
Volume 318, 15 April 2014
ISSN 0378-1127
ELSEVIER
Forest Ecology and Management

Forest Ecology and Management 318 (2014) 183–193

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Bird communities of reference and altered mixed-pine forests: Implications for restoring fire-dependent forest ecosystems

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ARTICLE INFO

Article history:
Received 22 October 2013
Received in revised form 18 December 2013
Accepted 9 January 2014
Available online 8 February 2014

Keywords:
Red pine
Restoration
Fire
Wildlife
Eastern white pine

ABSTRACT

Changes have occurred to disturbance regimes that drive composition, structure, and function in many forest ecosystems. In the northern Lake States, USA land use change has impacted fire-dependent mixed-pine forests of red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.). Although restoration is now being conducted on many federal and state forestlands, we currently lack baseline data on wildlife communities. To address the need for such information we sampled 25 reference and 29 altered mixed-pine sites in a wetland-upland landscape mosaic representative of eastern Upper Michigan. We put forward three questions: (1) do bird communities differ between reference sites and altered sites?; (2) what forest compositional and structural attributes are associated with differences in bird communities and how might they be related to fire history?; and (3) how does heterogeneity of natural land cover affect bird communities? Analyses revealed that richness of forest bird species was greater in reference sites ($T = -1.93$, $P = 0.06$), even though reference sites exist within 20-ha patches with less forest and more wetlands compared to altered sites. Bird assemblages also differed between reference and altered sites (Multiple Permutation Procedure, $T = -5.26$, $A = 0.02$, $P \leqslant 0.001$). Eight indicator species were associated with reference sites, and four species were found in altered sites. Although correlations among environmental variables were generally low, they suggested the important role fire played in this ecosystem. Our findings support the hypothesis that mixed-pine ecosystem restoration can be an important management tool in restoring bird communities.

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1. Introduction

Vegetation structure is a major driving force in the use of forest ecosystems by different bird species (MacArthur and MacArthur, 1961). Forest structure and composition are largely driven by landforms, edaphic facets, site quality, availability of seed sources and other propogules, competition, and past disturbances such as fire (Pregitzer et al., 2000; Frelich, 1995). Spatial attributes that characterize the heterogeneity of forests also affect bird communities (Boulinier et al., 1998), with terms such as area sensitivity being coined to describe the influence of patch characteristics on bird species occupancy (Robbins et al., 1989).

Across much of North America and elsewhere, alterations have occurred to natural disturbance regimes that drive forest structure and composition (Nowacki and Abrams, 2008; Schulte et al., 2007). In the northern Lake States, USA for instance, changes to fire regimes have reduced the dominance of mixed-pine forests of red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.) that during pre-EuroAmerican times occupied nearly three million ha (Leahy and Pregitzer, 2003; Stearns and Likens, 2002; Frelich, 1995). In eastern Upper Michigan, extensive wildfires outside the natural range of variability and subsequent fire suppression and forest management have promoted jack pine (*P. banksiana* Lamb.) on many former red pine-dominated sites (Corace et al., 2013; Drobyshev et al., 2008a). These changes in structure and composition have produced ladder fuels that increase the risk of high-severity crown fires in a landscape comprised of ecosystems that

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http://dx.doi.org/10.1016/j.foreco.2014.01.013
0378-1127/Published by Elsevier B.V.

were historically maintained by low or mixed-severity fires (Drobyshev et al., 2008b). Elsewhere in the northern Lake States, aspen (*Populus* spp.), maple (*Acer* spp.), other deciduous species, and monotypic plantations are now more common on sites that were historically mixed-pine (Fraver and Palik, 2012; Bender et al., 1997).

Like many federal and state agencies, the U.S. Fish and Wildlife Service's National Wildlife Refuge System has policies that foster the restoration of historical conditions (Meretsky et al., 2006). Management is promoting the regeneration of red pine and eastern white pine while reducing the dominance of jack pine (Nyamai, 2013; Corace et al., 2009). These actions are in lock-step with the related fire management concerns that current conditions are more likely to burn in a manner more difficult to manage safely. Consequently, many National Forests in the northern Lakes States are conducting similar treatments (B. Palik, *pers. comm.*). However, mixed-pine restoration is occurring with little knowledge of associated wildlife communities found in reference forests (sites) that provide targets for management actions [in this context, we define reference forests as those that have never been logged (i.e., are virgin), are comprised of native flora, and are maintained by a relatively intact natural disturbance regime, see below]. Theory suggests that reference mixed-pine forests should provide structural conditions which a unique wildlife community, not represented in more altered forests, would favor (Block et al., 2001). However, no tests to validate this assumption have been made even though past work has indicated that mechanical treatments to enhance structure of red pine forests yields different bird communities after three years (Atwell et al., 2008).

While evaluating bird communities of reference and altered mixed-pine sites, we examine potential drivers of bird communities across different forest conditions in a wetland-forest landscape mosaic. We hypothesize that observed differences in forest structure and fire history correspond to different bird communities, but that bird communities are constrained by the spatial attributes of these forest patches and their surrounding land covers.

Specifically, we address the following questions:

1. Do bird communities differ between reference sites and altered mixed-pine sites?
2. What compositional and structural attributes are associated with observed differences in bird communities and how might they be related to fire history?
3. How does heterogeneity of natural land cover affect bird communities?

2. Study area

This study was conducted at the 38,542-ha Seney National Wildlife Refuge (NWR) (N46.271594° W86.057078°), Schoolcraft County, Michigan, USA. Seney NWR lies within the Seney Sand Lake Plain ecoregion (Albert, 1995), itself characterized by having 85% area in public lands (Corace et al., 2012), a low human populations density (~6 people/km), and lacustrine landforms with broad, poorly drained embayments containing beach ridges, swales, dunes, and sandbars. The climate is influenced by its close proximity to both Lakes Superior and Michigan. Average annual precipitation is approximately 81 cm and average annual snowfall is approximately 312 cm. According to the system of Burger and Kotar (2003), 58% of the upland soil types at Seney NWR can support forests of mixed-pine growing with blueberry (*Vaccinium* spp.), sedges (*Carex* spp.), and bracken fern (*Pteridium aquilinum* L.).

The fire history of Seney NWR was reconstructed by Drobyshev et al. (2008b). During drought conditions over the last 300+ years, the mosaic of upland and wetland (peatland) fuels became linked and fire burned across the landscape relatively unchecked, with at least one landscape-scale fire approximately every 60 years. The estimated fire cycle (148 years) in the Seney Wilderness Area of Seney NWR was found to be consistent over the pre-European settlement time period (1707–1860). This observation suggests that currently this part of Seney NWR (in which is contained most of our reference sites) has a fire cycle very close to the long-term average documented before extensive timber harvesting commenced in eastern Upper Michigan. Therefore, this area represents a valuable baseline for other studies of natural mixed-pine forests and a benchmark for restoration efforts. Moreover, because our red pine-dominated reference sites are similar in overstory structure and composition with references sites in Minnesota (Fraver and Palik, 2012) we consider the range of structure and composition that we have documented in past studies (Corace et al., 2013; Drobyshev et al., 2008a,b) to fall within the natural range of variability found in benchmark red pine-dominated ecosystems of the northern Lake States.

Past studies have documented the red pine dominance of our reference sites and the shift in dominance to jack pine on altered sites (Corace et al., 2013; Drobyshev et al., 2008a). Unlike reference sites that have no history of logging, are dominated by a cohort of individuals up to 350 years old, and have a relatively intact fire regime, altered sites have all been logged (often repeatedly, Rist, 2008) and have altered fire regimes due to the proximity of anthropogenic impoundments and active fire suppression (Drobyshev et al., 2008b). Explanations why some sites are reference and some sites are altered rests largely with land use since EuroAmerican settlement (~1860), and especially since refuge establishment (1935). The wetter area of this landscape thwarted attempts to log at the turn of the 20th century as logging with horses and oxen across a wetland was not possible. When Seney NWR was established in 1935 a system of dikes, ditches, and impoundments (pools) were built by supplementing and altering previous (turn-of-the-century) ditching efforts for agricultural purposes. Efforts to create pools for waterfowl started in the eastern portion of the landscape and preceded west until funding ceased in the 1950s. The result was a landscape that was half altered by impoundments, gated gravel roads, and dikes to the east and a landscape that was half untouched by these actions (or other actions) to the west, hence Wilderness Area status starting in 1970 (Losey, 2003; Fig. 1). This resulting pattern of half altered and half reference resulted in different fire patterns due to impounded water, other anthropogenic developments, and active fire suppression on the non-Wilderness portions of the landscape.

3. Materials and methods

3.1. Bird surveys

We conducted unlimited-radius bird point counts within 54 plots also used to quantify forest composition and structure in this and past studies (Corace et al., 2013; Drobyshev et al., 2008a,b): 25 plots represented reference sites and 29 represented altered sites (Fig. 1). All sites were pine-dominated and naturally regenerated. Vegetation plots were randomly located within sites that were selected based on past management history (Rist, 2008). Counts were conducted from each plot center, with all plots being > 250 m from the center of any other plot so as to reduce the likelihood of counting the same bird twice while using unlimited-radius count methods (Ralph et al., 1993). Two point counts for each plot occurred between 6 June and 13 July 2009, a period coinciding with most bird breeding activity in Upper Michigan (Brewer et al., 1991). We observed a minimum interval of two weeks between visits and initiated counts no earlier than 15 min before sunrise (roughly 0545–0600 h), concluding them no later than 1100 h. The second

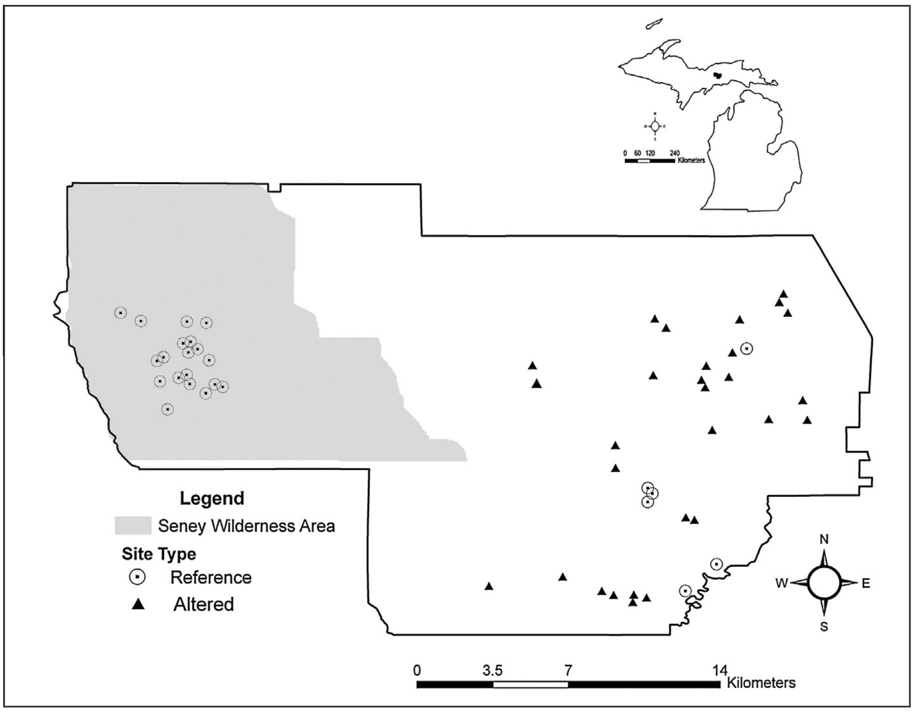

Fig. 1. The location of 25 reference and 29 altered mixed-pine sites relative to one another and the Seney Wilderness Area at Seney National Wildlife Refuge in Upper Michigan.

round of surveying replicated the daily routes from the initial round, but inverted the order of site visitation so as to minimize bias in the average time of day in which points were sampled at a given plot. We did not conduct point counts in rain or in wind conditions >16 kph.

Each point count lasted for five minutes during which we noted the songs of all discrete breeding males or, in the case of common snipe (*Gallinago gallinago* L.), ruffed grouse (*Bonasa umbellus* L.), raptors, and a few other species, their breeding display or other visual cues. Because past studies (Crozier and Niemi, 2003) and ongoing monitoring (U.S. Geological Survey Breeding Bird Survey *unpub. data*) have indicated that bird abundance in this landscape does not differ substantially over multiple years of sampling and because the remoteness of many of the reference sites (1.5-h one-way walk to plots in the Wilderness Area), bird data were only collected for one year and using a five minute (rather than 10-min) sampling frame. Point counts were conducted by a single, trained and experienced observer. Although we did not conduct tests of detectability we believe our methods were appropriate to compare and contrast bird communities of naturally regenerated pine stands within a given landscape devoid of anthropogenic noise.

3.2. Vegetation and fire history

We characterized vegetation at two separate scales: a patch scale of 20 ha and a plot scale of 0.05 ha. The 20-ha scale was chosen so as to encompass an area greater in size than the home territories of most passerines. At both scales, we focused on vegetation variables that represent features that can be a focus of restoration. At the patch scale, we used a geographic information system (GIS) and 2004 aerial imagery (grain size ~1 ha) classified to the National Vegetation Classification Standard (NVCS; USGS, 2012). NVCS classes were then converted into a total of 47 land covers. Within 20-ha circular patches (250 m radius) centered around each of the 0.05-ha vegetation plots (see below), we used FRAGSTATS (McGarigal et al., 2002) to determine the proportion of area comprised of forest and other vegetation land covers, the number of patches, patch density (number patches 10 ha^{-1}), patch richness, and Shannon's (H′) diversity. Other metrics were not calculated because our 20-ha patch invariably cut off the boundaries of cover types and imposed arbitrary patterns.

We used forest structure and composition data collected from within 50-m × 10-m (500-m^2) plots used in past studies (Corace et al., 2013; Drobyshev et al., 2008a,b). The centers of these plots were used as the place from which point counts were conducted. We recorded the species and diameter breast height (DBH, 1.37 m above ground) of all trees > 10.0 cm DBH for the entire plot and for saplings (2.5–10.0-cm DBH) in the central 30-m x 10-m portion of the plot. We established four 2-m^2 (1 m by 2 m) quadrats at equal distances along a lengthwise transect and recorded counts of all seedlings (stems < 2.5-cm DBH) and saplings (2.5–10.0-cm DBH) for all tree species. To measure forest fuels (coarse woody debris, CWD, ⩾12.50 cm in diameter; fine woody debris, FWD, <12.50 cm in diameter), we used methods adapted from the U.S. Forest Service Forest Inventory and Analysis Program (Reams et al., 2005).

We used the dendrochronological analysis of Drobyshev et al. (2008b) to develop descriptors of fire history. Fire-scarred live trees, stumps, and snags were sampled through the use of wedge sampling (Swetnam, 1996). Visual cross-dating approach dated fire scars and annual rings in all samples. We developed local and master 300-year-long point-year chronologies for red pine (Schweingruber et al., 1990) using ring widths, early and latewood widths, and early and latewood densities. We verified the point-year chronologies using existing red pine chronologies for the region and used them to aid in fire dating. Our descriptors of fire history were: (a) time since last fire (TLF), (b) number of fires over the last 50 years, 1956–2006 (NF50), and (c) number of fires over the last 142 years, 1864–2006 (NF142). Our reason for selecting the 50-year time frame was because it represents the most recent fire history in the study area. We selected the 142-year time frame because all sites had samples dating back to 1864 which allowed for comparisons among sites, and 1864 was also an active fire year in the study area.

3.3. Data analysis

We characterized the bird community for each site using the pooled list of species encountered during the two point counts and the maximum abundance of each species over both count periods. We determined the frequency of encounter (registration frequency) for each species by dividing the total number of plots in which it was encountered by the total number of reference and altered sites and the pooled sample. Based on literature review, we assigned each species into a breeding habitat category (wetland, generalist, forest), with most analyses focused on a combined forest-generalist species group that we believe best characterizes the bird communities associated with the mixed-pine forests in this landscape. We also grouped species into nest location, nest type, and forage type functional groups *a priori* by literature review and knowledge of breeding bird habitat use at Seney NWR (Appendix A; Crozier and Niemi, 2003).

Using *R* version 2.15.0 (2012) software, we calculated bird species richness and H′ for each site for: (1) all bird species in all habitat classes combined, (2) for bird species in each habitat class (e.g., forest, generalist, and wetland, respectively), and (3) for the combined forest-generalist species group. To test for differences between observations from reference and altered sites, we used a Student's *t*-test. Before running *t*-tests we examined all data for normality and all, except diversity metrics for the non-functional groupings, had normal distributions ($P > 0.01$). We performed transformations (e.g., natural log) as necessary. We used a chi-square test for association or non-independence on the registration frequency data to determine whether the frequency of encounter (registration frequency) for a given bird species differed between reference and altered sites.

We determined importance values for three different tree functional groups (i.e., pine tree species, other coniferous tree species (e.g., balsam fir, *Abies balsamea* (L.) Mill.; black spruce, *Picea mariana* Mill. B.S.P.), and deciduous tree species) to characterize the overstory and understory of each plot. The three groups represent different vegetation structural conditions that may relate to different conditions for bird use and fire behavior. For instance, we assumed a mixed-pine plot with high levels of other coniferous species would have more vertical strata because of the higher shade tolerance of balsam fir and black spruce. We used variables derived from our measurement of forest fuels to determine the volume ($m^3\ ha^{-1}$) of coarse woody debris and fine woody debris. A Mann–Whitney rank sum test in *R* was used to compare all vegetation characteristics between reference and altered plots.

We used bird abundance data and Multi-Response Permutation Procedure (MRPP) to test the hypothesis that bird community composition between reference and altered plots did not differ. We used PC-ORD5 software (McCune and Mefford, 1995) to conduct the MRPP, using a natural weighting factor and a Sørenson distance matrix (Mielke, 1984). To minimize spurious results due to an emphasis on rarer species, those species present at <5 plots (<∼10% of plots) were removed from the analysis resulting in an analysis of 34 forest-generalist species. MRPP was supplemented with an indicator analysis based upon methods of Dufrêne and Legendre (1997) using PC-ORD5. This analysis uses both the proportional abundance of a bird species in a particular habitat type and its relative frequency within a habitat type. Individual species are ranked from 0 to 100, with zero indicating no indication and 100 indicating perfect indication. The significance of Indicator Values (IV) for each habitat type was determined using a Monte Carlo test with 2000 permutations.

We examined the relationships among the abundances of the forest-generalist bird species and patch and plot explanatory variables using canonical correspondence analysis (CCA) (ter Braak and Šmilauer, 1997). Combining variables from the patch and plot scales, we used a total of 20 variables representing vegetation structure, other environmental characteristics (patch metrics, fuel loading, etc.), and disturbance histories, but excluded patch richness and patch Shannon's diversity due to redundancy. We used PC-ORD5 to perform CCA and determined the significance of each axis using a Monte Carlo permutation test with 500 runs (ter Braak and Šmilauer, 1997). We ran analyses with plot and patch data relativized and not relativized, but visual inspection showed no difference in results nor were any summary statistics different. Because the number of sites (54) exceeded the number of variables (20), overfitting data was not thought to be an issue. We used $\alpha = 0.10$ for all analyses because the failure to recognize a significant finding (Type II error) was of greater concern here than incorrectly stating a significant result (Type I error).

4. Results

4.1. Bird communities

We encountered 77 bird species across the 54 sites and 108 point counts: 31 forest species, 26 generalist species (57 forest-generalist species), and 20 wetland species. No non-native bird species or brown-headed cowbirds (*Molothrus ater* Boddaert) were observed. Registration frequencies indicated that no one species was found in ⩾40% of the 54 sites. Of those 20 species found in ⩾10% of the pooled sample, eight were more commonly encountered in reference sites and 10 more commonly in altered sites (two ties). Of those 15 forest-generalist species found in ⩾10% of the pooled sample, we found five more common in reference sites and eight more common in altered sites (one tie). We found two forest-generalist species solely in reference sites: American redstart (*Setophaga ruticilla* L.) and chestnut-sided warbler (*Dendroica pensylvanica* L.). No species from the forest-generalist group was found only in altered sites (Appendix A). Maximum abundance values of *individual* forest-generalist birds across the two sampling periods for each of the 54 plots showed no difference between reference and altered sites, with the mean (±1 SD) total number of individuals encountered at each being 15.07 (±3.41).

Species richness and Shannon's Diversity (H′) for forest birds tended to be greater in reference sites compared to altered sites, but only richness differed ($T = -1.93$, $P = 0.06$). H′ differed for only the nest type functional group ($T = 20.7$, $P = 0.04$) for the pooled forest-generalist species and was greater in altered sites (Table 1). Results of MRPP reveal that there were significant differences in bird assemblages between reference and altered sites ($T = -5.26$, $A = 0.02$, $P \leqslant 0.001$). The strong chance corrected within-group agreement (*A*) and test statistic (*T*) indicated that groups occupied different regions of species space, suggesting significant differences in the overall assemblage of species. We associated eight indicator species with reference sites, with four species indicative of altered sites (Table 2).

4.2. Vegetation and fire histories

Land covers within the 20-ha patches that surround each sampled 500-m^2 vegetation plot illustrate the heterogeneous nature of the landscape: eight land covers comprised (on average) ⩾5% of the patch area, with no one cover type comprising (on average) >23% of a patch. Wetland land covers predominated in all patches, especially within patches surrounding reference sites. Patches surrounding altered sites had (on average) more area in forests than

Table 1
Bird richness and Shannon's Diversity (H′) from 25 reference and 29 altered mixed-pine sites.

Diversity metric	Mean (±1SD)		*T*	*P*-value[a]
	Reference	Altered		
Overall species richness	16.08 (2.86)	15.66 (2.65)	−0.56	0.58
Forest species richness	7.40 (2.48)	6.14 (2.28)	−1.93	0.06*
Generalist species richness	4.56 (1.16)	4.86 (1.73)	0.76	0.45
Forest-generalist richness	11.96 (2.84)	11.00 (2.51)	−1.31	0.20
Wetland species richness	4.12 (2.03)	4.66 (3.27)	0.73	0.47
Overall H′	1.16 (0.08)	1.15 (0.08)	−0.52	0.61
Forest H′	0.81 (0.19)	0.73 (0.18)	−1.63	0.11
Generalist H′	0.62 (0.13)	0.64 (0.17)	0.36	0.72
Forest-generalist H′	1.03 (0.12)	1.00 (0.11)	−1.17	0.25
Wetland H′	0.53 (0.24)	0.53 (0.32)	−0.09	0.93
Habitat class forest-generalist H′	0.43 (0.06)	0.40 (0.07)	−1.51	0.14
Nest location forest-generalist H′	0.41 (0.08)	0.39 (0.07)	−0.87	0.39
Nest type forest-generalist H′	0.32 (0.14)	0.39 (0.12)	2.07	0.04*
Forage type forest-generalist H′	0.55 (0.08)	0.52 (0.10)	−1.42	0.16

[a] Significant values ($P \leqslant 0.10$) are indicated with an "*".

Table 2
Bird species significantly ($P \leqslant 0.10$) associated with 25 reference and 29 altered mixed-pine sites based on indicator species analysis.

Reference	*P*-value	Altered	*P*-value
Hairy woodpecker	0.07	American robin	0.03
Yellow warbler	0.01	Pileated woodpecker	0.06
American redstart	<0.01	Song sparrow	0.07
White-throated sparrow	0.02	Ruffed grouse	0.06
Least flycatcher	0.02		
Nashville warbler	0.04		
Chestnut-sided warbler	<0.01		
Veery	0.02		

patches surrounding reference sites (Fig. 2). Patches associated with altered sites had a higher patch density ($T = 2.46$, $P < 0.10$) compared to reference sites (Fig. 3).

We found more similarities between reference and altered sites at the plot scale than at the patch scale. Pine species dominated the overstory and the understory in both reference sites and altered sites, but altered sites had more fire-sensitive non-pine coniferous species (such as balsam fir and black spruce) in the overstory and much greater relative abundance of these other coniferous species in the understory (22% compared to <1%, $P = 0.01$). Although the overall number of fires recorded in the last 142 years did not differ between reference and altered sites, the number of fires in the last 50 years and the time since last fire indicated more frequent fire return interval (FRI) for the reference sites ($P = 0.02$ and $P = 0.03$, respectively). Correspondingly, there was both greater duff depth and litter depth in altered sites ($P = 0.02$ and $P = 0.05$, respectively) (Table 3).

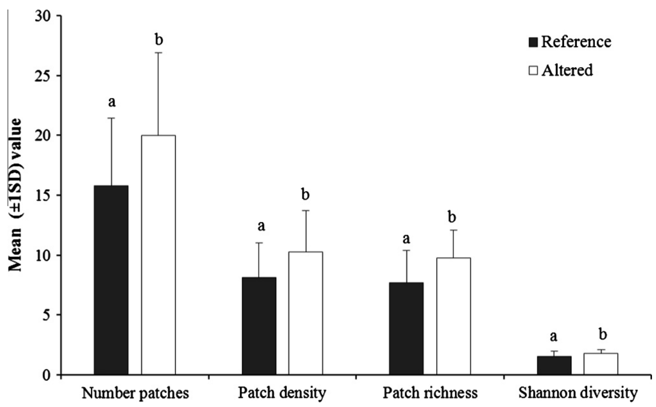

Fig. 3. Mean (±1SD) landscape metric values for 20-ha patches surrounding reference and altered mixed-pine sites. Significant values ($P \leqslant 0.10$) from pair-wise comparisons are indicated by different letters.

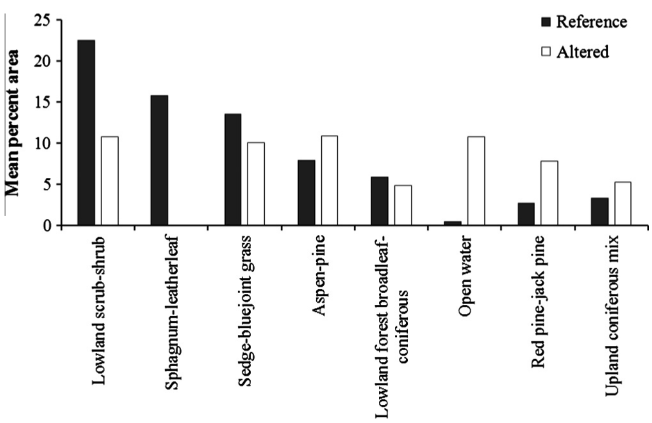

Fig. 2. Mean percent area across land covers comprising ⩾5% area of the 20-ha patch surrounding reference and altered mixed-pine sites.

4.3. Relationship of birds and environmental variables

The CCA of the abundances of 34 bird species as related to 20 patch and plot variables illustrated the variability in environmental factors among sites (Fig. 4). We found raw correlations among environmental variables to be generally low, with only seven variables being selected with a cutoff of $r^2 = 0.175$ and the analysis explaining only 22% of the variance in species. Axis 1, however, showed a significant relationship ($P < 0.001$, eigenvalue = 0.24) and appeared to be a fire history gradient associated with reference sites and the abundance of indicator species (e.g., American redstart, chestnut-sided warbler, hairy woodpecker (*Picoides villosus* L.), least flycatcher (*Empidonax minimus* Baird), Nashville warbler (*Vermivora ruficapilla* Wilson), veery (*Catharus fuscescens* Stephens), white-throated sparrow (*Zonotrichia albicollis* Gmelin), yellow warbler (*Dendroica petechial* L.)). These species tended to be most abundant in red pine-dominated reference sites (Den_RP) with more fires in the last 142 years (NF_142). Axis 2 appears to be related to the structure of sites, with increased hardwood understory (HDWD_U) and duff depth (DUFF_DEP) the result of altered fire regimes.

Table 3
Mean (±1SD) values for vegetation metrics for 25 reference and 29 altered 500 m^2 mixed-pine plots.

Metric	Reference	Altered	P-value[a]
Overstory tree density (ha^{-1})			
Jack pine	13.60 (35.93)	220.00 (419.25)	0.00*
Red pine	590.40 (303.88)	541.38 (410.43)	0.70
White pine	53.60 (82.61)	42.07 (70.98)	0.63
Overstory importance value (%)			
Pine	90.53 (20.83)	95.75 (6.90)	0.34
Other conifer	0.09 (0.46)	0.64 (1.77)	0.13
Deciduous	9.38 (20.87)	3.62 (6.31)	0.22
Understory importance value (%)			
Pine	57.98 (38.38)	60.00 (40.37)	0.99
Other conifer	0.42 (2.1)	22.24 (38.90)	0.01*
Deciduous	33.60 (35.92)	17.76 (26.56)	0.15
Tree dbh (cm)	24.47(4.22)	23.44 (4.66)	0.31
Snag dbh (cm)	16.70 (12.89)	19.28(13.58)	0.41
Tree density (ha^{-1})	905.60 (289.17)	922.86 (410.63)	0.99
Snag density (ha^{-1})	41.60 (36.93)	69.29 (71.07)	0.21
Fire history			
No. fires last 142 yr	5.84 (2.25)	5.97 (3.02)	0.77
No. fires last 50 yr	0.88 (0.60)	0.59 (1.01)	0.02*
Time since last fire (yr)	39.52 (23.03)	61.10 (29.78)	0.03*
Fuel loading (m^3 ha^{-1})			
Coarse woody debris (CWD)	3.73 (10.46)	2.30 (2.85)	0.16
Fine woody debris (FWD)	8,834.19 (11,773.31)	12,019.19 (9,171.68)	0.25
Duff depth (cm)	4.38 (2.06)	5.91 (2.32)	0.02*
Litter depth (cm)	20.53 (8.75)	23.13 (7.5)	0.05*
Fuel bed depth (cm)	14.63 (5.03)	14.93 (3.84)	0.43

[a] Significant values ($P \leqslant 0.10$) are indicated with an "*".

5. Discussion

Studies of bird communities in the western USA have examined the effects of low, mixed, and high-severity fires in a number of dry, pine-dominated ecosystem types (Bond et al., 2012; Hurteau et al., 2008). In particular, the role of fire in ponderosa pine (*P. ponderosa* Douglas ex C. Lawson) ecosystems has been well studied (Moore et al., 1999). In the southeastern USA the role and interrelationship of frequent, low-severity fire in the management of longleaf pine (*P. palustris* Mill.) ecosystems inhabited by Endangered red-cockaded woodpecker (*Picoides borealis* Vieillot) has also been well studied (Wilson et al., 1995; Jackson, 1994). Conversely, far fewer studies have been conducted that have examined fire effects and bird communities in dry, pine ecosystems of the northern Lake States. In fact, the few regional studies involving birds and fire of pine forests have involved the Endangered Kirtland's warbler (*Setophaga kirtlandii* Baird) and jack pine ecosystems of northern Lower Michigan that were historically maintained by high-severity (stand replacing) wildfire (Probst, 1986). Ours is the first study we are aware of in the northern Lake States that characterized bird communities across reference mixed-pine sites and related these findings to forest composition and structure, low to mixed-severity fire histories, and landscape heterogeneity.

Because we conducted our study in a naturally heterogeneous landscape we hypothesized that 20-ha patch-scale factors, such as dominance of forest land covers within a patch, would constrain bird communities. To our surprise we observed no difference in *individual* bird abundance between reference and altered sites, but instead documented greater richness of forest bird species in references sites even when forest land covers did not dominate at the 20-ha patch scale. In fact, non-forest land covers generally surrounded our reference sites, making mixed-pine a relatively small component of the overall 20-ha patch. We suggest that factors we did not measure at this scale (e.g., distance to nearest road, etc.) and the increased patchiness of altered sites may in part explain why forest bird species richness was greater in reference sites. Other research has indicated that the effect of landscape heterogeneity on bird communities differs among landscape types (Rodewald and Yahner, 2001). In particular, Schiek et al. (1995) found that patch size had little influence on bird diversity in remnant old-growth forests of the Pacific Northwest and suggested evolution prepared bird species to account for the natural heterogeneity that surrounded those sites. It is possible that the lack of roads in the Seney Wilderness Area may cause those reference mixed-pine sites to be functionally larger or that enhanced patchiness due to anthropogenic activities such as open water produced by impoundments may have a negative effect on forest bird richness in altered sites. Nonetheless, because we observed very few individuals of area-sensitive bird species, such as black-throated blue warbler (*Setophaga caerulescens* Gmelin), we cannot discount that the heterogeneity of the Seney NWR landscape potentially imposes a constraint on the overall bird community as others have suggested (Corace et al., 2012; Crozier and Niemi, 2003).

We found bird communities of reference and altered mixed-pine sites to be dissimilar. Besides differences in the dominance of red pine and jack pine in the overstory of reference and altered sites and increased abundance of understory conifers in altered sites, however, we found relatively few other differences in many of the structural attributes we measured in 500-m^2 plots. We provide three possible explanations for the incongruity of these findings. First, past analyses of disturbance history based on fire (Drobyshev et al., 2008b) and timber harvesting (Rist, 2008) suggest that enough time may have occurred between disturbances in altered sites such that their successional development has caused some structural convergence with reference sites. Working in northern Lower Michigan, Spaulding and Rothstein (2009) found convergence in structure between wildfire-regenerated jack pine and plantations over 40 yr. In our study, all sites were naturally regenerated and past analyses (Rist, 2008) and other field observations suggest none were clear-cut. The biological legacies of retained red pine and other structures (e.g., snags) may have promoted similar convergence. Second, we suggest that our meth-

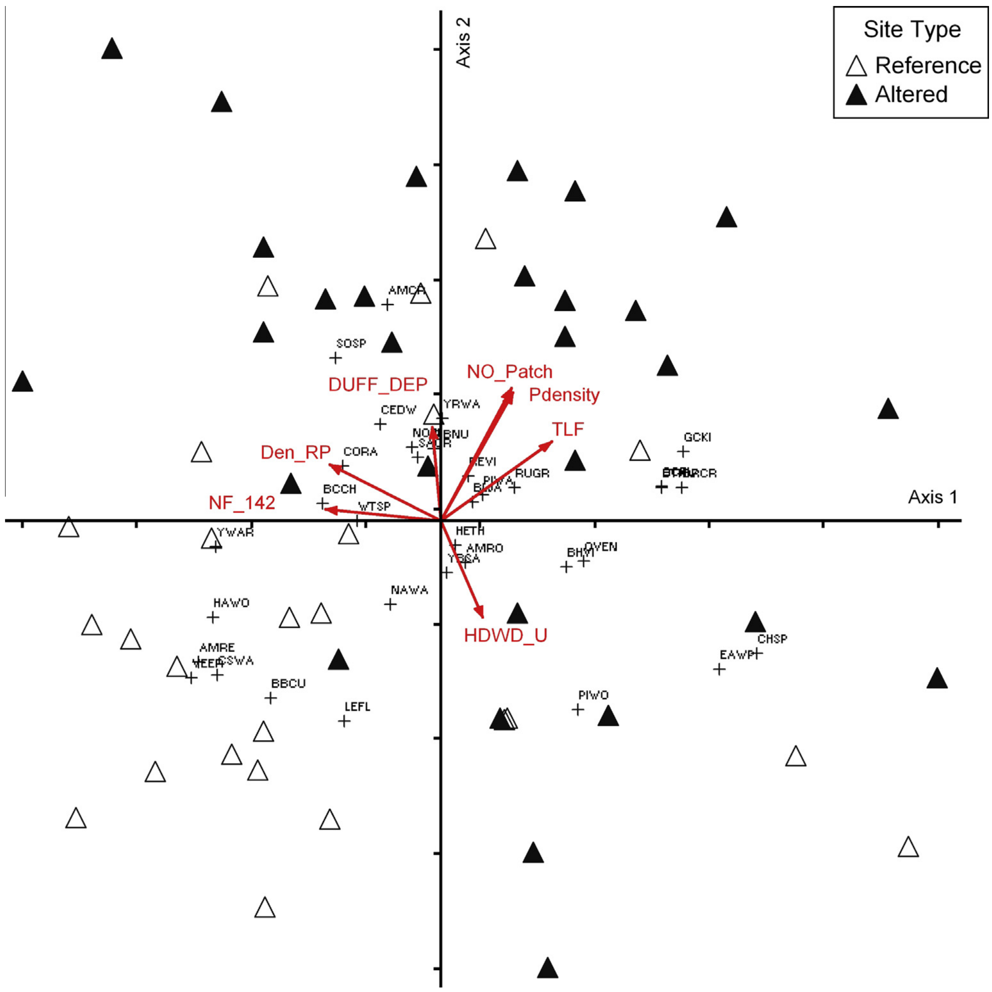

Fig. 4. Canonical correspondence analysis ordination triplot relating bird species abundance with patch and plot characteristics. See Appendix A for species codes.

ods did not account for the potential structural complexity provided by canopy development in reference sites. Canopy structure has been shown to influence bird communities in studies of pine systems in the Sierra Nevada of California (Beedy, 1981). Reference sites in our study are comprised of red pines that have been naturally pruned by a relatively intact fire regime. These reference sites likely have a higher canopy than the jack pine-dominated altered sites as jack pine is a poor self-pruning species. Our methods did not measure height of canopy (or other canopy features) and we suggest there may be additional structural complexity that we did not measure. Finally, it is possible that plot-scale factors have less influence on our bird community observations compared to patch-scale factors (see above).

Results from studies of dry, pine-dominated forests of central Washington indicate that forest restoration treatments aimed at reducing understory fuels (small trees) had neutral to positive effects on focal bird species (Gaines et al., 2010; Lyons et al., 2008; Gaines et al., 2007). In dry pines of northern Florida, studies examining the effects of restoration treatments aimed at reducing understory deciduous dominance within longleaf pine ecosystems suggests that fire treatments affect structure in such a way that the resulting bird community is more similar to reference sites (Steen et al., 2013). Although no similar studies involving the use of prescribed fire have been conducted in the northern Lake States that we are aware of, Atwell et al. (2008) showed how canopy release involving mechanical treatments to *enhance* structure in red pine forests in Minnesota resulted in a positive response to forest understory growth and an increase in bird abundance, richness, and diversity after three years. In our study, understories with greater conifer abundance seemingly had no positive effect on bird richness or the presence of unique bird species in altered sites. Coniferous tree species (such as black spruce and balsam fir) that are intolerant of fire and that likely exist on our altered sites due to fire suppression produced the composition we documented, which likely resulted in more layers in the understory. This suggests that the value of understory structure, as indicated by composition in mixed-pine forests, has limits and may have geographic variability in terms of value to the bird community. Future studies should be conducted in the northern Lake States that examine effects of fuels treatments (especially fire treatments) on wildlife communities.

6. Conclusions

Reference sites are critical for establishing restoration benchmarks and for understanding the development of ecosystems. Our mixed-pine reference sites provided a unique opportunity to quantify patterns and processes that may guide future mixed-pine management and our findings support the global hypothesis that bird communities associated with reference sites are different than altered sites. In particular, we found that the variation in fire histories associated with reference sites were related to the abundance of eight indicator forest-generalist bird species.

The structure, composition, and spatial attributes of forests are common themes in forest bird conservation plans, but rarely considered explicitly in these plans are the resulting patterns that arise from natural disturbance regimes (Rich et al., 2004). Although we did not actually test efficacy of restoration treatments in this study, our results (combined with those of Atwell et al., 2008) suggest that restoration of mixed-pine forests, and the fire that in part yields their structure and composition, could produce similar bird communities to reference sites. This may be especially true if conducted within landscapes in which native land covers dominate as studies have indicated that restoration treatments within natural landscapes are more likely to meet management goals and objectives (Moreno-Mateos et al., 2012). We also suggest the increased dominance of conifers in the understory that likely result from altered fire histories do not add to bird diversity in our study landscape. Thus, treatments that reduce fire hazard by reducing sub-canopy fuels to the range of values we documented in our reference sites may not have adverse effects on bird communities, but future study is required to support this contention. Finally, because of the unlimited-radius point count methodology we used and the fact that recent fires were not sampled, this study did not deduce any patterns related to species that may be potential "flagships" for mixed-pine forests, such as black-backed woodpecker (*Picoides arcticus* Swainson). Future studies should be conducted that target this and other less charismatic species of mixed-pine forest ecosystems.

Acknowledgments

Funding was provided by the Joint Fire Sciences Program, Seney National Wildlife Refuge, the Seney Natural History Association, Wayne State University, and The Ohio State University. We thank the following for assisting: B. Deemer, J. Downs, C. Fado, E. Grover, D. Marsh, D. McCormick, S. Rist, A. Stout, and H. Whitman. We also thank the staff of Seney NWR for logistical support. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Appendix A. All bird species encountered within 54 research plots at Seney National Wildlife Refuge

Birds are listed by decreasing pooled registration frequency (i.e., percentage of plots, sampled twice, with a given species). Habitat classification, nest location, nest type, and forage technique were assigned by literature review, tempered by site-specific experience. Significance ($P \leqslant 0.10$) of a λ^2 test is denoted by an *; $P \leqslant 0.05$ is denoted by an **. Also shown are *Partners in Flight* (PIF) regional conservation scores (2006, see Carter et al., 2000). Species of greater conservation priority have numerically higher scores.

Common name	Binomial	Species code	Habitat[a]	Nest location[b]	Nest type[c]	Forage technique[d]	PIF score	Registration frequency (%)		
								Reference (*n* = 25)	Altered (*n* = 29)	Pooled (*n* = 54)
Common yellowthroat	*Geothlypis trichas* L.	COYE	Wetland	SH	CU	FG	14	42	37	39
Hermit thrush	*Catharus guttatus* Pallas	HETH	Forest	GR	CU	GG	9	39	35	37
Pine warbler	*Dendroica pinus* Wilson	PIWA	Forest	TR	CU	BG	10	29	38	34
Nashville warbler	*Vermivora ruficapilla* Wilson	NAWA	Generalist	GR	CU	FG	13	36	28	32
White-throated sparrow	*Zonotrichia albicollis* Gmelin	WTSP	Generalist	GR	CU	GG	12	36	23	29
Swamp sparrow	*Melospiza georgiana* Latham	SWSP	Wetland	SH	CU	GG	13	34	23	28
Ovenbird	*Seiurus aurocapilla* L.	OVEN	Forest	GR	OV	GG	13	24	31	28
Sedge wren	*Cistothorus platensis* Latham	SEWR	Wetland	GS	SP	GG	14	33^{**}	8^{**}	20
Blue jay	*Cyanocitta cristata* L.	BLJA	Generalist	TR	CU	GG	10	17	22	20
Red-eyed vireo	*Vireo olivaceus* L.	REVI	Forest	SH	CU	HG	11	18	15	16
Song sparrow	*Melospiza melodia* Wilson	SOSP	Generalist	GR	CU	GG	12	11	22	17
Alder flycatcher	*Empidonax alnorum* Brewster	ALFL	Wetland	SH	CU	HA	11	15	15	15
Red-breasted nuthatch	*Sitta canadensis* L.	RBNU	Forest	TR	CA	BG	9	12	17	15
Sandhill crane	*Grus canadensis* L.	SACR	Generalist	GR	SA	PR	–	11	18	15
Yellow-rumped warbler	*Dendroica coronata* L.	YRWA	Forest	TR	CU	FG	9	10	18	14
Black-capped chickadee	*Poecile atricapillus* L.	BCCH	Forest	TR	CA	FG	11	16	11	13
Trumpeter swan	*Cygnus buccinator* Richardson	TRUS	Wetland	GR	PL	SP	–	2^{*}	21^{*}	12
Blue-headed vireo	*Vireo solitarius* Wilson	BHVI	Forest	TR	CU	FG	11	11	11	11

Appendix A (*continued*)

Common name	Binomial	Species code	Habitat[a]	Nest location[b]	Nest type[c]	Forage technique[d]	PIF score	Registration frequency (%)		
								Reference (*n* = 25)	Altered (*n* = 29)	Pooled (*n* = 54)
American crow	*Corvus brachyrhynchos* Brehm	AMCR	Generalist	TR	CU	GG	10	5	14	10
Common snipe	*Gallinago gallinago* L.	COSN	Wetland	GR	SC	PR	–	5	13	10
Common loon	*Gavia immer* Brünnich	COLO	Wetland	GR	PL	SD	–	2	15	9
Northern flicker	*Colaptes auratus* L.	NOFL	Generalist	SN	CA	GG	15	7	10	9
American redstart	*Setophaga ruticilla* L.	AMRE	Forest	TR	CU	HG	12	16**	0**	9
Red-winged blackbird	*Agelaius phoeniceus* L.	RWBL	Wetland	RE	CU	GG	9	3	11	7
Belted kingfisher	*Ceryle alcyon* L.	BEKI	Wetland	BA	BU	HD	16	1	1	7
Black-billed cuckoo	*Coccyzus erythropthalmus* Wilson	BBCU	Forest	TR	PL	FG	16	9	3	6
Chestnut-sided warbler	*Dendroica pensylvanica* L.	CSWA	Forest	SH	CU	FG	14	12*	0*	6
Yellow-bellied sapsucker	*Sphyrapicus varius* L.	YBSA	Forest	TR	CA	BG	14	7	5	6
Yellow warbler	*Dendroica petechia* L.	YWAR	Generalist	SH	CU	FG	11	9	2	6
Black-throated green warbler	*Dendroica virens* Gmelin	BTNW	Forest	TR	CU	FG	14	2	8	5
Pied-billed grebe	*Podilymbus podiceps* L.	PBGR	Wetland	FL	PL	SD	–	7	3	5
Eastern wood-pewee	*Contopus virens* L.	EAWP	Forest	TR	CU	HA	13	4	5	5
Least flycatcher	*Empidonax minimus* Baird	LEFL	Forest	TR	CU	HG	14	8	1	5
American bittern	*Botaurus lentiginosus* Rackett	AMBI	Wetland	GR	PL	SS	–	8	0	4
Bobolink	*Dolichonyx oryzivorus* L.	BOBO	Wetland	GR	CU	GG	15	8	0	4
Canada goose	*Branta canadensis* L.	CAGO	Wetland	GR	SC	SP	–	2	6	4
Common raven	*Corvus corax* L.	CORA	Generalist	CL	CU	GG	9	3	5	4
Ruffed grouse	*Bonasa umbellus* L.	RUGR	Forest	GR	SC	FB	14	1	7	4
Savannah sparrow	*Passerculus sandwichensis* Gmelin	SAVS	Wetland	GR	CU	GG	12	8	0	4
Cedar waxwing	*Bombycilla cedrorum* Vieillot	CEDW	Forest	TR	CU	FG	13	3	4	4
Chipping sparrow	*Spizella passerina* Bechstein	CHSP	Generalist	TR	CU	GG	11	3	4	4
Veery	*Catharus fuscescens* Stephens	VEER	Forest	GR	CU	GG	16	7	0	4
American robin	*Turdus migratorius* L.	AMRO	Generalist	TR	CU	GG	9	0	6	3
Brown creeper	*Certhia americana* Bonaparte	BRCR	Forest	TR	UB	BG	11	1	5	3
Golden-crowned kinglet	*Regulus satrapa* Lichtenstein	GCKI	Forest	TR	PE	FG	12	1	5	3
Great crested flycatcher	*Myiarchus crinitus* L.	GCFL	Generalist	TR	CA	HA	13	3	3	3
Hairy woodpecker	*Picoides villosus* L.	HAWO	Generalist	TR	CA	BG	11	5	1	3
Pileated woodpecker	*Dryocopus pileatus* L.	PIWO	Generalist	SN	CA	BG	11	0	6	3
Bay-breasted warbler	*Dendroica castanea* Wilson	BBWA	Forest	TR	CU	FG	17	4	0	3
Cape May warbler	*Dendroica tigrina* Gmelin	CMWA	Forest	TR	CU	FG	12	4	0	2
Common grackle	*Quiscalus quiscula* L.	COGR	Generalist	TR	CU	GG	9	0	4	2
Le Conte's sparrow	*Ammodramus leconteii* Audubon	LCSP	Wetland	GR	CU	GG	13	4	0	2

(*continued on next page*)

Appendix A (*continued*)

Common name	Binomial	Species code	Habitat[a]	Nest location[b]	Nest type[c]	Forage technique[d]	PIF score	Registration frequency (%)		
								Reference (*n* = 25)	Altered (*n* = 29)	Pooled (*n* = 54)
Vesper sparrow	*Pooecetes gramineus* Gmelin	VESP	Generalist	GR	CU	GG	12	3	1	2
Yellow-bellied flycatcher	*Empidonax flaviventris* Baird	YBFL	Forest	TR	CA	HA	12	3	1	2
Baltimore oriole	*Icterus galbula* L.	BAOR	Generalist	TR	PE	FG	13	3	0	2
Mourning dove	*Zenaida macroura* L.	MODO	Generalist	TR	SA	GG	6	1	2	2
Warbling vireo	*Vireo gilvus* Vieillot	WAVI	Forest	TR	CU	FG	11	3	0	2
Downy woodpecker	*Picoides pubescens* L.	DOWO	Generalist	SN	CA	BG	10	1	1	1
Lincoln's sparrow	*Melospiza lincolnii* Audubon	LISP	Generalist	GR	CU	GG	10	1	1	1
Magnolia warbler	*Dendroica magnolia* Wilson	MAWA	Forest	TR	CU	HG	10	2	0	1
Mourning warbler	*Oporornis philadelphia* Wilson	MOWA	Forest	GR	CU	FG	16	2	0	1
Purple finch	*Carpodacus purpureus* Gmelin	PUFI	Generalist	TR	CU	GG	16	0	2	1
Ring-billed gull	*Larus delawarensis* Ord	RBGU	Wetland	GR	SA	GG	–	0	2	1
White-breasted nuthatch	*Sitta carolinensis* Latham	WBNU	Forest	TR	CA	BG	11	1	1	1
Winter wren	*Troglodytes troglodytes* L.	WIWR	Forest	SN	CA	GG	12	1	1	1
American goldfinch	*Carduelis tristis* L.	AMGO	Generalist	SH	CU	FG	13	0	1	1
Blackburnian warbler	*Dendroica fusca* Müller	BLBW	Forest	TR	CU	FG	14	0	1	1
Caspian tern	*Hydroprogne caspia* Pallas	CATE	Wetland	GR	SC	HD	–	0	1	1
Cooper's hawk	*Accipiter cooperii* Vieillot	COHA	Forest	TR	PL	AP	11	0	1	1
Eastern bluebird	*Sialia sialis* L.	EABL	Generalist	SN	CA	HA	10	0	1	1
Great blue heron	*Ardea herodias* L.	GBHE	Wetland	TR	PL	SS	–	0	1	1
Indigo bunting	*Passerina cyanea* L.	INBU	Generalist	SH	CU	FG	10	0	1	1
Rose-breasted grosbeak	*Pheucticus ludovicianus* L.	RBGR	Forest	TR	CU	FG	16	0	1	1
Sharp-tailed grouse	*Tympanuchus phasianellus* L.	STGR	Generalist	GR	SC	GG	13	0	1	1
Sora	*Porzana carolina* L.	SORA	Wetland	FL	SA	GG	–	0	1	1
Gray catbird	*Dumetella carolinensis* L.	GRCA	Generalist	SH	CU	GG	12	2	1	1
Mallard	*Anas platyrhynchos* L.	MALL	Wetland	GR	SC	DA	-	0	3	1

[a] Brewer et al. (1991).
[b] Ehrlich et al. (1988): FL, floating; GR, ground; RE, reeds; SH, shrub; SN, snag; TR, tree (coniferous or deciduous).
[c] Ehrlich et al. (1988): BU, burrow; CA, cavity; CU, cup; OV, oven; PE, pendant; PL, platform; SA, saucer; SC, scrape; SP, sphere; UB, under bark.
[d] Ehrlich et al. (1988): AP, aerial pursuit; BG, bark glean; DA, dabbles; FB, foliage browse; FG, foliage glean; GG, ground glean; HA, hawks; HD, high dives; HG, hover & glean; PR, probes; SD, surface dives; SP, surface dips; SS, stalk & strike.

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