the midstory calculations detailed in Section 2.5.

Data Formatting

Before modeling, we needed to answer two questions: 1) Do any variables need to be excluded due to multicollinearity or other factors?, and 2) Which species should include non-forest points in their models?

Despite having multiple observers with varying experience levels, we were not able to include observer as covariate in our models. Due to having two relatively inexperienced observers that only observed in 2016, it was impossible to fit both year and observer effects because inexperienced observers only surveyed in one year. We chose year effects over observer effects because we believed that between-year population fluctuations were more likely to influence bird detections than observer, and we usually had all five observers visit every point.

We removed three habitat covariates from consideration in our models. We excluded forest patch size because there were only four, largely unbroken forest patches in our study area, each >1500 ha in size, exceeding the critical patch size for area-sensitive Midwestern forest bird species by multiple orders of magnitude (Ambuel and Temple, 1983). After excluding forest patch size, we used the 'vif' function in R package 'car' (Fox and Weisberg, 2019) to assess multicollinearity for all habitat variables with generalized variance inflation factor (GVIF), using a cutoff off of < 3 (Zuur et al., 2010). Initially, five (5) variables exceeded the cutoff (Table A2). We removed Bird Conservation Area as a covariate because it had the highest GVIF of any landscape covariate, and we removed canopy closure because it had the highest GVIF of any vegetation survey covariate; removing these covariates reduced variance inflation factor (VIF) for all other covariates to < 3 (Table A2). GVIF was not necessary in our second round of multicollinearity assessment due to lack of categorical variables, hence the shift to VIF (Fox and Monette, 1992).

Due to a high number of zero values in open areas for variables such as basal area, we were concerned that the inclusion of non-forest points in models for forest obligate species could result in uninformative modeled relationships between bird densities and habitat metrics. Therefore, we identified forest obligate species and excluded non-forest points from models for forest obligates. Birds were deemed “forest obligates” in our system if their detections at forest points were significantly greater than expected based on a one-tailed exact binomial test with success probability = 407/493 (0.826; the proportion of points in forest) and $\alpha = 0.05$.

Prior to analysis, all continuous covariates were center-scaled using the default “scale” function in R (R Core Team, 2019). Quadratic forms of covariates were calculated from center-scaled covariates and then re-center-scaled to create a distinct vertex at the mean value of each covariate. Coefficients are reported center-scaled due to lack of interpretability even when back-transformed; we instead compare relative coefficient values between species using coefficient signs and 95% confidence intervals.

Hierarchal Models

We used hierarchical distance sampling (HDS) models using the ‘gdistsamp’ function in R package ‘unmarked’ to evaluate relationships between habitat characteristics and bird densities (Chandler et al., 2011; Fiske and Chandler, 2011; R Core Team, 2019). HDS models in ‘unmarked’ use a site-specific likelihood for data collected at each “site,” in our case the 100-m radius plot around a point. We used this definition of site because we only had one year of vegetation survey data and we were not specifically interested in annual densities. We defined the superpopulation for each point as the abundance during the year with the highest abundance at each point, though we used data from all eight visits (four years) to estimate this value. Site-level abundance was treated as a random effect, and analysis was based on the integrated likelihood or on a function of the parameters of the detection function, detectability covariates, possible availability outcomes, availability covariates, abundance, and abundance covariates, with the number of model components varying based on the inclusion or exclusion of covariates at each stage of the hierarchy (Chandler et al., 2011; Royle, 2004; Royle et al., 2004). Distance sampling without availability corrections assumes that (1) detection is perfect at distance 0 from the observer, (2) individuals are detected at their initial location, and (3) individuals are counted in the correct distance bins (Buckland et al. 2001). The inclusion of availability allows the "perfect detection at the point" assumption to be relaxed. Availability is the probability that an individual will make itself available for detection, given that is occupying a site; detectability is conditional on a bird being available. Two different phenomena can contribute to an individual being unavailable for detection: 1) temporary emigration from a site, and 2) a bird being present but not vocalizing (Yamaura and Royle, 2017). Our study employed multiple visits to estimate availability (Chandler et al., 2011). When using both availability and detectability in a model, detection probability for a single visit is defined as the probability that an individual will be detected given it is occupying a site and is calculated as the product of availability and detectability (Yamaura and Royle, 2017). We define non-detection probability as the compliment of detection probability. We define cumulative detection probability the probability that an individual will be detected at least once across all eight (8) visits as is calculated as 1 – (the product of non-detection probabilities across all visits).

We fit models in a multi-stage process similar to that of Kendrick et al. (2013), and we evaluated model support using AIC at each stage (Akaike, 1987). We first determined if a uniform or half-normal function was better supported as a detection function by fitting HDS models with no covariates. We then used the most-supported key function and evaluated candidate models for availability in relationship to time since sunrise (TSSR), the quadratic of TSSR, Julian date (JDAY), and the quadratic of JDAY, and year (YEAR) as a fixed effect with df = 3, singly and in all additive combinations, excluding covariates from other hierarchy stages. JDAY and TSSR (including their quadratic terms) are associated with availability for multiple species of songbird (Sólymos et al., 2013). Year was included as a fixed effect as a species not occupying a site can be considered "temporary emigration" in this modeling framework so long as the habitat suitability does not change and the species has the ability to recolonize the site later. We used the best supported covariate combination for availability and evaluated detectability in relation to observer and wind speed singly and in all additive combinations, excluding abundance covariates. Higher wind speeds can also affect detectability by obscuring more distant aural cues (Rigby and Johnson, 2019).

Using the top covariate sets for both availability and detectability, we evaluated candidate models for abundance, starting with an all-abundance-covariates model. These models included thirteen different coefficients on abundance, not counting the intercept (Table 3.1). We broke all abundance coefficients into five sequential stages of a hierarchy: 1) landscape, 2) distance to edge, 3) tree attributes, 4) midstory layer, and 5) shrub and ground layer (Table 3.1). Starting with the first stage of the hierarchy, we evaluated all covariates of that hierarchy stage singly and in combination, keeping all lower stages of the hierarchy constant. Once we found the best combination of covariates for a hierarchy stage, we held the covariate combination at that hierarchy stage constant and moved to the next lowest hierarchy stage. We repeated the process of running all combinations for a single stage, holding lower stages constant, fixing the covariates for that stage, and moving to the next stage until all stages of the hierarchy were completed. This resulted in 58 models per species, with the exact covariate composition of models varying between species. Running all combination of models was computationally unrealistic; running approximately 2^{13} HDS models with our dataset in ‘unmarked’ would take several months per species given the speed of the high-performance computing clusters available to us. Ad hoc methods of fixing covariates in other hierarchical ecological modeling frameworks perform similarly to frameworks using all combinations of models (Doherty et al., 2012).

Our abundance covariate hierarchy has the following biologically rooted justification. Migrating birds returning to the breeding grounds can first assess habitat at a landscape scale, with certain forest species avoiding areas with small forest patches or low proportion of forest habitat on a landscape scale in spite of otherwise suitable site-scale conditions (Ambuel and Temple, 1983; Bakermans and Rodewald, 2006). Once reaching a suitable patch, an individual may avoid or gravitate toward the edge of the habitat, depending on the species (Kroodsma, 1984; Le et al., 2018). Once at an otherwise suitable area within a habitat patch, birds use structural characteristics of vegetation to select a breeding territory (MacArthur and MacArthur, 1961). In our hierarchy, we divided site-level structural characteristics into three subsections: tree attribute, midstory layer, and shrub-ground layer. Tree attributes were the first subsection, as they are derived from a comparatively large variable radius plot, and trees represent the largest vegetation structures in a forest. Tree species richness and proportion oak were surrogates for otherwise hard-to-measure structural differences. Variability in leaf and bark structure between tree species may impact foraging and nesting opportunities for forest birds, with oaks potentially providing above-average foraging opportunities for insectivores due to furrowed bark and short leaf petioles (Holmes and Robinson, 1981; Jackson, 1970; Rodewald and Abrams, 2002). The midstory and the shrub-ground layer represent distinct habitats for birds and thus were considered as separate hierarchy stages. We considered midstory before the shrub-ground layer because of its relatively higher altitude in the forest strata and its generally has larger vegetative structures (e.g., small trees and branches of large trees).

To estimate detection probability, we first estimated the mean and 95% confidence intervals for σ of half normal detection functions for each survey and species using survey covariates for each survey and the 'predict' function methods in 'unmarked.' To convert σ to a detection probability, we integrated from 0 – 100 m using the circular half normal function 'grhn' in 'unmarked' (Fiske and Chandler 2011). For each species, we report an arithmetic mean of all survey-scale mean detection probabilities across all surveys, and a standard deviation of the distribution of survey-scale means.

Discussion

A broad suite of habitat characteristics, ranging from landscape scale to site-level, are associated with bird species of management and conservation concerning breeding in and near forests in south-central Iowa. Landscape-scale forest cover appeared in top models for more than half of our study species, with positive associations for six species. Consistent with our results, positive associations with landscape scale forest cover has previously been demonstrated for species such as Acadian Flycatcher and Wood Thrush (Bakermans and Rodewald, 2006; Lee et al., 2002). Field Sparrow showed the opposite trend of other species; its site-level population density was negatively associated with forest cover at both scales examined, a sensible result for a primarily open area species (Carey et al., 2020). The positive association of Common Yellowthroat densities with forest cover at a 10 km was surprising given that Common Yellowthroats primarily use more open habitats such as marshes, scrublands, and prairies (Guzy and Ritchison, 2020); however, a study in Missouri showed that some scrubland species, such as Yellow-breasted Chat, are positively associated with increasing landscape scale forest cover

(Reidy et al., 2014). Some species in our study, such as Yellow-billed Cuckoo, Eastern Wood-Pewee, and Ovenbird, have previously been shown to be associated with landscape scale forest cover (Lee et al., 2002; Reidy et al., 2014), but did not have associations in our study. This may in part be due to narrow ranges of landscape forest cover in Iowa's agriculturally dominated landscape; forest cover at a 10 km scale in our study only ranged from 19%-36%. It also possible that other landscape-scale factors or specific characteristics of BCAs could account for relationships observed at the 10 km scale; we only observed three BCAs and excluded BCA as a covariate due to multicollinearity.

Of all thirteen habitat covariates, distance to forest edge was the most prevalent individual covariate in top models, appearing in top models for seven of ten species. Even after excluding non-forest points, all forest obligate species except Northern Flicker had distance to edge as a positive coefficient in their top model. This finding is consistent with other studies on forest obligate species, including most of the species in our study (Kroodsma, 1984; Le et al., 2018; Wenny et al., 1993). Field Sparrow and Common Yellowthroat both had negative relationships with distance to edge, a reasonable result for species that primarily use open areas as habitat (Carey et al., 2020; Guzy and Ritchison, 2020).

Relationships between tree characteristics and bird densities in our study were sparse and often difficult to interpret. For live tree basal area, we included both a linear and quadratic term in our models, expecting potential negative quadratic coefficients for species that may occur more frequently in open woodlands but less so in dense forest. However, three species, Eastern Wood-Pewee, Ovenbird, and Scarlet Tanager had a positive quadratic coefficient for live basal area, indicating a potential increase in density at very high or very low basal area values within forested habitat. In contrast to our study, Kendrick et al. (2013) found a positive linear relationship between Eastern Wood-Pewee density and tree stocking, a metric similar to basal area. Other studies have found relationships between Yellow-billed Cuckoo and Acadian Flycatcher densities and other tree density-related metrics, but we did not find such relationships (Reidy et al., 2014). Dead tree basal area did not appear in the top model for either species of woodpecker in our study (Red-headed Woodpecker and Northern Flicker), but appeared as a negative coefficient in the Yellow-billed Cuckoo model and a positive coefficient in the Ovenbird model, neither of which has a strong biological rationale. The only species with tree species richness in its top model, Wood Thrush, had a negative association of tree species richness and bird density. There is not a clear explanation for Wood Thrush density being higher in low species diversity tree stands, but the lack of positive relationships across the entire suite of study species suggests that higher tree species richness at a site does not lead to increased densities of our study species in our study area. This finding runs contrary to a study in Illinois showing positive relationships between tree species diversity forest bird densities Midwestern United States (Sierzega, 2016). Only one species, Eastern Wood-Pewee, was positively associated with proportion oak in our system; this species is also positively associated with oak in forests in Illinois (Sierzega, 2016). Both Yellow-billed Cuckoo and Red-headed Woodpecker densities had negative relationships with proportion oak. Red-headed Woodpeckers depend on oak and other hard mast trees as a food source and are generally associated with habitats containing oak trees (Conner, 1980; Rodewald et al., 2005), so the negative relationship in our study seems spurious; we have no strong biological justification for Yellow-billed Cuckoo densities being negatively associated with the proportion of oak.

Midstory density did not have any consistent patterns across species and appeared in models for relatively few species. The negative relationship between Red-headed Woodpecker density and midstory density at 2.5 m may reflect this species' preference for open woodland and savanna habitats. Acadian Flycatcher and Field Sparrow, two opposites in terms of other habitat associations, both had densities that were positively associated with midstory density at 2.5 m. For Field Sparrows, this may reflect a use of forest edges and successional habitat with small trees and tall shrubs in our study area. This result is unexpected for Acadian Flycatcher, as this species tends to both nest and forage at or above 3 m in other habitats (Allen et al., 2020). The negative relationship between Wood Thrush density and midstory density at 5 m may be an indicator of some other habitat characteristic, as this layer of the forest has not been previously documented as important to Wood Thrush, a species that nests in the lower midstory and shrubs and forages mostly on the ground (Evans et al., 2020). Ovenbirds use vegetation in the upper midstory and subcanopy as signing perches, thus providing a plausible explanation for the positive relationship between Ovenbird density and midstory density at 5 m in height (Porneluzi et al., 2020). The lack of midstory SD in our models may be a result of our novel method of calculating midstory heterogeneity; we suggest a comparative study of the methodology we used with other methods of measuring midstory heterogeneity and density, such as those of MacArthur and MacArthur (1961), the aerial LiDAR-based methods of Young et al. (2013), and newer ground-based LiDAR metrics more typically used for non-avian research (Loudermilk et al., 2009).

Leaf litter was the most prevalent site-level covariate in our models, appearing in top models for six of ten species; all other shrub and ground covariates considered appeared in the top model of at least one species. Unsurprisingly, both Ovenbird and Wood Thrush densities were positively related with leaf litter cover; both of these species rely on leaf litter as a foraging substrate (Holmes and Robinson, 1988). Grass likely represents an unsuitable foraging substrate for these two species, hence the negative relationship between grassy cover and bird densities for Ovenbird and Wood Thrush. Eastern Wood-Pewee and Acadian Flycatcher also had positive density relationships with leaf litter cover, but both are aerial insectivores (De Graaf et al., 1985) and are not unlikely to benefit from leaf litter itself. Instead, leaf litter may be an indicator of some other aspect of forest quality that influences densities of these species. Field Sparrow density was also positively associated with leaf litter cover. Two non-exclusive explanations are that Field Sparrows were detected from forest points in a nearby opening or Field Sparrows in our study area may be occurring along forest edges with leaf litter, as they do occasionally in other areas (Shugart and James, 1973). The positive association between Field Sparrow density and grass cover was expected, given that this species uses grasses for both foraging and nesting (Best, 1978; De Graaf et al., 1985). Common Yellowthroat was the only species whose density was negatively associated with leaf litter cover; this species is a ground and shrub gleaning insectivore likely not suited to foraging in leaf litter (De Graaf et al., 1985). Common Yellowthroat density had a positive relationship with green ground cover, consistent with findings that Common Yellowthroats in Iowa grasslands chose nesting sites with relatively high density of forbs (Murray and Best, 2014). Both Red-headed Woodpecker and Yellow-billed Cuckoo densities were positively associated with green ground cover; this result is unexpected, but the presence of herbaceous ground cover may be an indicator of the more open woodland types these species prefer (Le et al., 2018; Reidy et al., 2014). Acadian Flycatcher density had a negative relationship with shrub density, a result consistent with other studies of this species (Bakermans and Rodewald, 2006; Reidy et al., 2014). Surprisingly, Field Sparrow did not have shrub density in its top model despite this species’ association with shrubs elsewhere in the Midwest (Best, 1978; Reidy et al., 2014).

In our current study framework, we were unable to reliably model bird-habitat relationships for species with fewer than 200 observations, and some of the species we were able to model suffered from low cumulative detection probabilities. Yellow-billed Cuckoo, Red-headed Woodpecker, and Northern Flicker each had cumulative detection probabilities of <0.15, and these species had relatively few points with several repeat detections compared to other species. These species also had unexpected results in their habitat models. Northern Flicker had no habitat covariates in its top model, despite another in Tennessee finding relationships between Northern Flicker presence and habitat variables such as tree density (Anderson and Shugart, 1974); the modeled relationships between densities of Red-headed Woodpecker and Yellow-billed Cuckoo and oak were previously discussed. We believe some of the relationships for these difficult-to-redetect species may be spurious results of uncertainty in detection in our models. A study design with more visits per year and conditional replicates for rare species based on the methods of Specht et al. (2017) could allow for estimates of habitat relationships for less common species and increase cumulative detection probabilities for hard-to-detect species. In our study, logistical constraints and other study objectives caused us to prioritize better spatial coverage in favor of a greater number of visits per point.

Conclusions

Even with only ten bird species in our study, habitat associations varied considerably between species. Of thirteen habitat characteristics, nine had both negative and positive associations with bird density, with the direction of the relationship varying between species. The two edge and open area species in our study system, Field Sparrow and Common Yellowthroat, often had habitat relationship opposite those of other species. Field Sparrow was the only species with negative associations with landscape scale forest cover, Common

Yellowthroat was the only species with a negative association with leaf litter cover, and both Field Sparrow and Common Yellowthroat were the only species with positive associations with forest edge. From a management perspective, no single prescription will benefit all species of conservation concern in this area.

Six of ten species had a positive association with landscape scale forest cover at some scale, making it one of the most prevalent positive associations. Five of ten species had a positive association with distance from forest edge, making distance to edge another common positive association. Areas with high landscape-scale forest cover were positively associated with many species, though the observational nature of this study and the limited number of study areas make it difficult to untangle this relationship from confounding variables such as agricultural disturbance. Protecting large forest patches from the creation of edges, i.e., fragmentation, is also likely to benefit the many of the bird species in our study within this area; however, a minority of species, namely Common Yellowthroat and Field Sparrow in our study, may benefit from edge creation.

Leaf litter was the most consistent site-level covariate, with a positive relationship between leaf litter and bird density for five of ten species. Leaf litter provides foraging habitat for ground-foraging species such as Ovenbird and Wood Thrush. It may also serve as an indicator of higher quality habitat for forest species such as Eastern Wood-Pewee and Acadian Flycatcher despite leaf litter not directly benefiting them.

Aside from leaf litter cover, relationships between bird densities and site-level characteristics related to trees, the midstory, shrubs, and ground cover were largely species-specific, or, in the case of live tree basal area and high tree species richness, relatively unimportant for all study species in this area. However, some species-specific relationships may inform management for species such as the Acadian Flycatcher, a species negatively associated with shrubs in both our study area and in other systems. For future studies, we recommend assessing midstory characteristics using a variety of methods and employing a conditional replicate study design to better assess bird-habitat relationships for rare and hard to detect species of conservation concern.

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Tables

Table 3.1. Stages of a hierarchy of abundance covariates used to model relationships between habitat and breeding bird densities in and near south-central Iowa forests, 2016-2019. "Support" includes citations of papers that used similar covariates when modeling forest bird populations and communities in the Midwestern, Southern, or Eastern United States. *Reidy et al. (2014) use percent stocking, an alternative to basal area (Hovind and Rieck, 1961). ** MacArthur and MacArthur (1961) use the Shannon diversity index of foliage 1.5 m – 7.6 m in height for midstory heterogeneity; we based our standard deviation metric on Young et al. (2013).

Stage	Metrics	Support
1) Landscape	a) Proportion forest land cover within 10 km radius	Reidy et al., 2014; Thompson et al., 2012
	b) Proportion forest land cover within 1 km radius	Bakermans and Rodewald, 2006; Rodewald and Yahner, 2001
2) Edge	a) Distance to forest edge (m)	Kroodsma, 1984; Le et al., 2018
3) Tree attributes	a) Live tree basal area (m^2 ha^{-1})	Ambuel and Temple, 1983; Reidy et al., 2014*
	b) (Live tree basal area)^2	Reidy et al., 2014*
	c) Dead tree basal area (m^2 ha^{-1})	Sierzega, 2016; Stauffer and Best, 1980
	d) Proportion of live basal area consisting of oak (*Quercus spp.*)	Ambuel and Temple, 1983; Sierzega, 2016
	e) Tree species richness	Au et al., 2008; Le et al., 2018
4) Midstory layer	a) Mean foliage density at 2.5 m	Twedt et al., 1999
	b) Mean foliage density at 5 m	Twedt et al., 1999
	c) Midstory heterogeneity (SD of foliage density at 2.5 m and 5 m)	MacArthur and MacArthur, 1961**
5) Shrub and ground layer	a) Shrub density (stems m^{-2})	Le et al., 2018; Reidy et al., 2014
	b) Green ground cover	Le et al., 2018; Twedt et al., 1999
	c) Grassy ground cover	Au et al., 2008
	d) Leaf litter cover	Au et al., 2008; Le et al., 2018

Table 3.2. Descriptive statistics for habitat and birds survey variables collected in and near south-central Iowa forests, 2016-2019. Prop = proportion. Variables in italics were ultimately excluded from analyses.

Variable	Variable Type	Min	Quartile (25%)	Median	Quartile (75%)	Max	Unique values
Julian day	Continuous	136	163	184	206	228	92
Time since sunrise (hrs)	Continuous	-0.7	0.7	1.6	2.6	6.0	333
Observer	*Categorical*	-	-	-	-	-	*5*
Average wind speed (km/hr)	Continuous	0	8	11	15	38	45
Forest landcover within 1 km (prop)	Continuous	0.24	0.54	0.63	0.68	0.76	479
Forest landcover within 10 km (prop)	Continuous	0.19	0.22	0.25	0.31	0.36	493
Nearest forest patch size (ha)	*Continuous*	*1742*	*2721*	*2757*	*4503*	*4503*	*4*
Distance to edge of forest (m)	Continuous	0	22	136	279	759	408
Tree species richness	Continuous	0	2	4	6	11	12
Live tree basal area (m^2/ha)	Continuous	0	7	13	18	38	35
Dead tree basal area (m^2/ha)	Continuous	0	0	1	3	21	15
Oak proportion (of basal area)	Continuous	0	0	0.38	0.69	1	137
Canopy closure	*Continuous*	*0*	*0.7*	*0.9*	*0.95*	*1*	*20*
Midstory density at 2.5 m (prop cover)	Continuous	0	0.21	0.4	0.59	1	428
Midstory density at 5.0 m (prop cover)	Continuous	0	0.22	0.38	0.56	1	433
Midstory density standard deviation	Continuous	0	0.19	0.31	0.39	0.52	166
Shrub density (stems/m^2)	Continuous	0	0.88	1.63	2.62	7.85	21
Grassy ground cover (prop)	Continuous	0	0.05	0.15	0.4	1	21
Green ground cover (prop)	Continuous	0	0.55	0.7	0.85	1	21
Leaf litter ground cover (prop)	Continuous	0	0.05	0.6	0.95	1	21

Table 3.3. Detections of ten breeding bird species of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point.

Common name	**Scientific name**	**No. detections**
Yellow-billed Cuckoo	*Coccyzus americanus*	841
Red-headed Woodpecker	*Melanerpes erythrocephalus*	212
Northern Flicker	*Colaptes auratus*	692
Eastern Wood-Pewee	*Contopus virens*	3317
Acadian Flycatcher	*Empidonax virescens*	522
Wood Thrush	*Hylocichla mustelina*	574
Field Sparrow	*Spizella pusilla*	1003
Ovenbird	*Seiurus aurocapilla*	2061
Common Yellowthroat	*Geothlypis trichas*	1614
Scarlet Tanager	*Piranga olivacea*	710

Table 3.4. Summary of encounter histories for point counts of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point. Each column is the number of visits where at least one individual of a species was detected. Each cell is the number of survey points where the species was detected on the specified number of visits. All values of “0” are left blank. Numbers of visits are binned for readability; all species had at least one point with four repeat detections, and 7+ repeat detections indicates a bird was detected every year at a point and detected twice annually at that point for at least three years.

	No. visits detected					
Species	**0**	**1**	**2-4**	**5**	**6**	**7-8**
Yellow-billed Cuckoo	88	178	221	6		
Red-headed Woodpecker	337	132	24			
Northern Flicker	117	206	169	1		
Eastern Wood-Pewee	41	40	130	65	89	128
Acadian Flycatcher	308	72	90	13	9	1
Wood Thrush	241	125	120	4	3	
Field Sparrow	291	40	87	28	27	20
Ovenbird	128	51	197	57	43	17
Common Yellowthroat	222	56	115	45	27	28
Scarlet Tanager	156	145	185	4	3	

Table 3.5. Mean cumulative detection probabilities for point counts of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point. Cumulative detection was the probability that an individual was detected at least once across all visits. Standard deviation is of the 493 estimates of cumulative detection probability (one per point) and does not account for the uncertainty of point-scale cumulative detection probability estimates.

Species	**Mean**	**Sample SD**
Yellow-billed Cuckoo	0.084	0.008
Red-headed Woodpecker	0.083	0.012
Northern Flicker	0.141	0.016
Eastern Wood-Pewee	0.841	0.024
Acadian Flycatcher	0.698	0.030
Wood Thrush	0.414	0.054
Field Sparrow	0.739	0.023
Ovenbird	0.791	0.048
Common Yellowthroat	0.762	0.030
Scarlet Tanager	0.226	0.014

Table 3.6. Selected detection probability, availability, and detectability estimates for breeding bird species in south-central Iowa, 2016-2019. Estimates are for single visits to a point count station. Estimates were selected by taking the point with the cumulative detection probability across all visits (n = 8) for each species that was closest to the mean cumulative detection probability for that species at all points (n = 493). For the that point, we selected the fifth highest detection probability and its associated availability and detectability estimates. Detection probability for a single visit is calculated as the product of availability and detectability. See Table 3.5 for means of cumulative estimates across all visits.

		Availability		**Detectability**	
Species	**Detection Probability**	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**
Yellow-billed Cuckoo	0.009	0.017	(0.003, 0.099)	0.530	(0.475, 0.583)
Red-headed Woodpecker	0.007	0.011	(0.002, 0.054)	0.639	(0.468, 0.774)
Northern Flicker	0.020	0.026	(0.019, 0.035)	0.767	(0.628, 0.862)
Eastern Wood-Pewee	0.204	0.439	(0.363, 0.518)	0.465	(0.436, 0.495)
Acadian Flycatcher	0.126	0.472	(0.326, 0.622)	0.266	(0.241, 0.294)
Wood Thrush	0.048	0.059	(0.038, 0.09)	0.818	(0.668, 0.906)
Field Sparrow	0.155	0.212	(0.164, 0.269)	0.730	(0.645, 0.8)
Ovenbird	0.137	0.300	(0.237, 0.373)	0.456	(0.427, 0.485)
Common Yellowthroat	0.131	0.357	(0.282, 0.439)	0.367	(0.344, 0.391)
Scarlet Tanager	0.027	0.072	(0.03, 0.161)	0.381	(0.344, 0.42)

Table 3.7. Signs of coefficients for availability and detectability covariates from hierarchical distance sampling models of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point. Wind speed was the only detectability covariate; all others are availability covariate. All year effects are relative to the year 2016. Blank = covariate not in top model, JDAY = Julian date, TSSR = time since sunrise, * = 95% confidence interval overlapped zero; sign of the mean coefficient is reported. Covariates used in these analyses were center-scaled prior to analyses, and quadratic terms, denoted by "(variable)^2" were calculated from center-scaled covariates.

Species	**Year (2017)**	**Year (2018)**	**Year (2019)**	**JDAY**	**(JDAY)^2**	**TSSR**	**(TSSR)^2**	**Wind speed**
Yellow-billed Cuckoo	-	-	+	-		-	-*	-
Red-headed Woodpecker	+	+	-*	-	+		+*	-*
Northern Flicker	+	+	+	+			-*	-
Eastern Wood-Pewee	+	+	+	+	+	-	+*	-
Acadian Flycatcher	-*	+*	+	+*	-	-		
Wood Thrush	+	+*	+*	-	-	-	+	-
Field Sparrow	+*	+	-*		-	-*	+*	-*
Ovenbird	+	+	+	-	-	-	+	-
Common Yellowthroat	+	+	+	-	-	-*		-
Scarlet Tanager	-*	+*	+		-	-		

Table 3.8. Coefficients for landscape and edge covariates in density models of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point. Mean values and 95% confidence intervals are given for each coefficient. All covariates were center-scaled prior to analysis; coefficients are not back transformed. Coefficients in italics have 95% confidence intervals overlapping 0. Northern Flicker was also analyzed but did not have any of the coefficients below in its top model.

	Forest landcover within 10 km		**Forest landcover within 1 km**		**Distance to forest edge**	
Species	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**
Yellow-billed Cuckoo			0.054	(-0.024, 0.132)		
Red-headed Woodpecker	0.170	(0.022, 0.318)				
Eastern Wood-Pewee					0.135	(0.081, 0.188)
Acadian Flycatcher	0.241	(0.119, 0.363)			0.260	(0.145, 0.374)
Wood Thrush	0.115	(0.010, 0.221)	0.190	(0.057, 0.323)	0.182	(0.077, 0.287)
Field Sparrow	-0.176	(-0.273, -0.078)	-0.152	(-0.248, -0.056)	-2.544	(-2.946, -2.142)
Ovenbird			0.127	(0.044, 0.210)	0.195	(0.127, 0.263)
Common Yellowthroat	0.165	(0.091, 0.239)			-0.941	(-1.113, -0.770)
Scarlet Tanager	*0.069*	*(-0.019, 0.158)*	0.188	(0.080, 0.295)	0.132	(0.042, 0.222)

Table 3.9. Coefficients for tree-related covariates in density models of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point. Mean values and 95% confidence intervals are given for each coefficient. All covariates were center-scaled prior to analysis; coefficients are not back transformed. (Live basal area)^2 was calculated as the quadratic of center-scaled live basal area. Coefficients in italics have 95% confidence intervals overlapping 0. Northern Flicker, Acadian Flycatcher, Wood Thrush, and Field Sparrow were also analyzed but did not have any of the coefficients below in their top models.

	Live basal area		**(Live basal area)^2**		**Dead basal area**		**Proportion oak**	
Species	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**
Yellow-billed Cuckoo	*-0.076*	*(-0.157, 0.004)*			-0.087	(-0.166 -0.007)	-0.079	(-0.156 -0.003)
Red-headed Woodpecker	*-0.145*	*(-0.310, 0.021)*	*0.113*	*(-0.068, 0.295)*			-0.199	(-0.368 -0.030)
Eastern Wood-Pewee	*-0.047*	*(-0.112, 0.017)*	0.097	(0.033, 0.161)			0.098	(0.034, 0.162)
Ovenbird			0.108	(0.035, 0.180)	0.084	(0.025, 0.143)		
Common Yellowthroat			*-0.070*	*(-0.177, 0.038)*	*-0.089*	*(-0.194, 0.015)*	*-0.095*	*(-0.199, 0.009)*
Scarlet Tanager			0.137	(0.047, 0.228)			*0.061*	*(-0.027, 0.149)*

Table 3.10. Coefficients for midstory covariates in density models of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point. Mean values and 95% confidence intervals are given for each coefficient. All covariates were center-scaled prior to analysis; coefficients are not back transformed. Yellow-billed Cuckoo, Northern Flicker, Eastern Wood-Pewee, Common Yellowthroat, and Scarlet Tanager were also analyzed but did not have any of the coefficients below in their top models.

	Midstory density 2.5 m		**Midstory density 5 m**	
Species	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**
Red-headed Woodpecker	-0.225	(-0.403 -0.047)		
Acadian Flycatcher	0.196	(0.064, 0.327)		
Wood Thrush			-0.129	(-0.238, -0.020)
Field Sparrow	0.102	(0.001, 0.202)		
Ovenbird			0.069	(0.002, 0.136)

Table 3.11. Coefficients for shrub and ground cover covariates in density models of ten breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) for a total of eight (8) visits per point. Mean values and 95% confidence intervals are given for each coefficient. All covariates were center-scaled prior to analysis; coefficients are not back transformed. Coefficients in italics have 95% confidence intervals overlapping 0. Northern Flicker was also analyzed but did not have any of the coefficients below in its top model.

	Shrub stem density		**Grassy cover**		**Green cover**		**Litter cover**	
Species	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**	**Mean coef.**	**95% CI**
Yellow-billed Cuckoo					0.078	(0.005, 0.151)		
Red-headed Woodpecker	*-0.127*	*(-0.289, 0.034)*			0.148	(0.001, 0.296)		
Eastern Wood-Pewee			*-0.064*	*(-0.133, 0.005)*			0.071	(0.001, 0.142)
Acadian Flycatcher	-0.480	(-0.637 -0.322)	*-0.155*	*(-0.329, 0.019)*			0.400	(0.237, 0.563)
Wood Thrush	*-0.098*	*(-0.212, 0.015)*	-0.252	(-0.396 -0.109)	*-0.098*	*(-0.209, 0.012)*	0.249	(0.127, 0.371)
Field Sparrow			0.183	(0.094, 0.272)			0.166	(0.030, 0.301)
Ovenbird			-0.132	(-0.221 -0.043)			0.206	(0.129, 0.284)
Common Yellowthroat					0.081	(0.023, 0.139)	-0.461	(-0.596 -0.326)
Scarlet Tanager			*-0.098*	*(-0.205, 0.010)*				

Figures

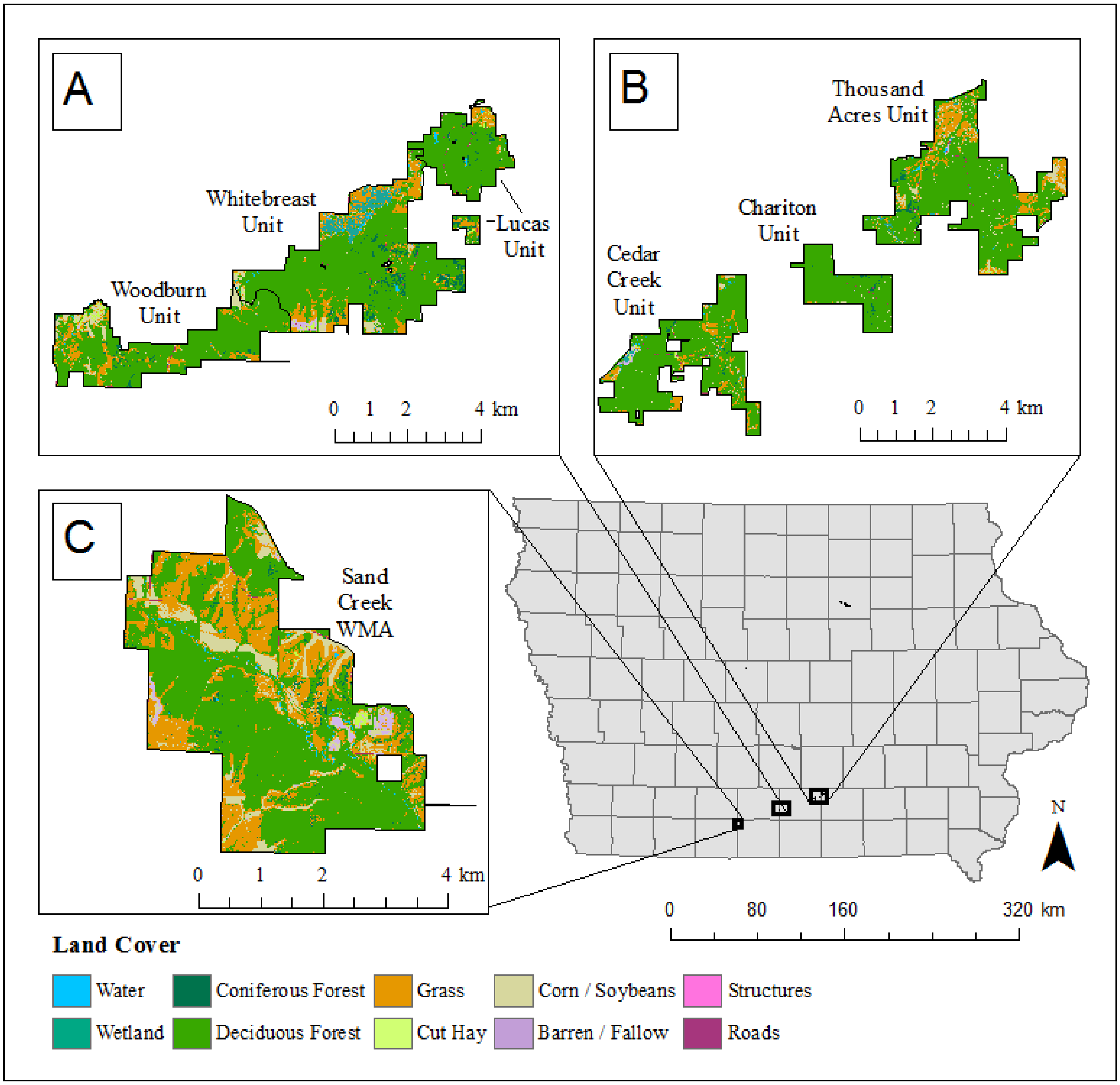

Figure 3.1. Land cover maps of the study areas used for breeding bird point counts in south-central Iowa, 2016-2019. Maps A and B represent the units of Stephen State Forest with the Stephens Forest and Stephens Forest – Thousand Acres Bird Conservation Areas (BCAs), respectively. Map C is of the Sand Creek Wildlife Management Area, located within the Sand Creek Woodland Savanna BCA. Land cover maps are modified from the Iowa Department of Natural Resource's 2009 High Resolution Land Cover of Iowa.

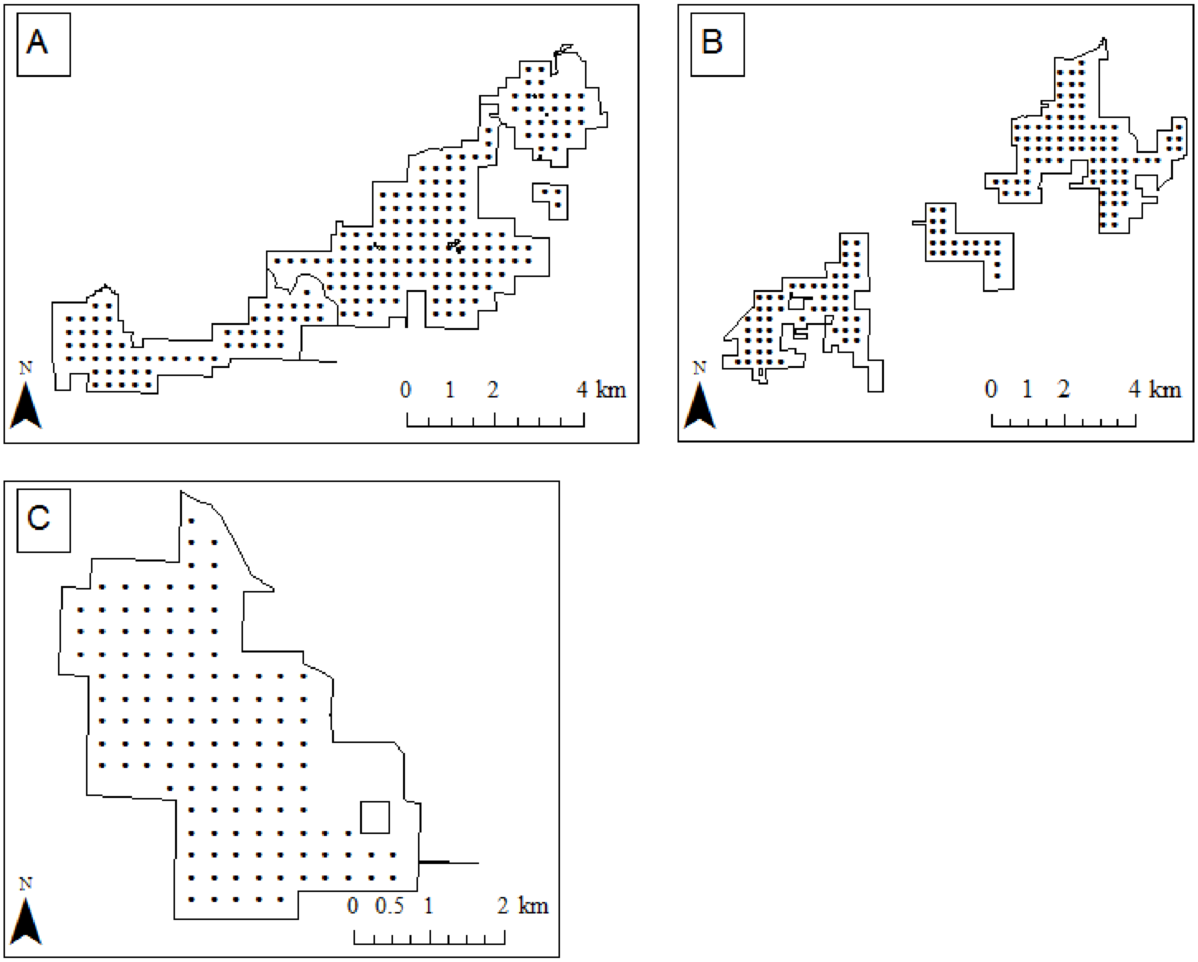

Figure 3.2. Point count locations used for surveys of breeding birds in south-central Iowa, 2016-2019, within the cores of three Iowa Bird Conservation Areas (BCAs): A) Stephens Forest BCA, B) Stephens Forest – Thousand Acres BCA, and C) Sand Creek Woodland Savanna BCA.

CHAPTER 4. BIRD DIVERSITY-HABITAT RELATIONSHIPS IN SOUTH-CENTRAL IOWA

A manuscript to be submitted to *The Wilson Journal of Ornithology*

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Abstract

With recent declines in avian populations, it is important to identify areas of high avian diversity and to determine habitat characteristics associated with that diversity. Our study focused on breeding bird communities three Bird Conservation Areas in south-central Iowa; these areas are primarily forested but also contain successional and agricultural habitats and are home to several Iowa Species of Greatest Conservation Need (SGCN). Our goals for the overall breeding bird community and the SGCN community specifically were to: 1) compare diversity metrics which do and do not consider imperfect detection probability, 2) determine if antilog Shannon-Weaver index and species richness produced similar estimates within our study system, 3) determine relationships between species diversity and habitat metrics, and 4) compare estimated diversity-habitat relationships between diversity metrics. We visited a grid of 493 points twice each breeding season from 2016 to 2019, using point counts with hierarchical distance sampling (HDS) to estimate individual species densities at a point scale. For every year at each point we calculated 1) species richness, and 2) antilog Shannon diversity using both raw data and HDS estimates, then averaged across years. We then related diversity to habitat using linear models with up to thirteen habitat variables, ranging in scale from landscape to site-level. We detected a total of 77 breeding birds meeting several criteria needed for analysis, 24 of which

were listed as SGCN. Point-scale species richness estimates using HDS data ranged from 16.7 to 25.7 and were, on average, 7.7 species higher than species richness values calculated using raw data. We found positive diversity-habitat relationships for landscape scale forest cover at a 10 km scale and tree species richness, which suggested that sites with greater forest cover and greater tree species richness in our study area benefitted bird diversity, though other unaccounted-for landscape-scale factors may be the ultimate cause of relationships. We also found a negative relationship between bird diversity and leaf litter cover. Our findings affirmed that these Bird Conservation Areas are important avian hotspots in Iowa, and provided evidence that landscape scale forest cover and unfragmented, large forest patches should be maintained or potentially increased where feasible to benefit the southern Iowa bird community.

Introduction

At both continental and regional scales in North America, vegetation and primary productivity explain the majority of patterns of avian diversity; more productive environments tend to have higher avian species richness (Hawkins and Porter 2003; Rowhani et al. 2008). Deciduous forests are one of the most productive ecosystems in temperate North America (Turner et al. 2003), and in the Midwestern United States alone, more than 120 bird species breed in forests and woodlands (Niemi et al. 2016). Despite the plethora of bird species in the eastern deciduous forest biome, which spans the Atlantic Coast of the United States and extends as far northwest as Minnesota and as far southwest as northeastern Texas (Dyer 2006), over 60% of which breed primarily in this biome are in decline (Rosenberg et al. 2019). This decline of avian biodiversity makes assessments of bird diversity and diversity-habitat relationships in this region a high priority.

On local landscape scale, disturbance by agriculture and suburban development within 1-2 km negatively impacts bird diversity in eastern deciduous and mixed forests (Askins and Philbrick 1987; Rodewald and Yahner 2001), although landscape-scale reforestation efforts in the wake of disturbance can allow bird communities to recover (Askins and Philbrick 1987). Habitat fragmentation and increasing edge habitat can also negatively impact bird diversity, as some species require a minimum area, and interior forest species often avoid forest edges (Kroodsma 1982; Ambuel and Temple 1983). At a stand scale, vegetation structure is the primary driver of bird diversity in eastern deciduous forest, with more structurally complex stands usually housing higher species diversity (MacArthur and MacArthur 1961). Conversion of structurally diverse mixed species forest to even-age, single species silvicultural plantations can negatively impact bird diversity (Twedt et al. 1999), but thinning forests to increase regeneration of oak trees can positively impact bird diversity by leaving ample canopy habitat while increasing habitat structure below the canopy (Newell and Rodewald 2012).

In response to the decline of bird diversity and bird habitat in Iowa and the Midwest as a whole, the Iowa Department of Natural Resources (DNR), in cooperation with the Partners in Flight Midwest Working Group, established the Bird Conservation Areas (BCA) program with goals including reducing habitat fragmentation and improving private land management (Iowa DNR 2010; Ehresman 2015). In 2015, BCAs as a whole harbored 83 out of the 85 bird species designated by the Iowa DNR as Species of Greatest Conservation Need (SGCN; Ehresman 2015). Our study focused on three primarily forested BCAs in south-central Iowa, with the objective of quantifying bird diversity and relationships between bird diversity and habitat. Because perfect detection of all species and individuals at a site is unrealistic and failing to account for undetected individuals and species can bias estimates of bird diversity (Norvell et al.

2003; Tyre et al. 2003; Yamaura et al. 2011), we employed methods which account for imperfect detection.

Our goals for the overall breeding bird community and the SGCN community specifically were to: 1) compare diversity metrics which do and do not consider imperfect detection probability, 2) determine if antilog Shannon-Weaver index and species richness produce similar estimates within our study system, 3) determine relationships between species diversity and habitat metrics, and 4) compare estimated diversity-habitat relationships between diversity metrics. We predicted that diversity metrics accounting for imperfect detection probability would produce significantly greater estimates of diversity and that the antilog Shannon-Weaver index and species richness would perform similarly. We also predicted that at least some habitat metrics would have significant relationships with diversity and that diversity-habitat relationships would be similar within the two species groupings (overall and SGCN) regardless of diversity metric. To test these predictions, we used hierarchical distance sampling (HDS) models to account for imperfect detection, used HDS model-derived estimates and raw species counts to calculate diversity metrics at a point scale, and then related those metrics to habitat variables at each survey point.

Methods

Study Area

Our study area comprised six units of Stephens State Forest and Sand Creek Wildlife Management Area, spanning Clarke, Decatur, Lucas, Monroe, and Ringgold counties in south-central Iowa, USA. These properties are the “cores” of three primarily forested Bird Conservation Areas (BCA), areas designated as containing habitat important to Iowa bird populations (Ehresman 2015). The Woodburn, Whitebreast, and Lucas Units of Stephens State

Forest are almost entirely contiguous and are located within the Stephens Forest BCA; these units combined are 2,767 ha and will hereafter be collectively called “Stephens” (Figure 4.1A). The Cedar Creek, Chariton, and Thousand Acres Units of Stephens State Forest are separated from each other by a distance of 1-4 km and are located within Stephens Forest -Thousand Acres BCA; these units combined are 2,361 ha and will hereafter be collectively called “Thousand Acres” (Figure 4.1B). Sand Creek Wildlife Management Area (hereafter “Sand Creek”), is 1,457 ha and is located within the Sand Creek Woodland Savanna BCA (Figure 4.1C).

These areas are comprised primarily of deciduous forest and woodlands, especially upland oak (*Quercus* spp.)-hickory (*Carya* spp.) forest, but also bottomland cottonwood (*Populus deltoides*)-silver maple (*Acer saccharinum*) woodlands. Small portions of these forests are actively managed; activities include girdling to create standing dead wood and selective harvesting of trees to create a more open canopy. The topography of these forests is characterized primarily by ridges and ravines; many ravines have seasonal streams. Some larger perennial streams and rivers are also present; bottomland forests tend to occur along these waterways. Other habitats present in smaller patches are pine plantations, wetlands, grassland, pasture, and crop fields; grasslands were more prevalent at Sand Creek compared to the other two study areas, and wetlands were largely confined to a small corner of Stephens (Figure 4.1). Dominant tree species were white, northern red, and bur oaks (*Quercus alba*, *Q. rubra*, and *Q. velutina*), shagbark hickory (*Carya ovata*), and American elm (*Ulmus americana*). Three species of ash (*Fraxinus* spp.) were also present, but most individuals were standing deadwood killed by emerald ash borer (*Agrilus planipennis*). Common woody plants in the understory and in clearings included ironwood (*Ostrya virginiana*), coralberry (*Symphoricarpos orbiculatus*), multiflora rose (*Rosa multiflora*), black raspberry (*Rubus occidentalis*), blackberry (*Rubus allegheniensis*), and eastern redcedar (*Juniperus virginiana*).

Bird Surveys

We conducted point counts from mid-to-late May through early-to-mid August 2016-2019. We randomly placed a grid of points 300 m apart at each site, and we removed points within 150 m of a study area boundary, resulting in 503 total points (Figure 4.2). We conducted 10-min, 100-m radius multispecies bird point counts. Data were collected on all bird detections, but we excluded visual-only detections and detections of known females and juveniles. For consistency with other studies, we would have ideally used only singing males for most species but due to slight changes in data collection protocol between years, we were unable to reliably determine singing males versus other types of detections. Our survey condition parameters were to conduct surveys between 0.7 hours before and 4.5 hours after sunrise with wind speeds <20 km/h and no precipitation. Both wind speed and time since sunrise were considered as covariates in models to account for deviations from our protocol (see Hierarchical Models). Out of 503 original points, 493 were surveyed twice each year for an early and late season visit; the cutoff between the seasons was approximately 1 July, and 10 of the original points were missed at least one of four years due logistical issues such as flooding. There were five total observers and two observers per season; when possible (85% of cases), each observer visited each point once during a season to minimize observer bias. Two relatively inexperienced observers surveyed in 2016 only, one experienced observer surveyed 2017-2019, one moderately experienced observer surveyed in 2017 and 2018, and a separate experienced observer surveyed in 2019 only.

Selection of Study Species and Species Groups

We included breeding birds whose primary habitat was forest, forest edge, shrubland, or grassland in our density and diversity calculations. We excluded species if they fit into any of the following categories: 1) passage migrant species, 2) species confined to wetlands or other habitats not listed above, due to the small amount of suitable habitat and our primary interest in forest and forest edge species, 3) primarily aerial species that were usually detected visually as flyovers, such as Turkey Vulture (*Cathartes aura*), Chimney Swift (*Chaetura pelagica*) and swallows (family: Hirundinidae), due to difficulty in ascertaining territoriality and appropriate distance bins, 4) primarily nocturnal species, due to our diurnally-focused protocol, 5) species with <5 detections within 100 m of our point count stations, due to difficulty in modeling densities, and 6) incidental species detected within our study area but not within 100 m of a point as a non-flyover during a survey.

The general cutoff for number of detections in distance sampling analyses is ~60 (Buckland et al. 2001), but species with similar song volume, quality, and frequency can be modeled with shared detection functions to improve sample size (Alldredge, Pollock, et al. 2007). We grouped species with <60 detection into one of ten different groups containing species with similar song quality and habitat preferences. We grouped Northern Bobwhite (*Colinus virginianus*) with Ring-necked Pheasant (*Phasianus colchicus*) on account of both being gallinaceous birds of open habitats with loud vocalizations; this grouping will be called the "gallinaceous group" (Brennan et al. 2020; Giudice and Ratti 2020). Yellow-billed Cuckoo (*Coccyzus americanus*) and Black-billed Cuckoo (*Coccyzus erythropthalmus*), both SGCN, were grouped due to similar vocalizations and a shared preference for shrubby habitat away from deep forest; this group will be called the "cuckoo group" (Hughes 2020a; Hughes 2020b). We grouped

Red-shouldered Hawk (*Buteo lineatus*), Broad-winged Hawk (*Buteo platypterus*), Cooper's Hawk (*Accipiter cooperii*) and Red-tailed Hawk (*Buteo jamaicensis*), this group will collectively be called the "hawk group". Although vocalizations and habitat preferences differ between these hawk species, all are members of the family Accipitridae and have at least moderately loud vocalizations (Dykstra et al. 2020; Goodrich et al. 2020; Preston and Beane 2020; Rosenfield et al. 2020). Eastern Kingbird (*Tyrannus tyrannus*) was grouped with Eastern Bluebird (*Sialia sialis*); both species prefer savanna-type habitat, engage in aggressive and vocal territory defense, and have a combination of soft and loud vocalizations; this group will be referred to as "the savanna group" (Gowaty and Plissner 2020; Murphy and Pyle 2020). We grouped Willow Flycatcher (*Empidonax traillii*), Warbling Vireo (*Vireo gilvus*), and Orchard Oriole (*Icterus spurius*) due to a shared preference for riparian habitat and moderately loud songs; this group will be referred to as "the riparian group" (Gardali and Ballard 2020; Scharf and Kren 2020; Sedgwick 2020). We grouped Bell's Vireo (*Vireo bellii*), Brown Thrasher (*Toxostoma rufum*), White-eyed Vireo (*Vireo griseus*), and Yellow-breasted Chat (*Icteria virens*). Each of these four species is relatively secretive, prefers scrubland and thicket habitats, and has a moderately loud song; this group will be referred to the as "the scrubland grouping" (Cavitt and Haas 2020; Eckerle and Thompson 2020; Hopp et al. 2020; Kus et al. 2020). We grouped Yellow-throated Vireo (*Vireo flavifrons*) with Hooded Warbler (*Setophaga citrina*) into "forest group 1;" Hooded Warbler was grouped with a similar vireo species, Blue-headed Vireo (*Vireo solitarius*), in another distance sampling analysis, and both Yellow-throated Vireo and Hooded Warbler share a preference for forest gaps and edges (Alldredge, Simons, et al. 2007; Chiver et al. 2020; Rodewald and James 2020). We grouped Sedge Wren (*Cistothorus platensis*), Grasshopper Sparrow (*Ammodramus savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*), three

SGCN, into a “quiet grassland grouping.” All are all secretive grassland species with quiet songs; previous research suggests that Grasshopper Sparrows are somewhat harder to detect than the other two species, but Henslow’s Sparrow and Sedge Wren generally have similar detection probabilities (Rigby and Johnson 2019). Given our low number of Grasshopper Sparrow detections we believed this grouping was our best option to estimate density that species’ density. We grouped Veery (*Catharus fuscescens*) and Cerulean Warbler (*Setophaga cerulea*), two SGCN, along with the non-SGCN, Summer Tanager (*Piranga rubra*) and (*Piranga olivacea*) as “forest group 2.” There is previous precedent for grouping Scarlet Tanager and Veery in distance sampling analyses (Alldredge, Pollock, et al. 2007), and all of these species are area-sensitive forest birds that have moderately loud songs (Buehler et al. 2020; Heckscher et al. 2020; Mowbray 2020; Robinson 2020). We grouped European Starling (*Sturnus vulgaris*), Common Grackle (*Quiscalus quiscula*), and Brown-headed Cowbird (*Molothrus ater*) as the “disturbance group” due to a shared preference for disturbed, open habitats, a similar metallic vocal quality, and frequent loud vocalizations (Cabe 2020; Lowther 2020; Peer and Bollinger 2020). We grouped Song Sparrow (*Melospiza melodia*) and Lark Sparrow (*Chondestes grammacus*) as the “sparrow group” due to a shared preference for open habitat, taxonomic similarity, and loud, similar-sounding songs (Arcese et al. 2020; Martin and Parrish 2020). We grouped Eastern Meadowlark *(Sturnella magna)* and Bobolink *(Dolichonyx oryzivorus)*, two SGCN, into a “loud grassland group” due to being loudly singing, easy-to-detect grassland species (Rigby and Johnson 2019).

Bird Survey Covariates

We obtained precipitation data and average wind speed data from climate stations at municipal airports in Chariton, Iowa, USA (Station ID: WBAN:04913) and Osceola, Iowa, USA

(Station ID: WBAN:54942), as these variables may affect an observer's ability to hear a bird vocalization. The Chariton station was ~21 km from the center of Thousand Acres, ~14 km from the center of Stephens, and ~57 km from the center of Sand Creek. The Osceola station was ~48 km from the center of Thousand Acres, ~16 km from the center of Stephens, and ~34 km from the center of Sand Creek. Despite the somewhat long distances, these were the closest weather stations to our study areas, and we lacked consistent weather data from the survey points. At both stations, weather data were recorded at 15 minutes, 35 minutes, and 55 minutes after each hour. Precipitation was defined as at least one station having a present weather code indicating rain, fog, etc., and thus we likely overestimated the proportion of surveys with precipitation. Due to a low proportion of surveys with precipitation and lack of survey site-specific data, we did not ultimately include precipitation as a model covariate.

When both weather stations were functional, we averaged wind speeds for Chariton and Osceola for all sites. Occasionally, one of the two stations was offline; in these cases, we only used data from the functional station. We excluded one aberrant wind speed reading at the Chariton weather station (>1000 km/h) and used only the Osceola data. There were seven (7) instances out of 629 where neither station recorded data; in these cases; we found a time within 40 minutes of the missing value and used the averaged wind speed from that time. For each bird survey, we used the wind speed value that was closest in time to the start of the bird survey; e.g., if a bird survey started at 8:01 a.m., we would use the wind speed data from 7:55 a.m.

We obtained sunrise times for the Iowa municipalities of Grand River, Woodburn, Lucas, and Russell from the Astronomical Observations Department of the United States Naval Observatory (3450 Massachusetts Ave NW, Washington, DC 20392). We used Grand River sunrise times for Sand Creek, Woodburn for the Woodburn and Whitebreast Units in Stephens, Lucas for the Lucas Unit in Stephens, and Russell for all units of Thousand Acres.

Landscape and Forest Patch Metrics

To assess forest cover at a landscape scale, obtained landscape cover data for 2016-2019 at 30-m spatial resolution from the Cropland Data Layer (CDL; USDA NASS, 2019, 2018, 2017, 2016). Using Esri® ArcGIS Pro®, we clipped the CDL rasters for each year to 1 km and 10 km buffers around each bird survey point, saving each clipped raster as a separate image file. We imported image files for each combination of point, year, and buffer size into R using package ‘raster’ (R Core Team, 2019). We defined mature forest cover as CDL cells with values 141, 142, 143, and 190 (deciduous forest, mixed forest, coniferous forest, and woody wetland, respectively; USDA NASS, 2019). We note that “forest” in the CDL dataset can include as little as 25% canopy cover within a 300 m x 300 m cell (USDA NASS, 2019). Woody wetland was included as “forest” because aerial imagery and ground-truthing both suggested that the majority of “woody wetlands” in our study area were bottomland cottonwood-silver maple woodlands. To assess the relative abundance of mature forest within each buffer as a percentage (“percent forest cover”), we imported clipped image files into R using package ‘raster’, (Hijmans, 2019), used the ‘getValues’ function to find the number of raster cells matching the criteria for forest, and then divided the number of forest cells by the total number of cells in the clipped image file. We averaged percent forest cover at each scale (1 and 10 km) across all four years for each point to get single covariate values.

To calculate distance to edge and forest patch size, we digitized forest polygons in ArcGIS Pro® using 2016-2018 Iowa Spring Color Infrared Orthophotos, which were taken prior to leaf-out (Iowa State University, 2018). We identified deciduous forest as large, dark reddish-brown patches, and coniferous trees and shrubs as bright red, irregularly shaped patches, categorizations corroborated by our vegetation surveys. Forest only split by streams and narrow gravel roads was considered continuous and was digitized as a single patch, as narrow non-forest corridors do not seem to affect deciduous forest bird habitat use (Rich et al., 1994). Internal fields and lakes were counted as edges and did not contribute to forest area. We did not categorize cedar groves with open canopy (i.e., visible spacing between trees) as forest. We calculated forest patch size as the area of each digitized forest polygon. We selected “forest points” as bird survey points within forest polygons using the Intersect tool in ArcGIS Pro®, setting distance to edge for all points outside of forest polygons to 0 m. To measure distance to forest edge for forest points, we converted forest polygons to polylines to create forest boundaries and measured distance from each forest point to the nearest forest boundary using the "Near" tool in ArcGIS Pro®; we used geodesic distance and a 1-km search radius.

Vegetation Surveys

Our vegetation survey protocols were derived from three standardized vegetation survey protocols for forest birds (Hamel, 1996; James and Shugart, 1970; Martin et al., 1997). Ultimately, we sought to avoid seasonal vegetation changes by using a short survey period while also meaningfully describing forest structure as it relates to avian habitat. We surveyed vegetation at each bird survey point between 16 July and 28 August 2019, with the assumption of minimal vegetation structure change from 2016 to 2019. Each vegetation metric we collected was justified by previous forest bird studies, primarily in the Midwestern United States (Table 4.1).

We used five metrics to assess tree community and structure: live tree basal area, dead tree basal area, relative amount live tree basal area comprised of oaks (genus *Quercus*) as a proportion (“proportion oak”), tree species richness, and canopy closure. Trees were defined as woody stems at 1.4 m with diameter >8 cm; stems meeting these criteria were counted separately even if they shared a base (James and Shugart, 1970; Martin et al., 1997). All tree metrics except canopy closure were calculated from a variable radius forestry prism sample centered on a bird survey point; we counted every other “borderline” tree in the prism sample (Figure A27; Hovind and Rieck 1961). Prism-sampled basal area can be collected in a more time-efficient manner than fixed radius plots while covering a larger area. To maximize the number of trees in our sample and increase our average survey radius, we used a 1-m basal area factor cruising prism (Cruise-Master Prisms, Sublimity, Oregon). We identified each tree in our prism sample to species and counted all dead trees in a separate category. We separated live and dead trees because dead trees provide habitat for woodpeckers and secondary cavity nesters, while the foliage of live trees provides foraging opportunities for foliage gleaners and cover for tree-nesting birds. Proportion oak was calculated as the basal area of living oaks divided by total live BA. When basal area was equal to zero, we set proportion oak to 0. We calculated tree species richness as the number of tree species in a prism sample. Canopy closure was measured using a periscope-style densitometer (Geographic Resource Solutions, Arcata, California). There were 20 presence/absence observations of canopy closure recorded along two 20-m transects centered on the survey point and oriented in the cardinal directions. We made ten observations along each transect spaced every 2 m, excluding the survey point itself. Canopy was marked was “present” if, when the densitometer was oriented straight upward, there was vegetation in the densitometer’s crosshairs, and the proportion of canopy closed was calculated by multiplying the number of “present” observations by 0.05 (Hamel 1996). Canopy closure was excluded from analyses due to multicollinearity (see Covariate Assessment below).

We used three metrics to quantify horizontal midstory structure: foliage density at 2.5 m in height, foliage density at 5 m, and standard deviation of foliage density. Studies quantifying deciduous forest midstory in the Midwestern United States are lacking (though see Yahner, 1982 for work on shelterbelt midstory in Minnesota), but studies in the Southern United States have found relationships between midstory foliage density and breeding forest bird species (Burger et al. 1998; Twedt et al. 1999). We modified the midstory protocol from Hamel (1996). Instead of using a checker pattern, our board was a 50 cm x 50 cm piece of plexiglass painted with OSHA Safety Orange spray paint over a coat of white primer attached to a telescoping aluminum pole. With the observer at the survey point, we situated the board 10 m away in three different randomly-selected cardinal directions, with the board facing the observer at heights of 2.5 m and 5 m in each selected direction (Figure A27. We elected not to take photographs at 0 m in height because we felt our ground cover and shrub metrics (below) adequately captured that vegetation layer. To keep our vegetation survey period as short as possible, we excluded one of the four cardinal direction via a random number generator, although we deviated on rare occasions from this selection if there was an obstruction or obstacle in the selected direction, such as a steep ravine or recently downed tree that would have been upright during the breeding season. When a board was entirely exposed or entirely obstructed from the observer vantage point, we recorded proportion covered as 0 or 1, respectively. For intermediate levels of obstruction, we photographed the board at each position from observer eye level (~1.6 m) using a Fujifilm FinePix XP120 Digital Camera (Fujifilm, Tokyo, Japan; Figure A28). For consistency, we set camera ISO to 800 and white balance to fluorescent light setting #3. When necessary, we altered the exposure bias of the camera manually to avoid extremely dark photos, washed out (i.e., white) board pixels, and blurry photos. At two (2) survey points we were only able to take photographs in two directions. For each board, we estimated the proportion covered by vegetation using a novel image analysis technique (see Midstory Image Analysis below). We calculated mean foliage density at both 2.5 m and 5 m by averaging percent cover for all boards at a point at the specified height. Variability in midstory foliage density is associated with differences in bird communities in some North American forests (MacArthur and MacArthur 1961; Young et al. 2013); we assessed midstory variability as the standard deviation of proportion covered of all boards at a point ("midstory SD").

We assessed four different metrics for the shrub and ground layer of the forest: shrub stem density, and percentage of ground covered by "green" vegetation, "grassy" vegetation, and leaf litter cover. We counted shrub stems covered or intercepted by an observer's outstretched arms along two perpendicular 1.8 m wide x 22.6 m long transects running north-south and east-west; both centered on the survey point (James and Shugart 1970). Shrubs were defined as woody stems under 8 cm in diameter and >0.5 m in height. We did not count shrubs and saplings separately, but we did count stems that split at a height of 10 cm or lower separately (Martin et al. 1997). Density was calculated as number of stems divided by 78 m^2, the approximate transect area. All ground cover metrics were measured using a periscope-style densitometer. There were 20 presence/absence observations of three ground cover types recorded along two 20-m transects centered on the survey point and oriented in the cardinal directions. We made ten observations along each transect spaced every 2 m, excluding the survey point itself. A ground cover type was marked was "present" if, when the densitometer was oriented straight downward, that ground cover type was in the densitometer's crosshairs, and the proportion of ground covered was calculated by multiplying the number of "present" observations by 0.05 (Hamel et al. 1996). Multiple ground cover types could be contained in a sample due to vertical stratification, e.g., herbaceous plants growing over leaf litter. We defined green cover as the proportion of ground covered by herbaceous plant foliage or foliage from woody plants that were too small to be considered shrubs, e.g., seedling trees. We defined grassy cover as the proportion of ground covered by graminoids, including grasses (Family: Poaceae) and sedges (Family: Cyperaceae). We defined litter cover as the proportion of ground covered by leaf litter, brown coniferous needles, or dead woody vegetative matter.

Midstory Image Analysis

Our goal in analyzing midstory photos was to calculate the proportion of a 50 cm x 50 cm orange board covered by vegetation. The relative size of the orange board in the midstory photos varied due to factors such as tilt of the board, the slope of the ground, and error in the measurement between the board and the photographer, meaning we could not simply count orange pixels and divide by a constant number for the majority of the photos. When the location of the edges of a partially obscured orange board could be determined or estimated within a photograph (n = 1798), we traced a quadrilateral shape bounded by the edges of orange board using the Polygon Lasso in Adobe® Photoshop® CS6. We filled the background with blue (red = 0, green = 0, blue = 255); the resulting image was saved as a JPEG file (Figure A28). We counted the blue pixels using the ‘rectangularRange’ function in R package ‘countcolors,’ and subtracted that value from the total number of pixels to get the board size in that image (R Core Team, 2019; Weller, 2019). R generally uses values between 0 and 1 as opposed to standard 0 to 255 for RGB (red-green-blue) values, so we used an upper vector of (red = 0.092, green = 0.092, blue = 1) and a lower vector of (red = 0, green = 0, blue = 0.91); there is a range of values due to JPEG image compression. This range did not overlap any pixels in our photographs. When the board edges could not be determined (n = 211), we followed a similar protocol, except that photos were cropped to an arbitrary shape containing all exposed areas of the orange board as opposed to a quadrilateral, and for this small proportion of photos we assumed the total board size was equal to the median board size at a board height of either 2.5 m or 5 m in height (805,370 px or 741,480 px, respectively).

For our first attempt at quantifying the number of orange board pixels in each photo, we used the following broad definition of an “orange” pixel to account for a variety of lighting conditions: 1) hue value in the ranges of 0°-59° (red to warm yellow) or 300°-359° (magenta to red); 2) saturation of 14%-100%; and 3) luminance of 8% - 75%. We used package ‘imager’ to load JPEG images into R as 4-dimensional ‘cimg’ objects and convert them from RGB to HSL (hue-saturation-luminance; Barthelme, 2020). We reduced the 4D HSL cimg objects to three dimensional arrays by taking only the first “slice” of dimension 3 of the cimg object, converted all hue values >299° to 0, and divided all hue values by 360 to get a scale from 0-1. We then used the ‘rectangularRange’ function in R package ‘countcolors’ using an upper vector of (0.166, 1.00, 0.75) and a lower vector of (0.00, 0.14, 0.08) to do two things: 1) count the number of pixels meeting the criteria we set for orange, and 2) create a 3D array replacing the putative orange pixels with hue = 267°, saturation = 100%, and luminance = 62% (purple). The 3D arrays with replaced orange pixels were converted to cimg objects and then from HSL to RGB to create an initial set of indicator images (Figure A28). Indicator images were compared to the original images; orange pixel counts were deemed satisfactory if the corresponding indicator image had 1) the entire exposed board covered by purple, and 2) no leaves, clusters of twigs, or branches mostly covered by purple. Small, isolated twigs and small portions of branches covered by purple were deemed acceptable; 1812 out of 2009 initial indicator images met these criteria.

For the remaining 197 images, we first tried an upper HSL vector (0.166, 1.00, 0.8) and a lower HSL vector (0.00, 0.25, 0.20), again setting all hue values >299° to zero and dividing hues by 360 prior to putting values in a vector. This set of values excludes more brown and dark plant material by upping lower limits for saturation and luminance at the cost of missing shaded parts of the orange board; it also includes some brighter board patches by increasing upper luminance. This second fixed set of criteria produced satisfactory indicator images for 114 out of 197 remaining images. For the remaining 83 images, we manually set the upper and lower vector values for each individual image to include the orange board and exclude plant material. Hue generally stayed in the original range, but we occasionally included more bluish-gray values for very backlit and washed out photographs (250-299°). Both saturation and luminance limits varied anywhere from 0 to 1 based on the lighting of the photograph. After obtaining orange board pixel counts, we divided the orange pixel counts by the board size (calculated or median per above) to get proportion of the board covered; we used these proportions for the midstory calculations detailed in Section 2.5.

Covariate Assessment

We removed three habitat covariates from consideration in our models. We excluded forest patch size because there were only four, largely unbroken forest patches in our study area, each >1500 ha in size, exceeding the critical patch size for area-sensitive Midwestern forest bird species by multiple orders of magnitude (Ambuel and Temple 1983). After excluding forest patch size, we used the 'vif' function in R package 'car' (Fox and Weisberg 2019) to assess multicollinearity for all habitat variables with generalized variance inflation factor (GVIF), using a cutoff off of < 3 (Zuur et al. 2010). Initially, five (5) variables exceeded the cutoff (Table A2). We removed Bird Conservation Area as a covariate because it had the highest GVIF of any landscape covariate, and we removed canopy closure because it had the highest GVIF of any vegetation survey covariate; removing these covariates reduced variance inflation factor (VIF) for all other covariates to <3 (Table A2). GVIF was not necessary in our second round of multicollinearity assessment due to lack of categorical variables, hence the shift to VIF (Fox and Monette 1992).

Hierarchical Models

We used hierarchical distance sampling (HDS) models using the 'distsamp' and 'gdistsamp' functions in R package 'unmarked' to estimate bird densities; these functions produced identical results within our analysis framework (Chandler et al. 2011; Fiske and Chandler 2011; R Core Team 2019). HDS models in 'unmarked' use a site-specific likelihood for data collected at each site. For this analysis, we defined "site" as the 100-m radius plot around a point on a single visit, meaning each point count station served as the location of eight separate "sites" from 2016 to 2019. We chose this definition so we could estimate separate densities for each year, and because preliminary analyses using both visits to a point within a year as a single site resulted in unreasonably small and imprecise detection probabilities.

In hierarchical distance sampling in 'unmarked,' site-level abundance is treated as a random effect, and analysis is based on the integrated likelihood or on a function of the parameters of the detection function, detectability covariates, abundance, and abundance covariates, with the number of model components varying based on the inclusion or exclusion of covariates at each stage of the hierarchy (Royle et al. 2004; Royle 2004; Chandler et al. 2011). Distance sampling assumes that (1) detection is perfect at distance 0 from the observer, (2) individuals are detected at their initial location, and (3) individuals are counted in the correct distance bins (Buckland et al. 2001).

We used a half-normal detection function for all hierarchical distance sampling models and a Poisson distribution for abundance (the default in 'unmarked'). The distance bins matched those described in "Bird Surveys" for most species; the two exceptions were the hawk group and American Crow (*Corvus brachyrhynchos*), which used distance bins of 0-75 m and 75-100 m due to relatively few detections close to the sampling point. Possible detection covariates for models included time since sunrise (TSSR), the quadratic of TSSR, Julian date (JDAY), and the quadratic of JDAY, observer, and wind speed; each of these covariates has previously been demonstrated to affect detection probability (Alldredge, Simons, et al. 2007; Sólymos et al. 2013; Rigby and Johnson 2019). The linear forms of these covariates were center-scaled prior to analyses, and quadratic terms were calculated from center-scaled covariates to create a distinct peak within the range of observed values, and then were re-center-scaled. Possible abundance covariates depended on the species being modeled. For single species, we only considered binary forest versus non-forest. For all multispecies groups, we also considered species as a fixed effect on abundance. For the hawk group only, we also considered a species X forest interaction in combination with both species and forest as covariates due to the differing habitat preferences of the species in that group. Per guidelines for abundance models accounting for imperfect detection probability, we attempted to consider models with all combinations of both detectability and abundance covariates, and we selected the top model using AIC (Doherty et al. 2012). This modeling framework resulted in 128 possible models for single species, 256 possible models for most multispecies groups, and 320 possible models for the hawk group. However, due to some species with small sample size, not all combinations of covariates produced converging models; models which failed to converge were discarded from consideration. Due to the need for a single model per species or multispecies group to estimate year-specific and area-specific densities, we did not model average (Cade 2015).

To estimate detection probability, we first estimated the mean and 95% confidence intervals for σ of half normal detection functions for each survey and species using survey covariates for each survey and the 'predict' function methods in 'unmarked.' To convert σ to a detection probability, we integrated from 0 – 100 m using the circular half normal function 'grhn' in 'unmarked' (Fiske and Chandler 2011). For each species or multispecies grouping, we report an arithmetic mean of all survey-scale mean detection probabilities across all surveys.

We estimated abundances for individual species at each combination of point and year ("point-year") using visit-specific probability distributions calculated by the 'ranef' function methods in 'unmarked.' This function uses empirical Bayes methods to estimate site-scale densities (Fiske and Chandler 2011). When calculating a visit-specific density, 'unmarked' adds the observed count of individuals to a distribution of possible unobserved counts, ~Poisson in this case, calculated from detection and abundance coefficients. Because we visited each point twice within a year, each point-year had two observed counts and two distributions of unobserved counts. We subtracted the observed counts from the mean of each 'ranef' distribution to obtain the mean (λ) of the unobserved count Poisson distribution. For each point-year, we selected the higher observed count because we assumed a closed population within each year. We selected the unobserved count distribution with the lower λ because abundance covariates were constant between visits, so a lower λ estimate corresponded to the visit with a higher detection probability. To calculate the abundance of a species at a given point-year, we added the selected λ estimate to the observed count.

To calculate an occupancy probability at each point-year, we first considered if the bird species was observed at that point year at either visit. If it was observed, we set the occupancy probability to “1.” If it was not observed, we used the ppois() function in R to calculate the probability the site had 0 individuals given the estimated λ for that point-year, i.e., the probability that the site was unoccupied. We used the compliment of this probability as the occupancy probability.

To calculate an area-wide abundance, we summed the selected λ values and selected observed counts across all point-years. To convert abundance to birds/ha, we divided abundance by the number of point-years (n = 1972) and the area of a point count circle (~3.14 ha).

Diversity Calculations

For all diversity metrics, we started by calculating a diversity metric for each point-year, then were averaged across years to get a single point-scale estimate. “Raw” signifies a metric that does not account for imperfect detection probability and “estimated” signifies a metric that accounts for imperfect detection probability using data derived from HDS models. To calculate raw species richness on a point-year scale, we tallied the number of species observed at each point within a year between the two annual visits; averaging point-year estimates across years sometimes led to fractional species richness values. To calculate estimated species richness on a point-year scale, we summed occupancy probabilities of all species, per the methods of Yamaura and Royle (2017). Note that because occupancy probabilities are continuous between 0 and 1, species richness estimates were not necessarily integers. To calculate a raw antilog Shannon-Weaver index for each point, inputted raw counts of all species for each point year into the ‘diversity’ function in R package ‘vegan’ and exponentiated the result (Oksanen et al. 2019). We used antilog form of the Shannon-Weaver index because it is more interpretable than its standard form; when all species are equally common, the antilog Shannon-Weaver index is equal to species richness (Peet 1974). To calculate estimated antilog Shannon-Weaver index for each point year, we used the same protocol as for the raw index, but instead of raw counts, we used mean estimated abundances derived from the HDS models. We performed each of these calculation for two different groups of species: all study species, and only species with SGCN designation, resulting in a total of eight diversity metrics per point.

Linear Models

To compare differences between diversity metrics, we used two repeated measures ANOVA tests with Bonferroni-adjusted paired sample t-tests as pairwise post-hoc tests. Before performing ANOVA analyses, we assessed normality using quantile-quantile plots and found no issues. We treated point as the "experimental" unit, and we used diversity index type ("index type"; species richness versus antilog Shannon-Weaver index) and "data source" (raw data or HDS model-derived data) as the two "treatments." In addition to post-hoc tests for statistical significance, we also calculated pairwise measures of effect size with bootstrapped 95% confidence interval using the default settings for Cohen's d in R package 'rstatix' with $d > 0.8$ as the cutoff for 'large' effect size (Cohen 1992; Kassambara 2020). We performed separate ANOVA tests for the all-species group of metrics and SGCN-specific group of metrics. We used $\alpha = 0.05$ for all tests. ANOVA and pairwise diversity metric comparisons were conducting using R package 'rstatix' (Kassambara 2020).

To estimate relationships between bird diversity and habitat, and to compare estimated habitat relationships between diversity metrics, we used linear regression models and multi-stage AIC-based model selection separately for each of the eight diversity metrics (Akaike 1987). We considered thirteen different covariates, not counting the intercept (Table 4.1). Due a prediction that edge habitat and interior forest would both have relatively high diversity and that habitat metrics would be contrasting between these habitat types, we considered both quadratic and linear coefficients for all covariates. The linear forms of these covariates were center-scaled prior to analyses, and quadratic terms were calculated from center-scaled covariates to create a distinct peak within the range of observed values, and then were re-center-scaled. We broke all habitat coefficients into five sequential stages of a hierarchy: 1) landscape, 2) distance to edge, 3) tree attributes, 4) midstory layer, and 5) shrub and ground layer (Table 4.1). Starting with the first stage of the hierarchy, we evaluated all covariates of that hierarchy stage singly and in combination, keeping all lower stages of the hierarchy constant. For that stage of the hierarchy, we selected competitive models using the criteria of $\leq$2.0 ΔAIC from the top model and excluding uninformative parameters that did not appear in the top model (Arnold 2010). We used all competitive combinations of covariates from the first stage in all the following stages, only eliminating these combinations if they no longer appeared in the top model(s) for a stage. We repeated the process of running all combinations for a single stage, holding lower stages constant, fixing competitive combinations of covariates for that stage, and moving to the next stage until all stages of the hierarchy were completed. For each diversity metric, we report the parameters in the top model and the model(s) with the fewest number of parameters within 2.0 ΔAIC of the top model, as well as whether the 95% confidence intervals of coefficients associated these parameters overlap zero. We report coefficient values only if a parameter appeared in the top model for more than one diversity metric. Running all combination of models was computationally unrealistic ($2^{26} \approx 6.7 \cdot 10^{7}$ models), but ad hoc methods of fixing covariates in other hierarchical ecological modeling frameworks perform similarly to frameworks using all combinations of models (Doherty et al. 2012). We used the ‘stats’ R package for all habitat linear models and model selection (R Core Team 2019).

Our abundance covariate hierarchy has the following biologically rooted justification. Migrating birds returning to the breeding grounds can first assess habitat at a landscape scale, with certain forest species avoiding areas with small forest patches or low proportion of forest habitat on a landscape scale in spite of otherwise suitable site-scale conditions (Ambuel and Temple 1983; Bakermans and Rodewald 2006). Once reaching a suitable patch, an individual may avoid or gravitate toward the edge of the habitat, depending on the species (Kroodsma, 1984; Le et al., 2018). Once at an otherwise suitable area within a habitat patch, birds use structural characteristics of vegetation to select a breeding territory (MacArthur and MacArthur 1961). In our hierarchy, we divided site-level structural characteristics into three subsections: tree attribute, midstory layer, and shrub-ground layer. Tree attributes were the first subsection, as they are derived from a comparatively large variable radius plot, and trees represent the largest vegetation structures in a forest. Tree species richness and proportion oak were surrogates for otherwise hard-to-measure structural differences. Variability in leaf and bark structure between tree species may impact foraging and nesting opportunities for forest birds, with oaks potentially providing above-average foraging opportunities for insectivores due to furrowed bark and short leaf petioles (Jackson 1970; Holmes and Robinson 1981; Rodewald and Abrams 2002). The midstory and the shrub-ground layer represent distinct habitats for birds and thus were considered as separate hierarchy stages. We considered midstory before the shrub-ground layer because of its relatively higher altitude in the forest strata and its generally has larger vegetative structures (e.g., small trees and branches of large trees).

Graphics

To better visualize non-linear relationships between habitat metrics and densities, we created plots for all covariates with both linear and quadratic terms in the top model for either overall estimated species richness or SGCN estimated species richness. We chose estimated species richness for visualization because it accounted for imperfect detection probability and was more interpretable than antilog Shannon-Weaver indices. We chose covariate values that roughly spanned the observed rage of values for that covariate. Mirroring the methods outlined in the “Linear Models” section, we converted raw values to center-scaled linear coefficients using means and standard deviations from the original habitat dataset, and we calculated quadratics by squaring the center-scaled linear coefficients and re-center-scaling the derived values using the mean and standard deviation of entire set (n = 493) of original center-scaled linear values for each covariate. To predict estimated species richness with a 95% confidence interval for a particular covariate value, we inputted calculated center-scaled values into the ‘stats’ package’s ‘predict’ function, holding all other covariates at their mean value (0 for all linear values and 0.998 for all quadratic values due to center-scaling). We created plots using ‘ggplot2’ with predicted values, including 95% confidence intervals as error bars, on the y-axis and original covariate values on the x-axis (Wickham 2016). We created a smoothed spline through the plotted points using the ‘spline’ function in the ‘stats’ R package to increase readability of our plots (R Core Team 2019).

To visualize geographic distributions of breeding bird species diversity within our study areas, we used ArcGIS Pro® to create 300 m x 300 m square buffers centered on each point and depicted point-scale diversity metrics within each buffer using a discrete version of the ‘viridis’ color scale. We used integers in our legends to increase interpretability, but values were up to 0.499 units higher or 0.500 units lower than the integer.

Results

Bird Survey Covariates and Habitat Surveys

Most bird survey covariates and habitat metrics had relatively wide and continuous ranges of values (Table 4.2). Exceptions for variables included in models were zero inflation of dead tree basal and proportion oak, a narrow range of proportions of forest within 10 km of each point, and notably skewed distributions of both green and grassy ground cover. For broad habitat classifications, 407 points were classified as forest and 86 were classified as non-forest. We measured a total of 32 tree species in our prism samples with a mean live tree basal area of 14.9 m^2/ha at the 407 forest points; oak and hickory dominated the tree community (Table A1).

Bird Survey and HDS Model Results

We detected a total of 126 bird species within our study areas from 2016 to 2019; 77 of these species met our criteria for HDS modeling and 24 of the 77 were SGCN (Table 4.3, Table A4). One additional SGCN, Horned Lark (*Eremophila alpestris*), was detected but ultimately excluded due to detection on only one occasion. Mean detection probabilities by species ranged from 0.03 (Ruby-throated Hummingbird, *Archilochus colubris*) to 0.86 (Wood Thrush); the mean detection probability across all 77 species was 0.38 (Table 4.3). Overall density estimates varied considerably between species, ranging between 0.002 birds/ha (Hooded Warbler) to 1.028 birds/ha (Gray Catbird), with a median species-specific density of 0.067 birds/ha (Table 4.3). All detectability covariates appeared in the top models for multiple species; in general, relationships between detection probability and wind speed, Julian day, and time since sunrise were negative, but signs of coefficients varied between species (Table 4.4, Table 4.5). Forest appeared as an abundance coefficient in 47 of 56 species/multispecies groups with a nearly even split between positive and negative relationships (Table 4.4, Table 4.5). Species as a fixed effect was in the top model for 9 of 10 multispecies groups (Table 4.4).

Species Diversity Metrics

In general, metrics using data estimated from HDS models produced higher estimates than raw data. For raw data metrics, the antilog Shannon-Weaver indices were lower than species richness; for estimated HDS data metrics, and antilog Shannon-Weaver indices were lower than species richness (Table 4.6). Point-scale diversity estimates for all species ranged from 8.3 (minimum raw species richness) to 29.8 (maximum estimated antilog Shannon-Weaver). Point-scale diversity estimates for SGCN ranged from 1.0 (minimum raw species richness) to 8.3 (maximum estimated antilog Shannon-Weaver). For both species groupings, there was strong evidence of statistical differences between species richness and antilog Shannon-Weaver indices (two-way repeated measures ANOVA, all spp.: $F_{1, 492} = 3086.9$, $P < 0.001$, SGCN: $F_{1, 492} = 1830.1$, $P < 0.001$); this was also the case between metrics using raw versus HDS estimated data (two-way repeated measures ANOVA, all spp.: $F_{1, 492} = 49{,}150.2$, $P < 0.001$, SGCN: $F_{1, 492} = 8457.1$, $P < 0.001$). There was also a significant interaction between species group and diversity metric type (two-way repeated measures ANOVA, all spp.: $F_{1, 492} = 25{,}898.2$, $P < 0.001$, SGCN: $F_{1, 492} = 5988.8$, $P < 0.001$). For both species' groupings, there was strong statistical evidence of pairwise differences between all metric types with a large effect size for each comparison (Table 4.7).

When examining the spatial distribution estimated species richness, there is a noticeable "hotspot" of high overall richness and SGCN richness in the northern corner of Thousand Acres, and the central part of Sand Creek has noticeably low species richness for both species' groupings (Figure A29, Figure A30).

Diversity-Habitat Relationships

Forested landcover within 10 km was a positive linear coefficient in the top model of six of eight diversity metrics and all competitive models for these metrics (Table 4.8, Table 4.9). Forested landcover within 10 km was a positive quadratic coefficient for five of eight diversity metrics and all competitive models for these metrics (Table 4.8, Table 4.9). For estimated SGCN species richness, the combination of linear and quadratic coefficients led to similar predictions of species richness from 20% to 25% forest cover within 10 km, but a higher estimate at 35% forest cover (Figure 4.3). Forested landcover within 1 km was not an informative parameter in any top model (Table 4.8). For all eight metrics, distance to forest edge had a negative linear coefficient and positive quadratic coefficient in the top model and all competitive models (Table 4.8, Table 4.9). For both overall species richness and SGCN species richness, the combination of linear and quadratic coefficients led to predictions of relatively high diversity at the forest edge that declined until approximately 400 m from the edge. For overall species richness, there was an increasing trend in overall species richness between 400 m and 800 m from the edge. For SGCN, the increase between 400 m and 800 m was more dramatic; 800 m had the highest estimate of SGCN richness of any distance we examined (Figure 4.3).

Tree species richness was a positive linear coefficient for all top models and competitive models for all overall species metrics, but it did not appear in any top models for SGCN metrics (Table 4.8, Table 4.9). Proportion oak was an informative parameter in one competitive model for SGCN species richness, but the 95% confidence interval overlapped zero in the top model for SGCN species richness (Table 4.8).

For midstory metrics, midstory foliage density at 2.5 m did not appear as an informative covariate in any top model (Table 4.8). Midstory foliage density at 5 m as was a positive linear coefficient for 5 of 8 metrics (Table 4.8, Table 4.10). Three top models for overall species metrics had a positive quadratic coefficient for midstory foliage density at 5 m (Table 4.8, Table 4.10). For overall species richness, the combination of linear and quadratic coefficients for midstory foliage density at 5 m led to wide confidence intervals for predicted values with no clear trend in species richness with midstory foliage density values between 0 and 1 (Figure 4.4). Midstory SD was a negative quadratic coefficient for the top model for six of eight metrics, and was a linear coefficient in the top model for overall raw Shannon index only (Table 4.8, Table 4.10).

Shrub density was a positive linear coefficient and negative quadratic for all overall species metric top models as well as all competitive models (Table 4.8, Table 4.10). Shrub density was a negative linear coefficient of three of four SGCN species metrics, although coefficients were small (Table 4.8, Table 4.10). For overall species richness, the combination of linear and quadratic coefficients led to a slight positive trend in species richness between 0 and 4 stems/m^2, with a possible decline between 4 and 8 stems/m^2 (Figure 4.4).

Grassy ground cover had a positive linear coefficient and negative quadratic coefficient for all top models for overall species metrics. No SGCN top models had a grassy ground cover as an informative covariate (Table 4.8, Table 4.11). For overall species richness, the combination of linear and quadratic coefficients for grass ground cover showed no clear trends in species richness with grassy ground cover values between 0 and 1 (Figure 4.4). Green ground cover had a positive linear coefficient for seven of eight species metrics (Table 4.8, Table 4.11). There was a positive quadratic coefficient for green ground cover in all overall species metrics, but there were no informative quadratic coefficients of green cover for SGCN species metrics (Table 4.8, Table 4.11). For overall species richness, the combination of linear and quadratic coefficients for grass ground cover showed no clear trends in species richness with green ground cover values between 0 and 1 (Figure 4.4). Leaf litter cover had a negative linear coefficient for all eight species metrics (Table 4.8, Table 4.11). Three of the overall species metrics had a positive quadratic coefficient for leaf litter (Table 4.8, Table 4.11). There were no informative quadratic coefficients of litter cover for SGCN (Table 4.8, Table 4.11). For overall species richness, the combination of linear and quadratic coefficients for leaf litter cover showed a clear negative trend of species richness with increasing leaf litter with a potential plateau starting between 60% and 80% ground coverage (Figure 4.4).

Discussion

Deciduous forests in the Midwest host a wide variety of bird species, but many of these are in decline (Niemi et al. 2016; Rosenberg et al. 2019). This decline in avian biodiversity makes assessments of bird diversity and diversity-habitat relationships in this region a high priority. In our study, we detected and modeled densities for 77 species that breed in Iowa deciduous forest and nearby environments, 24 of which were Species of Greatest Conservation Need. Vegetation changes, disturbances, and management activities affect bird diversity at scales ranging from the entire North American continent to vegetation structure within a forest stand (MacArthur and MacArthur 1961; Askins and Philbrick 1987; Rowhani et al. 2008). We accounted for spatial scales ranging from local landscape to forest stand microhabitats using an array of quantitative habitat metrics and related these metrics to average annual bird diversity with 100-m radius point count plots. To produce more accurate estimates of bird diversity within our study area, we employed hierarchical distance sampling models that allowed us to account for undetected species and individuals at the scale of a 100-m point count radius.

We predicted that diversity metrics derived from methods that incorporate imperfect detection would produce significantly higher estimates than those which use “raw” data. Across both species’ groupings and both diversity metric types, derive values were always significantly higher with a large effect size. For the overall bird community, estimated species richness was 7.7 species higher when using HDS data; for SGCN, estimated species richness was 1.2 species higher when using HDS data. Both of these gaps have the potential to be significant to management, as additional bird species, especially SGCN, may increase the conservation value of sites and alter management decisions (Yoccoz et al. 2001). Other studies on breeding bird communities accounting have predicted the presence of multiple undetected species (Tyre et al. 2003; Yamaura et al. 2011), although these other studies occur across larger study areas instead of single point count locations, making direct comparison difficult. One shortcoming of our study is that we did not incorporate model validation into our study design. Future studies involving prediction of undetected species using HDS should consider incorporating model validation; potential methods to accomplish this goal could include using more visits to a subset of sites or comparing species richness estimates between sites with similar habitat characteristics.

Contrary to our prediction, antilog Shannon-Weaver indices and species richness did not perform similarly. In pairwise comparisons of the two metrics, antilog Shannon-Weaver produced significantly lower values than species richness calculated using raw data, but significantly higher values than species richness when using estimates from HDS models. This difference in lower versus higher estimates for antilog Shannon-Weaver versus richness is likely due to the inclusion of many fractional estimated counts of undetected species, potentially making this estimator unreliable, as antilog Shannon-Weaver should be equal to or lower than species richness (Peet 1974). While antilog Shannon-Weaver may be appropriate at an area scale when estimated counts are generally ≥1, we believe HDS-estimated species richness it a better estimator for small scale diversity calculations.

One result common to both overall bird species and SGCN was an association between high landscape scale forest cover at 10 km scale and high bird species richness, especially at the highest observed values for landscape scale forest cover. To the best of our knowledge, most studies considering landscape-scale effects of deciduous forest on North American breeding birds consider effects on individual species as opposed to species richness (Bakermans and Rodewald 2006; Thompson et al. 2012; Reidy et al. 2014), making this one of few studies to consider the relationship between species richness and landscape scale deciduous forest cover in North America. However, there is evidence from a study on mixed-coniferous-deciduous forest in Connecticut that increasing forest cover at a landscape scale over the course of several year may increase bird diversity, especially diversity among long-distance migrants (Askins and Philbrick 1987). Caveats to this finding include a narrow range of observed landscape scale forest cover values (0.19 – 0.36), and that we did not consider other factors such as landscape scale disturbance or characteristics of individual BCAs that could also affect bird species diversity; we specifically excluded the latter from our analyses due to multicollinearity. Another study considering landscape effects on bird diversity found that agricultural disturbance at a 1-km radius scale has a negative association with forest bird diversity in Pennsylvania (Rodewald and Yahner 2001). Most of the land surrounding our study areas is agricultural (USDA NASS 2019), meaning agricultural disturbance and forest cover are likely highly correlated in our system.

Other compelling diversity-habitat relationships in our study included distance to edge, tree species richness, and leaf litter ground cover. For both overall species richness and SGCN we had higher values at both the forest edge and in the forest interior (>600 m from edge), with lower values in between. Elevated species richness for the forest interior was especially pronounced for SGCN. This pattern of high diversity at the edge and forest interior (but not in between) matches the findings of Kroodsma (1982) in Tennessee, although in that study diversity started increasing much closer to the edge (~200 m from the edge). We observed a positive relationship between bird diversity and tree species richness. Other studies have found mixed relationships between bird diversity and tree species diversity; in Mississippi bottomland forests and Arkansas forests, there is a positive association between bird diversity and tree species richness (James 1971; Twedt et al. 1999), while in Minnesota oak woodlands and savannas, there is a negative relationship (Au et al. 2008). Given that the majority of our study area was forest as opposed to woodland or savanna, the positive relationship makes sense in the context of other studies. We also found a negative relationship between leaf litter and bird diversity, which matches the pattern observed in Minnesota oak woodlands and savannas (Au et al. 2008). Au et al. (2008) attribute the negative relationship to canopy closure, which was highly collinear with leaf litter in their system. We removed canopy closure from our analysis due to multicollinearity; due to the observational nature of our study we were unable to determine whether leaf litter or a related factor such as canopy closure was the causative mechanism of the decreasing diversity with increased leaf litter cover. Although midstory density at 5 m, shrub density, grassy ground cover, and green ground cover were consistently in top models, predicted values and confidence intervals calculated using the range of observed covariate values revealed unclear patterns

(Figure 4.4), a valuable reminder to consider predictions using realistic covariate values as opposed to blindly following top models or confidence intervals associated with coefficients.

Despite accounting for imperfect detection probability in some of our metrics, we were not able to consider the entire breeding bird community. Specifically, we did not account for nocturnal species, a variety of species mostly detected as "flyovers," and species which were extremely rare or undetected during point count surveys. Bayesian models have been developed that incorporate undetected breeding bird species across an entire study area through the use of functional groups, although in current applications they produce imprecise estimates of the number of species missed (Yamaura et al. 2011). Nocturnal surveys and better methods for surveying "flyover" species would positively contribute to estimates of species richness in our area in both a numerical and conservation sense.

Overall, we affirmed that diversity metrics which account for imperfect detection probability produce significantly higher estimates of diversity than metrics using raw data. For studies analyzing many small areas, such as this one, we recommend using estimated species richness accounting for imperfect detection probability as a primary metric of diversity, as opposed to Shannon-Weaver-based estimates. We found high estimated species richness at both forest edges and forest interiors, but not in between, emphasizing the importance of both habitats to the breeding bird community in our study area. For SGCN, interior forest had the highest species richness. In this vein, we recommend management practices in this area which avoid creating new edges in large forest patches to preserve interior habitat 800 m or more away from the forest edge. We found positive diversity-habitat relationships for landscape scale forest cover at a 10 km scale and tree species richness, suggesting that sites with high forest cover and high tree species richness in our study area. For the benefit of bird diversity in this area, we recommend preserving landscape-scale forest cover where possible, and to consider restoration efforts that increase the amount of forest at a landscape scale. We also recommend that any selective harvests maintain tree species richness at a site by not completely eliminating any tree species. We also found a negative relationship between bird diversity and leaf litter cover, although the mechanism and management implications for this finding are unclear; this relationship may be attributable to decreased canopy closure, a variable we excluded from analyses due to multicollinearity.

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Tables

Table 4.1. Stages of a hierarchy of habitat covariates used to model relationships between habitat metrics and breeding bird diversity in and near south-central Iowa forests, 2016-2019. "Support" includes citations of papers that used similar covariates when modeling forest bird populations and communities in the Midwestern, Southern, or Eastern United States. *Reidy et al. (2014) use percent stocking, an alternative to basal area (Hovind and Rieck 1961). ** MacArthur and MacArthur (1961) use the Shannon diversity index of foliage 1.5 m – 7.6 m in height for midstory heterogeneity; we based our standard deviation metric on Young et al. (2013).

Table 4.2. Descriptive statistics for habitat and birds survey variables collected in and near south-central Iowa forests 2016-2019. Prop = proportion. Variables in italics were ultimately excluded from analyses.

Variable	Variable Type	Min	Quartile (25%)	Median	Quartile (75%)	Max	Unique values
Julian day	Continuous	136	163	184	206	228	92
Time since sunrise (hrs)	Continuous	-0.7	0.7	1.6	2.6	6.0	333
Observer	*Categorical*	-	-	-	-	-	*5*
Average wind speed (km/hr)	Continuous	0	8	11	15	38	45
Forest landcover within 1 km (prop)	Continuous	0.24	0.54	0.63	0.68	0.76	479
Forest landcover within 10 km (prop)	Continuous	0.19	0.22	0.25	0.31	0.36	493
Nearest forest patch size (ha)	*Continuous*	*1742*	*2721*	*2757*	*4503*	*4503*	*4*
Distance to edge of forest (m)	Continuous	0	22	136	279	759	408
Tree species richness	Continuous	0	2	4	6	11	12
Live tree basal area (m^2/ha)	Continuous	0	7	13	18	38	35
Dead tree basal area (m^2/ha)	Continuous	0	0	1	3	21	15
Oak proportion (of basal area)	Continuous	0	0	0.38	0.69	1	137
Canopy closure	*Continuous*	*0*	*0.7*	*0.9*	*0.95*	*1*	*20*
Midstory density at 2.5 m (prop cover)	Continuous	0	0.21	0.4	0.59	1	428
Midstory density at 5.0 m (prop cover)	Continuous	0	0.22	0.38	0.56	1	433
Midstory density standard deviation	Continuous	0	0.19	0.31	0.39	0.52	166
Shrub density (stems/m^2)	Continuous	0	0.88	1.63	2.62	7.85	21
Grassy ground cover (prop)	Continuous	0	0.05	0.15	0.4	1	21
Green ground cover (prop)	Continuous	0	0.55	0.7	0.85	1	21
Leaf litter ground cover (prop)	Continuous	0	0.05	0.6	0.95	1	21

Table 4.3. Detections, density estimates and detection probabilities for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Detections ("dets.") are across all surveys. Density and detection probability ("det. prob.") estimates were derived from hierarchical distance sampling models. Densities are in birds/ha. A letter under the "Group" column signifies species with shared detection functions on account of low detections for at least one species in that group; these species use similar habitats and have similar vocalization habits. Species with the same letter share a detection function. * = Iowa Species of Greatest Conservation Need.

Common Name	**Scientific Name**	**Dets.**	**Density**	**Det. prob.**	**Group**
Northern Bobwhite*	*Colinus virginianus*	39	0.007	0.67	a
Ring-necked Pheasant	*Phasianus colchicus*	43	0.008	0.67	a
Wild Turkey	*Melanerpes erythrocephalus*	68	0.018	0.34	
Mourning Dove	*Zenaida macroura*	264	0.045	0.62	
Yellow-billed Cuckoo*	*Coccyzus americanus*	841	0.181	0.50	b
Black-billed Cuckoo*	*Coccyzus erythropthalmus*	48	0.011	0.50	b
Ruby-throated Hummingbird	*Archilochus colubris*	104	0.278	0.03	
Cooper's Hawk	*Accipiter cooperii*	54	0.009	0.60	c
Red-shouldered Hawk*	*Buteo lineatus*	172	0.029	0.60	c
Broad-winged Hawk	*Buteo platypterus*	28	0.005	0.60	c
Red-tailed Hawk	*Buteo jamaicensis*	30	0.005	0.60	c
Red-headed Woodpecker*	*Melanerpes erythrocephalus*	212	0.045	0.49	
Red-bellied Woodpecker	*Melanerpes carolinus*	1295	0.194	0.76	
Downy Woodpecker	*Dryobates pubescens*	1218	0.381	0.29	
Hairy Woodpecker	*Dryobates villosus*	333	0.106	0.28	
Northern Flicker*	*Colaptes auratus*	692	0.126	0.65	
Pileated Woodpecker	*Dryocopus pileatus*	160	0.027	0.72	
Great Crested Flycatcher	*Myiarchus crinitus*	525	0.137	0.36	
Eastern Kingbird*	*Tyrannus tyrannus*	77	0.021	0.33	d
Eastern Wood-Pewee*	*Contopus virens*	3317	0.698	0.44	
Acadian Flycatcher*	*Empidonax virescens*	522	0.199	0.23	
Willow Flycatcher	*Empidonax traillii*	48	0.015	0.31	e
Eastern Phoebe	*Sayornis phoebe*	140	0.096	0.12	
Bell's Vireo*	*Vireo bellii*	32	0.010	0.29	f
White-eyed Vireo	*Vireo griseus*	18	0.006	0.29	f
Yellow-throated Vireo	*Vireo flavifrons*	355	0.111	0.32	g
Warbling Vireo	*Vireo gilvus*	19	0.006	0.31	e
Red-eyed Vireo	*Vireo olivaceus*	2401	0.742	0.28	
Blue Jay	*Cyanocitta cristata*	2334	0.383	0.67	
American Crow	*Corvus brachyrhynchos*	436	0.071	0.63	
Black-capped Chickadee	*Poecile atricapillus*	1188	0.39	0.30	
Tufted Titmouse	*Baeolophus bicolor*	644	0.148	0.45	
White-breasted Nuthatch	*Sitta carolinensis*	2391	0.971	0.22	
Carolina Wren	*Thryothorus ludovicianus*	176	0.055	0.33	
House Wren	*Troglodytes aedon*	733	0.287	0.23	
Sedge Wren*	*Cistothorus platensis*	59	0.027	0.20	h

Table 4.3 continued

Common Name	Scientific Name	Dets.	Density	Det. prob.	Group
Blue-gray Gnatcatcher	*Polioptila caerulea*	108	0.062	0.15	
Eastern Bluebird	*Sialia sialis*	38	0.011	0.33	d
Veery*	*Catharus fuscescens*	11	0.003	0.36	i
Wood Thrush*	*Hylocichla mustelina*	574	0.084	0.86	
American Robin	*Turdus migratorius*	287	0.085	0.34	
Gray Catbird	*Dumetella carolinensis*	1982	1.028	0.17	
Brown Thrasher*	*Toxostoma rufum*	80	0.027	0.29	f
European Starling	*Sturnus vulgaris*	33	0.014	0.21	j
Cedar Waxwing	*Bombycilla cedrorum*	273	0.140	0.18	
American Goldfinch	*Spinus tristis*	1252	0.223	0.53	
Eastern Towhee	*Pipilo erythrophthalmus*	1863	0.351	0.53	
Chipping Sparrow	*Spizella passerina*	141	0.067	0.19	
Field Sparrow*	*Spizella pusilla*	1003	0.154	0.68	
Grasshopper Sparrow*	*Ammodramus savannarum*	45	0.019	0.20	h
Henslow's Sparrow*	*Ammodramus henslowii*	65	0.028	0.20	h
Song Sparrow	*Melospiza melodia*	725	0.153	0.45	k
Lark Sparrow	*Chondestes grammacus*	24	0.006	0.45	k
Bobolink*	*Dolichonyx oryzivorus*	39	0.010	0.41	l
Eastern Meadowlark*	*Sturnella magna*	34	0.008	0.41	l
Orchard Oriole	*Icterus spurius*	22	0.007	0.31	e
Baltimore Oriole*	*Icterus galbula*	94	0.037	0.23	
Red-winged Blackbird	*Agelaius phoeniceus*	564	0.162	0.31	
Brown-headed Cowbird	*Molothrus ater*	1028	0.437	0.21	j
Common Grackle	*Quiscalus quiscula*	13	0.006	0.21	j
Ovenbird	*Seiurus aurocapilla*	2061	0.495	0.36	
Louisiana Waterthrush	*Parkesia motacilla*	155	0.035	0.48	
Blue-winged Warbler	*Vermivora cyanoptera*	129	0.049	0.26	
Kentucky Warbler*	*Geothlypis formosa*	112	0.024	0.44	
Common Yellowthroat*	*Geothlypis trichas*	1614	0.421	0.35	
Hooded Warbler	*Setophaga citrina*	5	0.002	0.32	g
American Redstart	*Setophaga ruticilla*	221	0.112	0.17	
Cerulean Warbler*	*Setophaga cerulea*	10	0.003	0.36	i
Northern Parula	*Setophaga americana*	181	0.068	0.25	
Yellow Warbler	*Setophaga petechia*	168	0.081	0.18	
Yellow-breasted Chat	*Icteria virens*	10	0.003	0.29	f
Dickcissel	*Spiza americana*	358	0.099	0.33	
Indigo Bunting	*Passerina cyanea*	1867	0.596	0.29	
Northern Cardinal	*Cardinalis cardinalis*	1824	0.336	0.55	
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	532	0.176	0.28	
Scarlet Tanager	*Piranga olivacea*	710	0.195	0.36	i
Summer Tanager	*Piranga rubra*	101	0.029	0.36	i

Table 4.4. Top covariate combinations for hierarchical distance sampling models as determined by AIC for breeding bird densities in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Multispecies groups contain species with shared detection functions on account of low detections for at least one species in that group; these species use similar habitats and have similar vocalization habits; groups are detailed as a footnote. “Species” as a categorical main effect was only used in multispecies group. “Species * forest” denotes an interaction between species and forest in addition to a main effect of each covariate; this interaction was only considered for the hawk group. We attempted to perform all combinations of models, but not all models converged. “No. models” is the number of models that converged out of one of the total possible models: 128 for single species, 256 for most multispecies groups, and 320 for the hawk group. OBS = categorical main effect of observer (df = 4), WIND = wind speed, JDAY = Julian date, TSSR = time since sunrise. “Forest” was a binary covariate denoting whether point surveys occurred in forest (1) or non-forest (0). Continuous covariates used in these analyses were center-scaled prior to analyses, and quadratic terms, denoted by “$(\text{variable})^2$” were calculated from center-scaled covariates.

Species or group	**No. models**	**Detection covariates**	**Abundance covariates**
Wild Turkey	42	JDAY + $(\text{JDAY})^2$	forest
Mourning Dove	57	OBS + JDAY + $(\text{JDAY})^2$ + TSSR	forest
Ruby-throated Hummingbird	20	JDAY + $(\text{JDAY})^2$	(none)
Red-headed Woodpecker	113	OBS + $(\text{JDAY})^2$ + $(\text{TSSR})^2$	(none)
Red-bellied Woodpecker	118	OBS + WIND + JDAY + TSSR	forest
Downy Woodpecker	127	OBS + WIND + JDAY + $(\text{JDAY})^2$ + TSSR	forest
Hairy Woodpecker	112	OBS + JDAY + (TSSR)2	forest
Northern Flicker	123	OBS + WIND + JDAY + TSSR + $(\text{TSSR})^2$	forest
Pileated Woodpecker	68	OBS + TSSR	forest
Great Crested Flycatcher	83	OBS + JDAY + $(\text{JDAY})^2$ + TSSR	forest
Eastern Wood-Pewee	128	OBS + WIND + JDAY + $(\text{JDAY})^2$ + TSSR + (TSSR)2	forest
Acadian Flycatcher	123	OBS + WIND + JDAY + $(\text{JDAY})^2$ + TSSR	forest
Eastern Phoebe	69	OBS + TSSR	forest
Red-eyed Vireo	128	OBS + JDAY + TSSR + $(\text{TSSR})^2$	forest
Blue Jay	128	OBS + JDAY + $(\text{JDAY})^2$ + $(\text{TSSR})^2$	forest
American Crow	128	OBS + WIND + JDAY + $(\text{JDAY})^2$ + TSSR + $(\text{TSSR})^2$	(none)
Black-capped Chickadee	127	OBS	forest
Tufted Titmouse	125	OBS + WIND + JDAY + $(\text{JDAY})^2$ + TSSR + $(\text{TSSR})^2$	forest
White-breasted Nuthatch	128	OBS + WIND + JDAY + TSSR	forest
Carolina Wren	103	OBS + JDAY	forest
House Wren	127	OBS + JDAY + $(\text{JDAY})^2$	forest
Blue-gray Gnatcatcher	60	JDAY + $(\text{JDAY})^2$ + TSSR	forest
Wood Thrush	61	JDAY + $(\text{JDAY})^2$ + TSSR	forest

Table 4.4 cont.

Species or group	No. models	Detection covariates	Abundance covariates
American Robin	121	OBS + WIND + $(JDAY)^2$ + TSSR + $(TSSR)^2$	forest
Gray Catbird	128	OBS + TSSR + $(TSSR)^2$	forest
Cedar Waxwing	123	OBS + WIND + JDAY + TSSR	(none)
American Goldfinch	122	OBS + WIND	forest
Eastern Towhee	128	OBS + WIND + JDAY + TSSR	forest
Chipping Sparrow	90	OBS + WIND + JDAY + TSSR	forest
Field Sparrow	127	OBS + JDAY + $(JDAY)^2$ + TSSR	forest
Baltimore Oriole	38	JDAY + $(JDAY)^2$	(none)
Red-winged Blackbird	92	OBS + WIND + JDAY + $(JDAY)^2$ + TSSR + $(TSSR)^2$	forest
Ovenbird	99	OBS + JDAY + $(JDAY)^2$	forest
Louisiana Waterthrush	58	JDAY + (JDAY)2 + TSSR	forest
Blue-winged Warbler	28	$(JDAY)^2$	forest
Kentucky Warbler	33	WIND + JDAY	forest
Common Yellowthroat	128	OBS + WIND + JDAY + $(JDAY)^2$ + TSSR	forest
American Redstart	111	OBS + JDAY + $(JDAY)^2$ + TSSR	forest
Northern Parula	110	OBS + WIND + JDAY + $(JDAY)^2$	(none)
Yellow Warbler	106	OBS + JDAY + (JDAY)2 + $(TSSR)^2$	forest
Dickcissel	108	OBS + WIND + JDAY + $(JDAY)^2$	forest
Indigo Bunting	128	OBS + $(JDAY)^2$ + TSSR + $(TSSR)^2$	forest
Northern Cardinal	128	OBS + WIND + JDAY + TSSR	(none)
Rose-breasted Grosbeak	117	OBS + JDAY + $(JDAY)^2$	(none)
Gallinaceous group	40	OBS + TSSR	forest
Cuckoo group	239	OBS + WIND + JDAY + TSSR + $(TSSR)^2$	species
Hawk group	320	OBS + WIND	species * forest
Savanna group	123	OBS + JDAY	species + forest
Riparian group	248	OBS	species + forest
Scrubland group	177	OBS + WIND + JDAY + TSSR	species + forest
Forest group 1	128	(JDAY)2	species + forest
Quiet grassland group	251	OBS + WIND + JDAY + $(TSSR)^2$	species + forest
Forest group 2	230	OBS + $(JDAY)^2$ + TSSR	species + forest
Disturbed group	188	OBS + JDAY	species + forest
Sparrow group	245	OBS + JDAY + $(JDAY)^2$	species + forest
Loud grassland group	103	OBS + TSSR + $(TSSR)^2$	forest

Gallinaceous group = Northern Bobwhite + Ring-necked Pheasant, Cuckoo group = Yellow-billed Cuckoo + Black-billed Cuckoo, Hawk group = Cooper's Hawk + Red-shouldered Hawk + Broad-winged Hawk + Red-tailed Hawk, Savanna group = Eastern Kingbird + Eastern Bluebird, Scrubland group = Bell's Vireo + White-eyed Vireo + Brown Thrasher + Yellow-breasted Chat, Forest group 1 = Yellow-throated Vireo + Hooded Warbler, Quiet grassland group = Sedge Wren + Grasshopper Sparrow + Henslow's Sparrow, Forest group 2 = Veery + Cerulean Warbler + Scarlet Tanager + Summer Tanager, Disturbed group = European Starling + Common Grackle + Brown-headed Cowbird, Sparrow group = Lark Sparrow + Song Sparrow, Loud grassland group = Eastern Meadowlark + Bobolink

Table 4.5. Signs of coefficients for continuous detectability and abundance covariates from hierarchical distance sampling models for breeding bird densities in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys). Multispecies groups contain species with shared detection functions on account of low detections for at least one species in that group; these species use similar habitats and have similar vocalization habits; groups are detailed as a footnote. “Forest” is the only abundance coefficient listed; all others are for detectability JDAY = Julian date, TSSR = time since sunrise, † = model has a species X forest interaction in addition to a main effect, * = 95% confidence interval overlapped zero; sign of the mean coefficient (+ or -) is reported. “Forest” was a binary covariate denoting whether point surveys occurred in forest (1) or non-forest (0). All continuous covariates used in these analyses were center-scaled prior to analyses, and quadratic terms, denoted by “(variable)^2” were calculated from center-scaled covariates.

Species or group	**Wind speed**	**JDAY**	**(JDAY)^2**	**TSSR**	**(TSSR)^2**	**Forest**
Wild Turkey		-	+			-*
Mourning Dove		-	+*	-		-
Ruby-throated Hummingbird		-	+*			
Red-headed Woodpecker			+		-	
Red-bellied Woodpecker	-	-		-		+
Downy Woodpecker	-*	+	-	-		+
Hairy Woodpecker		-			-*	+
Northern Flicker	-	+		+	-*	+
Pileated Woodpecker				-		+
Great Crested Flycatcher		-	+	-		-*
Eastern Wood-Pewee	-	+	+	-	+*	+
Acadian Flycatcher	-*	+*	-	-		+
Eastern Phoebe				-		+
Red-eyed Vireo		-		-	+	+
Blue Jay		+	+		-	+
American Crow						
Black-capped Chickadee						+
Tufted Titmouse	-	-	+	+	-	+
White-breasted Nuthatch	-*	+		-		+
Carolina Wren		+*				+
House Wren		-	-			-
Blue-gray Gnatcatcher		-	-	-*		+
Wood Thrush		-	-	-		+
American Robin	+		+	-*	+*	-
Gray Catbird				-*	+*	-
Cedar Waxwing	+*	-*		+*		

Table 4.5 continued

Species or group	**Wind speed**	**JDAY**	**$(JDAY)^2$**	**TSSR**	**$(TSSR)^2$**	**Forest**
American Goldfinch	-					-
Eastern Towhee	-	+		-		-
Chipping Sparrow	-*	-		+*		-
Field Sparrow		+	-	-		-
Baltimore Oriole		-	+			
Red-winged Blackbird	-	-	-	-*	+*	-
Ovenbird		-	-			+
Louisiana Waterthrush		-	-*	-		+
Blue-winged Warbler			+			-*
Kentucky Warbler	+*	-				+
Common Yellowthroat	-	-	-	-		-
American Redstart		-	+	+		+*
Northern Parula	-*	-	-			
Yellow Warbler		-	-		+*	-
Dickcissel	-	-	-			-
Indigo Bunting			-	-	+	-
Northern Cardinal	-	-		-		
Rose-breasted Grosbeak		-	-			
Gallinaceous group				+		-
Cuckoo group	-	-		-*	-	
Hawk group						+*†
Savanna group		+				-
Riparian group						-
Scrubland group	-*	-		-		-
Forest group 1			-			+
Quiet grassland group	-	-			+	-
Forest group 2			-	-		+
Edge group		-				-
Sparrow group		+	-			-
Loud grassland group				+	+*	-

Gallinaceous group = Northern Bobwhite + Ring-necked Pheasant, Cuckoo group = Yellow-billed Cuckoo + Black-billed Cuckoo, Hawk group = Cooper's Hawk + Red-shouldered Hawk + Broad-winged Hawk + Red-tailed Hawk, Savanna group = Eastern Kingbird + Eastern Bluebird, Scrubland group = Bell's Vireo + White-eyed Vireo + Brown Thrasher + Yellow-breasted Chat, Forest group 1 = Yellow-throated Vireo + Hooded Warbler, Quiet grassland group = Sedge Wren + Grasshopper Sparrow + Henslow's Sparrow, Forest group 2 = Veery + Cerulean Warbler + Scarlet Tanager + Summer Tanager, Disturbed group = European Starling + Common Grackle + Brown-headed Cowbird, Sparrow group = Lark Sparrow + Song Sparrow, Loud grassland group = Eastern Meadowlark + Bobolink

Table 4.6. Descriptive statistics for point-scale diversity metrics for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. The “overall” species group consists of 77 breeding birds with at least five detections from 2016-2019. “SGCN” is a subset of 24 species with Species of Greatest Conservation Need designation in Iowa. Diversity metrics are species richness (“Rich.”) and antilog Shannon-Weaver index (“Shann.”). Data used to calculate diversity metrics were either raw counts (“Raw) or data derived from hierarchical distance sampling (“HDS”) models.

Species Group	**Diversity Metric**	**Data**	**Min**	**Quartile (25%)**	**Median**	**Quartile (75%)**	**Max**
Overall	Rich.	Raw	8.3	11.8	12.8	14.3	18.5
		HDS	16.7	19.4	20.4	21.7	25.7
	Shann.	Raw	6.3	10.7	11.9	13.1	17.0
		HDS	18.5	24.1	25.0	26.0	29.8
SGCN	Rich.	Raw	1.0	2.3	3.0	3.5	6.0
		HDS	2.4	3.5	4.0	4.6	7.3
	Shann.	Raw	1.3	2.3	2.7	3.3	5.3
		HDS	3.6	4.8	5.3	5.9	8.3

Table 4.7. Pairwise comparisons of point-scale diversity metrics for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. The "overall" species group is consisting of 77 breeding birds with at least 5 detections from 2016-2019. "SGCN" is a subset of 24 species with Species of Greatest Conservation Need designation in Iowa. For the within and between groups, there are two diversity metrics, species richness ("Rich.") and antilog Shannon-Weaver index ("Shann."), and two sources of data used to calculate diversity metrics: raw counts and data derived from hierarchical distance sampling (HDS) models. "Mean diff." is the mean of the differences for a given metric at a point scale. A Bonferroni correction was used to adjust p-values and correct for multiple testing. Cohen's d is measure of effect size. *** = p < 0.001.

				Pairwise t-test			**Cohen's d**	
Species Group	**Within Group**	**Between Groups**	**Mean diff.**	**t**	**df**	**p_{adj}**	**d**	**95% CI**
Overall	HDS	Shann. - Rich.	-4.5	-94.8	492	***	-4.27	(-4.66, -3.90)
	Raw	Shann. - Rich.	1.0	55.3	492	***	2.49	(2.26, 2.78)
	Rich.	HDS - Raw	7.7	213.3	492	***	9.61	(9.05, 10.26)
	Shann.	HDS - Raw	13.1	216.3	492	***	9.74	(9.09, 10.43)
SGCN	HDS	Shann. - Rich.	-1.2	-58.3	492	***	-2.62	(-2.83, -2.46)
	Raw	Shann. - Rich.	0.1	19.3	492	***	0.87	(0.77, 0.98)
	Rich.	HDS - Raw	1.2	213.3	492	***	4.01	(3.75, 4.30)
	Shann.	HDS - Raw	2.6	216.3	492	***	4.06	(3.76, 4.41)

Table 4.8. Summary of AIC-based model selection results for models of diversity-habitat relationships for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. The “overall” species group contains 77 breeding birds with at least five detections from 2016-2019. “SGCN” is a subset of 24 species with Iowa Species of Greatest Conservation Need designation. Diversity metrics are species richness (“Rich.”) and antilog Shannon-Weaver index (“Shann.”). Data used for diversity metrics were either raw counts (“Raw) or data derived from hierarchical distance sampling (“HDS”) models. Only the top model and competitive model(s) within 2.0 ΔAIC with the fewest coefficients are shown. L = linear, Q = quadratic coefficient. * = 95% confidence interval of coefficient contains 0. “Forest 10km” and “forest 1km” are the proportion of forested land cover within 10 km and 1 km of point. “Edge” is distance to forest edge from inside the forest. “Live BA” and “dead BA” are basal area of all species of live and dead trees. “Oak” is the relative amount of live basal area comprised of oaks. “Tree spp.” is tree species richness. “Mid 2.5m” and “mid 5m” are midstory foliage density at 2.5 m and 5m heights. and “mid SD” is a metric of midstory heterogeneity. “Shrub” is shrub stem density. “Grass,” “green,” and “litter” are all ground cover metrics.

Species Group	**Metric**	**Data**	**Forest 10km**	**Forest 1km**	**Edge**	**Live BA**	**Dead BA**	**Tree Spp.**	**Oak**	**Mid 2.5m**	**Mid 5m**	**Mid SD**	**Shrub**	**Grass**	**Green**	**Litter**	**AIC**	**ΔAIC**
Overall	Rich.	Raw	L		L + Q			L			L + Q*	Q	L + Q	L + Q	L + Q	L + Q	1927.01	0.00
			L		L + Q			L			L + Q*	Q	L + Q		L + Q	L + Q	1928.55	1.54
		HDS	L		L + Q		L*	L			L + Q	Q*	L + Q*	L	L + Q	L + Q*	1671.85	0.00
			L		L + Q		L	L			L*		L + Q*	L	L + Q	L	1673.21	1.36
	Shann.	Raw	L		L + Q			L			L + Q*	L + Q	L + Q	L + Q	L + Q	L + Q	1898.16	0.00
			L		L + Q			L			L	Q	L + Q		L + Q	L + Q	1900.11	1.95
		HDS	Q		L + Q			L				Q*	L + Q*	L*	Q	L	1687.48	0.00
			Q		L + Q			L					L + Q		Q	L	1689.08	1.61
SGCN	Rich.	Raw	L + Q	Q*	L + Q		L*				L*	Q*	L		L	L	1106.44	0.00
			L + Q		L + Q								L		L	L	1107.95	1.51
		HDS	L* + Q	Q*	L + Q	L			L*	L*	L		L	L*	L	L*	1038.22	0.00
			L* + Q*	Q*	L + Q	L			L		L		L	L	L		1039.77	1.55
	Shann.	Raw	L + Q		L + Q							Q*	L + Q*	L* + Q*	L + Q*	L + Q*	1027.28	0.00
			L + Q		L + Q								L* + Q*	L* + Q*	L + Q*	L + Q*	1028.84	1.56
		HDS	Q		L + Q	L	L* + Q*	Q*	L*							L*	962.51	0.00

Table 4.9. Coefficients of top models of diversity-habitat relationships for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. The “overall” species group contains 77 breeding birds with at least 5 detections from 2016-2019. “SGCN” is a subset of 24 species with Iowa Species of Greatest Conservation Need designation. Only landscape-, edge-, and tree-related coefficients appearing in at least two top models with coefficient 95% CIs not overlapping are shown. Diversity metrics are species richness (“Rich.”) and antilog Shannon-Weaver index (“Shann.”). Data used for diversity metrics were either raw counts (“Raw) or data derived from hierarchical distance sampling (“HDS”) models. “Forest 10km” is the proportion of forested land cover with 10 km of a point. “Edge” is distance to forest edge from inside the forest in m. “Dead BA” is basal area of dead trees in m^2/ha. “Tree spp.” is tree species richness. Quadratics terms are denoted by (variable)^2 and are unitless due to center-scaling. Coefficients in italics have 95% confidence intervals overlapping 0.

			Forest 10km		**(Forest 10km)^2**		**Edge**		**(Edge)^2**		**Tree spp.**	
Species Group	**Metric**	**Data**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
Overall	Rich.	Raw	11.5	(8.3, 14.8)			-0.002	(-0.004, -0.001)	0.253	(0.034, 0.473)	0.167	(0.075, 0.260)
		HDS	7.8	(5.3, 10.3)			-0.004	(-0.005, -0.003)	0.391	(0.221, 0.561)	0.097	(0.026, 0.168)
	Shann.	Raw	10.0	(6.9, 13.2)			-0.002	(-0.004, -0.001)	0.217	(0.004, 0.431)	0.177	(0.087, 0.268)
		HDS			0.166	(0.045, 0.287)	-0.004	(-0.005, -0.003)	0.417	(0.247, 0.587)	0.096	(0.029, 0.164)
SGCN	Rich	Raw	2.1	(0.6, 3.7)	0.103	(0.028, 0.179)	-0.001	(-0.002, -0.001)	0.186	(0.091, 0.282)		
		HDS	1.4	(0.0, 2.8)	0.070	(0.004, 0.135)	-0.002	(-0.002, -0.001)	0.241	(0.157, 0.325)		
	Shann.	Raw	1.8	(0.3, 3.2)	0.099	(0.029, 0.169)	-0.001	(-0.002, -0.001)	0.187	(0.100, 0.274)		
		HDS			0.078	(0.018, 0.137)	-0.002	(-0.003, -0.002)	0.249	(0.167, 0.331)		

Table 4.10. Coefficients of top models of diversity-habitat relationships for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. The “overall” species group contains 77 breeding birds with at least 5 detections from 2016-2019. “SGCN” is a subset of 24 species with Iowa Species of Greatest Conservation Need designation. Only midstory- and shrub-related coefficients appearing in at least two top models with coefficient 95% CIs not overlapping are shown. Diversity metrics are species richness (“Rich.”) and antilog Shannon-Weaver index (“Shann.”). Data used for diversity metrics were either raw counts (“Raw) or data derived from hierarchical distance sampling (“HDS”) models. “Mid 5m” is midstory foliage density at 5m in height as a proportion, and “mid SD” is a metric of midstory heterogeneity. “Shrub” is shrub stem density in stems/m^2. Quadratics terms are denoted by $(\text{variable})^2$ and are unitless due to center-scaling. Coefficients in italics have 95% confidence intervals overlapping 0.

			Mid 5m		**(Mid 5m)^2**		**(Mid SD)^2**		**Shrub**		**(Shrub)^2**	
Species Group	**Metric**	**Data**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
Overall	Rich.	Raw	-1.084	(-1.982, -0.186)	*0.192*	*(-0.003, 0.387)*	-0.269	(-0.497, -0.041)	0.270	(0.106, 0.433)	-0.215	(-0.409, -0.021)
		HDS	-0.913	(-1.607, -0.219)	0.153	(0.002, 0.303)	*-0.172*	*(-0.348, 0.004)*	0.186	(0.060, 0.313)	-0.199	(-0.366, -0.032)
	Shann.	Raw	-1.220	(-2.170, -0.269)	0.223	(0.014, 0.432)	-0.278	(-0.500, -0.056)	0.284	(0.125, 0.444)	-0.211	(-0.399, -0.023)
		HDS					*-0.123*	*(-0.274, 0.028)*	0.256	(0.131, 0.381)	-0.166	(-0.325, -0.007)
SGCN	Rich	Raw	*-0.302*	*(-0.638, 0.033)*			*-0.080*	*(-0.162, 0.002)*	-0.081	(-0.138, -0.023)		
		HDS	-0.395	(-0.710, -0.080)					-0.064	(-0.113, -0.015)		
	Shann.	Raw					*-0.071*	*(-0.146, 0.005)*	-0.073	(-0.140, -0.007)	*0.021*	*(-0.056, 0.098)*
		HDS										

Table 4.11. Coefficients of top models of diversity-habitat relationships for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. The “overall” species group contains 77 breeding birds with at least 5 detections from 2016-2019. “SGCN” is a subset of 24 species with Iowa Species of Greatest Conservation Need designation. Only ground cover-related coefficients appearing in at least two top models with coefficient 95% CIs not overlapping are shown. Diversity metrics are species richness (“Rich.”) and antilog Shannon-Weaver index (“Shann.”). Data used for diversity metrics were either raw counts (“Raw) or data derived from hierarchical distance sampling (“HDS”) models. “Grass” is the proportion of the ground covered by graminoid plants (e.g., grasses, sedges). “Green” is the proportion the ground covered by herbaceous or small woody plants. “Litter” is the proportion of the ground covered by leaf litter. Quadratics terms are denoted by (variable)^2 and are unitless due to center-scaling. Coefficients in italics have 95% confidence intervals overlapping 0.

			Grass		**(Grass)^2**		**Green**		**(Green)^2**		**Litter**		**(Litter)^2**	
Species Group	**Metric**	**Data**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
Overall	Rich.	Raw	0.939	(0.065, 1.814)	-0.290	(-0.560, -0.021)	1.134	(0.322, 1.945)	0.291	(0.079, 0.503)	-1.597	(-2.093, -1.102)	0.224	(0.047, 0.401)
		HDS	0.539	(0.038, 1.040)			0.863	(0.235, 1.491)	0.255	(0.091, 0.419)	-1.307	(-1.689, -0.925)	*0.108*	*(-0.030, 0.245)*
	Shann.	Raw	0.873	(0.022, 1.724)	-0.298	(-0.560, -0.036)	0.906	(0.118, 1.695)	0.317	(0.111, 0.523)	-1.397	(-1.882, -0.912)	0.194	(0.022, 0.366)
		HDS	*0.463*	*(-0.042, 0.968)*					0.250	(0.112, 0.389)	-0.900	(-1.282, -0.517)		
SGCN	Rich	Raw					0.485	(0.194, 0.776)			-0.284	(-0.488, -0.079)		
		HDS	*0.225*	*(-0.010, 0.459)*			0.311	(0.058, 0.565)			*-0.168*	*(-0.386, 0.051)*		
	Shann.	Raw	*0.303*	*(-0.048, 0.655)*	*-0.048*	*(-0.155, 0.058)*	0.428	(0.102, 0.753)	*0.043*	*(-0.041, 0.128)*	-0.261	(-0.464, -0.059)	*-0.020*	*(-0.090, 0.050)*
		HDS									*-0.170*	*(-0.382, 0.042)*		

Figures

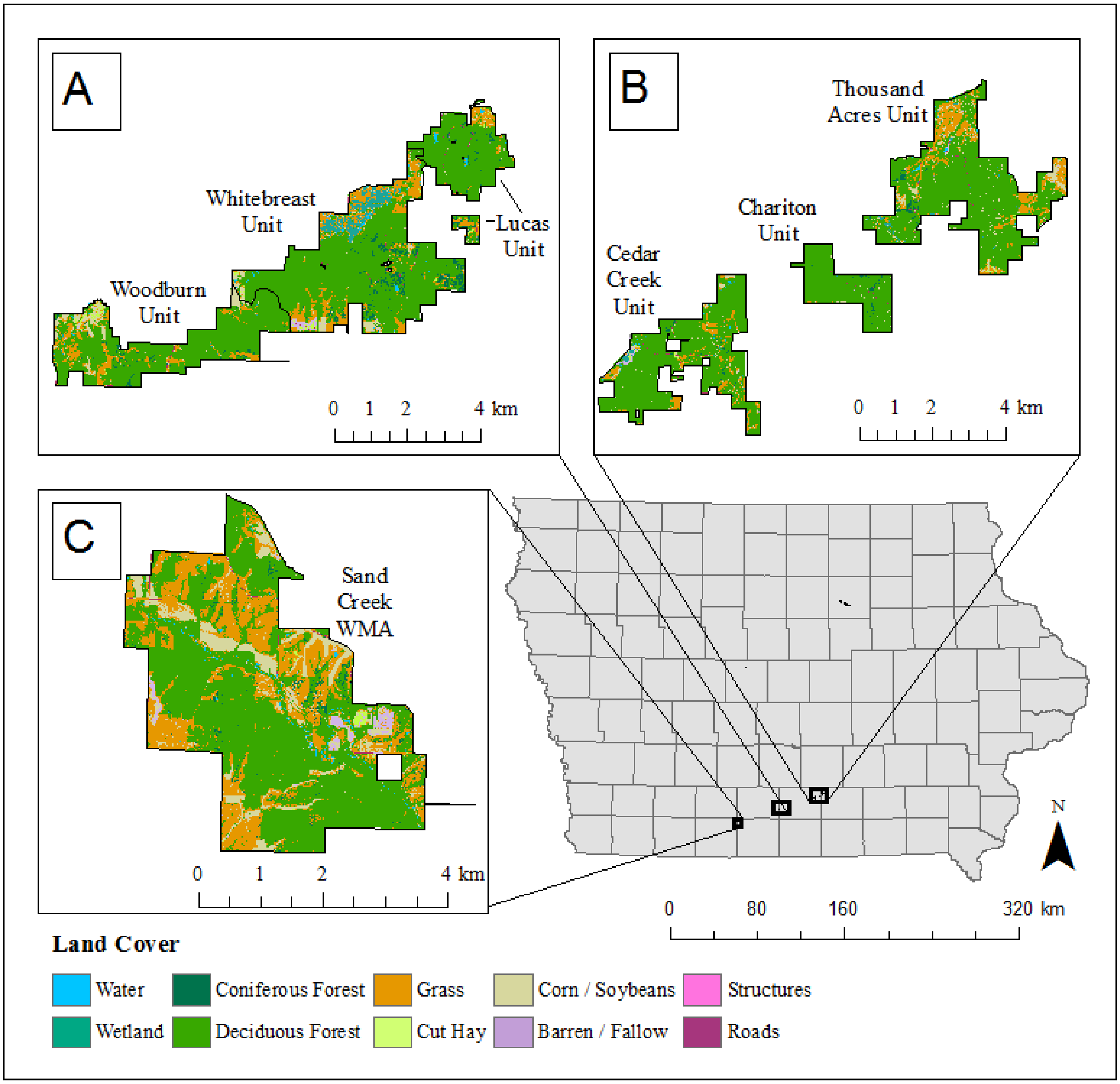

Figure 4.1. Land cover maps of the study areas used for breeding bird point counts in south-central Iowa, 2016-2019. Maps A and B represent the units of Stephen State Forest with the Stephens Forest and Stephens Forest – Thousand Acres Bird Conservation Areas (BCAs), respectively. Map C is of the Sand Creek Wildlife Management Area, located within the Sand Creek Woodland Savanna BCA. Land cover maps are modified from the Iowa Department of Natural Resource's 2009 High Resolution Land Cover of Iowa.

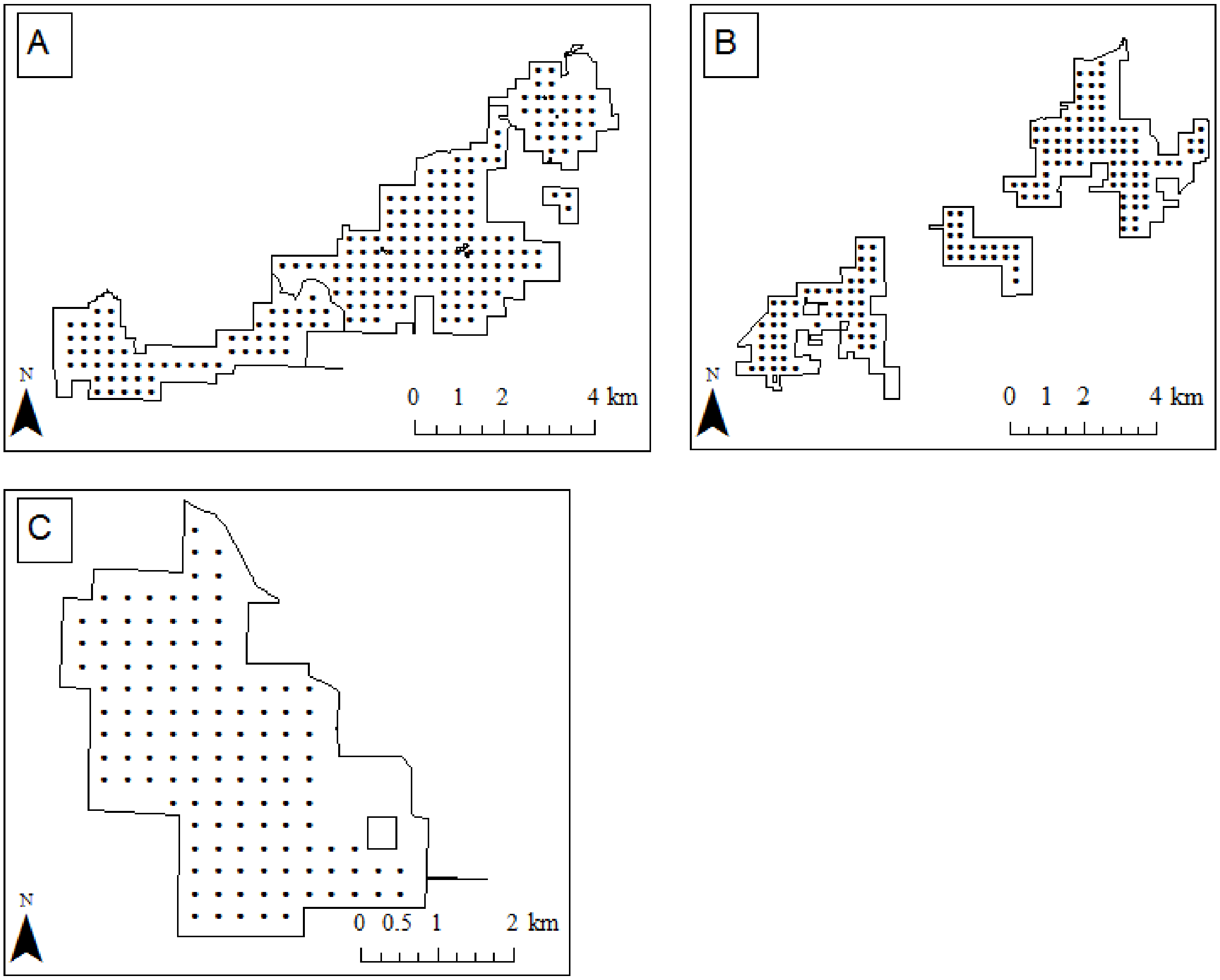

Figure 4.2. Point count locations used for surveys of breeding birds in south-central Iowa, 2016-2019, within the cores of three Iowa Bird Conservation Areas (BCAs): A) Stephens Forest BCA, B) Stephens Forest – Thousand Acres BCA, and C) Sand Creek Woodland Savanna BCA.

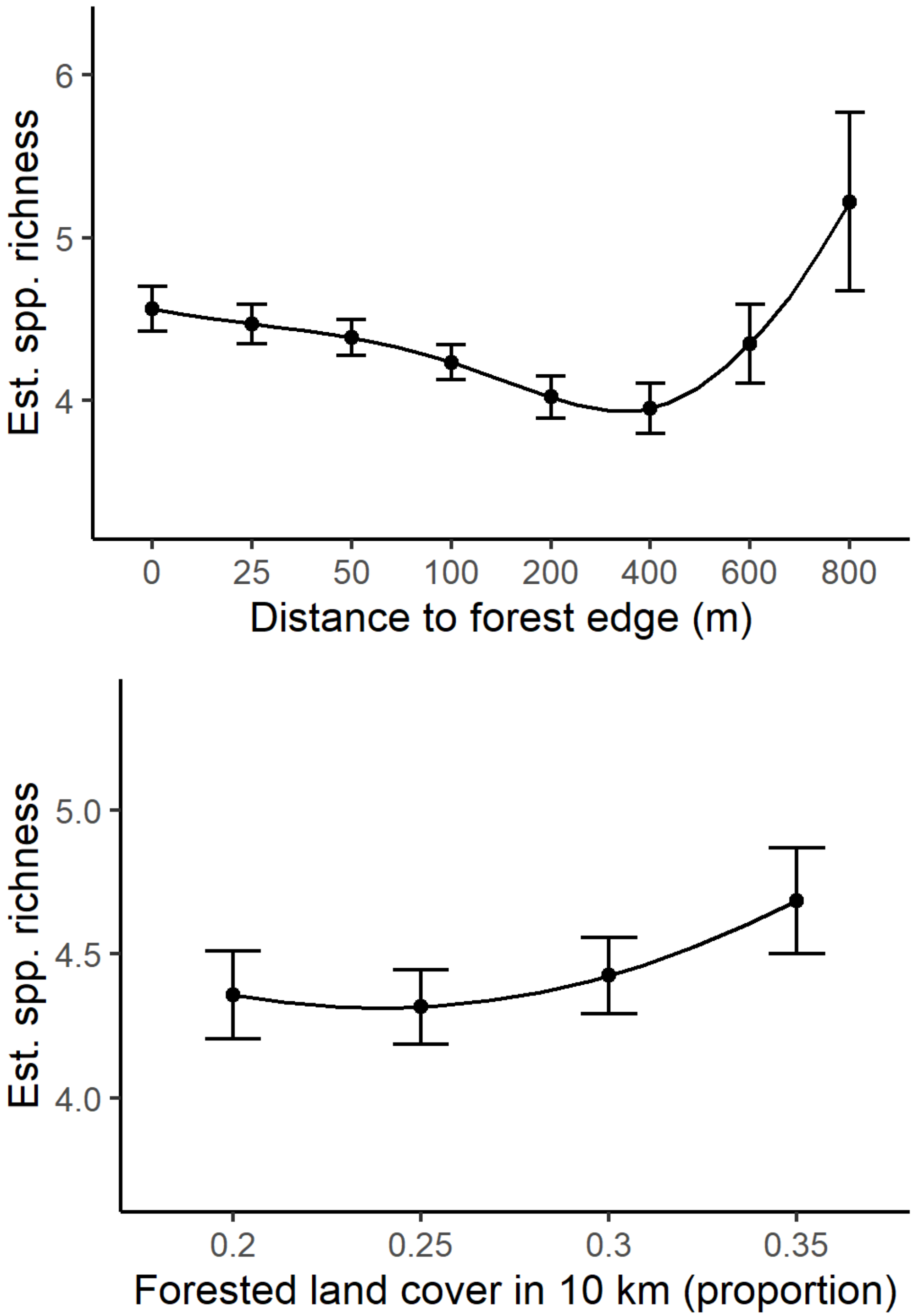

Figure 4.3. Species richness-habitat relationships for breeding bird Species of Greatest Conservation Need (SGCN) in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. Species richness was estimated by summing occupancy probabilities derived from hierarchical distance sampling models of 24 SGCN. Note differing y-axis scales and partially geometric x-axis scale for distance to forest edge. Error bars represent 95% confidence intervals.

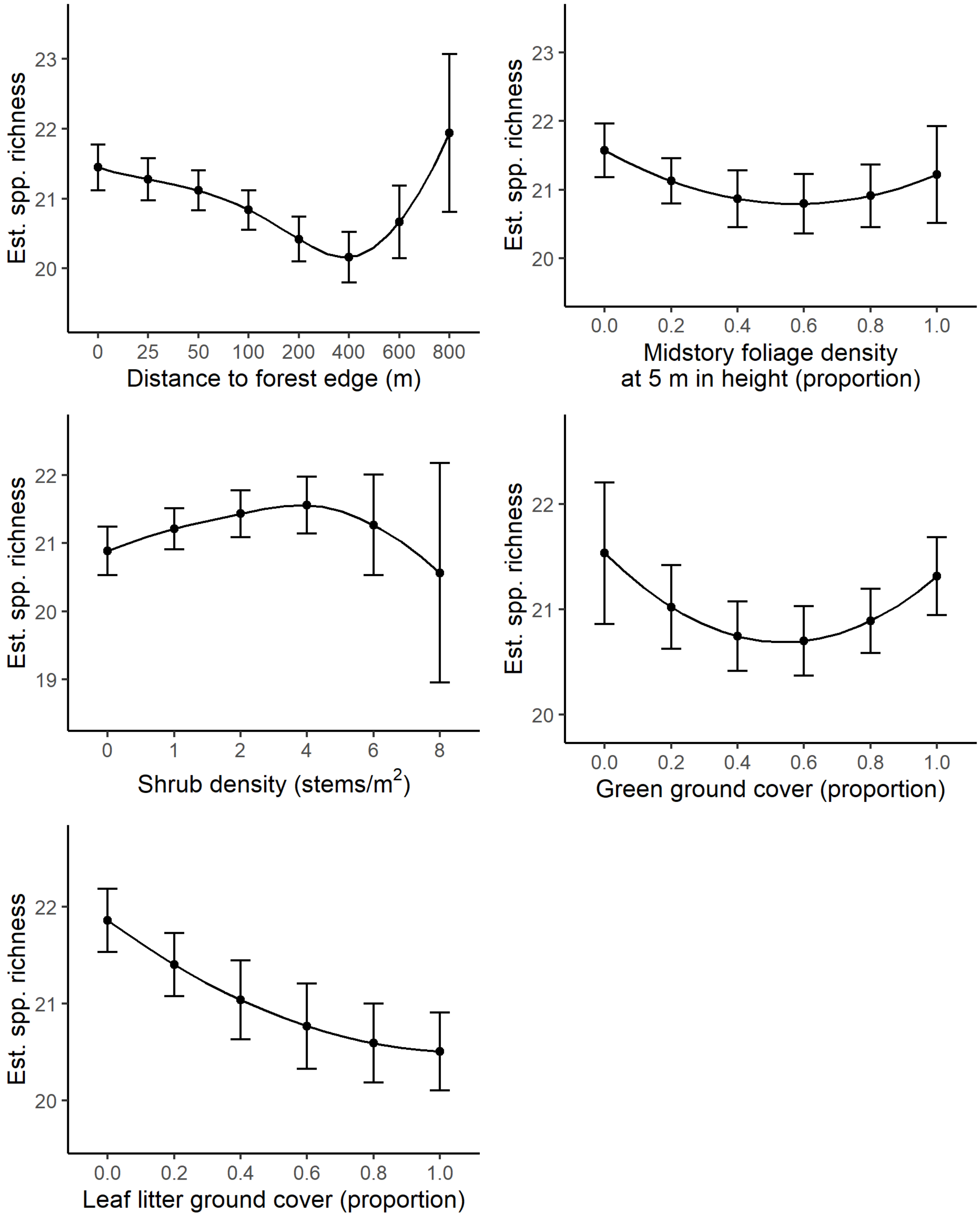

Figure 4.4. Species richness-habitat relationships for breeding birds in and near south-central Iowa forests, 2016-2019. Data are from point counts (k = 493 points) visited twice per breeding season (n = 3944 total surveys) and were averaged across all years and visits for each point. Species richness was estimated by summing occupancy probabilities derived from hierarchical distance sampling models of 77 species. Note differing y-axis scales and partially geometric axis scales for distance to forest edge and shrub density. Error bars represent 95% confidence intervals.

CHAPTER 5. GENERAL CONCLUSIONS

Our results affirm that the three primarily forested Iowa Bird Conservation Areas in south-central Iowa are important to Iowa Species of Greatest Conservation Need and overall forest bird communities. We found that sites within these BCAs with a higher proportion of landscape scale forest cover supported higher densities of SGCN such as Red-headed Woodpecker, Acadian Flycatcher, Wood Thrush, and Common Yellowthroat, higher general SGCN species richness, and higher overall species richness. These results are consistent with studies on Acadian Flycatcher and on bird communities as a whole within the eastern deciduous forest biome (Askins and Philbrick 1987; Bakermans and Rodewald 2006). Creation of forest edges and forest fragmentation are known to negatively impact forest bird diversity and density (Kroodsma 1982; Ambuel and Temple 1983), and we found that SGCN species richness was highest at the most interior forest points (~800 m from the edge), and that there were positive relationships between distance to edge and densities . Densities of forest-dwelling SGCN, such as Eastern Wood-Pewee, Acadian Flycatcher, and Wood Thrush, were also highest in the two most forested Bird Conservation Areas, Stephens and Thousand Acres. Taken together, these findings suggest that interior forests with minimal edge habitat are important for forest birds and should be conserved.

In contrast, there were some species within our study area that utilized edge habitats and open areas. Notably, Field Sparrow and Common Yellowthroat were among the top five most abundant SGCN in our study area. Both species had a positive relationship between density and distance to edge, and Field Sparrow density was negatively related to landscape scale forest cover. Edge and open areas were also important to other, less common SGCN, such as Henslow’s Sparrow and Bobolink, as evidenced by their relatively higher abundance at Sand

Creek, the least forested BCA, and their negative relationship between density and a binary forest cover covariate. To benefit the entire community of SGCN in this area, some edge and open habitat should be maintained in addition to conserving forest interiors.

Within forest stands, relationships between smaller habitat metrics and birds were less prevalent and less consistent. Tree species richness was positively associated overall bird species richness and Eastern Wood-Pewee densities were positively associated with oak, and Acadian Flycatcher densities were negative associated with shrubs, which is consistent with other studies (James 1971; Bakermans and Rodewald 2006; Sierzega 2016). Comparisons of other tree, midstory, and shrub metrics versus bird densities and diversity did not produce many other compelling relationships. Leaf litter cover was the most prevalent ground cover covariate in our models; it was positively associated with densities for five of ten individual species analyzed, but negatively associated with Common Yellowthroat densities, overall species richness, and SGCN species richness. However, in our study, we excluded canopy closure due to multicollinearity with variable such as leaf litter; other studies suggest that when these two factors are collinear, canopy closure may be the primary driver of bird community composition (Au et al. 2008).

Our results overall suggest that intact interior forest away from edges are especially beneficial to SGCN and the bird community as a whole, but that the maintenance of some edge and open habitat is needed for some SGCN. Landscape-scale forest cover was also positively associated with many SGCN and the bird community as a whole, though confounding factors such as agricultural disturbance or unquantified differences between BCAs make explain some of these relationships. Smaller scale habitat characteristics may be important to certain species, but overall, landscape and forest edge appear to be the primary drivers of bird densities and diversity in south-central Iowa forests.

The findings of this study served several practical purposes. First, they provided important baseline data about the distribution and abundance of conservation priority species in these areas. Second, these findings provided information on bird-habitat relationships and recommendations that can be used by forest managers in south-central Iowa. Third, the maps within the appendix of this document provided spatial information about the abundance of conservation priority breeding birds and overall breeding bird diversity which indicates hotspots for breeding birds; this information will be used by local organizations to inform construction of a birding trail.

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APPENDIX A: SUPPLEMENTAL TABLES

Table A1. Cumulative basal area of each living tree species and stranding dead trees observed in variable radius 1 m factor forestry prism plots (k = 493) in south-central Iowa forests in 2019. The ten (10) most abundant tree species are bolded. * Non-native, non-naturalized conifer only occurring in planted stands.

Common Name	Scientific Name	Total basal area (m^2/ha)
Red Pine*	Pinus resinosa*	7
White Pine*	**Pinus strobus***	**184**
Red Cedar	Juniperus virginiana	63
Cottonwood	Populus deltoides	112
willow sp.	Salix sp.	2
Bitternut Hickory	**Carya cordiformis**	**184**
Shagbark Hickory	**Carya ovata**	**907**
Black Walnut	**Juglans nigra**	**205**
White Oak	**Quercus alba**	**1452**
Bur Oak	**Quercus macrocarpa**	**505**
Shingle Oak	Quercus imbricaria	163
Red Oak	**Quercus rubra**	**469**
Black Oak	**Quercus velutina**	**399**
American Hophornbeam	Ostrya virginiana	105
Honey Locust	Gleditsia triacanthos	44
Black Locust	Robina pseudoacacia	71
Hackberry	**Celtis occidentalis**	**208**
Autumn Olive	Elaeagnus umbellata	1
Osage Orange	Maclura pomifera	26
mulberry sp.	Morus sp.	12
American Plum	Prunus americana	5
Black Cherry	Prunus serotina	76
Box Elder	Acer negundo	21
Silver Maple	Acer saccharinum	72
Ohio Buckeye	Aesculus glabra	37
American Elm	**Ulmus americana**	**488**
Slippery Elm	Ulmus rubra	104
Siberian Elm	Ulmus pumila	1
Basswood	Tilia americana	167
White Ash	Fraxinus americana	48
Black Ash	Fraxinus nigra	4
Green Ash	Fraxinus pennsylvanica	72
Standing dead wood (all species)		910

Table A2. Assessment of multicollinearity using generalized variance inflation factor (GVIF) and variance inflation factor (VIF). for south-central Iowa forest habitat characteristics, 2016-2019. We used a cutoff of GVIF (or VIF) < 3 and removed the variables with the highest VIF at a landscape scale (BCA) and a site scale (canopy closure). The first second column represents GVIF with all variables assessed simultaneously, the third column represents VIF after problematic variables were removed. GVIF was not necessary in our second round of multicollinearity assessment due to lack of categorical variables, hence the shift to VIF. Prop = proportion. GVIF values over 3 are in bold.

Variable	**Variable type**	**df**	**GVIF (all variables)**	**VIF (variables removed)**
Forest landcover within 1 km	Continuous	1	1.8	1.7
Forest landcover within 10 km	Continuous	1	**10.7**	1.3
Bird Conservation Area	Categorical	2	**12.5**	Removed
Distance to forest edge	Continuous	1	1.7	1.7
Live tree basal area	Continuous	1	**3.2**	2.7
Dead tree basal area	Continuous	1	1.2	1.1
Proportion oak	Continuous	1	1.8	1.7
Tree species richness	Continuous	1	2.5	2.2
Canopy closure	Continuous	1	**5.2**	Removed
Mean foliage density at 2.5 m	Continuous	1	1.8	1.7
Mean foliage density at 5 m	Continuous	1	2.1	2.0
Foliage density standard deviation	Continuous	1	1.5	1.5
Shrub density	Continuous	1	1.4	1.3
Grassy ground cover	Continuous	1	2.0	1.8
Green ground cover	Continuous	1	1.2	1.1
Litter ground cover	Continuous	1	2.6	2.5

Table A3. Results of exact binomial tests to determine forest obligate status for 10 breeding bird species of conservation and management concern in and near south-central Iowa forests, 2016-2019. Data were collected over the course of 3994 point count surveys at 493 unique points from 2016 to 2019. Birds were deemed "forest obligates" in our system if their detections at forest points were significantly higher than expected based on a one-tailed exact binomial test with success probability = 407/493 (0.826; the proportion of points in forest) and $\alpha = 0.05$. Species arranged by descending proportion of detections at forest points, and forest obligates are bolded.

Species	Detections (forest points)	Detections (all points)	Proportion of detections in forest	P-value
Acadian Flycatcher	**514**	**522**	**0.98**	**<0.00001**
Ovenbird	**2018**	**2061**	**0.98**	**<0.00001**
Wood Thrush	**552**	**574**	**0.96**	**<0.00001**
Scarlet Tanager	**682**	**710**	**0.96**	**<0.00001**
Eastern Wood-Pewee	**3173**	**3317**	**0.96**	**<0.00001**
Northern Flicker	**594**	**692**	**0.86**	**0.012**
Yellow-billed Cuckoo	695	841	0.83	0.5
Red-headed Woodpecker	170	212	0.80	0.8
Common Yellowthroat	805	1614	0.50	1.0
Field Sparrow	492	1003	0.49	1.0

Table A4. Species detected during breeding bird point count periods in and near south-central Iowan forests, 2016-2019, that were excluded from analyses. Reasons for exclusion include primary habitats that were not forest, shrubland, grassland, or similar habitat (usually wetland obligates; denoted by "habitat"), not being detected within 100 m of a survey point within the allotted 10-min survey ("incidental"), species that were almost exclusively detected as flyovers ("flyover"), species that migrate through the study area but do not breed ("migrant"), primarily nocturnal species ("nocturnal"), and species with few than 5 detections ("low detections") . We only supply the primary reason for exclusion; a species may meet multiple exclusion criteria.

Species	**Scientific**	**Exclusion Reason**
Canada Goose	*Branta canadensis*	habitat
Wood Duck	*Aix sponsa*	habitat
Northern Pintail	*Anas acuta*	habitat
Mallard	*Anas platyrhynchos*	habitat
Eurasian Collared-Dove	*Streptopelia decaocto*	incidental
Chimney Swift	*Chaetura pelagica*	flyover
Virginia Rail	*Rallus limicola*	habitat
American Bittern	*Botaurus lentiginosus*	habitat
Least Bittern	*Ixobrychus exilis*	habitat
Great Blue Heron	*Ardea herodias*	habitat
Green Heron	*Butorides virescens*	habitat
Yellow-crowned Night-Heron	*Nyctanassa violacea*	habitat
Turkey Vulture	*Cathartes aura*	flyover
Mississippi Kite	*Ictinia mississippiensis*	flyover
Bald Eagle	*Haliaeetus leucocephalus*	habitat
Killdeer	*Charadrius vociferus*	habitat
Least Sandpiper	*Calidris minutilla*	habitat
American Woodcock	*Scolopax minor*	nocturnal
Spotted Sandpiper	*Actitis macularius*	habitat
Eastern Screech-Owl	*Megascops asio*	nocturnal
Great Horned Owl	*Bubo virginianus*	nocturnal
Barred Owl	*Strix varia*	nocturnal
Belted Kingfisher	*Megaceryle alcyon*	habitat
American Kestrel	*Falco sparverius*	incidental
Yellow-bellied Flycatcher	*Empidonax flaviventris*	migrant
Alder Flycatcher	*Empidonax alnorum*	migrant
Least Flycatcher	*Empidonax minimus*	migrant
Horned Lark	*Eremophila alpestris*	low detections
Purple Martin	*Progne subis*	flyover
Tree Swallow	*Tachycineta bicolor*	flyover
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	flyover
Bank Swallow	*Riparia riparia*	flyover
Cliff Swallow	*Petrochelidon pyrrhonota*	flyover
Barn Swallow	*Hirundo rustica*	flyover
Marsh Wren	*Cistothorus palustris*	habitat
Swainson's Thrush	*Catharus ustulatus*	migrant

Table A4 continued

Species	**Scientific**	**Exclusion Reason**
Northern Mockingbird	*Mimus polyglottos*	low detections
House Finch	*Haemorhous mexicanus*	incidental
Clay-colored Sparrow	*Spizella pallida*	migrant
Northern Waterthrush	*Parkesia noveboracensis*	migrant
Tennessee Warbler	*Leiothlypis peregrina*	migrant
Mourning Warbler	*Geothlypis philadelphia*	migrant
Magnolia Warbler	*Setophaga magnolia*	migrant
Blackpoll Warbler	*Setophaga striata*	migrant
Yellow-throated Warbler	*Setophaga dominica*	migrant
Chestnut-sided Warbler	*Setophaga pensylvanica*	migrant
Black-throated Green Warbler	*Setophaga virens*	migrant
Wilson's Warbler	*Cardellina pusilla*	migrant
Blue Grosbeak	*Passerina caerulea*	incidental

APPENDIX B: SUPPLEMENTAL FIGURES

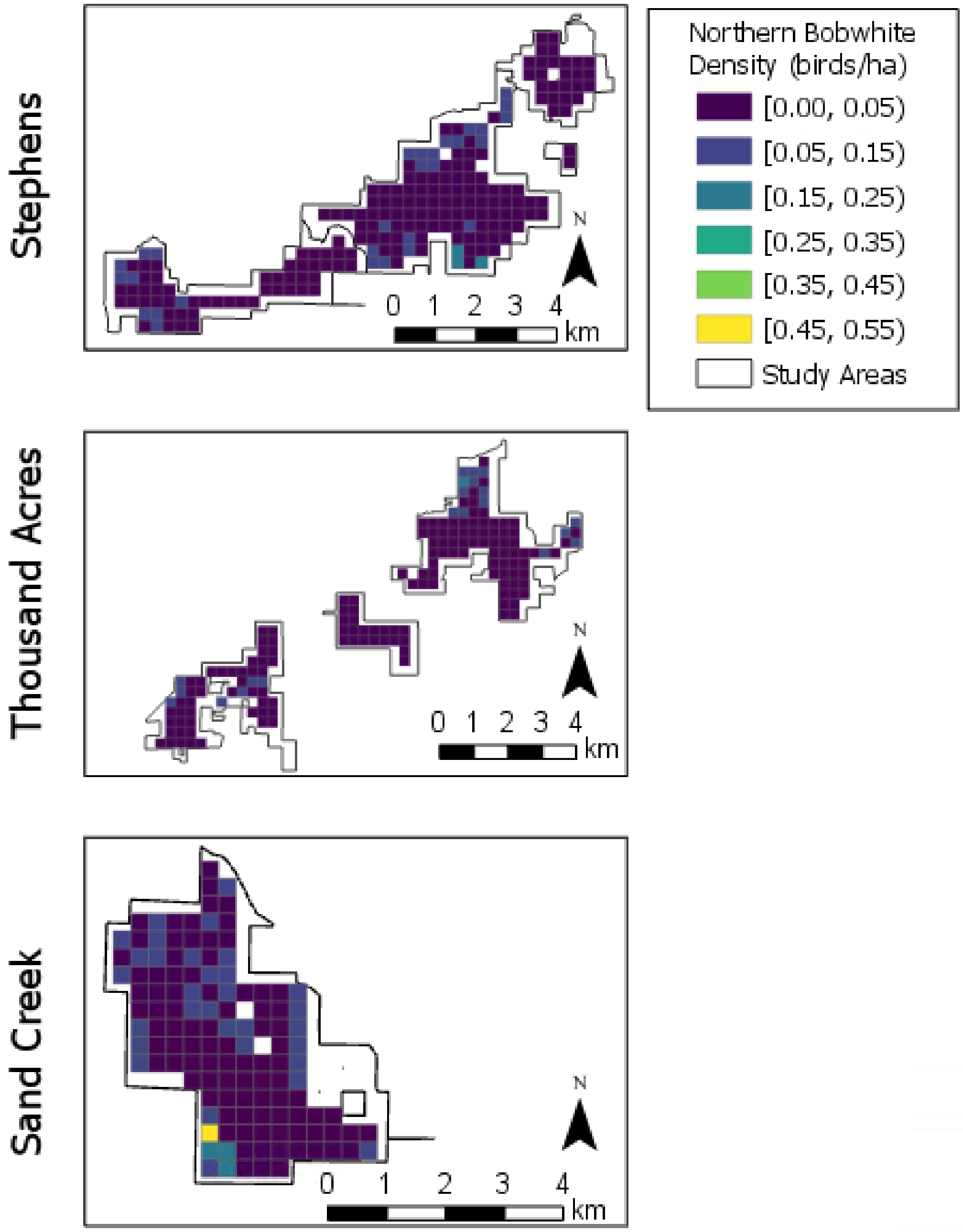

Figure A1. Density map of Northern Bobwhite in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

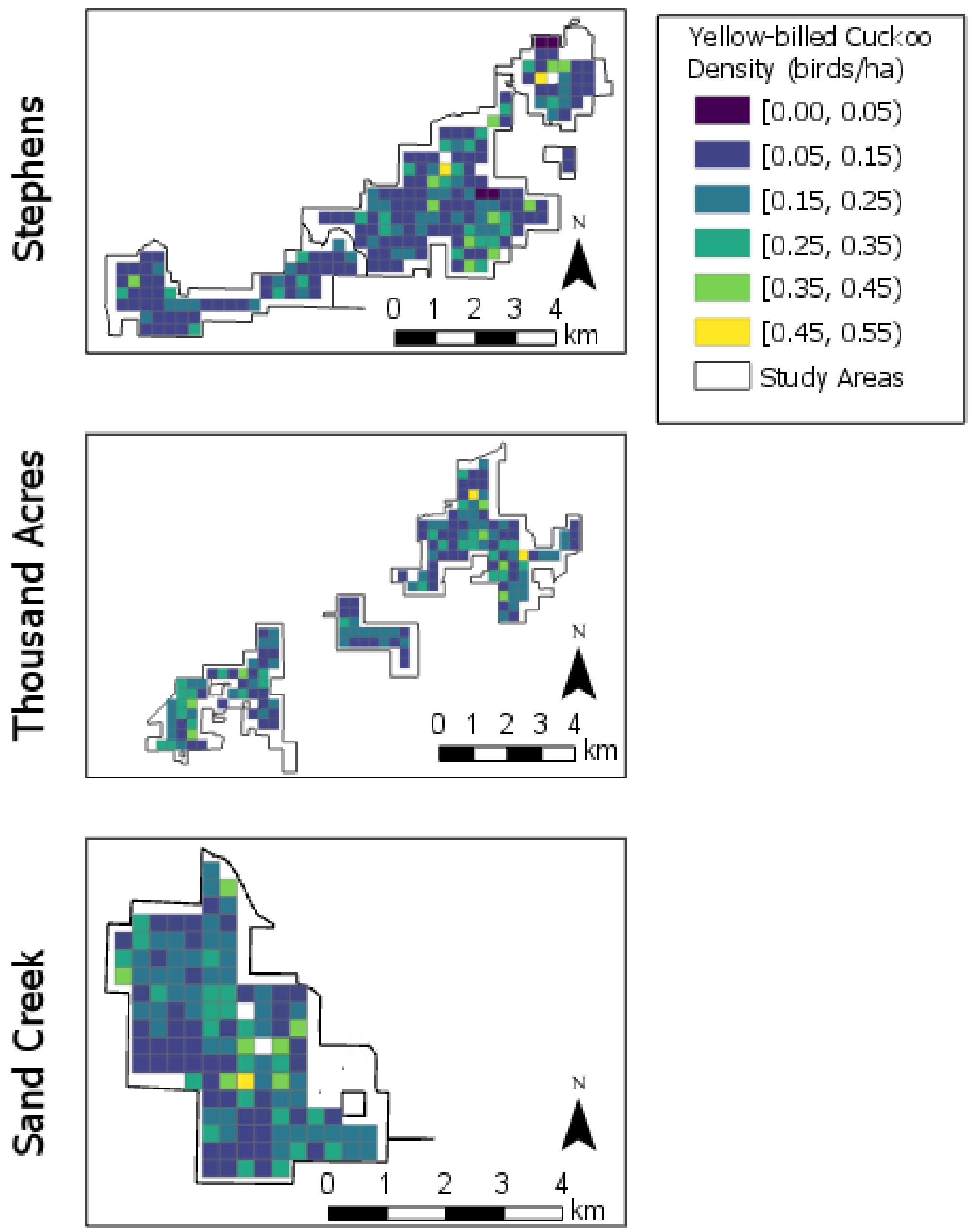

Figure A2. Density map of Yellow-billed Cuckoo in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

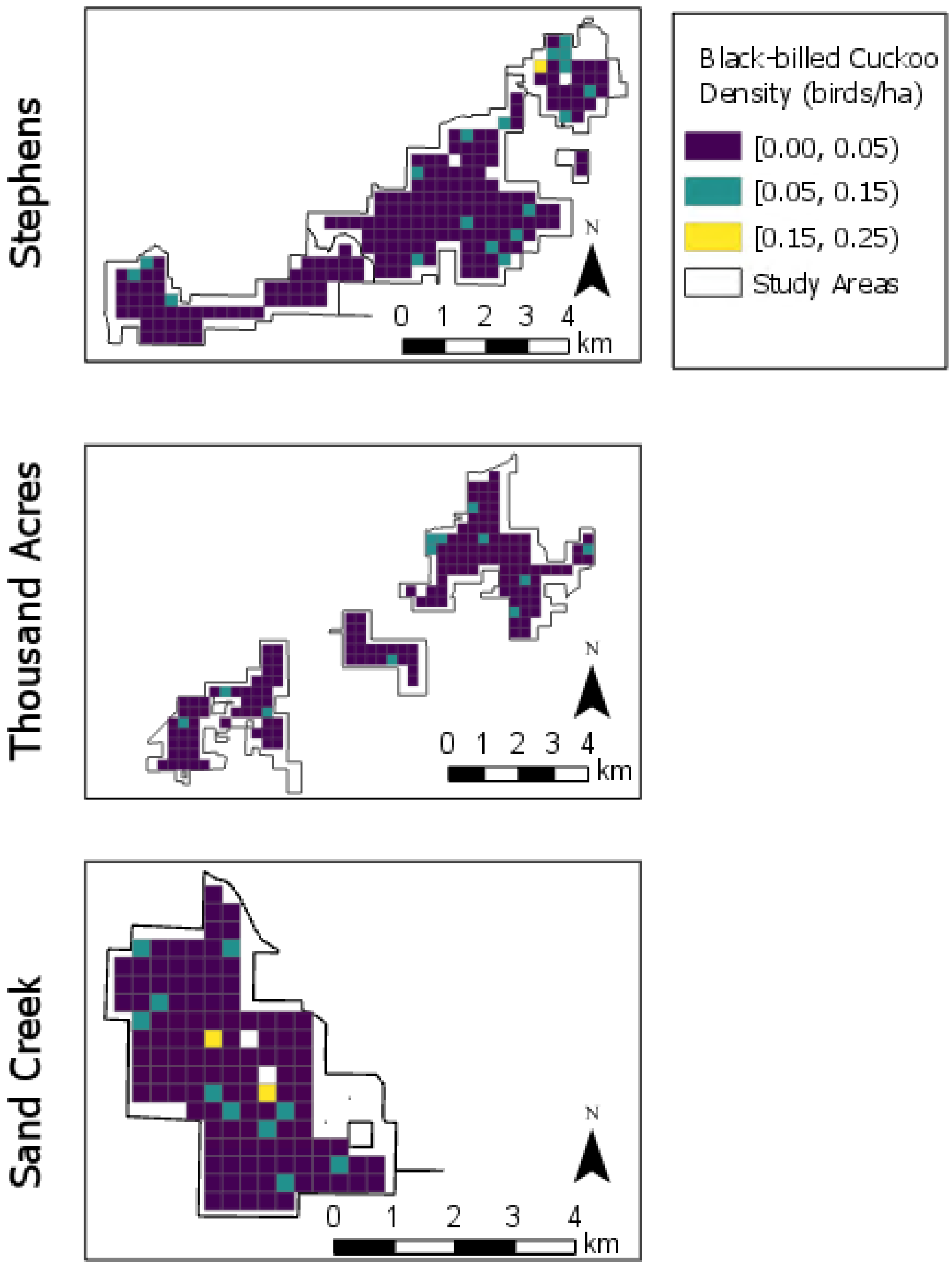

Figure A3. Density map of Black-billed Cuckoo in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

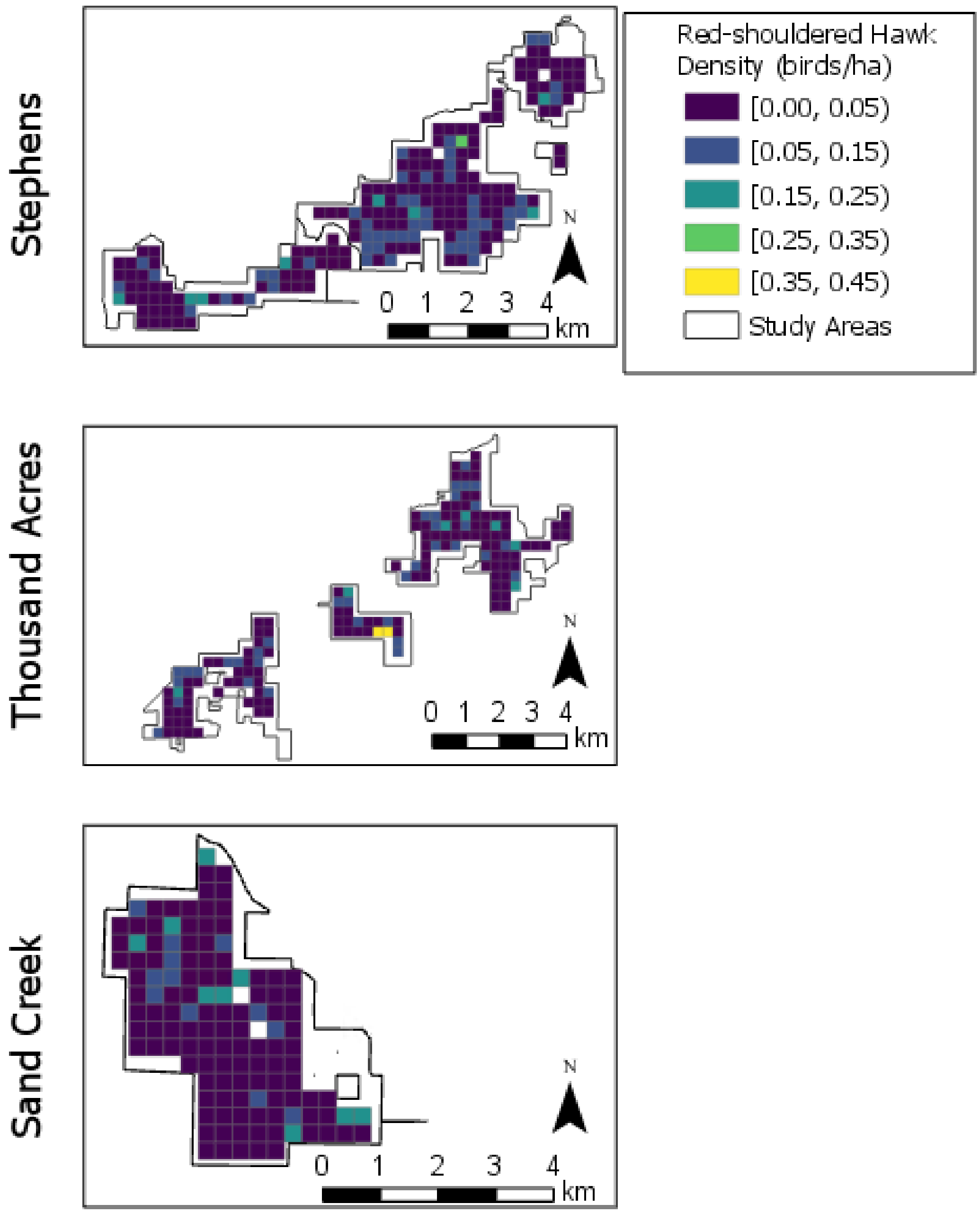

Figure A4. Density map of Red-shouldered Hawk in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

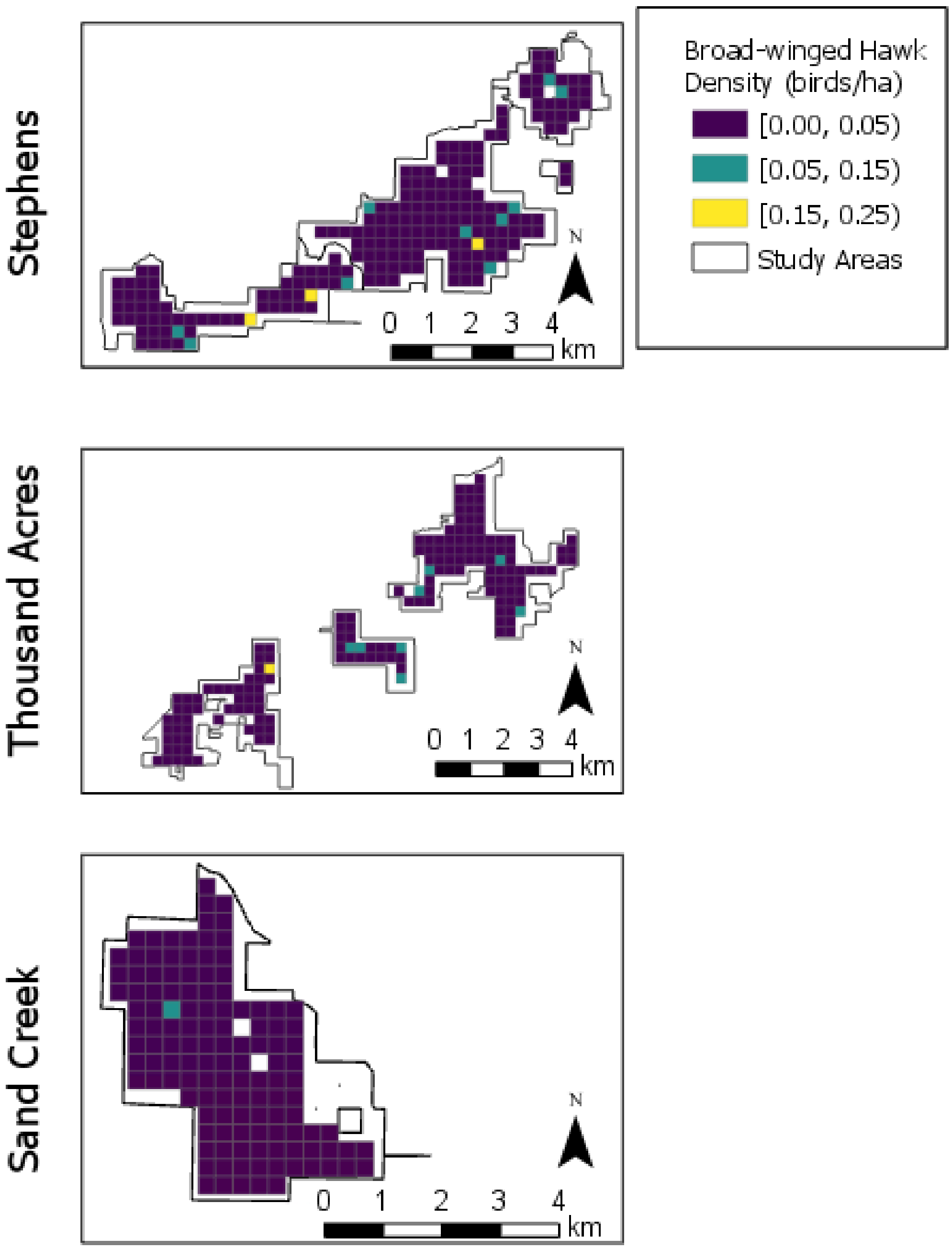

Figure A5. Density map of Broad-winged Hawk in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

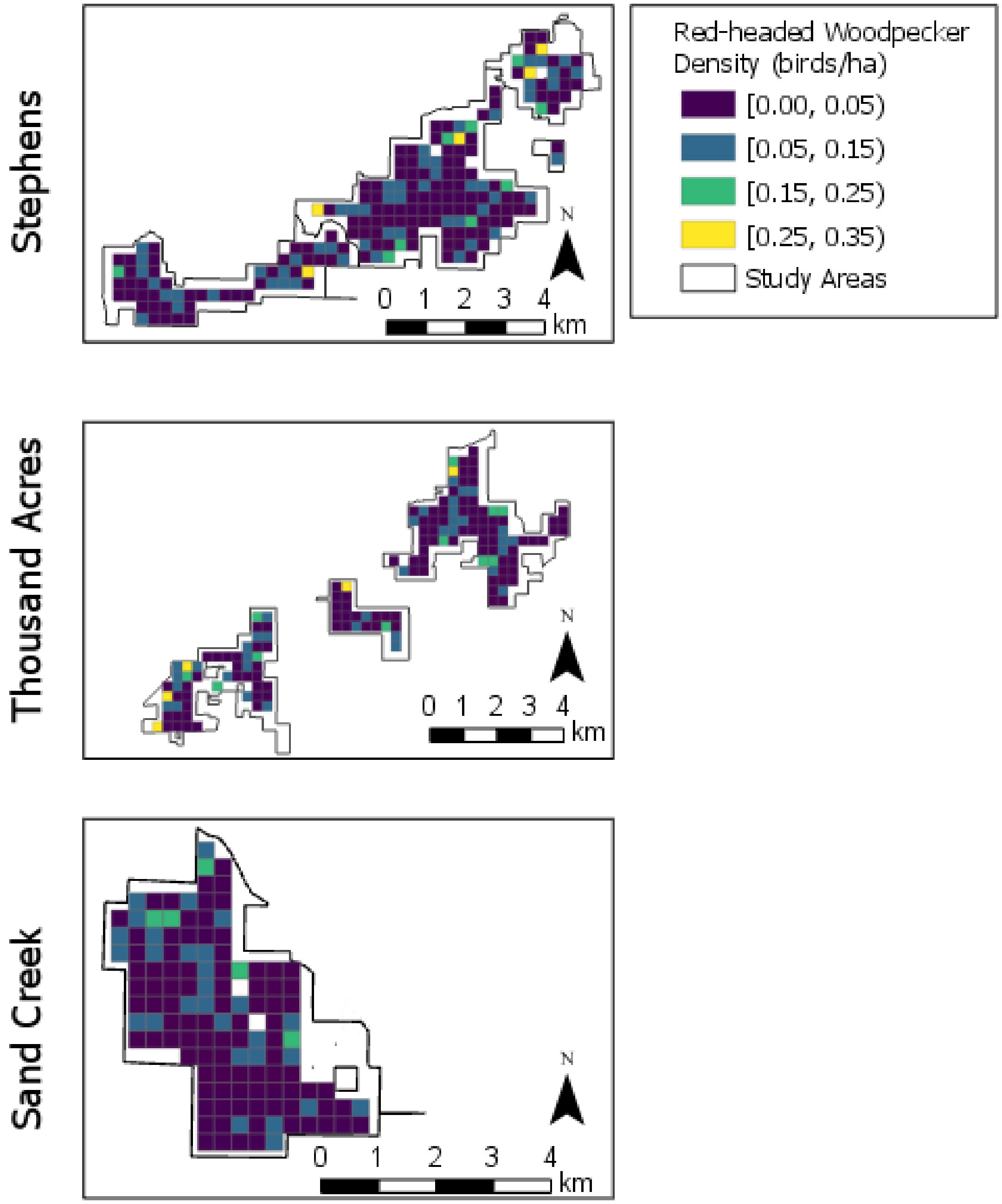

Figure A6. Density map of Red-headed Woodpecker in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

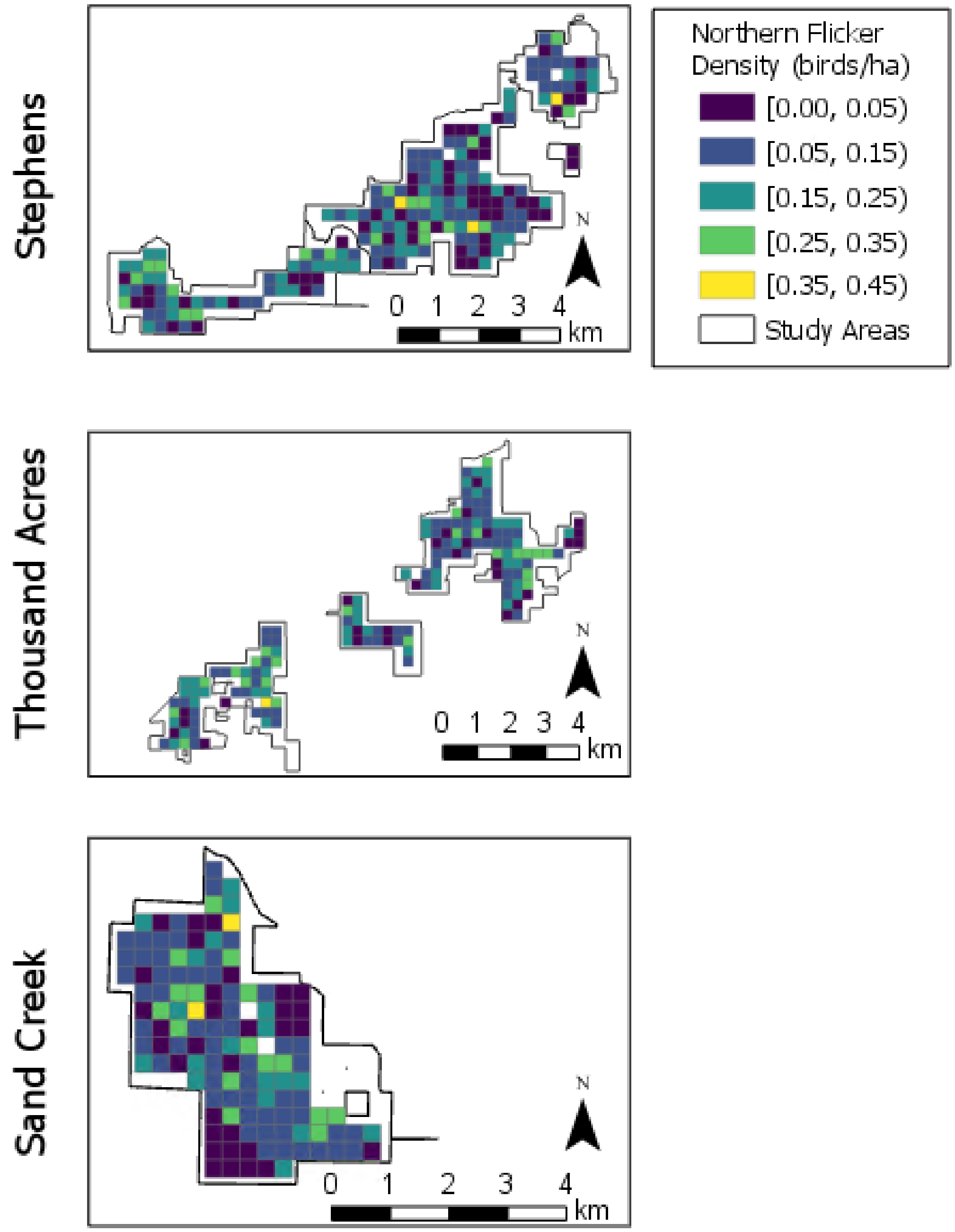

Figure A7. Density map of Northern Flicker in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

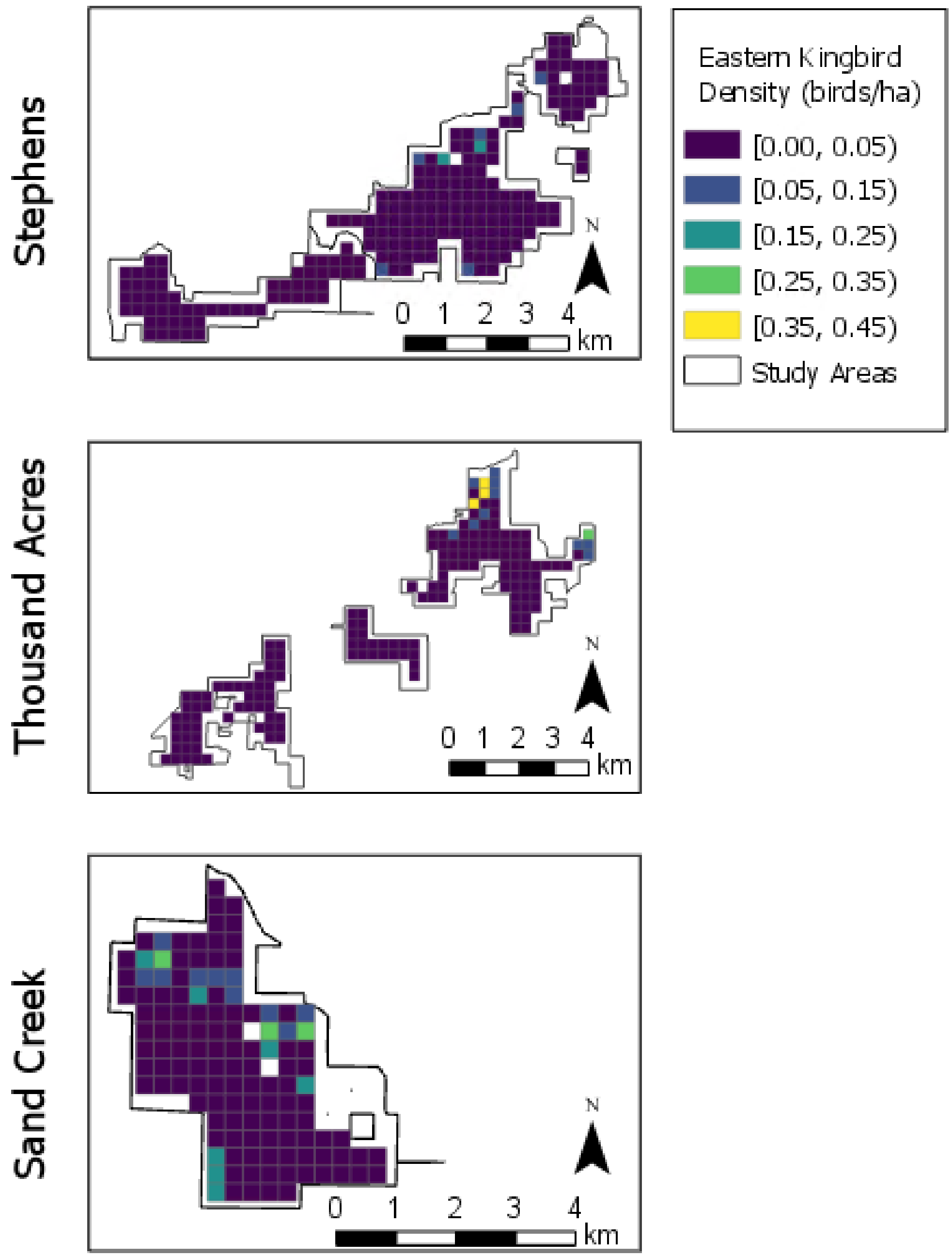

Figure A8. Density map of Eastern Kingbird in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

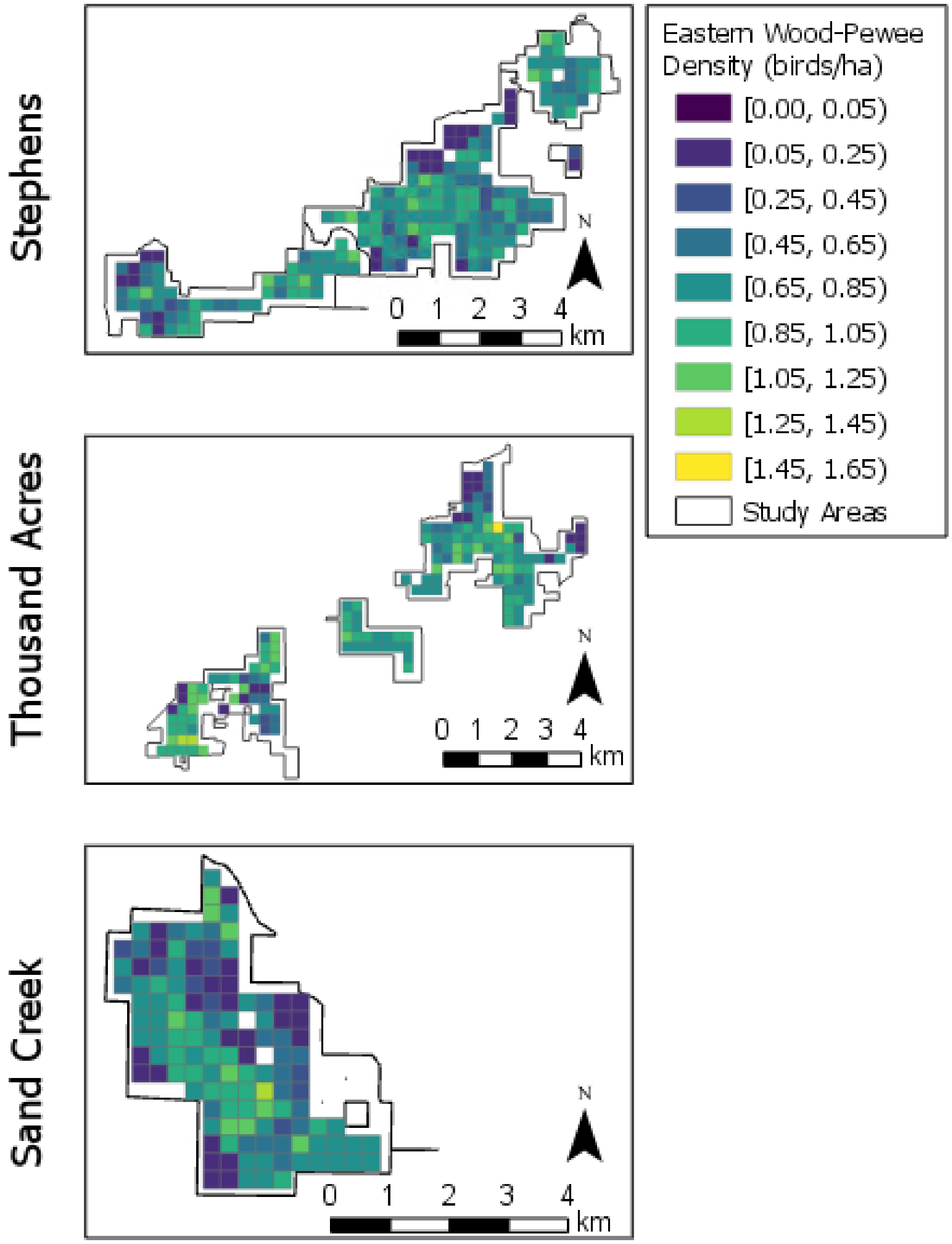

Figure A9. Density map of Eastern Wood-Pewee in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

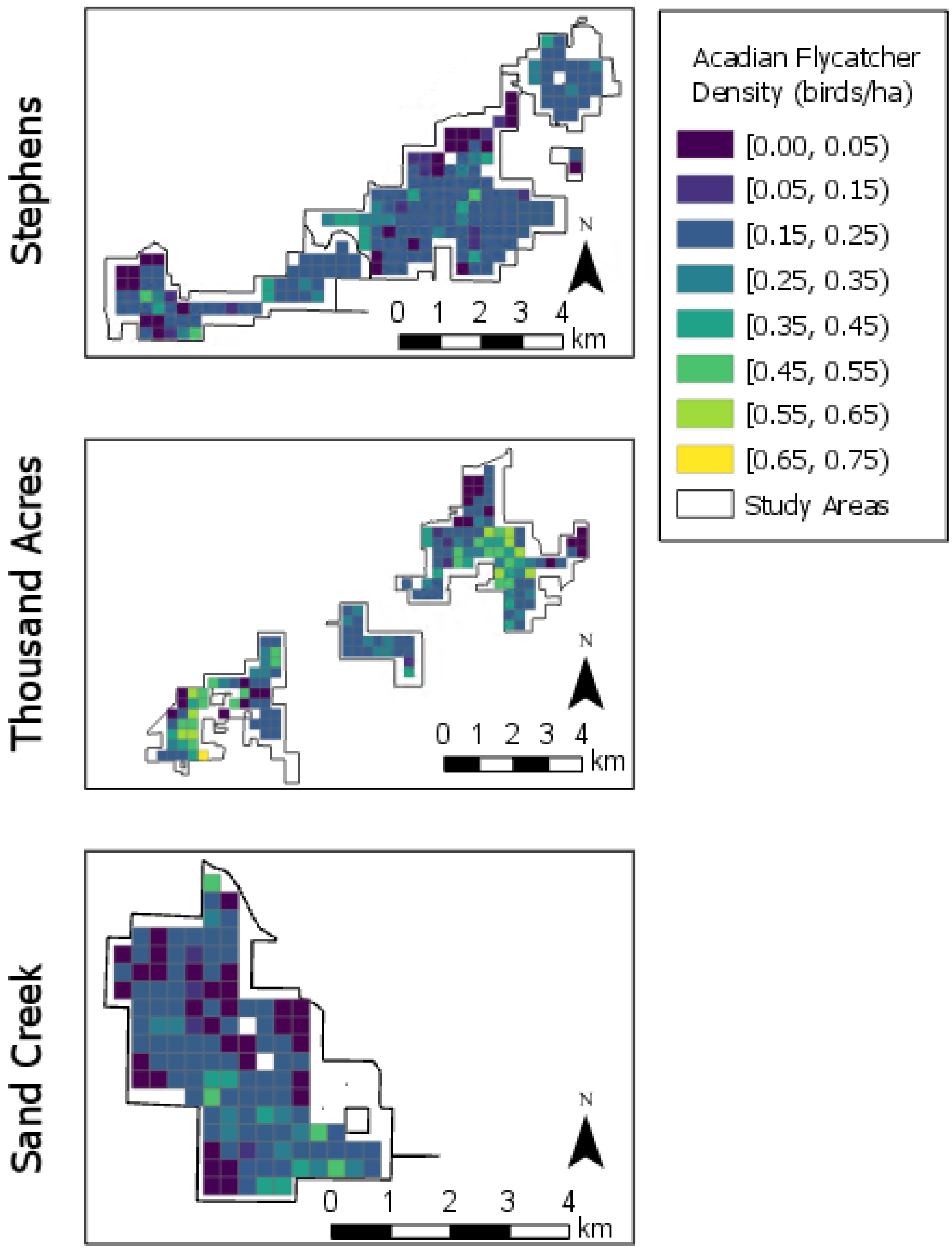

Figure A10. Density map of Acadian Flycatcher in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

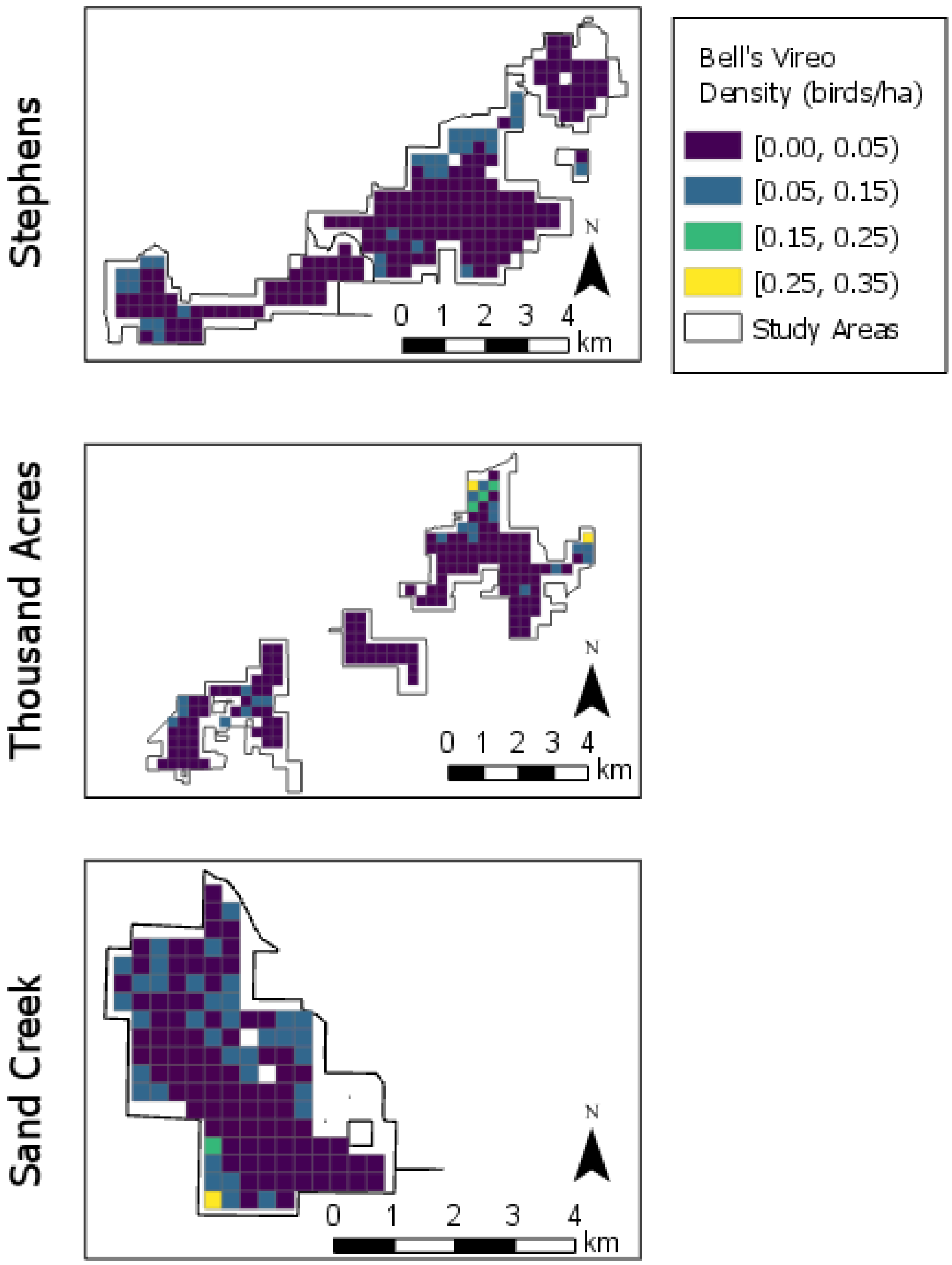

Figure A11. Density map of Bell's Vireo in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

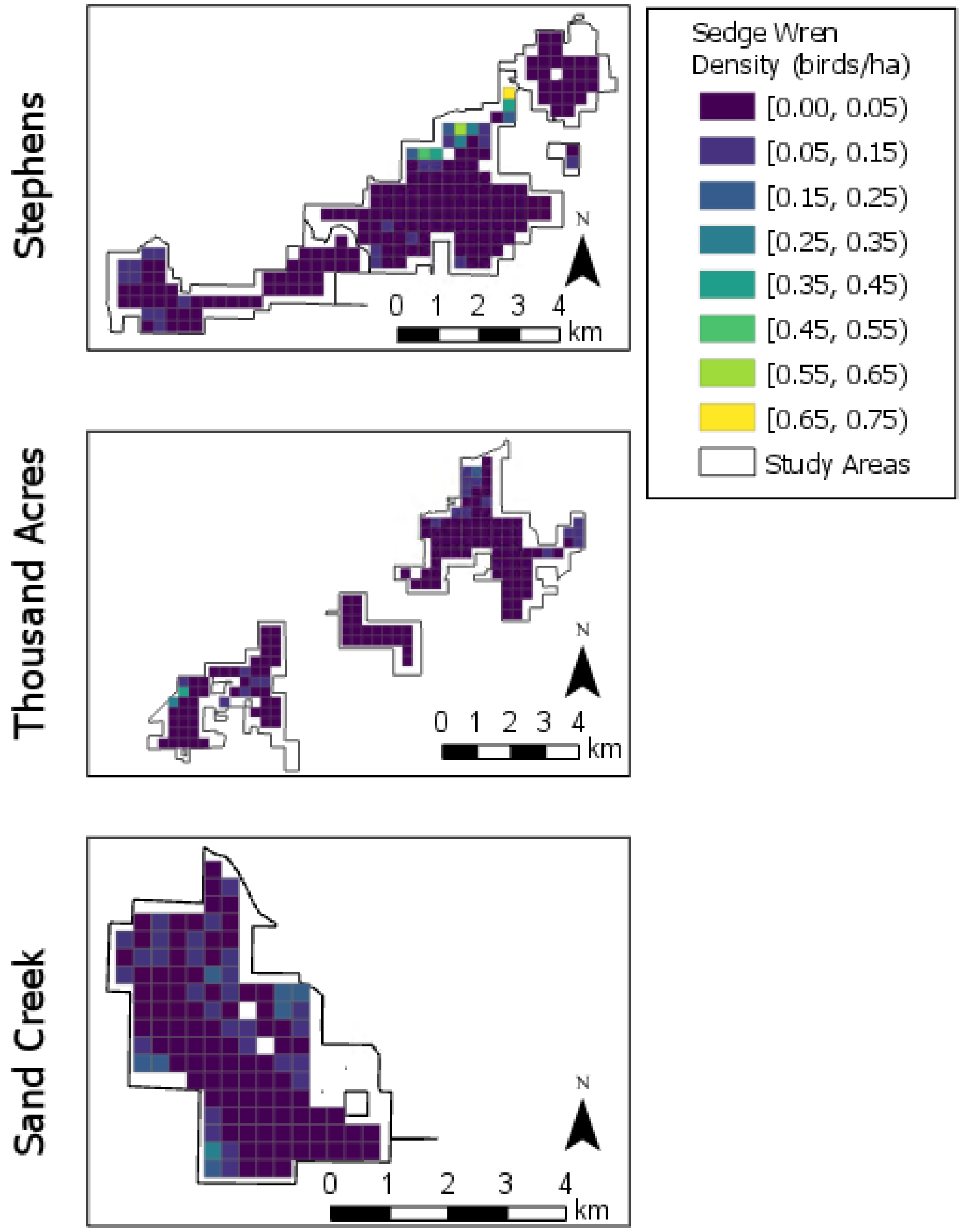

Figure A12. Density map of Sedge Wren in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

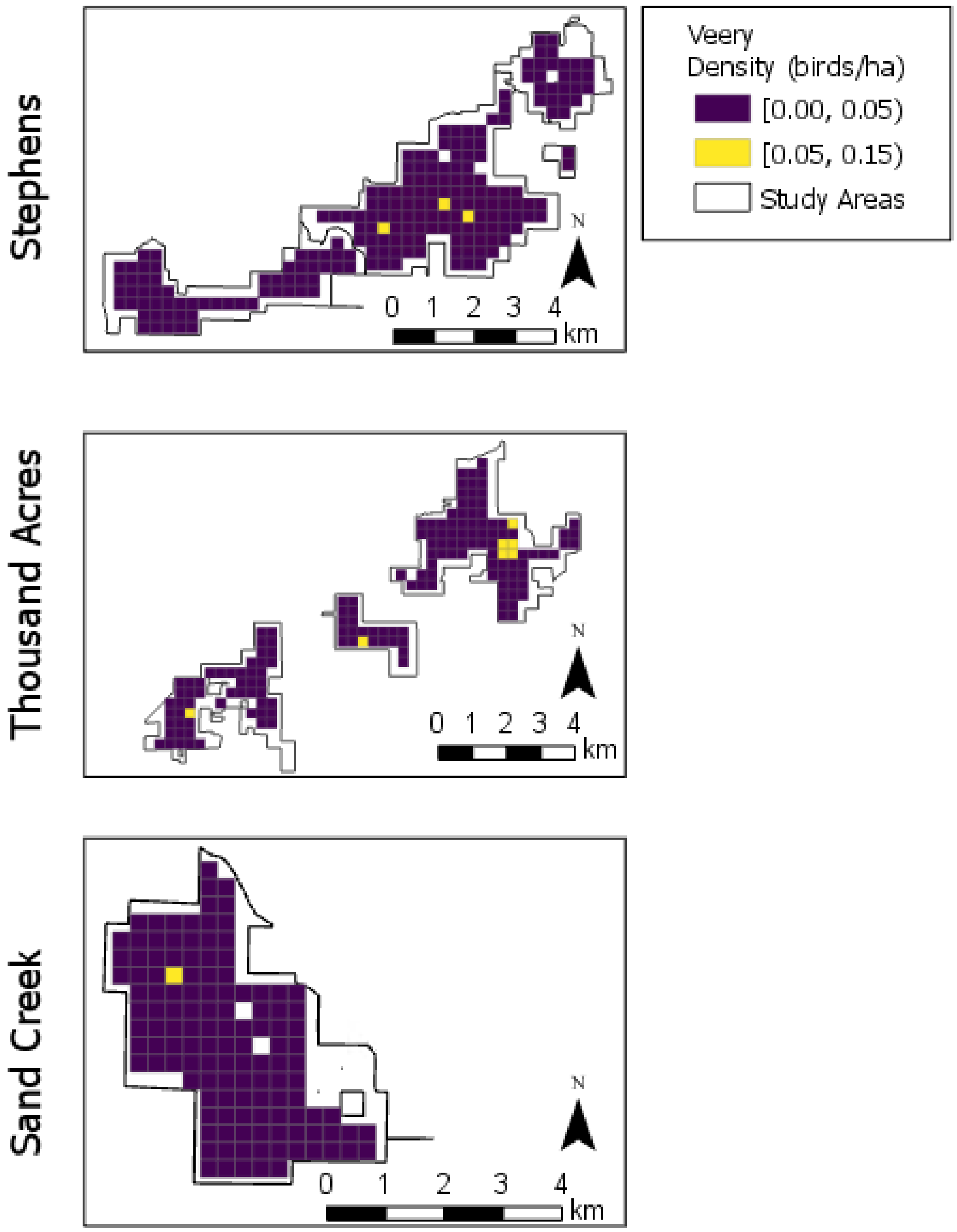

Figure A13. Density map of Veery in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

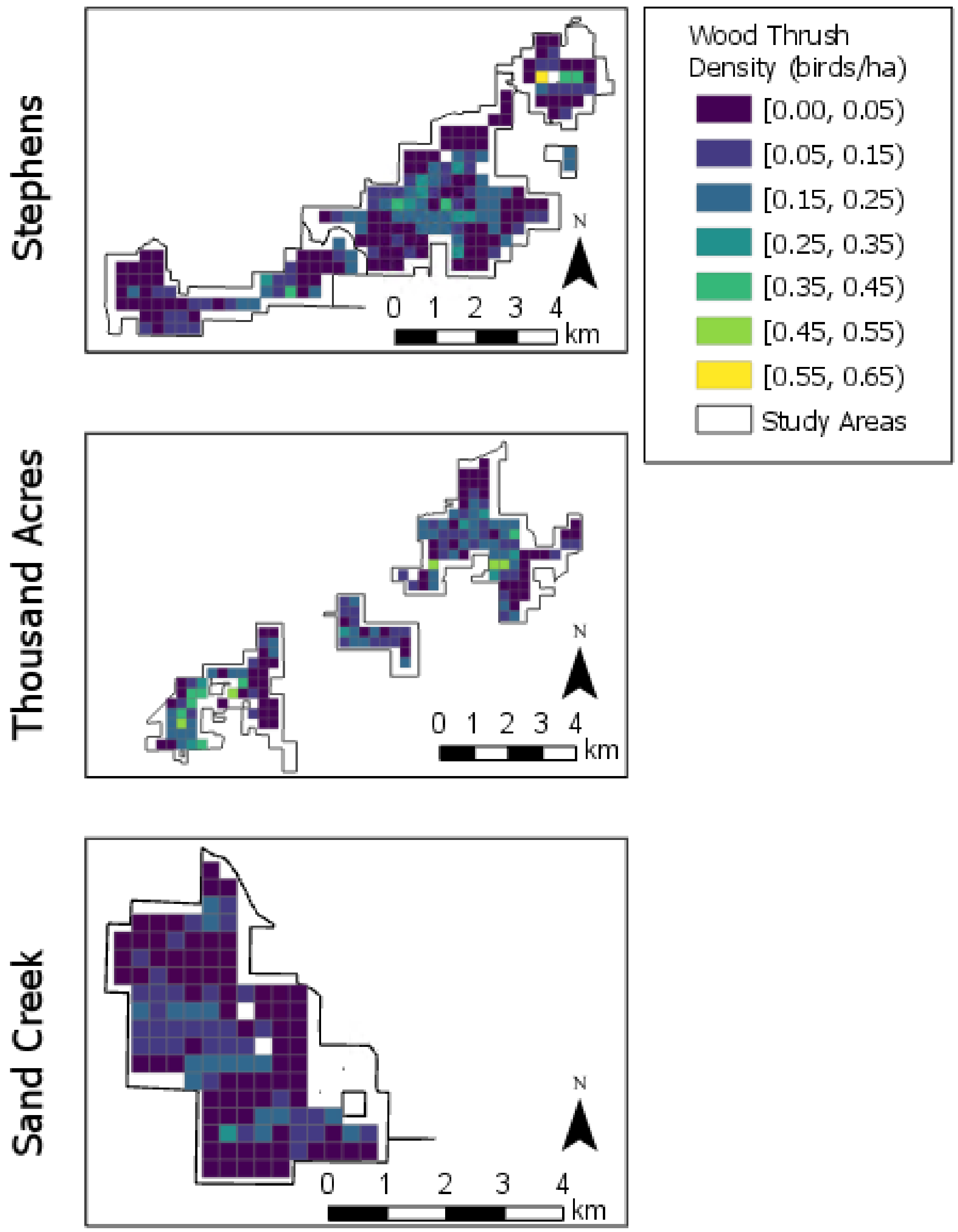

Figure A14. Density map of Wood Thrush in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

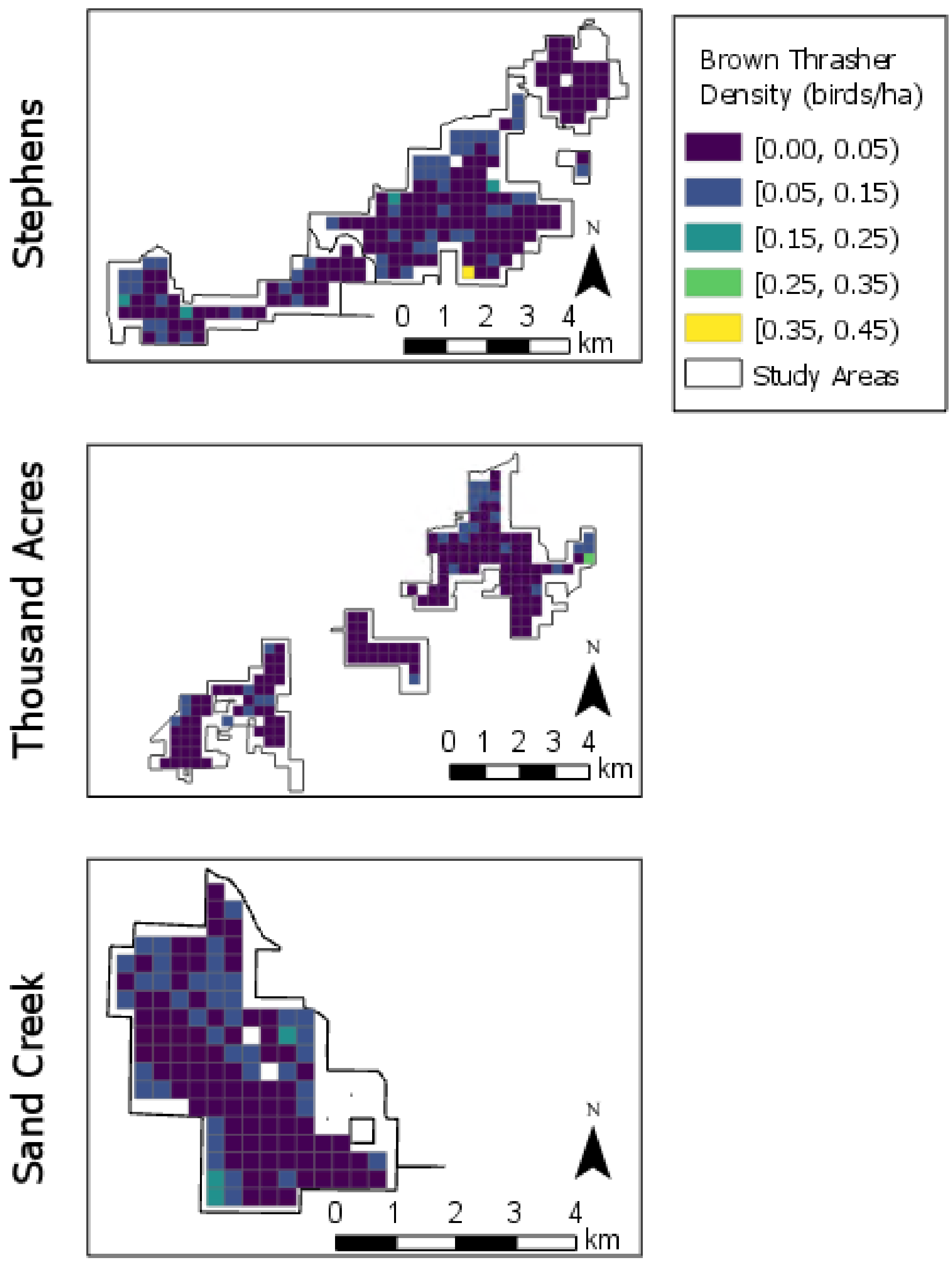

Figure A15. Density map of Brown Thrasher in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

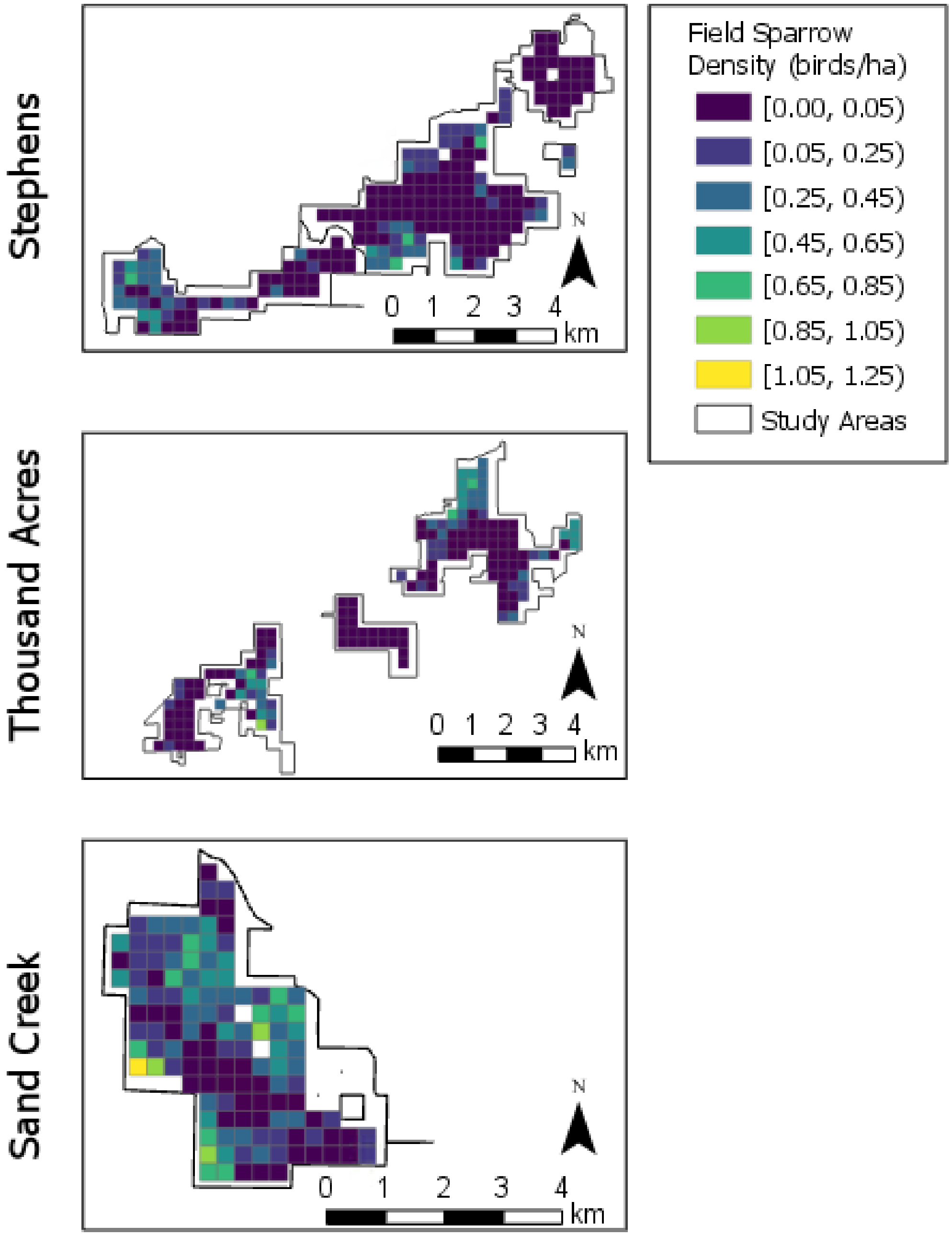

Figure A16. Density map of Field Sparrow in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

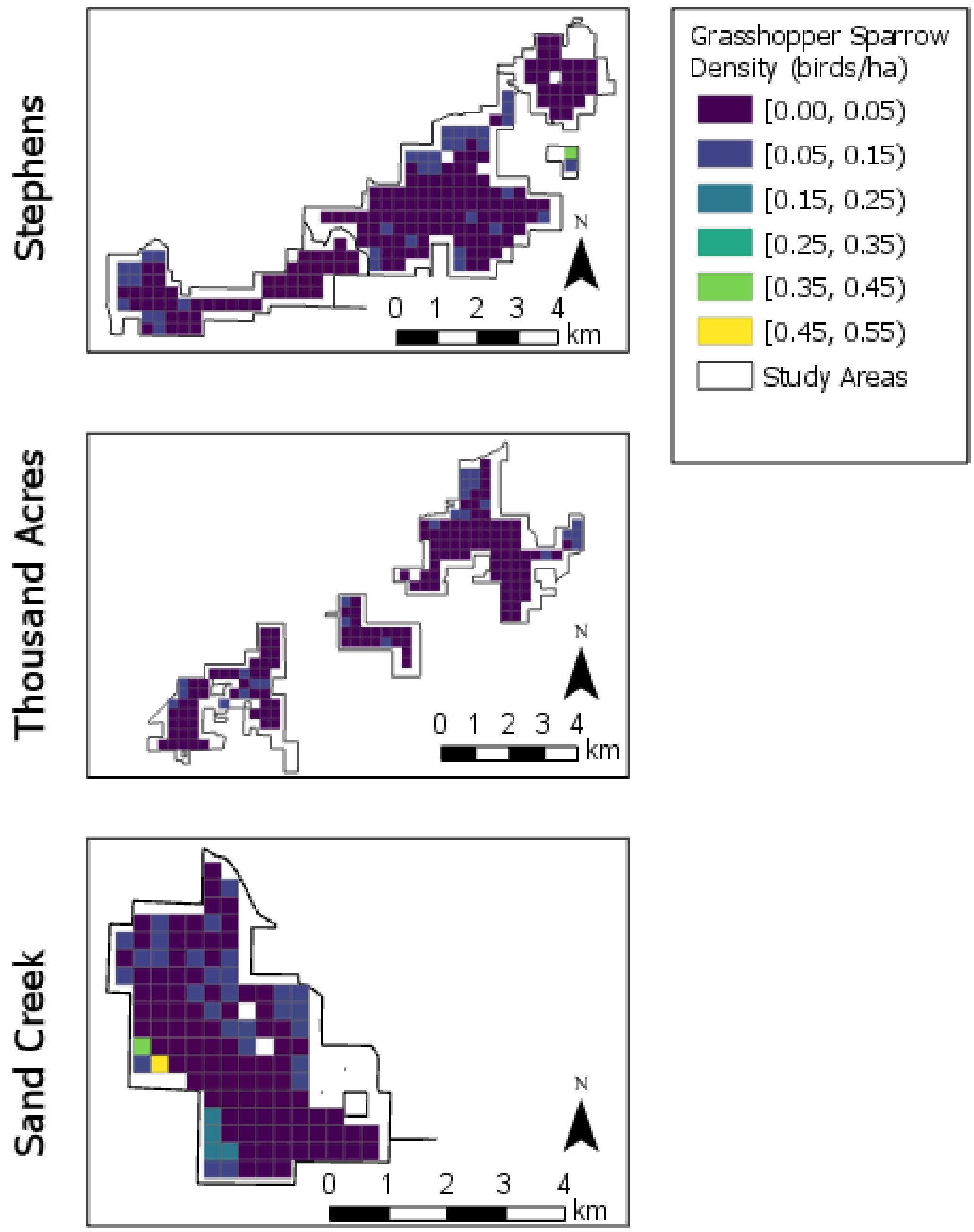

Figure A17. Density map of Grasshopper Sparrow in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

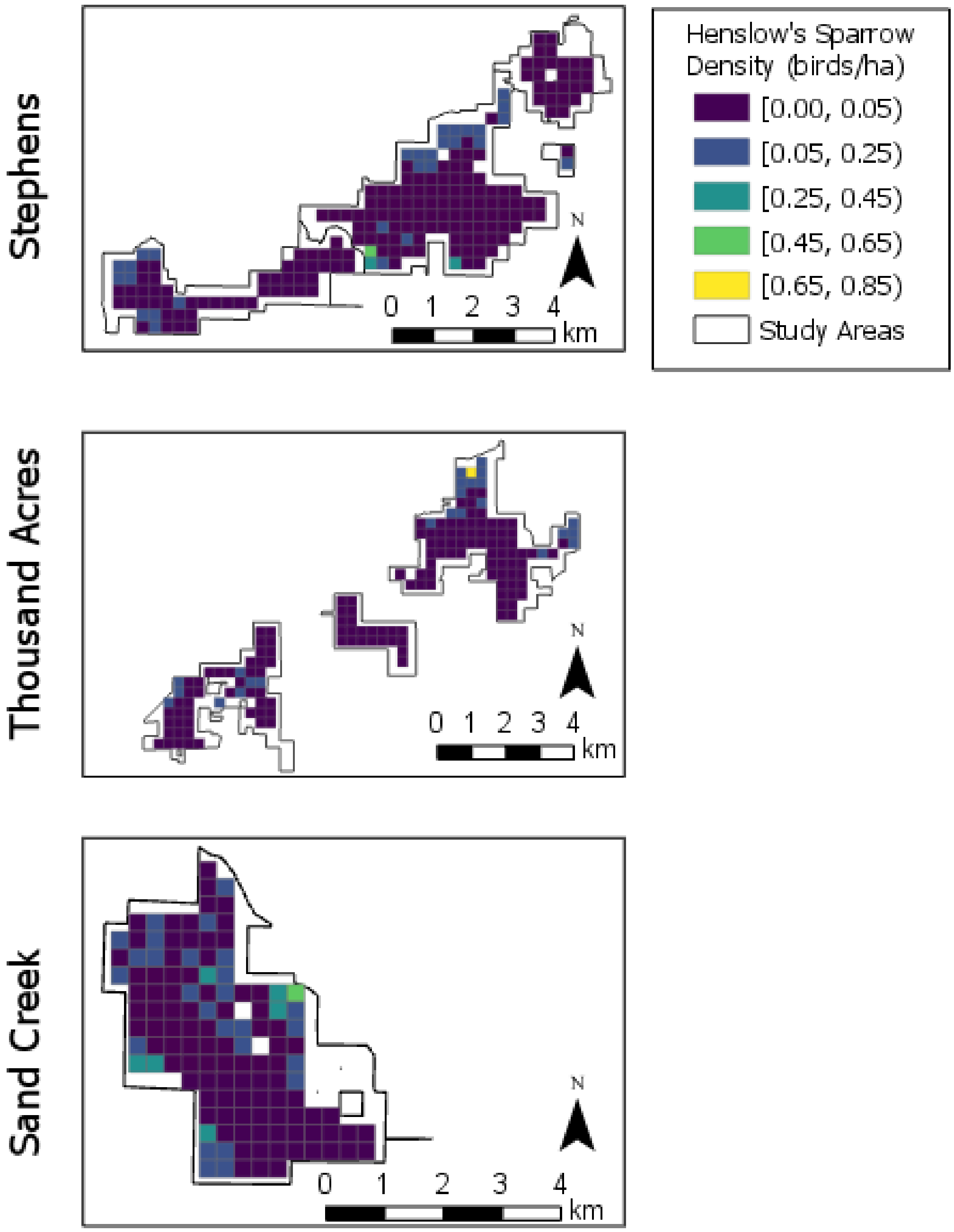

Figure A18. Density map of Henslow's Sparrow in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

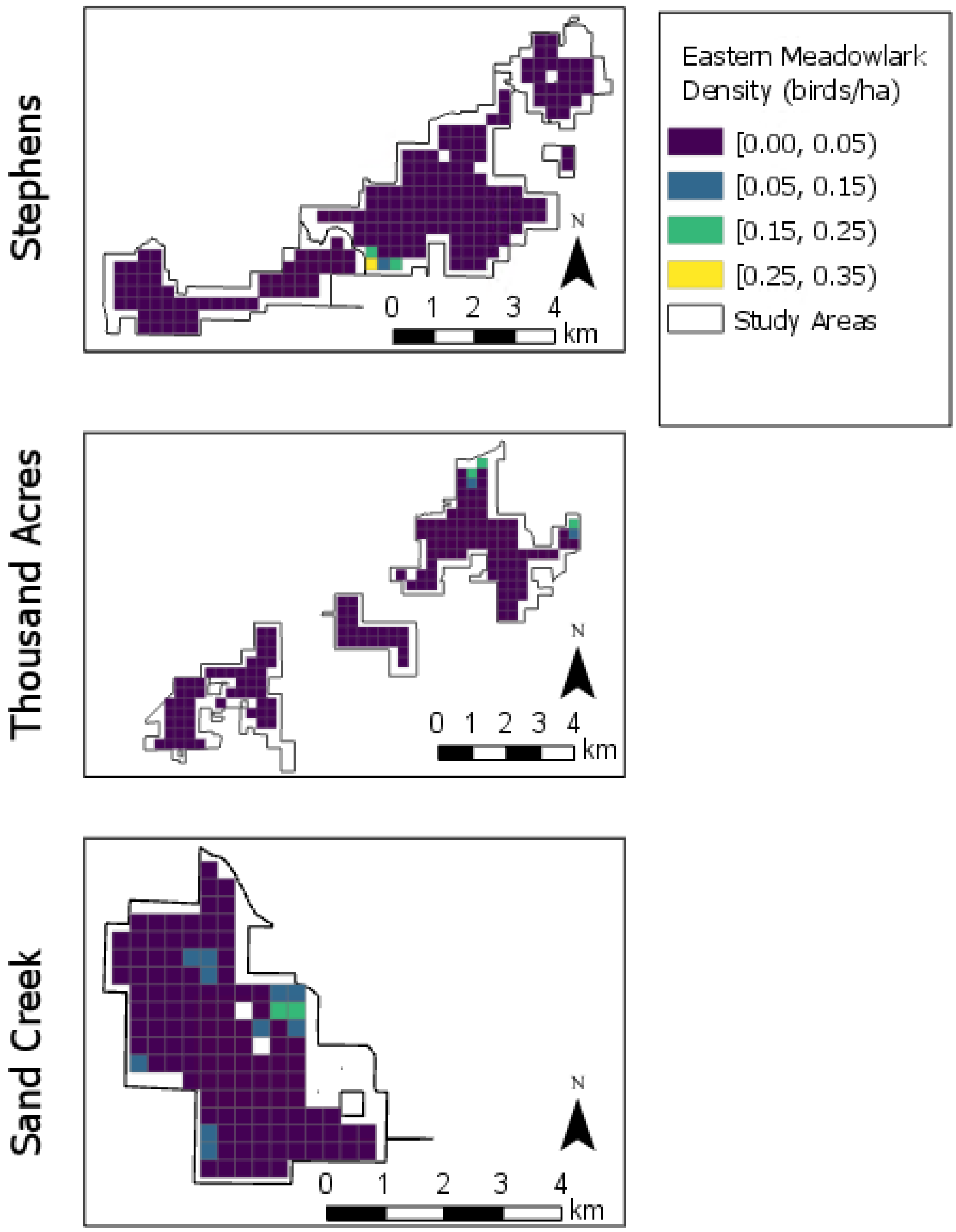

Figure A19. Density map of Eastern Meadowlark in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

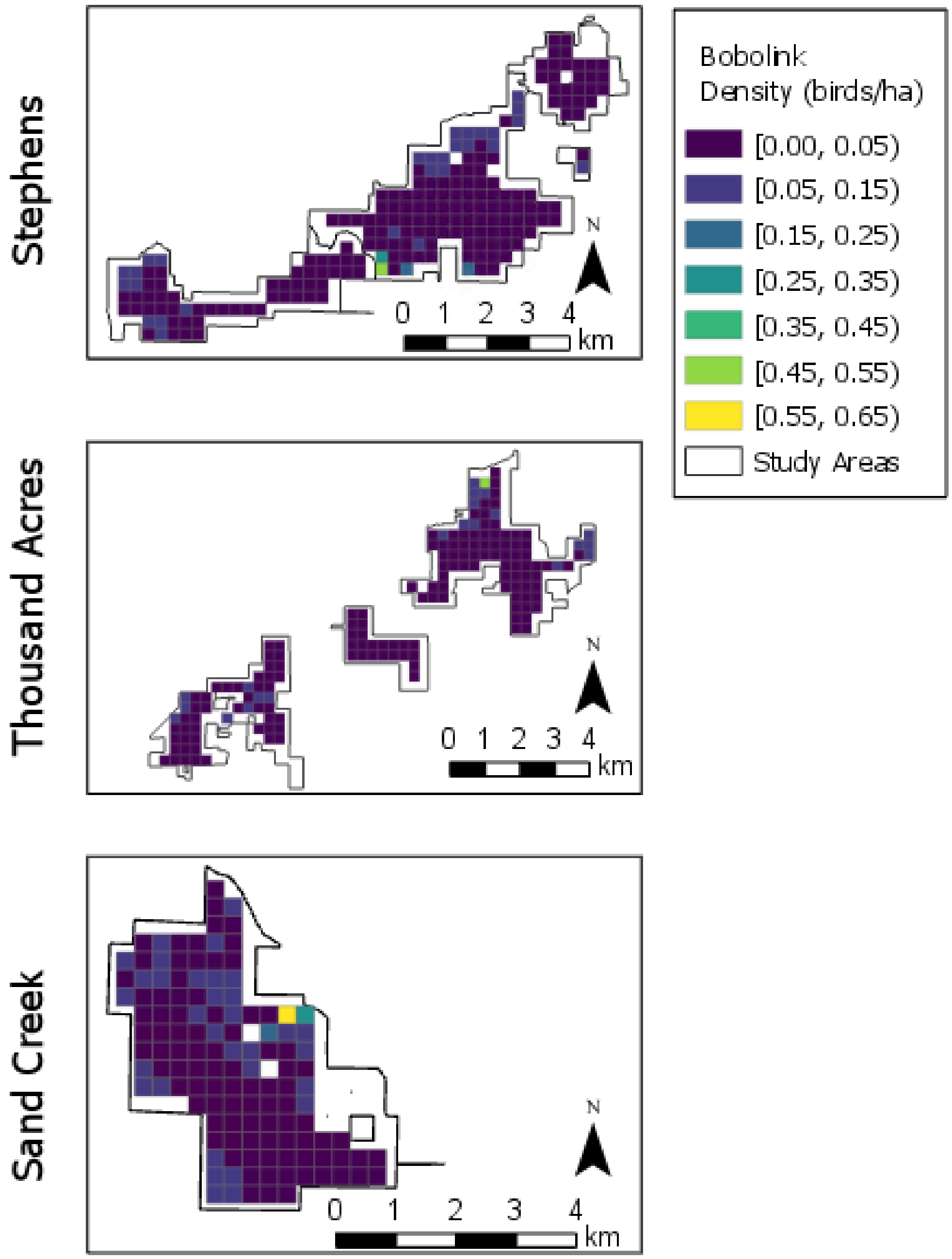

Figure A20. Density map of Bobolink in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

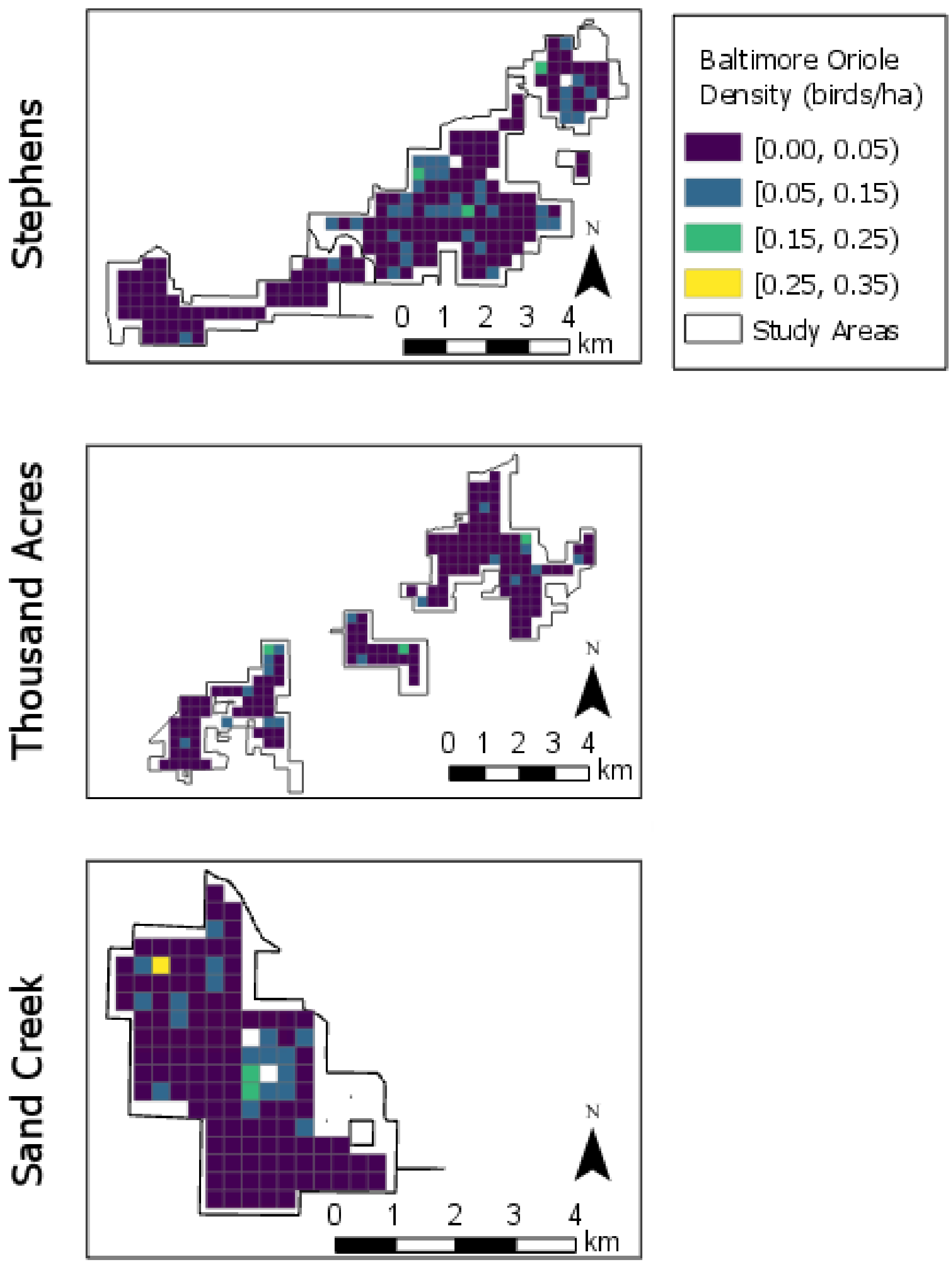

Figure A21. Density map of Baltimore Oriole in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

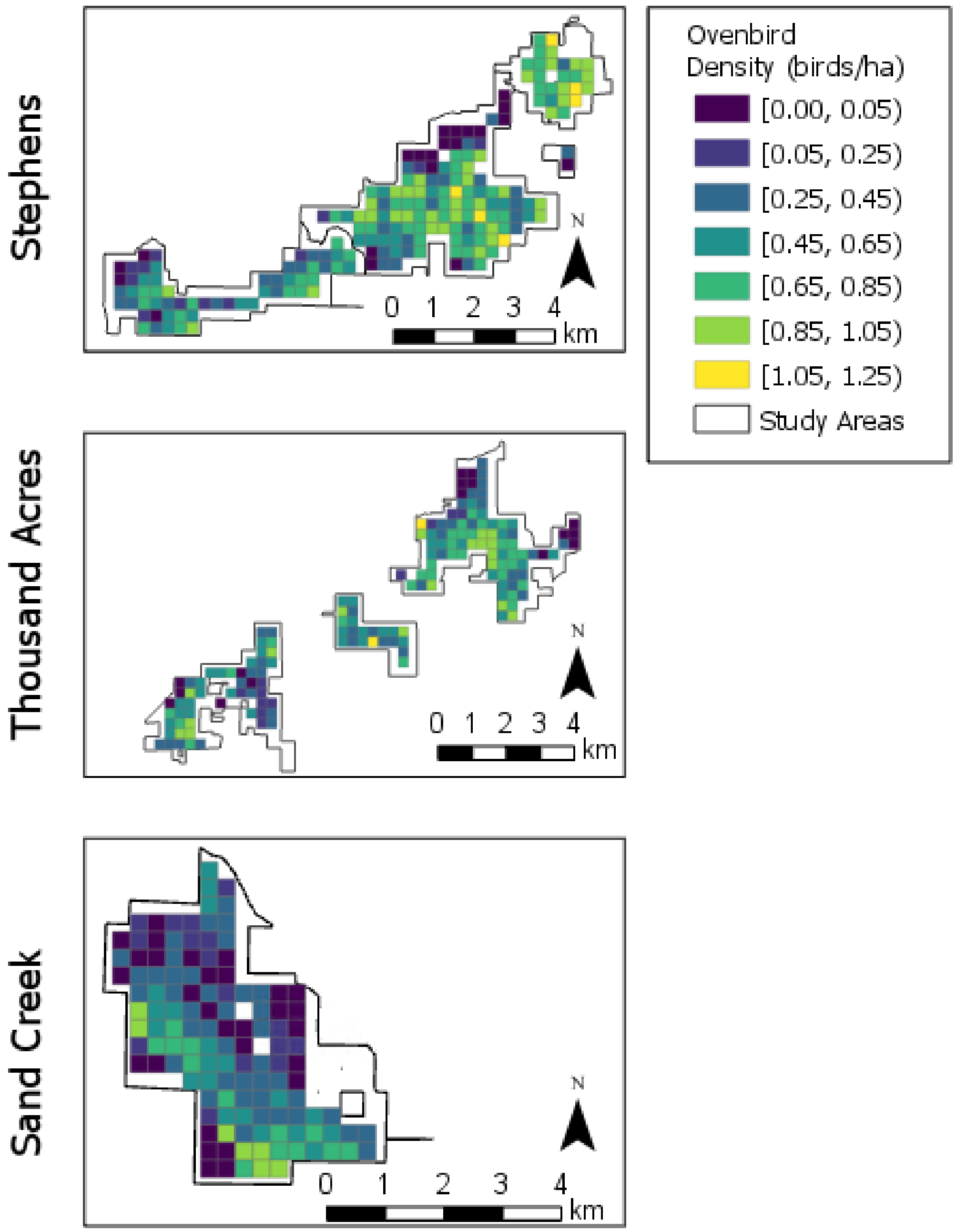

Figure A22. Density map of Ovenbird in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

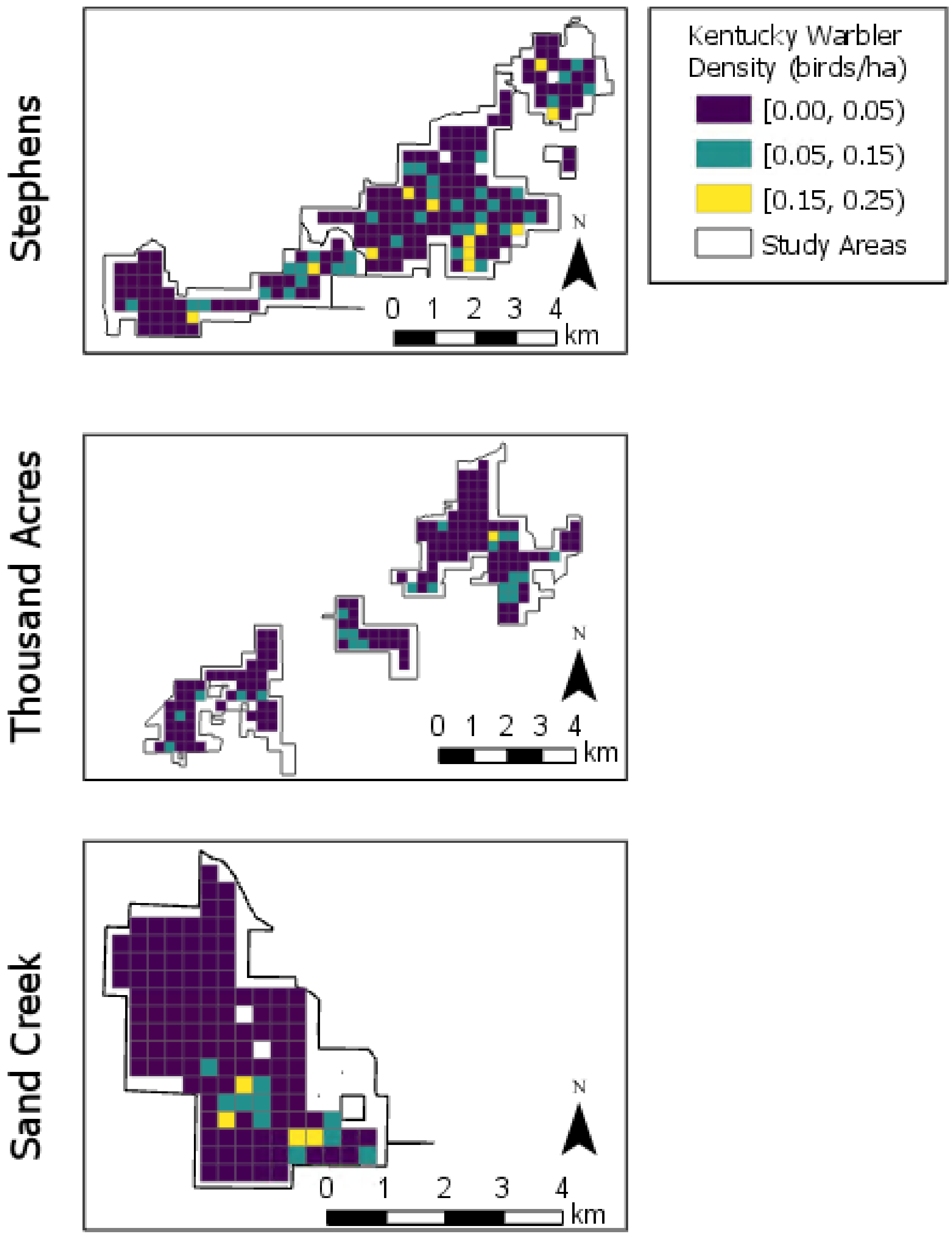

Figure A23. Density map of Kentucky Warbler in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

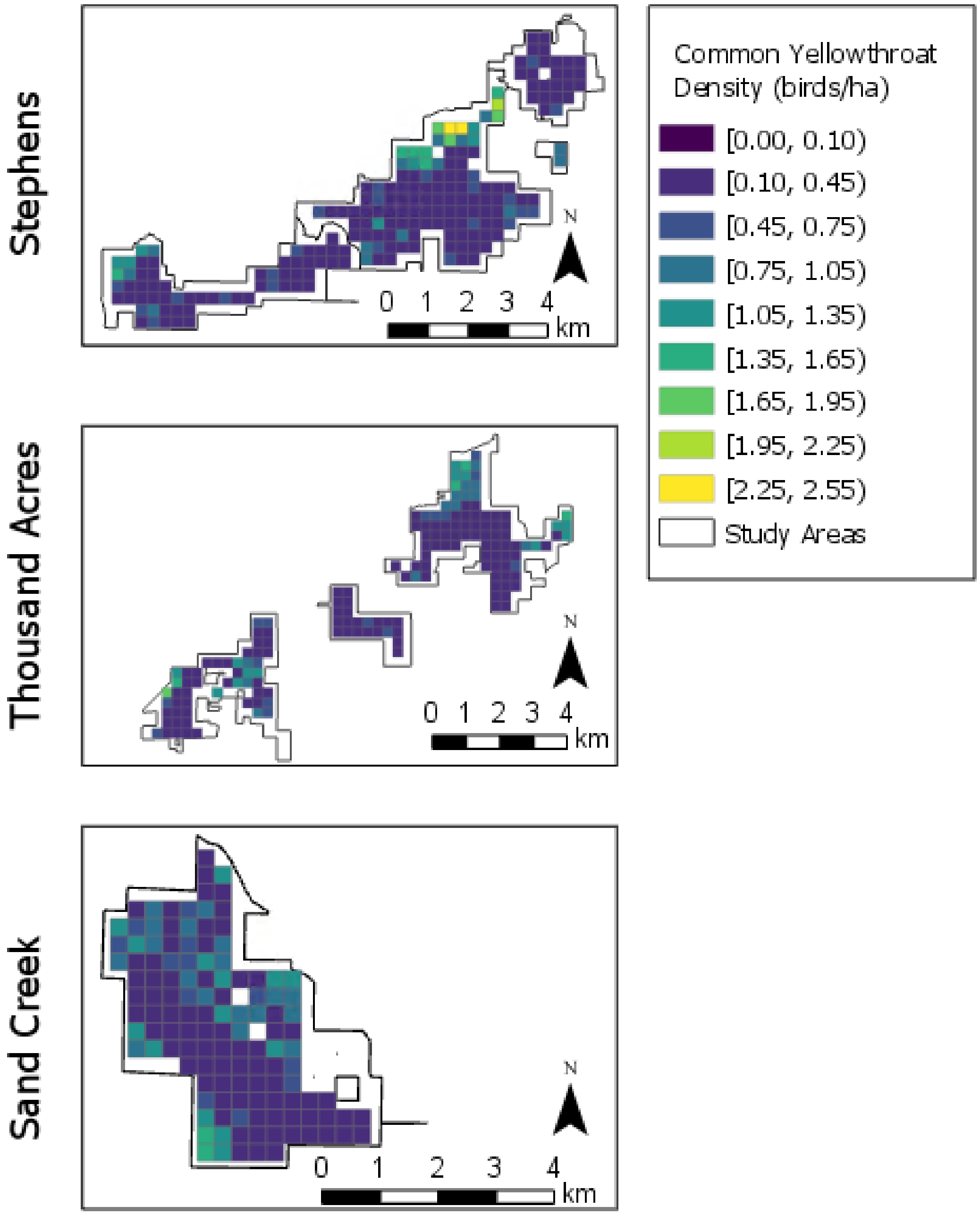

Figure A24. Density map of Common Yellowthroat in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first two density intervals are smaller than other intervals to highlight low estimated densities.

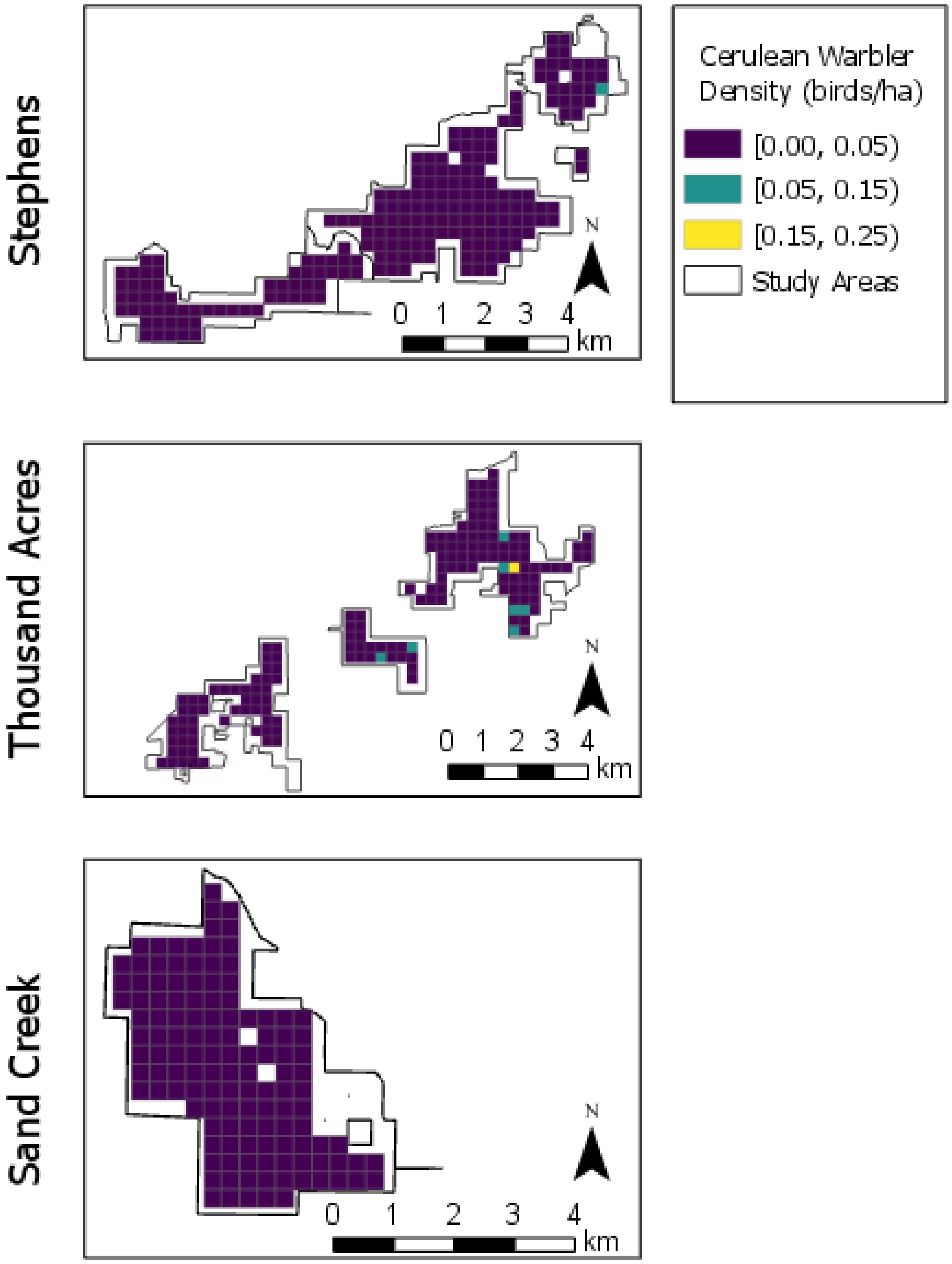

Figure A25. Density map of Cerulean Warbler in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

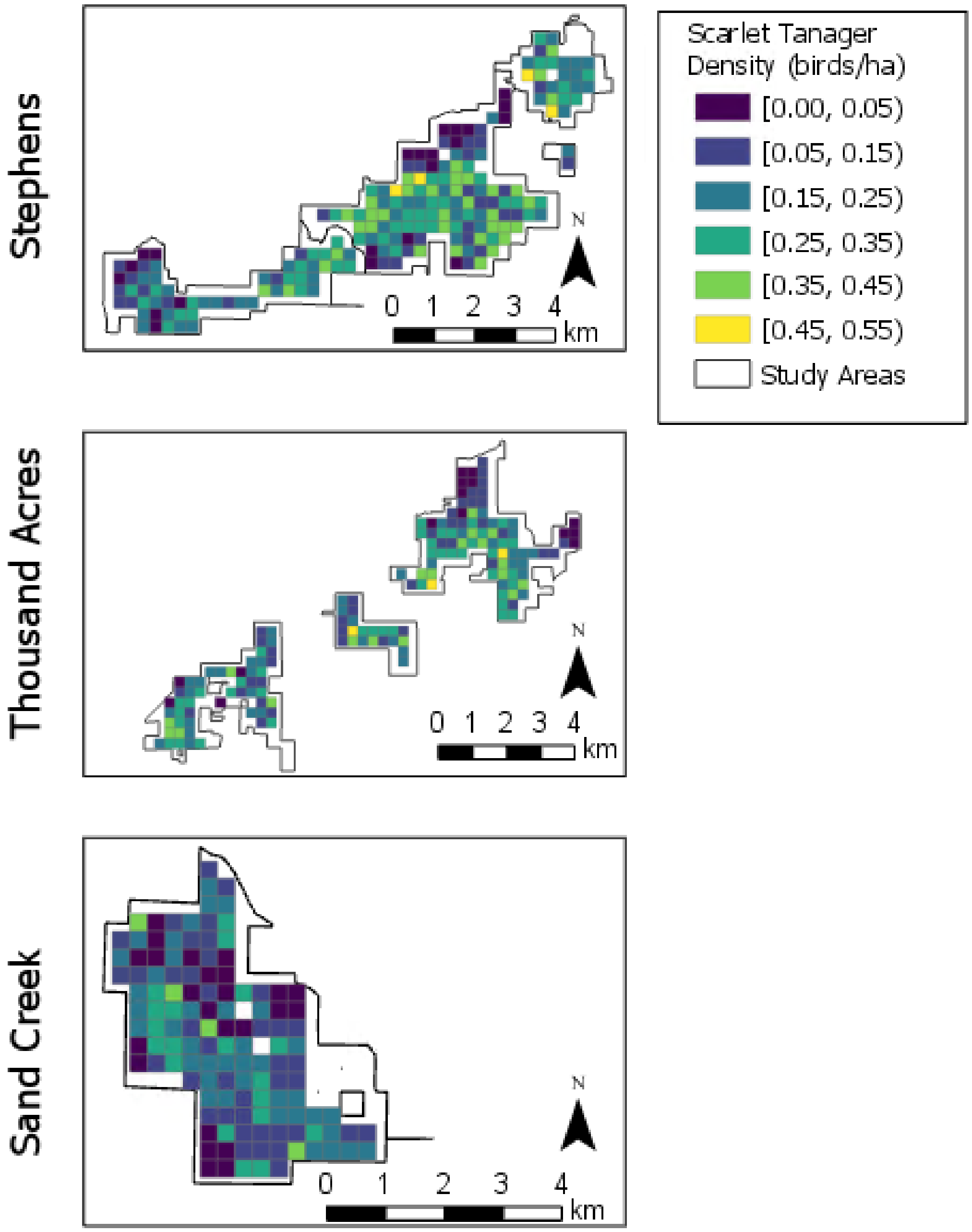

Figure A26. Density map of Scarlet Tanager in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

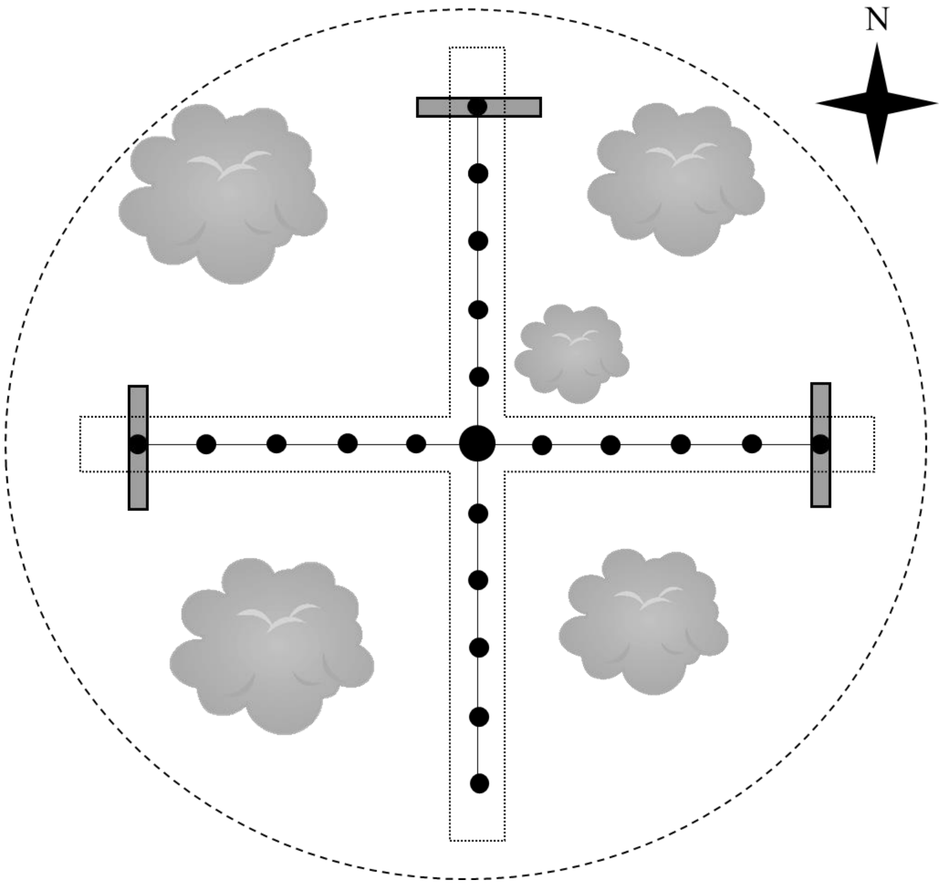

Figure A27. A diagram of the vegetation survey protocol used in and near south-central Iowa forests in 2019. The largest black circle in the center represents the center of a bird survey point, which is also the center of the vegetation survey. The outer dashed circle is a variable-radius plot contain a sample of trees (irregular gray shapes) determined by a 1-factor forestry prism. The cross with a dotted outline represents two perpendicular 1.8 m wide x 22.6 m long shrub measurement transects oriented in cardinal directions and centered on the survey point. The gray rectangles are density board positions, located 10 m from the survey point in each of the cardinal directions, with one . Density boards were used to assess foliage density at heights of 2.5 m and 5.0 m. The thin vertical and horizontal lines intersecting the smaller black circles are two transects (“veg transects”) along which we collected various vegetation metrics. Each veg transect is 20 m long, centered on the survey point, and oriented in the cardinal directions. Each veg transect has 10 vegetation measurement points spaced 2 m apart. At each measurement point, canopy closure, herbaceous ground cover, bare ground cover, and leaf litter cover were measured as a presence/absence measure using a GRS densitometer.

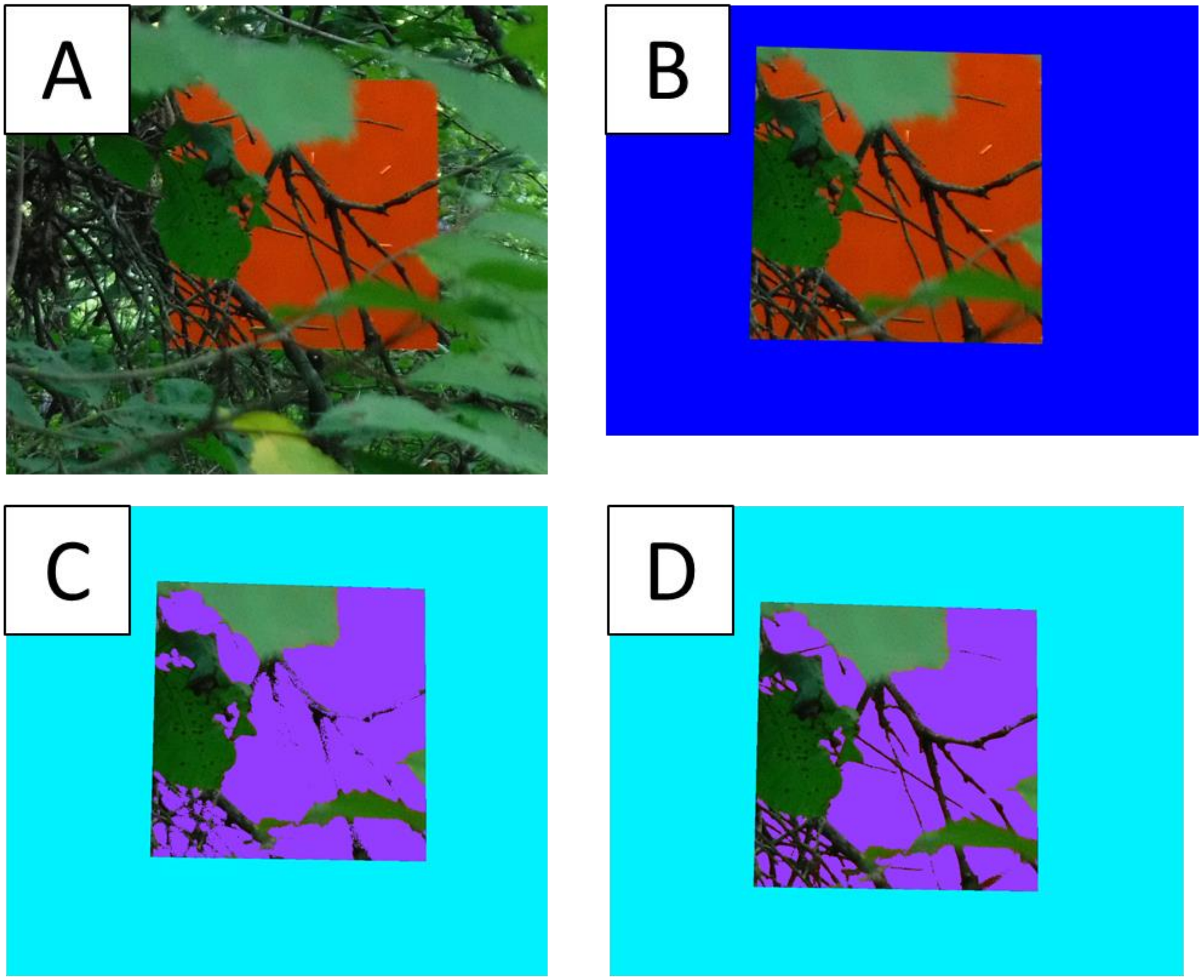

Figure A28. An illustration of the image analysis process used to calculate midstory foliage density for vegetation surveys conducted in south-central Iowa in 2019. All photos are cropped from their original size, hence the slight unevenness in size. A) An unaltered image of a 50 cm x 50 cm orange board 10 m away from an observer at a height of 2.5 m. B) The same photograph of an orange board with the background replace by a uniform blue color. C) A first, unsuccessful attempt at replacing orange board pixels with purple pixels while avoiding most vegetative matter, with the goal of counting orange board pixelss. D) A second, successful attempt at replacing orange board pixels with purple pixels with more restrictive brightness and saturation criteria.

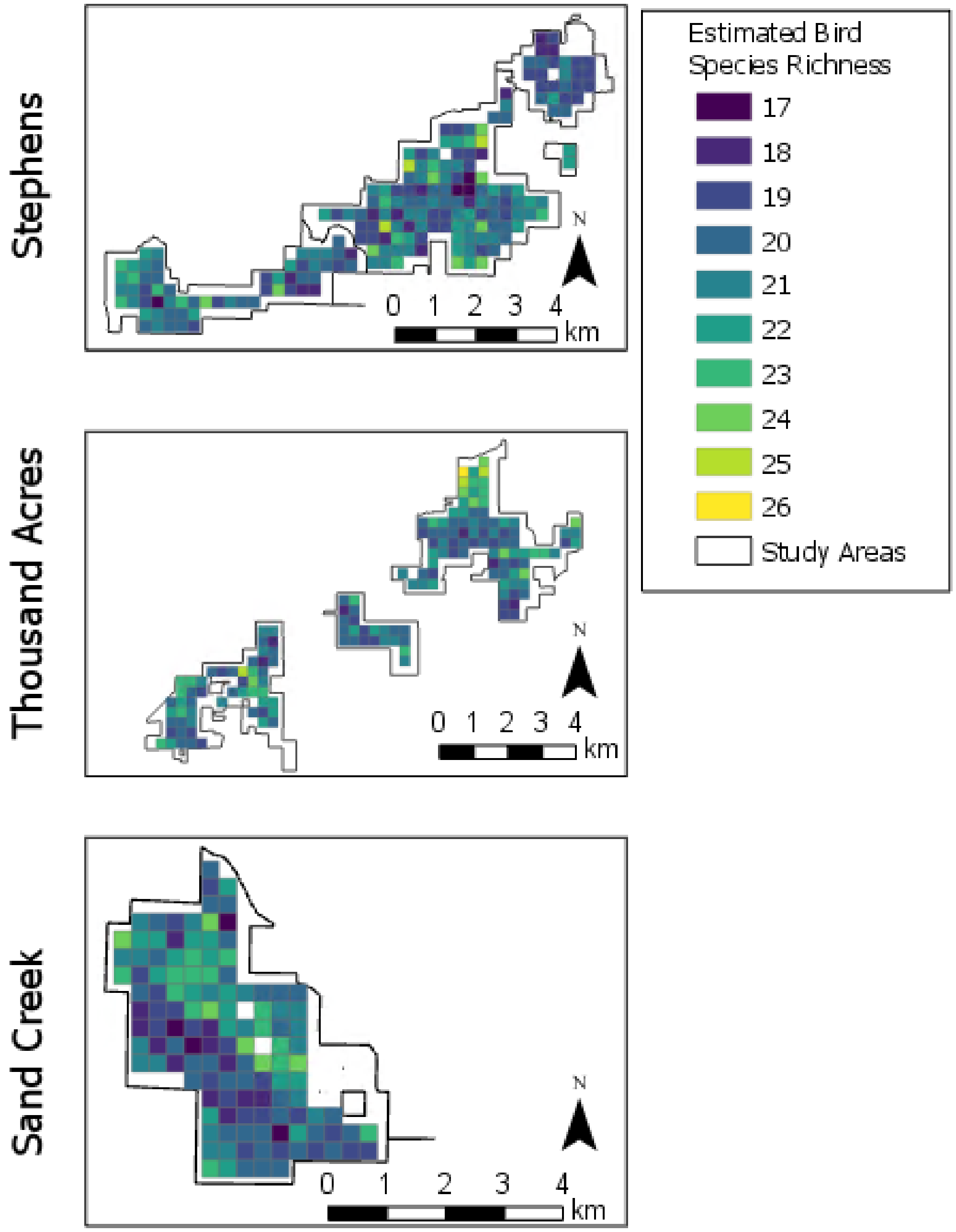

Figure A29. Maps of estimated species richness for forest, grassland, and edge breeding birds in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.

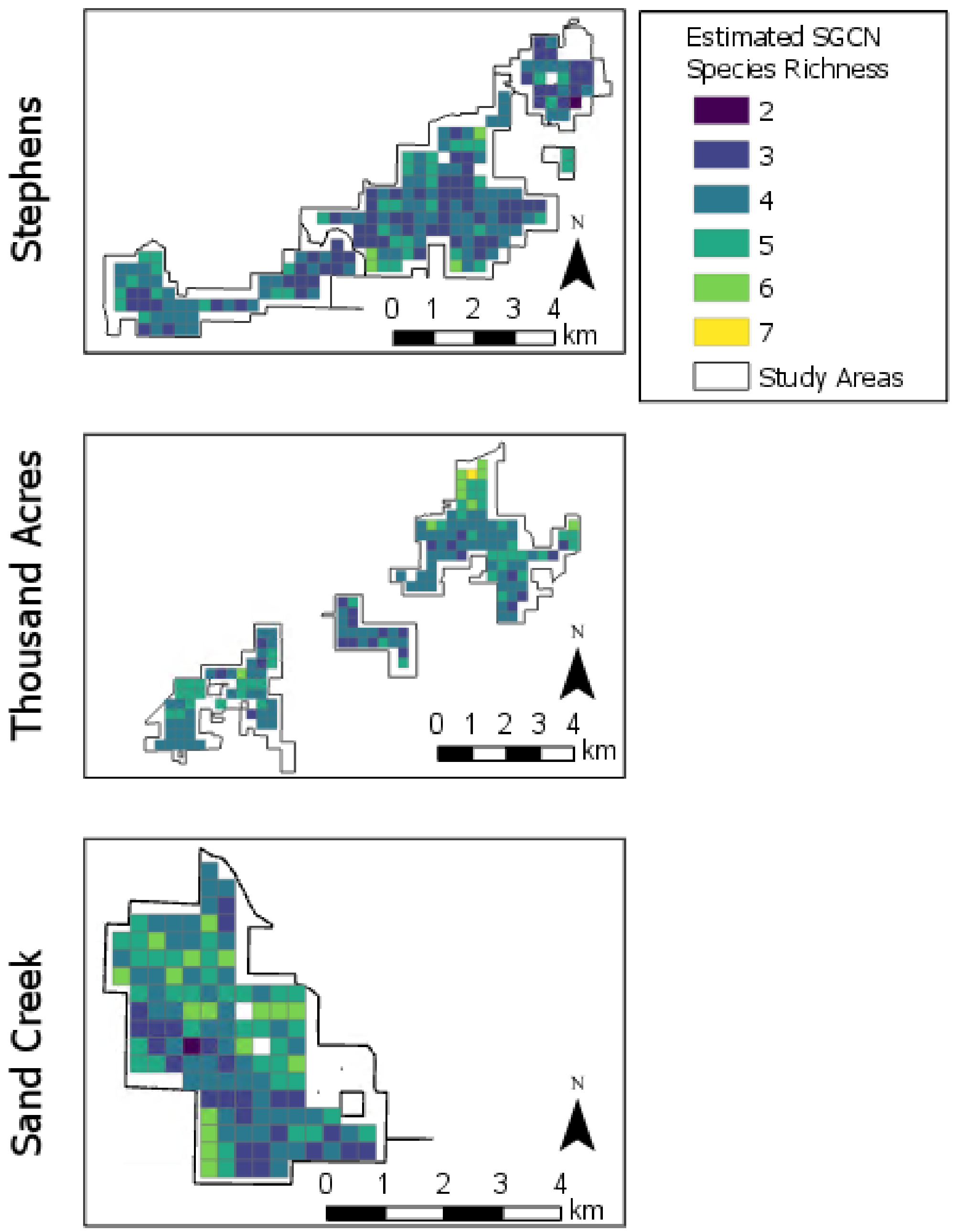

Figure A30. Maps of estimated species richness for breeding bird Species of Greatest Conservation Need in the cores of three primarily forested Bird Conservation Areas (BCA) in south-central Iowa, 2016-2019. Points (k = 493 points) were visited twice per breeding season (n = 3944 total surveys). Data used for estimates were derived from hierarchical distance sampling models and were averaged across years. Each square tile represents a 100-m radius point count circle; point count circle centers were 300 m apart. Stephens = Stephens Forest BCA, Thousand Acres = Stephens Forest -Thousand Acres BCA, Sand Creek = Sand Creek Woodland Savanna BCA. The first density interval is smaller than other intervals to highlight very low estimated densities.