

## Importance of scale, land cover, and weather on the abundance of bird species in a managed forest



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### ARTICLE INFO

#### Keywords:

Avian abundance  
Climate change  
Forest management  
Empirical model  
Laurentian mixed forests

### ABSTRACT

Climate change and habitat loss are projected to be the two greatest drivers of biodiversity loss over the coming century. While public lands have the potential to increase regional resilience of bird populations to these threats, long-term data are necessary to document species responses to changes in climate and habitat to better understand population vulnerabilities. We used generalized linear mixed models to determine the importance of stand-level characteristics, multi-scale land cover, and annual weather factors to the abundance of 61 bird species over a 20-year time frame in Chippewa National Forest, Minnesota, USA. Of the 61 species modeled, we were able to build final models with R-squared values that ranged from 26% to 69% for 37 species; the remaining 24 species models had issues with convergence or low explanatory power (R-squared < 20%). Models for the 37 species show that stand-level characteristics, land cover factors, and annual weather effects on species abundance were species-specific and varied within guilds. Forty-one percent of the final species models included stand-level characteristics, 92% included land cover variables at the 200 m scale, 51% included land cover variables at the 500 m scale, 46% included land cover variables at the 1000 m scale, and 38% included weather variables in best models. Three species models (8%) included significant weather and land cover interaction terms. Overall, models indicated that aboveground tree biomass and land cover variables drove changes in the majority of species. Of those species models including weather variables, more included annual variation in precipitation or drought than temperature. Annual weather variability was significantly more likely to impact abundance of species associated with deciduous forests and bird species that are considered climate sensitive. The long-term data and models we developed are particularly suited to informing science-based adaptive forest management plans that incorporate climate sensitivity, aim to conserve large areas of forest habitat, and maintain an historical mosaic of cover types for conserving a diverse and abundant avian assemblage.

### 1. Introduction

Climate change and land-use change are projected to be the two greatest drivers of biodiversity loss over the coming century (Sala et al., 2000). Climate change has the potential to alter ecosystem structure and function and have significant global and regional impacts to biodiversity (Matthews et al., 2011; Grimm et al., 2013a,b; Urban et al., 2016). It is generally accepted that mean global temperatures are increasing and the largest temperature increases from climate change are currently found in the boreal and hemiboreal forests (Hansen et al.,

1996; Balling et al., 1998; Serreze et al., 2000; IPCC, 2014). Significant changes in forest composition due to climate change and associated ecological processes have already been documented and are expected to increase in hemiboreal forests of the northern US (Iverson et al., 2008; Rodenhouse et al., 2009; Matthews et al., 2011; Wang et al., 2015). Drivers underlying these changes include overall increases in fire frequency, increases in insect infestation, and stand- and landscape-scale alteration of the mosaic composition of forests such as age, structure, and species composition (Mattson and Haack, 1987; Frelich and Reich, 1995; Fleming et al., 2002; Heilman et al., 2002; Wolter et al., 2012;

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Fischelli et al., 2013; Hansen et al., 2013; Wang et al., 2015; Niemi et al., 2016). Further, recent changes to economics and ownership structures in the forest products industry have forced significant changes in forest ownership (Miles et al., 2011; Lönnstedt and Sedjo, 2012), resulting in parcelization, loss of forestlands, and fragmentation of the forest landscape (Heilman et al., 2002).

Climate change and land-use change are likely to have substantial consequences on avian populations and communities (Meynard and Quinn, 2008; Eglington and Pearce-Higgins, 2012; Riordan and Rundel, 2014). Over 300 North American bird species are predicted to have significant range reductions over the next century due to direct effects of climate change (Langham et al., 2014). Additionally, indirect effects of climate change, including alterations to habitat composition, are predicted to alter the suitability of forests, resulting in widespread population declines in many forest bird species (Niemi et al., 1998). Because boreal and hemiboreal forests are already experiencing significant ecological changes, birds breeding in these biomes are especially vulnerable to the effects of climate change (Grinde and Niemi, 2016a). Moreover, bird populations throughout the United States are experiencing increased pressures from human-induced changes to the landscape through habitat degradation, fragmentation, and loss (Yahner, 2000; Benítez-López et al., 2010; Sih et al., 2011; Wade et al., 2013). The direct and indirect effects of climate change will likely exacerbate the impacts of landscape-level habitat pressures on birds (Lawler et al., 2009; Rodenhouse et al., 2009; Stralberg et al., 2009; Bateman et al., 2016; LeBrun et al., 2016). However, the overall impacts of climate change and land-use change may affect species differently; some species may be vulnerable to habitat fragmentation while other species may be more susceptible to direct or indirect impacts of climate change.

Adaptive forest management has the potential to mitigate climate-induced changes to wildlife by conserving and cultivating critical habitats – particularly within large blocks of public lands where land-use change is greatly restricted. Adaptive silviculture techniques can promote forest resilience, preserve forest composition, increase adaptive capacity, and enhance carbon sequestration (Duvencek et al., 2014). However, to create successful adaptive management plans, managers need to understand how habitat at the local and landscape scale, climate, and potential interactions impact the abundance of forest-dependent species. To address this knowledge gap we used a large-scale, long-term dataset to assess patterns and commonalities of factors influencing avian species abundance in northern Minnesota's forests.

The Minnesota National Forest Breeding Bird Monitoring Program was established in 1995 in response to concerns about biodiversity and population declines of migratory passerines (Hanowski and Niemi, 1995; Niemi et al., 2016). The program was designed to provide an estimate of population trends for forest bird species in National Forests in Minnesota (Fig. 1). Data from this monitoring program provide a unique opportunity to investigate the relative roles that stand-level characteristics, land cover factors at multiple spatial scales, and climatic factors (as inferred by variability in weather; Eglington and Pearce-Higgins, 2012) had on bird species annual abundance over a 20-year timeframe. We predicted that bird species would respond uniquely to variation in local habitat, land cover, and weather, but hypothesized that there are likely common factors and scales associated with changes in abundance within trait-based guilds, and that species classified as climate sensitive by the Audubon Climate Report (Langham et al., 2014) would be more likely to retain weather variables within the species-specific models (Urban et al., 2016). Specifically, our objectives for this project were to: (1) build empirical statistical models to determine the influence of land cover and climatic factors on the abundance of 61 bird species over a 20-year time frame and (2) assess common factors associated with changes in abundance by guild and climate sensitivity.

## 2. Methods

### 2.1. Study area

This study was conducted from 1995 to 2014 in the Chippewa National Forest (NF). Chippewa NF is located in north-central Minnesota (Fig. 1), near the ecotone of boreal and northern temperate forests and is therefore best defined as “hemiboreal” with a mix of forest cover types. The most representative tree species in Chippewa NF are aspen (*Populus* spp.), paper birch (*Betula papyrifera*), spruce (*Picea* spp.), balsam fir (*Abies balsamea*), tamarack (*Larix laricina*) and pine (*Pinus* spp.) forests. Common cover types in Chippewa NF include upland deciduous (~35%), lowland conifer (~25%), upland coniferous (~35%, primarily pine and spruce plantations), and upland mixed forest (~2%; Niemi et al., 2016). This region supports approximately 155 breeding species of forest-dwelling birds (Green, 1995) – amongst the most diverse in North America (Robbins et al., 1986; Niemi et al., 1998).

### 2.2. Sampling

At the onset of the Minnesota National Forest Breeding Bird Monitoring Program, avian point count sampling locations were distributed across the forest mosaic in a stratified random manner (Fig. 1; Hanowski and Niemi, 1995). The sample of stands is therefore representative of the percent of forest cover found in Chippewa NF. Selected stands were large enough to accommodate three replicate sampling sites separated by a minimum of 220 m. Point count sampling in the Minnesota National Forest Breeding Bird Monitoring Program followed national and regional standards (Ralph et al., 1995; Howe et al., 1997). Ten-minute point counts were conducted at each site between late June and early July (Etterson et al., 2009; Niemi et al., 2016). Point counts were conducted by trained observers from approximately 0.5 h before to 4 h after sunrise on days with little wind ( $< 15 \text{ km hr}^{-1}$ ) and little or no precipitation. All birds heard or seen from the site were recorded, and distance was estimated as 0–25 m, 25–50 m, 50–100 m, > 100 m (Howe et al., 1997; Niemi et al., 2016). We excluded birds recorded beyond the 100 m radius in our analyses to focus on birds observed in the forest stands we sampled.

### 2.3. Stand, land cover and weather variables

Forest birds are territorial during the breeding season and reported territory sizes vary depending on the species. Additionally, results from recent studies have shown that landscape factors at larger spatial scales were important drivers for many forest birds (Thogmartin, 2010; Streby et al., 2012; Lapin et al., 2013; LeBrun et al., 2016; Grinde and Niemi, 2016b). On the basis of this information and available land-cover data, we chose to calculate cover type and landscape variables at multiple spatial scales. A total of 48 predictor variables were used to build the statistical models, including 15 stand-level variables associated with a 100 m (3.14 ha) buffer around the site, 11 land cover variables calculated at the 200 m (12.5 ha) scale, seven land cover variables at the 500 m (78.5 ha) scale, nine land cover variables at the 1000 m (314.2 ha) scale, and six annual weather variables.

Land cover data were available from the Greater Border Lakes Region land cover classification and change detection project (Wolter et al., 2012). We used data from 1995 to 2000 as a base layer and extrapolated land cover layers for 2005 and 2010 using the University of Maryland's global forest change data (Hansen et al., 2013). Land cover data for 2005 and 2010 were therefore updated to include both forest loss and forest gain from 2000 to 2012. These 5-year increments of land cover data were summarized within various buffers for each site, where the closest year of land cover data available was used to correspond with the year in the bird samples. We also calculated road density as length (m) of road within a 1000 m buffer around each site based on

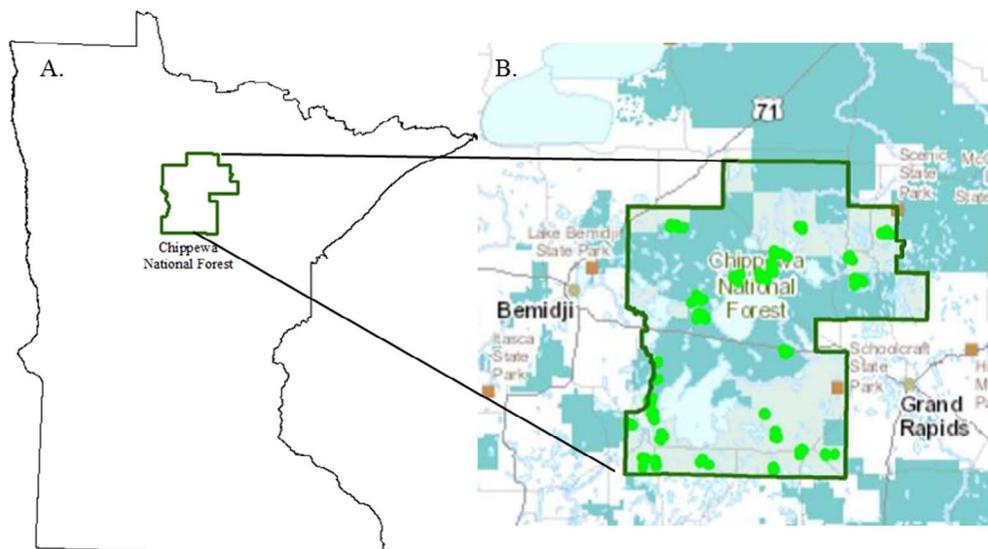


Fig. 1. (A.) Location of northern Minnesota's Chippewa National Forest and (B.) General locations of forest breeding bird point counts. Each point represents 3–5 forest stands, approximately 380 individual points are sampled annually in Chippewa National Forest.

TIGER roads from 2014 (U.S. Census Bureau, 2014).

We used a variety of data sources to quantify local stand-level characteristics (i.e., forest tree species composition, stand age, and annual disturbance), for each site over the 20-year time period of the study. Forest composition was derived from a detailed forest type map generated from multi-temporal Landsat analyses (Wolter et al., 1995; Wolter and White, 2002), where the proportions of each dominant tree species (or type) within a 100 m radius of the site were used as stand-level dependent variables. Stand records from the US Forest Service were used to identify stand age at the onset of the project; these data were then extrapolated to obtain a stand age for every year. Missing stand age data were estimated from the 5-year land cover data by using the year in which a cell converted from forest to non-forest as stand origin (Wolter et al., 2012). Insect defoliation disturbance data were obtained from the Minnesota EPIC program for 1995–1996 (Land Management Information Center, 1998) and USDA Forest Service, Forest Health Protection and its partner's aerial survey data for 1997–2014. Stand-level logging records were obtained from the US Forest Service to determine “logged” dates. We used diameter at breast height (dbh) data measured from 1/100th acre fixed-radius plots (minimum cut-off was 0.25 mm) at each site to calculate above ground tree biomass (hereafter biomass) using biomass regression equations outlined in Chojnacky et al. (2014) and compared with Jenkins et al. (2004).

Weather variables included annual average spring temperature and precipitation and Palmer Drought Severity Index (PDSI; Fig. 2) for each year and also for the year prior to the year the bird surveys were conducted. Average monthly temperature and precipitation data were extracted at each site from PRISM 4-km resolution historical climate grids; March through June were averaged to obtain average spring precipitation and temperature (PRISM Climate group, 2016). Regional PDSI was downloaded from NOAA and extracted at each site; March through June were averaged to obtain average spring PDSI values (Palmer, 1965).

#### 2.4. Predictive models

A generalized linear mixed-effects model with negative binomial error from the *lme4* R package (Bates et al., 2015) was used to model species abundance. We defined species abundance as the number of individuals of each species detected at each site within the 100 m radius. Models included both fixed effects associated with environmental covariates and random effects for site and year. We used Akaike's Information Criterion (AICc; Burnham and Anderson, 2002) for model

selection. Niemi et al. (2016) and Etterson et al. (2009) applied detectability analysis to data used in this analysis, and their results showed that adjusting for detectability did not change the results of trend analysis for the majority of species. Considering the lack of evidence for species detectability issues in our dataset (Etterson et al., 2009; Niemi et al., 2016), and the support from studies questioning assumptions and need for including detectability adjustments, especially when sample sizes are large (Hutto, 2016; Johnson, 2008), we used raw counts for our analyses.

We developed five subsets of candidate models according to type and scale, specifically stand-level characteristics (i.e., local biomass, stand records, or tree composition within a 100 m buffer), land cover characteristics at the 200 m, 500 m, and 1000 m scales (including road density for the latter), and weather variables, to assess the best predictors of species abundance at multiple scales (Appendix A). We added the variables of interest in two separate steps. In the first step we built models for each subset using a forward selection approach. For each model subset, we evaluated single predictor models and determined predictors with the highest model weight(s) based on AICc. We identified overall best models for each subset by including predictors that had greater than 5% support in a “full subset model” if needed. In the second step we combined predictor variables from the five “best subset models” to develop the overall “combined best model.” If the combined best models included more than one predictor, we evaluated variables for interactions and interaction terms were included in the best models as indicated by model weights. This step-by-step analytic procedure was selected because it minimizes the number of models examined and follows a hierarchical pattern, ending with the broadest encompassing scales that allow us to test for interactions between independent variables as needed. Nagelkerke's R-squared was used to evaluate goodness-of-fit for final models (Nagelkerke, 1991; Faraway, 2006).

#### 2.5. Guild associations

Each species was categorized within five different guild types to assess patterns within trait-based guilds and climate sensitivity status (migration, nesting, habitat preference, foraging, and climate sensitivity; Appendix B). Information for categorizing species was obtained primarily from Ehrlich et al. (1988), Freemark and Collins (1992), and Niemi et al. (2016). Climate sensitivity was assigned based on results from the Audubon Climate Report (Langham et al., 2014). Audubon's climate change sensitivity classifications suggest which bird species are most likely to be impacted by future climate.

We included only those guilds represented by four or more species

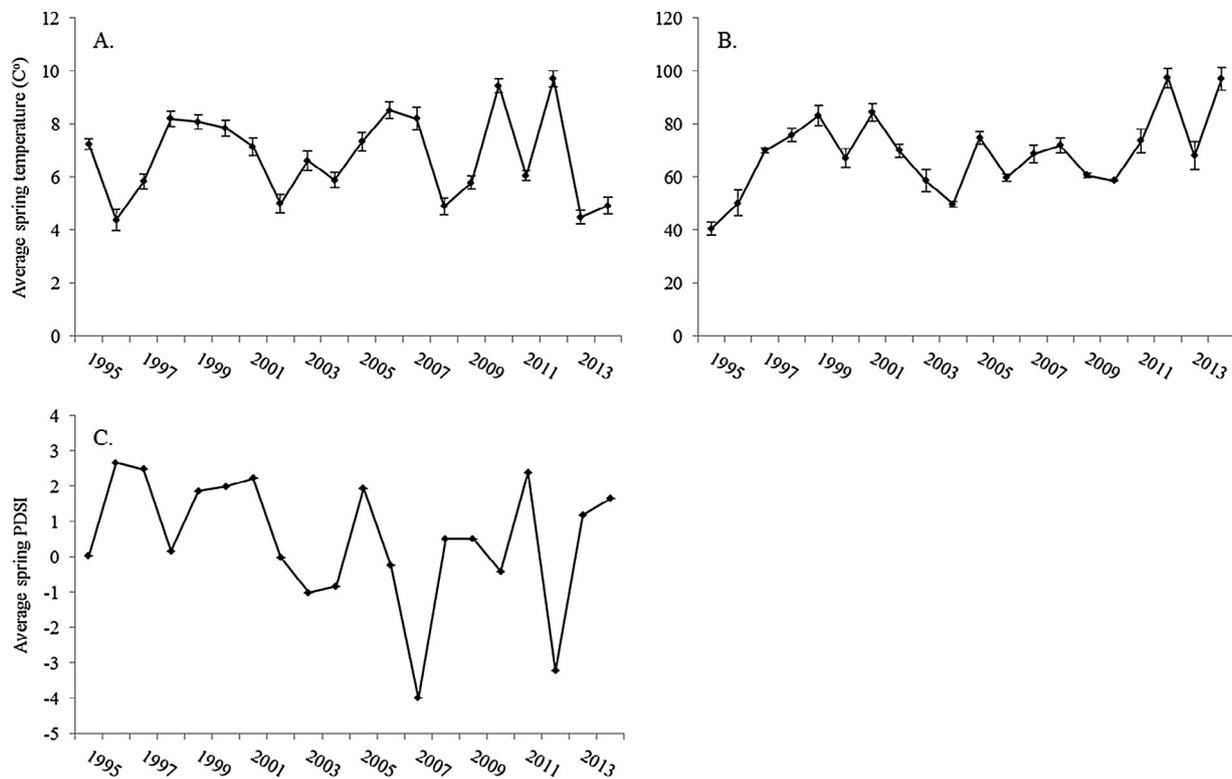


Fig. 2. Average spring (March–June) (A.) temperature (C°), (B.) precipitation (inches), and (C.) Palmer Drought Severity Index (PDSI) of point count locations in Chippewa National Forest from 1995 to 2014. Error bars represent standard deviations.

in our analyses. Three guilds were used to classify nesting location: sub-canopy or shrub (10 species), ground (16 species), and canopy (8 species) nesters. Five guilds were used to classify species habitat: coniferous forest (5 species), deciduous forest (9 species), early-successional (6 species), lowland conifer (7 species), and mixed forest (4 species). Two guilds were used to classify migration distance: long-distance migrants (23 species) and short-distance migrants (13 species). Three guilds were used to classify foraging strategy: flycatchers (5 species), foliage insects (16 species), and ground insects and seeds (5 species). We explored variables and spatial scales associated with drivers of abundance for four guilds and climate-sensitive bird species. Our null hypothesis was that membership in a guild has no influence on the frequency that its members include a variable from a given subset. We used a Chi-square test of independence to test the final models against the null hypothesis (Mangiafico, 2015). Given a significant Chi-square table, all possible pairwise comparisons were tested within nesting and foraging guilds using a Bonferroni correction of the  $P$  value. The post hoc comparisons between habitat guilds tested each habitat guild against all other habitat guilds and Bonferroni corrections were used for the comparisons.

### 3. Results

#### 3.1. Predictive models

Models were attempted for 61 species (Appendix B). Seven species had models with extensive convergence issues most likely due to small sample sizes ( $n$  ranged 71–491) and perhaps because the bird surveys occurred after the primary breeding period for permanent residents (Evening Grosbeak, Downy Woodpecker, and Hairy Woodpecker), and short-distance migrants (Eastern Towhee and Purple Finch). The two remaining species were long-distance migrants (Wood Thrush and Great-crested Flycatcher). Another 17 species had models with little explanatory power ( $R^2 < 0.20$ ). Six of these species were permanent residents (Pileated Woodpecker, Common Raven, Gray Jay, Black-

capped Chickadee, White-breasted Nuthatch, and Blue Jay), six were short-distance migrants (Northern Flicker, Cedar Waxwing, Brown-headed Cowbird, Blue-headed Vireo, Golden-crowned Kinglet, and American Goldfinch) and five were long-distance migrants (Magnolia Warbler, Yellow-throated Vireo, Yellow Warbler, Canada Warbler, and Indigo Bunting). The remaining 37 species had final models with  $R^2$  values ranging from 26% to 69% (Appendix C); we focused inference from the models for these species.

Our results, as expected, showed that specific responses to stand-level characteristics, multi-scaled land cover variables, and weather factors were dependent on the bird species (Appendix C). Overall, 15 species (41%) modeled had stand-level attributes (100 m) in their subset of best models. Ninety-two percent of species models included land cover variables at the 200 m scale, 51% of species models had 500 m scale variables in the best models, 46% of species had 1000 m scale variables in best models, and 38% of species had weather variables in best models (Appendix C). Three species (8%) included significant weather and land cover interaction terms (Appendix C).

A total of 25 (of 48 possible) predictor variables were included in final abundance models. The most common explanatory variables included in final models were tree biomass, lowland cover in 200 m, 500 m, and 1000 m buffers, and amount of open habitat in the 200 m buffer (Appendix C). Fourteen species (38%) had associations with biomass; final models for six species indicated negative associations with biomass and eight species were positively associated with biomass. The amount of lowland conifer in the 200 m buffer was included in 14 species models; five of these species had negative associations and nine had positive associations with lowland cover. Lowland conifer at the 500 m scale and 1000 m scale were each included in 10 final species models. Five species were negatively associated with the amount of lowland conifer in the 500 m buffer and five species had positive associations. Three species had negative associations with the amount of lowland conifer in the 1000 m buffer, seven had positive associations. Seven species included the amount of open cover at the 200 m scale in final models; all were positively associated with open areas (Appendix

C). The remaining 20 variables and model coefficients were related to species-specific habitat preferences.

Three species (Golden-winged Warbler, Black-throated Green Warbler, and Brown Creeper) included significant interaction terms between weather and land cover. These three species were classified as climate sensitive by the Audubon Climate Report (Langham et al., 2014). Golden-winged Warbler had a significant interaction between the percent of regenerating forest in the 1000 m buffer and temperature. The Golden-winged Warbler final model showed that abundance is higher in stands with more regenerating habitat at the 1000 m scale and abundance was lower in years with higher average spring temperatures (Appendix C). Final models for Black-throated Green Warbler indicated a positive relationship with abundance and the amount of forest at the 200 m scale and drought negatively impacted abundance. There was a significant interaction term between the amount of upland forest in the 500 m buffer and PDSI (Appendix C). Brown Creeper abundance was higher in stands with more forest in the 200 m buffer, negatively impacted by the amount of open cover in the 1000 m buffer and in years of lower precipitation, with a significant interaction term between the amount of open cover and precipitation (Appendix C).

### 3.2. Guilds and climate sensitivity

The Chi-square test of independence (Table 1) indicated sub-canopy or shrub nesting species were more likely than canopy-nesting species to have stand-level variables 100 m subset in their final models ( $\chi^2_1 = 5.95$ ,  $P = 0.01$ ; Fig. 3). This result demonstrates the importance of fine-scale heterogeneity for this group of species compared to canopy-nesting species. Short-distant migrants were more likely to have variables at the 500 m scale than long-distant migrants ( $\chi^2_1 = 5.90$ ,  $P = 0.02$ ; Fig. 3). Habitat guild membership and climate sensitivity were associated with the inclusion of weather variables in final abundance models. Species associated with deciduous forests were more likely to have weather variables in their final models compared to species in all other habitat guilds ( $\chi^2_1 = 8.16$ ,  $P = 0.004$ ; Fig. 3); and species classified as climate sensitive by the Audubon Climate Report (Langham et al., 2014) were more likely to have weather variables in their final models ( $\chi^2_1 = 5.26$ ,  $P = 0.02$ ; Fig. 3). Significant variables and scales of importance were equally distributed among foraging guild types (Table 1; Fig. 3).

## 4. Discussion

Habitat affinities of forest bird species have previously been reported (e.g., Bayne et al., 2010; Gnass Giese et al., 2015; Grinde and Niemi, 2016b), but this is the first study in this region using multiple spatial scales in land cover combined with weather. Models for 37 avian species occupying hemiboreal forest in the upper Midwestern United States showed that the strength of the relationships between species abundance and land cover factors were species-specific. Many species showed strong relationships with land cover variables over multiple spatial scales, while others were relatively weak or insignificant. Niemi et al. (2016) presented habitat analyses by forest cover type for 123

forest bird species in national forests of northern Minnesota and Wisconsin, including the Chippewa NF and the species presented here. Although Niemi et al. (2016) did not include multiple spatial scales or weather, the forest cover types important to the species models presented here were generally consistent with that study. For instance, strong forest cover type associations were found for species associated with lowland coniferous forests such as Yellow-bellied Flycatcher, Connecticut Warbler, and Palm Warbler and early-successional vegetation such as Chestnut-sided Warbler, Mourning Warbler, and Song Sparrow (Collins et al., 1982).

### 4.1. Stand-level characteristics and land cover factors

Species models showed that bird species respond differentially to stand-level characteristics and land cover characteristics at multiple spatial scales. This result is not surprising given the complex breeding cycle and diverse habitat requirements of forest birds. For example, a particular cover type may provide the essential microhabitat characteristics (e.g., nesting cavities or a dense shrub layer) required for nesting, but the larger-scale land cover composition may reflect post-breeding dispersal requirements (Streby et al., 2012) or large-scale population dynamics (Grinde and Niemi, 2016b; Niemi et al., 2016). Overall, landscape context in addition to forest structure and cover type should be considered in the development of breeding bird habitat models.

Niemi et al. (2016) reported that forest cover type composition remained relatively stable over the time period of this study within the Chippewa NF; however there was a reduction in harvest activity that occurred over the duration of the study. The average harvest level in the early 1990s was 85 million board feet and decreased to an average of 35 million board feet in the late 2000s (Niemi et al., 2016). Further, Niemi et al. (2016) noted that changes in data from the National Land Cover Database (NLCD) (Fry et al., 2009, 2011; Homer et al., 2001) indicated that open areas and grass/shrub cover types converted disproportionately to forested land cover, suggesting that open habitats within Chippewa NF may have declined during the period of bird sampling.

This change in composition is important because, across eastern forests, early-successional bird species have shown significant declines (King and Schlossberg, 2014; Sauer et al., 2017). Several early-successional associated bird species that are of conservation concern were modeled in this study and provide an important example of how the results of this study could provide guidance for forest management plans. Golden-winged Warblers are recognized as species of continental concern by the US Fish and Wildlife Service's Partners in Flight program (Rosenberg et al., 2016) and also recognized as Minnesota Stewardship Species by Minnesota Audubon (Pfanmuller, 2012); four additional species (Chestnut-sided Warbler, Nashville Warbler, Rose-breasted Grosbeak, and Veery) are also designated as Minnesota Stewardship Species (Pfanmuller, 2012). The final models for these five species included variables at multiple scales; the 200 m scale variables were primarily associated with regenerating forests, yet most species were positively associated with biomass within the regenerating cover types

**Table 1**

Results of Chi-square test of independence to assess relationships between climate sensitivity, nesting, habitat, migration, and foraging guild membership and common factors that were included in final abundance models for 37 species in Chippewa National Forest, MN. Bolded values indicate significant results.

Model subset	Nesting guild			Habitat guild			Migration guild			Foraging guild			Climate sensitivity		
	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P
Stand-level (100 m)	<b>6.23</b>	2	<b>0.04</b>	4.93	4	0.29	0.09	1	0.77	1.71	2	0.42	0.00	1	0.95
Land cover (200 m)	3.70	2	0.16	3.40	4	0.49	0.01	1	0.92	1.35	2	0.51	0.92	1	0.34
Land cover (500 m)	5.05	2	0.08	1.23	4	0.87	<b>5.91</b>	1	<b>0.02</b>	4.95	2	0.08	1.30	1	0.25
Land cover (1000 m)	1.39	2	0.50	3.62	4	0.46	1.67	1	0.20	1.33	2	0.51	2.01	1	0.16
Climate	0.71	2	0.70	<b>12.16</b>	4	<b>0.02</b>	0.24	1	0.62	2.87	2	0.24	<b>5.26</b>	1	<b>0.02</b>

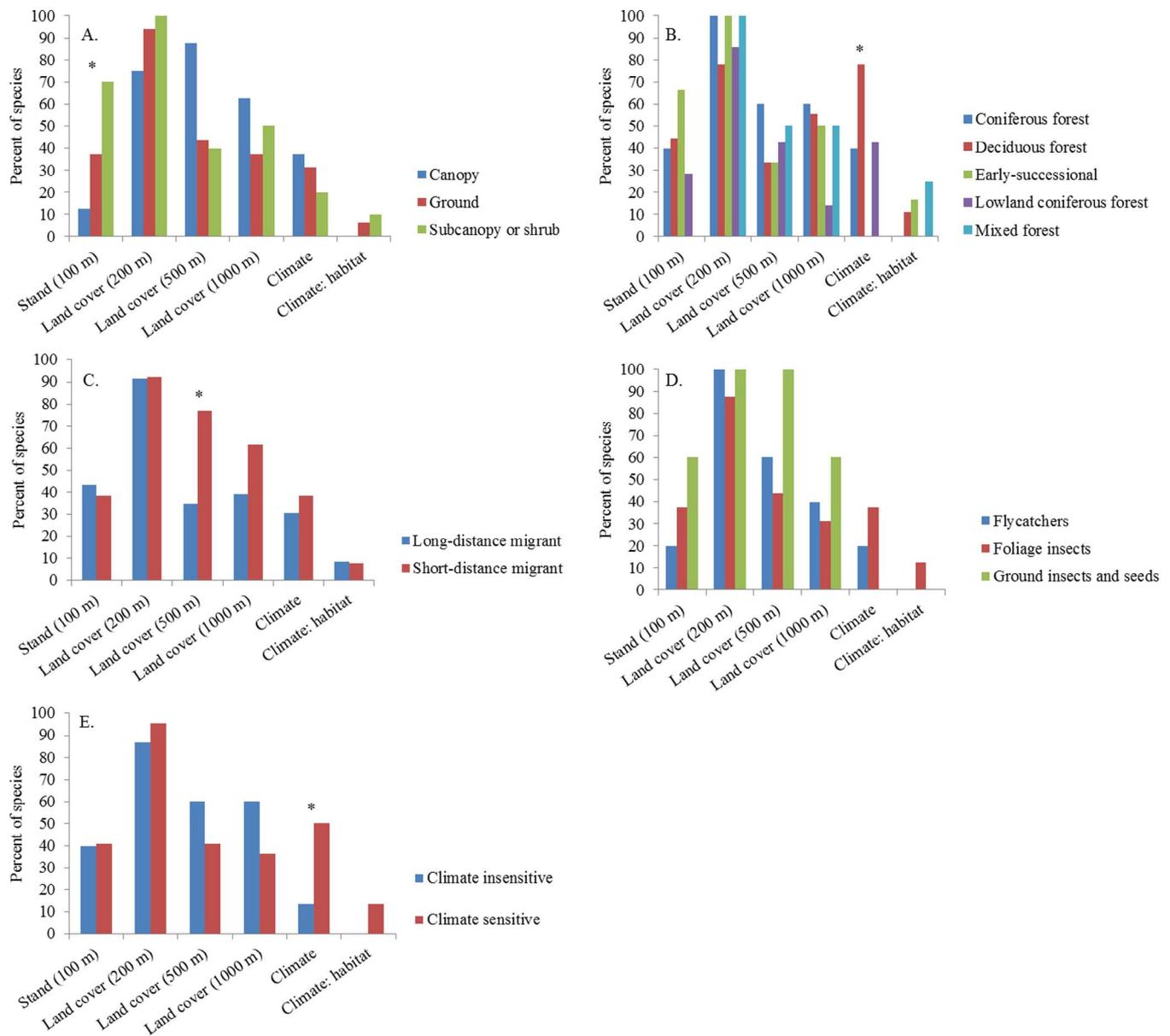


Fig. 3. Percent of species by (A.) Nesting guild, (B.) Habitat guild, (C.) Migration guild, (D.) Foraging guild, and (E.) Climate sensitivity that included explanatory variables associated with each subset in final abundance models used for predicting abundance of 37 species in Chippewa National Forest, MN from 1995 to 2015. \* indicate significance based on Chi-square test of independence with Bonferroni corrections of *P* values for multiple comparisons.

and the larger scale variables were species-specific. Our results emphasize the importance of smaller-scale habitat features such as retention of dead or live trees that provide song perches for many passerine species in recently logged areas, but also highlight the importance of considering larger scales in forest composition surrounding a recently cut area to maximize benefits of harvest to early-successional species. The Golden-winged Warbler is an especially good example of the combination of the need to manage for both local and larger scales (Thogmartin, 2010). The species requires shrubby habitat with scattered trees within its territory (Golden-winged Warbler Working Group, 2013), but also a landscape matrix of shrubby wetlands and more mature forest during the post-breeding season (Streby et al., 2015). Overall, the complexity of bird species response to cover type and scale emphasizes the importance of long-term regional monitoring of populations and adaptive forest management plans.

#### 4.2. Weather

The direct effects of weather variables were both positively and negatively associated with bird abundances (Fig. 2). Overall, models indicated that changes to precipitation and drought regimes are likely more important drivers of avian abundance than temperature per se, at least over the 20-year time frame of this study. The impact of weather variability on bird populations has not been studied over longer periods of time in this region, despite regional prediction of extensive climate-induced changes (Pastor and Post, 1988).

The results of the guild analyses showed that species breeding in deciduous forests were influenced by weather more than species in other habitat guilds. Blake et al. (1992, 1994) examined the effects of a drought over five- and seven-year periods in northern Wisconsin and Michigan, respectively. They found significant declines in abundance for two to three years following the most intense drought and declines were most intense in upland deciduous forests. While Langham et al. (2014) reported no clear associations between habitat affinities and

climate sensitivity when assessing bird species across North America, the results of this study and [Blake et al. \(1992, 1994\)](#) suggest that impacts of climate change in the Great Lakes Region may have differential impacts across forest types; this is an important result and warrants further study. The mechanisms of this relationship are unclear, but we speculate drought conditions may reduce availability of food resources (e.g., insects and fruit), especially those additional resources necessary to feed young. Further examination and tests of this potential mechanism are needed. Overall, the importance of weather to the abundance of species classified as climate sensitive demonstrates the need to include climate sensitivity in wildlife conservation plans.

Over the 20-year period of this study, significant interaction terms between land cover and weather were found for three species: Black-throated Green Warbler, Golden-winged Warbler, and Brown Creeper. We note that significant interaction terms must be interpreted with caution, and we acknowledge these relationships could be spurious. However, the interactions suggest possible associations between forest cover types at larger scales and climate. For example, the abundance of Black-throated Green Warbler may not be influenced as much by drying conditions when its landscape context consists of large upland forests. Similarly, Golden-winged Warbler abundance may not be as negatively impacted by higher temperatures when the surrounding landscape is primarily regenerating forests, which is preferred breeding habitat in Minnesota ([Streby et al., 2012](#); [Niemi et al., 2016](#)). However, the mechanisms for these interactions are unclear and beyond the scope of this study.

#### 4.3. Management implications

This study provides important insight into the drivers of species abundance and scientific guidance to assess species responses. Our results emphasize the importance of considering the differential impacts of weather across forest types and incorporating multiple scales in the development of management plans to maximize benefits of management for bird species.

Overall, the importance of land cover factors suggests that future forest changes may have a greater impact on species abundance than direct impacts of projected climate, but we acknowledge that 20 years of variation in weather may not be long enough to assess direct impacts of climatic trends. Nonetheless, Chippewa NF recently began incorporating adaptive management strategies for climate change into current forest vegetation management projects ([Swanston et al., 2011](#); [Handler et al., 2014](#)). Their management goals were to encourage diversity in forest community composition and incorporate the vulnerability of native plant communities to climate change in their conservation efforts. Our results support this overall strategy. In particular, our results suggest that no single management scenario will benefit all bird species because of their varied habitat and landscape requirements. Therefore, adaptive management strategies promoting the perpetuation of habitat and landscape mosaics that optimize benefits to the most species, especially those sensitive to future climate changes, should be considered ([Scheller and Mladenoff, 2005](#); [Duveneck et al., 2014](#)).

The importance of the lowland conifer forests to breeding birds in this study area was reflected in the prevalence of this cover type among species models. This is not unexpected because Chippewa NF is among the most aquatic of the national forests, with over a quarter of the surface covered in open water and emergent wetlands, and 35% of the forested land cover in lowlands – primarily lowland conifer. Among the greatest uncertainties facing Chippewa NF is how projected climate change might affect the hydrology of its extensive lowland system (John Almendinger, Minnesota Department of Natural Resources, pers. communication) and how projected temperature increases might affect the boreal conifer species currently dominating these systems ([Wolter et al., 1995](#)). Impacts of climate change are cumulative and interconnected, thus current forest species composition may be altered directly through changes in climate or indirectly through insect

infestation disturbance. For example, a recent regional outbreak in eastern larch beetle has been attributed to warming climate ([McKee and Aukema, 2015](#)). Our results indicate climate-related impacts to lowland conifer systems could have profound implications for bird populations in the Chippewa NF and elsewhere in the region.

## 5. Conclusions

Forests of the Great Lakes region support some of the richest breeding bird communities in North America ([Robbins et al., 1986](#); [Price and Root, 2005](#)), including numerous species of high conservation priority. Conservation of these forests is critical to help mitigate impacts of climate change on avian abundance and diversity. However, these systems are particularly vulnerable to a changing climate because of their geographic location and intensive use ([Pastor and Post, 1988](#)). For example, recent research suggests breeding birds in mixed northern conifer and deciduous forests at the edge of their current climate range are among the most vulnerable to warming ([Grinde and Niemi, 2016a](#)). Moreover, several important community types that are currently prevalent within the Great Lakes region, including bigtooth and quaking aspen (*Populus grandidentata* and *P. tremuloides*), sugar maple (*Acer saccharum*), balsam fir, red pine (*Pinus resinosa*), jack pine (*P. banksiana*), and paper birch as well as lowland conifer systems [i.e., spruce, tamarack, and northern white cedar (*Thuja occidentalis*)], are projected to decrease or disappear entirely from the conterminous US ([Hansen et al., 2001](#); [Swanston et al., 2011](#)). Important future work would be to examine the impacts predicted shifts in forest community types and precipitation and temperature changes could have on bird species under potential management and habitat loss scenarios. Process-based forest landscape and succession models allow for detailed simulations of forest landscape change to test and assess the combined effects of management and indirect impacts of climate change on vegetation under multiple adaptive management scenarios ([Scheller and Mladenoff, 2005](#); [Duveneck et al., 2014](#); [Lucash et al., 2017](#)). In a forthcoming study, we will evaluate the consequences of these alternative climate and management scenarios on bird populations by coupling the results of empirical models presented here with the simulated projections of forest, land cover, and climatic change (B.R. Sturtevant, unpublished manuscript). This approach will allow managers to examine alternative management and natural disturbance scenarios *a priori* to optimize bird populations and maintain biodiversity.

Our 20-year dataset is relatively long; however longer time frames are essential to better understand the dynamics of disturbance and climate across large landscapes. Overall, our results provide an important step to help develop science-based adaptive management plans that aim at maintaining a mosaic of forest habitat that optimize the conservation of bird species populations and diversity into the future.

## Acknowledgments

We thank Kelly Barrett from Chippewa National Forest for her expertise added to this project Stephen Matthews and Deahn Donner (USFS Northern Research Station) and two anonymous reviewers' helpful comments on earlier versions of this manuscript. Natural Resources Research Institute contribution number 620. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## Funding

This work was supported by the U.S. Department of Agriculture, Forest Service, through a Joint Venture Agreement, 14-JV-11242313-045, with the Northern Research Station. Funding for the breeding bird counts in the Chippewa National Forest have been completed through a variety of agreements with the Forest Service, most recently a Challenge Cost Share Agreement with the Chippewa and Superior

National Forests, 15-CS-11090300-031. Contributions by Sturtevant were supported by the USFS National Fire Plan.

**Appendix A. Variables used to build avian abundance candidate models in Chippewa National forest from 1995 to 2014. We developed five subsets of candidate models; 100 m stand-level characteristics, land cover characteristics at 200 m, 500 m, and 1000 m scales, and climatic variables, to assess the best predictors of species abundance at multiple scales**

#### 100 m Stand-level characteristics

age	Stand age
jpine100	Jack pine in 100 m buffer
ced100	Cedar in 100 m buffer
tam100	Tamarack in 100 m buffer
bspr100	Black spruce in 100 m buffer
acidbog100	Acid bog in 100 m buffer
nhard100	Northern hardwoods in 100 m buffer
grass100	Grassland in 100 m buffer
brush100	Brush in 100 m buffer
rpine100	Red pine in 100 m buffer
sprucefir100	Spruce fir habitat in 100 m buffer
aspenbirch100	Aspen birch in 100 m buffer
logged	Logged (binary)
insect	Insect damage (categorical: 0 = no damage; 1 = moderate damage; 2 = severe defoliation)
biomass	biomass calculated

#### 200 m Land cover characteristics

open200	Open area 200 m in buffer
forest200	Forest in 200 m buffer
nearwat	Distance to nearest waterbody
lc200	Lowland conifer in 200 m buffer
uc200	Upland conifer in 200 m buffer
um200	Upland mixed wood in 200 m buffer
uh200	Upland hardwood in 200 m buffer
reg200	Regeneration in 200 m buffer
sprucefir200	Spruce fir habitat in 200 m buffer
aspenbirch200	Aspen birch in 200 m buffer
redpine200	Red pine in 200 m buffer

#### 500 m Land cover characteristics

dev500	Developed area in 500 m buffer
wet500	Wetland 500 m
uf500	Upland forest 500 m
lf500	Lowland forest 500 m
forest500	Forest 500 m
logreg500	Regeneration in 500 m buffer
open500	Open area 500 m in buffer

#### 1000 m Land cover characteristics

rd1000	Road length in 1000 m buffer
forest1000	Forest in 1000 m buffer
uf1000	Upland forest in 1000 m buffer
lf1000	Lowland forest in 1000 m buffer
reg1000	Regeneration in 1000 m buffer
wet1000	Wetland in 1000 m buffer
w1000	Water in 1000 m buffer
dev1000	Developed area in 1000 m buffer
open1000	Open area in 1000 m buffer

#### Weather variables

pdsi	Palmer drought severity index (March–June)
precip	Mean annual precipitation (March–June)
temp	Mean spring temperature (March–June)
prevpdsi	Palmer drought severity index (March–June) of previous year
prevprecip	Mean annual precipitation (March–June) of previous year
prevtemp	Mean spring temperature (March–June) of previous year

**Appendix B. Species and associated guilds.** Each species was categorized within five guild types: nesting, habitat preference, migration, foraging, and climate sensitive. Information for categorizing species was obtained primarily from Ehrlich et al. (1988), Freemark and Collins (1992), and Niemi et al. (2016). Climate sensitivity was assigned based on results from Audubon climate Report (2014)

Common name	Nest guild	Habitat guild	Migration guild	Foraging guild	Climate sensitive
Alder Flycatcher	Subcanopy or Shrub	Shrub swamp	Long-distance migrant	Flycatchers	n
American Crow	Canopy	Deciduous forest	Short-distance migrant	Omnivores	n
American Goldfinch	Subcanopy or Shrub	Fields and meadows	Short-distance migrant	Seeds	n
American Redstart	Subcanopy or Shrub	Early-successional mixed	Long-distance migrant	Flycatchers	y
American Robin	Subcanopy or Shrub	Fields and meadows	Short-distance migrant	Ground insects and fruit	y
Black-and-white Warbler	Ground	Mixed forest	Long-distance migrant	Bark insects	n
Blackburnian Warbler	Canopy	Coniferous forest	Long-distance migrant	Foliage insects	y
Black-capped Chickadee	Cavity, Hole, or Bank	Deciduous forest	Permanent Resident	Foliage insects	n
Black-throated Green Warbler	Subcanopy or Shrub	Mixed forest	Long-distance migrant	Foliage insects	y
Blue Jay	Canopy	Deciduous forest	Permanent Resident	Omnivores	n
Blue-headed Vireo	Subcanopy or Shrub	Coniferous forest	Short-distance migrant	Foliage insects	n
Brown Creeper	Cavity, Hole, or Bank	Deciduous forest	Short-distance migrant	Bark insects	y
Brown-headed Cowbird	Nest Parasite	Fields and meadows	Short-distance migrant	Ground insects and seeds	n
Canada Warbler	Ground	Mixed forest	Long-distance migrant	Foliage insects	y
Cedar Waxwing	Subcanopy or Shrub	Ponds, lakes, rivers, streams	Short-distance migrant	Fruit	n
Chestnut-sided Warbler	Subcanopy or Shrub	Early-successional mixed	Long-distance migrant	Foliage insects	y
Chipping Sparrow	Canopy	Coniferous forest	Short-distance migrant	Ground insects and seeds	n
Common Raven	Canopy	Coniferous forest	Permanent Resident	Omnivores	y
Common Yellowthroat	Ground	Shrub swamp	Long-distance migrant	Foliage insects	n
Connecticut Warbler	Ground	Lowland coniferous forest	Long-distance migrant	Foliage insects	y
Downy Woodpecker	Cavity, Hole, or Bank	Deciduous forest	Permanent Resident	Bark insects	n
Eastern Towhee	Ground	Early-successional mixed	Short-distance migrant	Ground insects and seeds	n
Eastern Wood-Pewee	Canopy	Mixed forest	Long-distance migrant	Flycatchers	n
Evening Grosbeak	Canopy	Mixed forest	Permanent Resident	Foliage insects and seeds	y
Golden-crowned Kinglet	Canopy	Coniferous forest	Short-distance migrant	Foliage insects	y
Golden-winged Warbler	Ground	Early-successional mixed	Long-distance migrant	Foliage insects	y
Gray Catbird	Subcanopy or Shrub	Early-successional mixed	Long-distance migrant	Foliage insects and fruit	n
Gray Jay	Subcanopy or Shrub	Lowland coniferous forest	Permanent Resident	Omnivores	n
Great Crested Flycatcher	Cavity, Hole, or Bank	Deciduous forest	Long-distance migrant	Flycatchers	n
Hairy Woodpecker	Cavity, Hole, or Bank	Deciduous forest	Permanent Resident	Bark insects	y
Hermit Thrush	Ground	Mixed forest	Short-distance migrant	Ground insects and fruit	y

Indigo Bunting	Subcanopy or Shrub	Fields and meadows	Long-distance migrant	Foliage insects and seeds	n
Least Flycatcher	Subcanopy or Shrub	Deciduous forest	Long-distance migrant	Flycatchers	y
Magnolia Warbler	Subcanopy or Shrub	Coniferous forest	Long-distance migrant	Foliage insects	y
Mourning Warbler	Ground	Early-successional mixed	Long-distance migrant	Foliage insects	y
Nashville Warbler	Ground	Lowland coniferous forest	Long-distance migrant	Foliage insects	y
Northern Flicker	Cavity, Hole, or Bank	Fields and meadows	Short-distance migrant	Ground insects and fruit	n
Northern Parula	Canopy	Lowland coniferous forest	Long-distance migrant	Foliage insects	n
Northern Waterthrush	Ground	Lowland coniferous forest	Long-distance migrant	Foliage insects	n
Ovenbird	Ground	Deciduous forest	Long-distance migrant	Foliage insects	y
Palm Warbler	Ground	Lowland coniferous forest	Long-distance migrant	Foliage insects	y
Pileated Woodpecker	Cavity, Hole, or Bank	Deciduous forest	Permanent Resident	Bark insects	n
Pine Warbler	Canopy	Coniferous forest	Short-distance migrant	Foliage insects	y
Purple Finch	Canopy	Mixed forest	Short-distance migrant	Seeds	y
Red-breasted Nuthatch	Cavity, Hole, or Bank	Coniferous forest	Permanent Resident	Bark insects	y
Red-eyed Vireo	Subcanopy or Shrub	Deciduous forest	Long-distance migrant	Foliage insects	n
Red-winged Blackbird	Subcanopy or Shrub	Open wetlands	Short-distance migrant	Ground insects and seeds	n
Rose-breasted Grosbeak	Subcanopy or Shrub	Deciduous forest	Long-distance migrant	Foliage insects and fruit	n
Scarlet Tanager	Canopy	Deciduous forest	Long-distance migrant	Foliage insects	y
Song Sparrow	Ground	Fields and meadows	Short-distance migrant	Ground insects and seeds	n
Swamp Sparrow	Ground	Shrub swamp	Short-distance migrant	Ground insects and seeds	y
Veery	Ground	Deciduous forest	Long-distance migrant	Ground insects and fruit	y
White-breasted Nuthatch	Cavity, Hole, or Bank	Deciduous forest	Permanent Resident	Bark insects	y
White-throated Sparrow	Ground	Early-successional mixed	Short-distance migrant	Ground insects and seeds	y
Winter Wren	Ground	Lowland coniferous forest	Short-distance migrant	Foliage insects	n
Wood Thrush	Subcanopy or Shrub	Deciduous forest	Long-distance migrant	Ground insects and fruit	y
Yellow-bellied Flycatcher	Ground	Lowland coniferous forest	Long-distance migrant	Flycatchers	y
Yellow-bellied Sapsucker	Cavity, Hole, or Bank	Deciduous forest	Short-distance migrant	Nectar and Sap	y
Yellow-rumped Warbler	Canopy	Coniferous forest	Short-distance migrant	Foliage insects and fruit	n
Yellow-throated Vireo	Canopy	Deciduous forest	Long-distance migrant	Foliage insects	y
Yellow Warbler	Subcanopy or Shrub	Shrub swamp	Long-distance migrant	Foliage insects	n

## Appendix C. Summary of final species abundance models for Chippewa National forest from 1995 to 2014

Common name	Observations	AIC <sub>C</sub>	R-Squared	Variable subset	Variable	Variable estimate	Standard error
Alder Flycatcher	582	2957	0.50		Intercept	−3.62	0.53
				200 m	open200 <sup>a</sup>	0.70	0.13
				500 m	uf500	−0.05	0.01
American Crow	2430	9131	0.29		Intercept	−5.94	1.18
				500 m	dev500 <sup>a</sup>	0.31	0.06
				1000 m	w1000 <sup>a</sup>	0.38	0.03
				Climate	precip <sup>a</sup>	0.87	0.28
American Redstart	3573	8499	0.61			−0.36	0.16
				100 m	biomass <sup>a</sup>	0.02	0.01
				200 m	lc200 <sup>a</sup>	−0.73	0.09
				500 m	lf500 <sup>a</sup>	0.56	0.16
				1000 m	lf1000 <sup>a</sup>	−1.11	0.16
American Robin	2539	9603	0.29		Intercept	−4.46	0.00
				100 m	biomass	0.00	0.00
				200 m	uh200 <sup>a</sup>	−0.24	0.00
				500 m	dev500 <sup>a</sup>	0.39	0.00
				1000 m	lf1000 <sup>a</sup>	0.18	0.00
				Climate	precip <sup>a</sup>	0.69	0.00
Black-and-white Warbler	1636	8113	0.26		Intercept	−2.36	0.14
Blackburnian Warbler	1344	6635	0.36	200 m	open200 <sup>a</sup>	0.20	0.04
				200 m	uc200 <sup>a</sup>	0.41	0.00
				1000 m	open1000	−0.03	0.00
Black-throated Green Warbler	2418	8735	0.53		Intercept	−8.25	0.92
				200 m	forest200 <sup>a</sup>	1.92	0.22
				Interaction	uf500:pdsi	0.00	0.00
Brown Creeper	757	4577	0.31		Intercept	−3.08	2.11
				200 m	forest200 <sup>a</sup>	1.58	0.23
				1000 m	open1000	−0.17	0.07
				Climate	precip <sup>a</sup>	−1.44	0.43
				Interaction	open1000:precip <sup>a</sup>	0.03	0.02
Chestnut-sided Warbler	5772	13467	0.53		Intercept	−1.68	0.11
				100 m	biomass	0.00	0.00
				200 m	reg200 <sup>a</sup>	0.50	0.03
Chipping Sparrow	1671	6063	0.40		Intercept	−2.70	0.19
				100 m	biomass <sup>a</sup>	−0.04	0.01
				200 m	uc200 <sup>a</sup>	0.47	0.04
				500 m	lf500 <sup>a</sup>	−0.55	0.10
				1000 m	lf1000 <sup>a</sup>	0.35	0.11
Common Yellowthroat	3367	9768	0.54		Intercept	−2.35	0.28
				200 m	open200 <sup>a</sup>	0.60	0.06
				500 m	uf500	−0.04	0.01
				1000 m	uf1000	0.02	0.01
Connecticut Warbler	295	1484	0.45		Intercept	0.71	2.47
				200 m	lc200 <sup>a</sup>	1.26	0.09
				Climate	prevprecip <sup>a</sup>	−1.95	0.58
Eastern Wood – Pewee	2151	8097	0.45		Intercept	−1.27	0.11
				200 m	lc200 <sup>a</sup>	−0.48	0.07
				500 m	lf500 <sup>a</sup>	−0.33	0.12
				1000 m	lf1000 <sup>a</sup>	0.26	0.11
Golden-winged Warbler	524	2778	0.45		Intercept	−7.88	0.55
				100 m	biomass	0.00	0.00
				200 m	open200 <sup>a</sup>	0.93	0.11
				1000 m	reg1000 <sup>a</sup>	1.31	0.23
				Interaction	reg1000 <sup>a</sup> :temp	−0.08	0.03
Gray Catbird	308	1800	0.35		Intercept	−3.09	0.00

				100 m	biomass <sup>a</sup>	-0.04	0.00
				200 m	forest200 <sup>a</sup>	-1.22	0.00
Hermit Thrush	4155	13111	0.45		Intercept	-2.01	0.10
				200 m	lc200 <sup>a</sup>	0.46	0.05
				500 m	lf500 <sup>a</sup>	-0.49	0.10
				1000 m	lf1000 <sup>a</sup>	0.62	0.09
Least Flycatcher	4959	12205	0.62		Intercept	1.20	0.85
				200 m	lc200 <sup>a</sup>	-0.80	0.06
				Climate	precip <sup>a</sup>	-0.49	0.20
Mourning Warbler	1520	5986	0.41		Intercept	-3.28	0.13
				200 m	reg200 <sup>a</sup>	0.48	0.05
Nashville Warbler	6723	13671	0.58		Intercept	-3.73	0.68
				100 m	biomass <sup>a</sup>	0.02	0.01
				200 m	lc200 <sup>a</sup>	0.53	0.04
				500 m	lf500 <sup>a</sup>	0.17	0.05
				Climate	prevprecip <sup>a</sup>	0.42	0.16
Northern Parula	946	4343	0.44		Intercept	-4.13	0.18
				200 m	lc200 <sup>a</sup>	0.26	0.09
				500 m	lf500 <sup>a</sup>	0.33	0.10
Northern Waterthrush	452	2506	0.48		Intercept	-7.43	1.65
				1000 m	lf1000 <sup>a</sup>	1.24	0.14
				Climate	prevprecip <sup>a</sup>	0.91	0.38
Ovenbird	14873	21244	0.64		Intercept	-1.58	0.57
				100 m	biomass	0.00	0.00
				200 m	lc200 <sup>a</sup>	-0.25	0.03
				500 m	uf500	0.02	0.00
				Climate	prevprecip <sup>a</sup>	0.27	0.13
Palm Warbler	259	1203	0.49		Intercept	-6.33	0.00
				100 m	biomass <sup>a</sup>	-0.01	0.00
				200 m	lc200 <sup>a</sup>	1.16	0.00
Pine Warbler	1908	6686	0.55		Intercept	-5.23	0.22
				200 m	uc200 <sup>a</sup>	0.82	0.05
				500 m	uf500	0.02	0.00
				Climate	pdsi	-0.18	0.04
Red-breasted Nuthatch	1707	7708	0.31		Intercept	-2.77	0.13
				200 m	uc200 <sup>a</sup>	0.47	0.02
				Climate	pdsi	-0.16	0.06
Red-eyed Vireo	15686	21577	0.48		Intercept	0.94	0.07
				100 m	biomass <sup>a</sup>	0.01	0.00
				200 m	lc200 <sup>a</sup>	-0.27	0.02
				1000 m	lf1000 <sup>a</sup>	-0.06	0.04
Red-winged Blackbird	424	2117	0.46		Intercept	1.20	1.51
				200 m	nearwat <sup>a</sup>	-0.97	0.20
				500 m	wet500 <sup>a</sup>	0.81	0.21
				1000 m	uf1000	-0.04	0.01
Rose-breasted Grosbeak	1651	7287	0.28		Intercept	-2.05	0.25
				100 m	age <sup>a</sup>	-0.25	0.04
				100 m	biomass	0.00	0.00
				200 m	open200 <sup>a</sup>	0.25	0.04
				1000 m	reg1000 <sup>a</sup>	0.31	0.05
Scarlet Tanager	1361	7142	0.26		Intercept	-1.82	0.28
				500 m	lf500 <sup>a</sup>	-0.42	0.03
				Climate	temp	0.07	0.04
Song Sparrow	1130	4305	0.50		Intercept	-5.86	0.39
				100 m	biomass <sup>a</sup>	-0.05	0.01
				200 m	open200 <sup>a</sup>	0.90	0.11
Swamp Sparrow	938	3423	0.55		Intercept	-3.82	0.62
				200 m	open200 <sup>a</sup>	0.66	0.14

				500 m	uf500	−0.05	0.01
Veery	5831	14155	0.56		Intercept	0.19	0.27
				200 m	uc200 <sup>a</sup>	−0.42	0.03
				1000 m	lf1000 <sup>a</sup>	−0.47	0.04
				Climate	temp	0.08	0.03
White-throated Sparrow	5477	10755	0.68		Intercept	−4.24	0.18
				100 m	biomass <sup>a</sup>	−0.01	0.01
				200 m	lc200 <sup>a</sup>	0.29	0.06
				500 m	lf500 <sup>a</sup>	0.25	0.14
				1000 m	lf1000 <sup>a</sup>	0.88	0.14
Winter Wren	1555	6651	0.45		Intercept	−3.89	0.14
				200 m	lc200 <sup>a</sup>	0.20	0.05
				500 m	lf500 <sup>a</sup>	0.65	0.06
Yellow-bellied Flycatcher	687	3410	0.44		Intercept	−5.29	0.20
				200 m	lc200 <sup>a</sup>	0.97	0.05
Yellow-bellied Sapsucker	1934	8006	0.26		Intercept	−2.83	0.00
				100 m	biomass <sup>a</sup>	−0.01	0.00
				200 m	uh200 <sup>a</sup>	0.45	0.00
				Climate	pdsi	−0.10	0.00
Yellow-rumped Warbler	1673	7600	0.35		Intercept	−3.05	0.15
				200 m	lc200 <sup>a</sup>	0.52	0.06
				500 m	lf500 <sup>a</sup>	−0.36	0.13
				1000 m	lf1000 <sup>a</sup>	0.38	0.12

<sup>a</sup> Indicates natural log transformed variables.

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