RESEARCH ARTICLE

Kirtland's Warbler Habitat Management and Multi-species Bird Conservation: Considerations for Planning and Management across Jack Pine (*Pinus banksiana* Lamb.) Habitat Types

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ABSTRACT: Intensive management of jack pine (*Pinus banksiana* Lamb.) plantations has led to a population increase and breeding range expansion of the endangered Kirtland's Warbler (*Dedroica kirtlandii* Baird). However, no study has quantified the different bird communities that are associated with Kirtland's Warbler habitat management. We examined bird species conservation scenarios of warbler habitat management by addressing the following: (1) how do bird community structure and conservation scenarios differ among jack pine habitats of three discrete age classes (YOUNG, < 5 years; KW, 5-23 years; and OLD, > 23 years)?; (2) what functional groups (e.g., nest placement groups, foraging groups) of bird species are represented among these three habitat types?; and (3) what are the relationships between bird communities and the composition and structure of these habitat types? Sixty bird species were observed in 37 habitat patches across the three habitat types. Conservation metrics based upon the pooled species lists for each of the habitat types indicated no difference ($P > 0.05$) among them. Five bird species of U.S. Fish and Wildlife Service Regional Conservation Priority were found among the habitat types, with all but Kirtland's Warbler most common in the YOUNG habitat. Five indicator species associated with the YOUNG and KW habitat types were observed, while nine species were associated with the OLD habitat. A functional group analysis indicated that stand structure was important for breeding species across habitat types. We believe our results support increased ecologically-based planning and management across jack pine habitats for more than just Kirtland's Warbler.

Index terms: Endangered Species Act, habitat management, jack pine, Kirtland's Warbler, migratory birds

INTRODUCTION

An important aspect of the Endangered Species Act (ESA) of 1973 is to "provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved" (Flather et al. 1998). As such, the ESA has been critical in identifying where management efforts to conserve or recover species are most effective (Wilcove et al. 1993; Czech 2005). For many ESA-listed species, the conservation, rehabilitation, or restoration of critical habitat has multi-species consequences (Wilcove and Chen 1998). In other words, the impacts of endangered species habitat management are not confined to only the endangered species. Yet the multi-species benefits of habitat management for most ESA-listed species are relatively underappreciated, and too often the efficacy of species recovery efforts is narrowly evaluated (Gifford 2007).

One such example of this phenomenon is the intensive management of habitat for the Kirtland's Warbler (Dendroica kirtlandii Baird), a ground-nesting, Neotropical migrant that breeds in the fire-dependent jack pine (Pinus banksiana Lamb.) ecosystems of the Upper Midwest (Probst 1986; Probst 1988; Probst and Weinrich 2003). These ecosystems, typically found on xeric, sandy soils, once covered much of northern Michigan, Wisconsin, and adjacent Ontario. In the younger, wildfire-induced seral stages preferred by breeding Kirtland's Warblers, habitat is characterized by dense and patchy stands of jack pine. Historically, periodic wildfire once every 5 to 20 years maintained these conditions across outwash-dominated landscapes (Zou et al. 1992; Kashian et al. 2001). However, fire suppression and landscape fragmentation have significantly reduced Kirtland's Warbler habitat across the species' core breeding range. In 1971, the Michigan census revealed only 201 males, less than half of the number recorded 10 years earlier (Probst et al. 2003). As a result, the Kirtland's Warbler was listed under the ESA and intensive efforts to manage jack pine plantations for breeding habitat began in the northern Lower Peninsula of Michigan by the State of Michigan Department of Natural Resources (MDNR), the U.S. Forest Service, and the U.S. Fish and Wildlife Service (USFWS). The propagation and management of such plantations has since effectively increased the amount of suitable habitat, and has led to a concomitant increase in the Kirtland's Warbler population, as well as a recent range expansion into the Upper Peninsula of Michigan and Wisconsin (Probst et al. 2003; Levin et al. 2007; Donner et al. 2009). In 2008, for the seventh consecutive year, census results exceeded the established recovery objective of 1000 singing males. The 1792 singing male Kirtland's Warblers observed in Michigan in 2008 was the

greatest number of male birds ever recorded (MDNR, unpubl. data).

Presently, most Kirtland's Warbler breeding habitat consists of dense jack pine plantations that are 5 to 23 years old and 1.4 to 5.0 m in height (Probst 1986, 1988; Probst et al. 2003). Initial silvicultural treatments typically involve clear-cutting mature jack pine stands, which are then trenched and hand-planted with 2-yr old jack pine seedlings in an "opposing wave pattern" (Houseman and Anderson 2002) (Figure 1). This pattern of planting produces small (< 1 ha) openings in which adult birds forage, surrounded by dense (preferably > 3952 stems ha-1) patches of jack pine in which birds nest (Probst 1986, 1988). Other regeneration methods, such as prescribed fire and direct seeding, have also been utilized with mixed results (Probst and Weinrich 1993; Goebel et al. 2007).

While there is clearly a need to continue managing jack pine plantations as described above to maintain habitat for Kirtland's Warbler, efforts to further promote Kirtland's Warbler habitat may benefit from a shift to a "mesofilter" approach to biodiversity conservation (Hunter 2005), one that considers multiple species, ecoregional conservation scenarios (Corace 2007), and other ecosystem components (Rothstein et al. 2004; Spaulding and Rothstein 2009). Currently, most habitat management for Kirtland's Warbler exemplifies a "fine-filter" approach (Hunter 2005), whereby the critical needs of a single species justify intensive management actions that may yield uncharacteristic vegetation patterns, relative to those that arise from a natural disturbance (in this case, wildfire). However, the intensity and expense of these and other intensive management actions for single species have raised concerns about ecosystem (Holling and Meffe 1996) and economic (Abhat 2008) sustainability.

Before proposing the broad-scale application of a mesofilter approach to jack pine management for Kirtland's Warbler, a baseline of existing conservation opportunities provided by intensive jack pine plantation management is required. In particular, planners and land managers would benefit from knowing what bird species utilize all jack pine habitat types involved in warbler habitat management. For some species, warbler habitat management may already be providing an underappreciated source of habitat; for others, novel conservation opportunities may exist in the management of one or more jack pine successional stages or age classes (hereafter referred to as habitat types). However, to our knowledge no study has examined the multiple bird species conservation scenarios of Kirtland's Warbler habitat management.

Figure 1. Aerial view of jack pine at Kirtland's Warbler Wildlife Management area following intensive plantation management (left half of photo) and prescribed fire (right foreground).

The primary goal of this paper is to quantify the multi-species aspects of Kirtland's Warbler habitat management. Specifically, we address the following questions: (1) how do bird community structure and conservation scenarios differ among three jack pine habitat types (YOUNG habitat, recently clearcut jack pine patches < 5 years; KW habitat, Kirtland's Warbler-suitable patches 5-23 years old; and OLD habitat, jack pine patches > 23 years old and awaiting treatment for Kirtland's Warbler)?; (2) what functional groups of bird species are represented among the three habitat types?; and (3) what are the relationships between bird communities and habitat patch composition and structure?

STUDY AREA

We conducted our study at the USFWS's Kirtland's Warbler Wildlife Management Area (WMA), one of 57 land units in the National Wildlife Refuge System established under the authority of the ESA (Davison et al. 2006). The Kirtland's Warbler WMA is comprised of 125 tracts located within eight counties of the northern Lower Peninsula of Michigan (Figure 2). The total size of Kirtland's Warbler WMA is 2676 ha, with considerable variation existing in individual stand size. An average (± 1 SD) stand at the WMA is 22.6 (± 37.4) ha. The largest stand is 316 ha and is located in Oscoda County, and the two smallest stands each consist of < 1 ha in Ogemaw County (Goebel et al. 2007).

Due to its inland location and northern latitude, the Kirtland's Warbler WMA is characterized by a relatively severe climate. The growing season ranges from 70 to 130 days, with frequent spring freezes. Snowfall is heavy, with over 350 cm recorded annually in some localities. Average annual precipitation is relatively uniform across the area, ranging between 71 and 81 cm (Albert 1995).

Topographically, the land is flat to gently rolling, and landforms are glacially-derived. In terms of physiography and land classification, the majority (94%) of the stands are in the Highplains Landtype Association, with 6% in the Presque Isle Land-

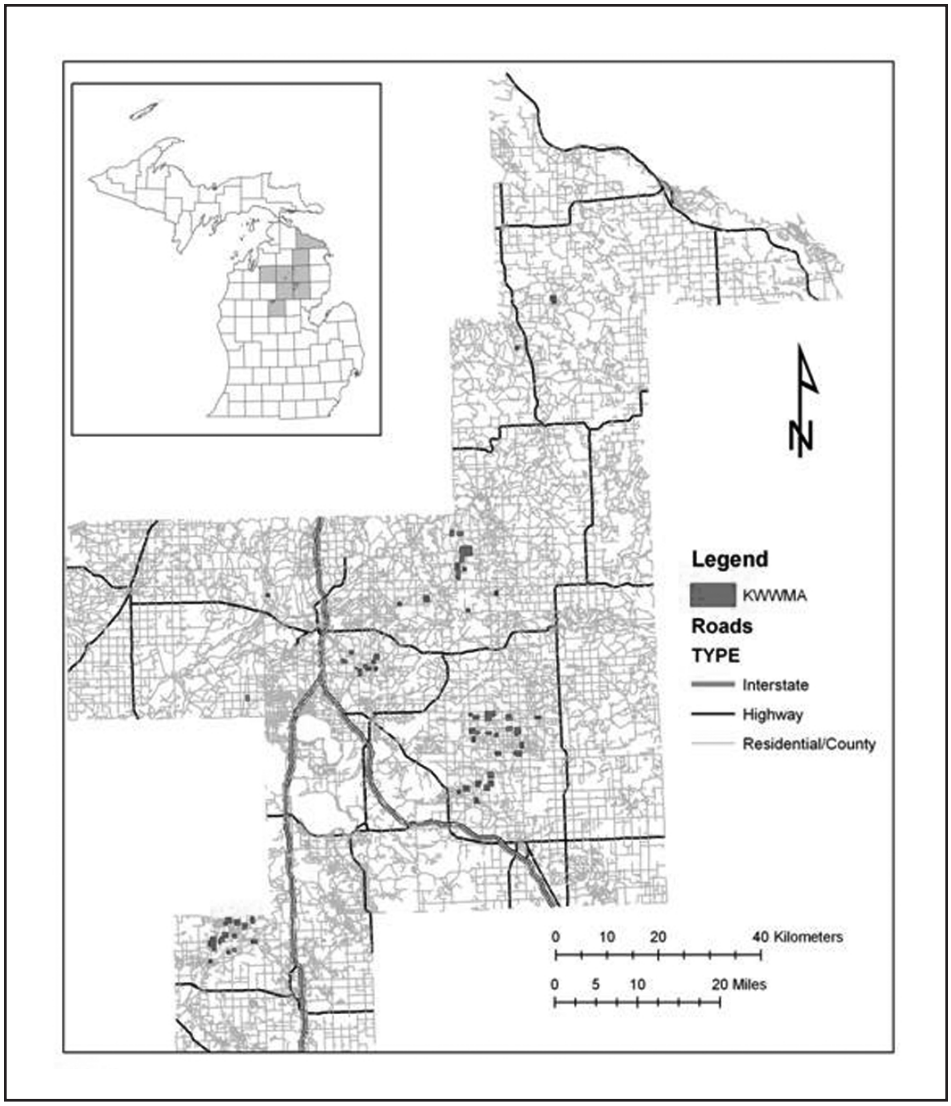

Figure 2. U. S. Fish and Wildlife Service Kirtland's Warbler Wildlife Management Area.

type Association (Albert 1995). Most of the area is comprised of sand-dominated soil associations well suited for the growth of jack pine and the production of Kirtland's Warbler habitat: Grayling–Graycalm–Au Gres (35%), Rubicon–Grayling–Croswell (34%), and Grayling–Rubicon–Au Gres (21%) (Goebel et al. 2007).

METHODS

Bird Communities

We conducted breeding bird surveys twice in 97 habitat patches across 37 jack pine tracts of Kirtland's Warbler WMA (or 30% of all WMA tracts). Because the amount of land in the WMA is not evenly divided among YOUNG, KW, and OLD jack pine habitat types, it was not possible to sample an equal number of point counts in each. Our resulting 194 total counts involved 21 YOUNG habitat patches, 30 KW habitat patches, and 46 OLD habitat patches as determined by examining tree ages from the dominant cohort utilizing either an increment borer or destructively sampling several stems (Goebel et al. 2007). Bird surveys were conducted using the unlimited point count method of Ralph et al. (1993), with methods adapted to local conditions. To minimize disturbance to breeding Kirtland's Warblers in patches that are closed to public entry during the breeding season, only one year of bird data was

collected. Each of 97 point count stations was surveyed twice between 6 June and 9 July 2006, a period coinciding with moderate to high levels of breeding activity for most terrestrial bird species in the northern Lower Peninsula of Michigan (Brewer et al. 1991). A minimum interval of two weeks was observed between visits to a given point count station. Counts were initiated no earlier than 15 minutes before sunrise (roughly 0545 to 0600 hr EST), and were concluded no later than 1100 hr. The second round of point counts replicated the daily routes from the initial round, but inverted the order of visitation so as to minimize bias in the average time of day in which points were sampled. Counts were not executed in rain or when winds exceeded 16 kph. Point locations were ≥ 250 m from each other to minimize double counting of birds and ≥ 50 m from patch edges to minimize the counting of off-patch individuals. Each count was conducted for five minutes, during which time all discrete breeding males were noted by manifestation of their song. Species without identifiable song (e.g., corvids, raptors, and woodpeckers) were noted by visual observation or by manifestation of their call.

Habitat Patch Composition and Structure

After reconnaissance of each habitat patch and examination of digital aerial photographs, we quantified the composition and structure of YOUNG habitat using MDNR sampling procedures for jack pine regeneration surveys. Specifically, we established a series of 0.008-ha plots that were distributed systematically across a habitat patch; the number of plots was dependent on the size and homogenous nature of the habitat patch. In each plot, we counted all woody stems by species and classified, if possible, each jack pine stem as either planted or volunteer. We also estimated the average height of the jack pine stems in each plot. For KW and OLD habitat patches, we systematically established a series of 0.008-ha plots across the habitat patch so as to characterize its variability in composition and structure. Within each plot, we measured the diameter breast height (dbh) of every tree > 10.0 cm dbh by species, and estimated the average height of the overstory jack pine using a clinometer. We also counted the number of understory trees (stems < 10.0 cm dbh and > 2.54 cm dbh) by species. Finally, we counted the number of seedlings (stems < 2.5 cm dbh) by species within three nested 1-m^2 quadrats.

Data Analysis

Bird species were tallied and sorted by habitat type into two metrics of occupancy: (1) registration frequency (i.e., the percentages of point counts in a given habitat type in which a particular species was observed) and (2) abundance. Registration frequencies consisted of presence-absence data per point count station and, therefore, were less prone to bias brought upon by trying to count all singing males of a given species.

To compile species lists for each of the three jack pine habitat types for community and species-specific conservation scenario comparisons, we required a minimum 10% registration frequency before characterizing a species as using a given habitat type. We felt that such a conservative approach was warranted due to the mobile nature of the species we studied. Using this approach allowed us to remove species that were documented at Kirtland's Warbler WMA, but which do not breed or consistently utilize one or more of the three habitat types studied. This process eliminated, for instance, some wetland-dependent species such as Red-winged Blackbird (*Agelaius phoeniceus* L.). We used a chi-square test ($\alpha < 0.05$) for association or non-independence (Krebs 1989) on the registration frequency data to determine whether they differed among habitat types.

For our analysis of the bird conservation value of each of the three jack pine habitat types, we evaluated each species based on (1) the USFWS Regional (Midwest) Conservation Priority species list (USFWS 2002) and (2) the Partners in Flight (PIF) regional conservation scores (PIF 2006). USFWS Regional Conservation Priority species are those in high need of conservation action in the collection of states that form the USFWS Midwest planning region, while PIF regional conservation scores are more ecoregional in nature. Both are derived from global abundance, threats on breeding and wintering grounds, total area of breeding distribution, the importance of areas based on abundance patterns, and population trends. However, whereas species are simply listed as a USFWS Regional Conservation Priority, PIF values are numerically assigned in reference to the relative conservation needs of the species (Carter et al. 2000). A Kirtland's Warbler, for example, receives a score of 22, while a Mourning Dove (*Zenaida macroura* L.) receives a score of 6. To compare bird community conservation values among habitat types, we calculated the summed PIF score for all species observed within YOUNG, KW, and OLD patches and compared the average PIF scores based on the species list of each jack pine habitat type. We also calculated a weighted score for each habitat type by summing individual species PIF scores by their overall registration frequency in each. Average and weighted PIF scores among habitat types were compared by analysis of variance (ANOVA) (Krebs 1989). Using a literature review (Ehrlich et al. 1988) tempered by our own regional knowledge of natural history, we examined how the bird species list pooled across jack pine habitat types broke down into functional groups based on bird nest location, nest type, and foraging technique. We then compared these findings using PIF conservation scores for the species included in each functional group.

Descriptive statistics were used to examine differences in vegetation structural characteristics by habitat type. We used the registration frequency data (without a minimum registration frequency requirement) and Multi-Response Permutation Procedure (MRPP) to test the hypothesis that bird composition among the three habitat types was not different. We used PC-ORD software (McCune and Mefford 1995) to conduct the MRPP, using a natural weighting factor and a Sørenson distance matrix as recommended by Mielke (1984). MRPP was supplemented with an Indicator Analysis based upon methods of Dufrêne and Legendre (1997) using PC-ORD software. 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 tested using a Monte Carlo permutation procedure.

To examine the relationships between bird abundance and habitat patch vegetation characteristics, we used canonical correspondence analysis (CCA), a direct gradient analysis ordination that is constrained by multiple regression of the factors used (ter Braak and Šmilauer 1997). Twelve variables representing habitat patch characteristics were used in the CCA (including the three habitat types, each as a binary variable): total overstory density, total understory density, total overstory density + total understory density, total seedling density, jack pine overstory density, jack pine understory density, total jack pine overstory density + total jack pine understory density, jack pine seedling density, and jack pine height. Prior to the analysis, those bird species that occurred in < 5% of the plots were deleted from the dataset (20 species), and all habitat patch characteristic variables were relativized to ensure all variables were on the same relative scale. CCA was performed with CANOCO ver. 4 software and the significance of each axis was determined using a Monte Carlo permutation test (ter Braak and Šmilauer 1997).

RESULTS

Bird Communities

Sixty bird species were documented across 194 point counts in 37 habitat patches of the Kirtland's Warbler WMA (Appendix). Registration frequencies for 12 (20%) of these species did not differ among habitat types (Table 1). Forty (67%) of these bird species had registration frequencies ≥ 10% in at least one of the three habitat types, and were included in species lists for a given habitat type. Acknowledging an uneven sample size among the three habitat types (e.g., a 120% larger sample in OLD habitat relative to YOUNG habitat) and the pre-requisite of ≥ 10% registration frequency for inclusion in a habitat type, 20 bird species were documented in YOUNG habitat, 25 species in KW habitat, and 22 species in OLD habitat.

On average (±1 SD), 34% (± 11%) of the bird species were observed in more than one habitat type. Considerably more bird species were observed in both YOUNG and KW habitats (45%) than in either KW and OLD (34%) or YOUNG and OLD (24%). Seven bird species avoided OLD habitat and utilized only the YOUNG and KW habitat combination (Black-billed Cuckoo, *Coccyzus erythropthalmus* Wilson; Field Sparrow, *Spizella pusilla* Wilson; Brown Thrasher, *Toxostoma rufum* L.; Clay-colored Sparrow, *Spizella pallida* Swainson; Vesper Sparrow, *Pooecetes gramineus* Gmelin; Lincoln's Sparrow, *Melospiza lincolnii* Audubon; Upland Sandpiper, *Bartramia longicauda* Bechstein). Five bird species (Cedar Waxwing, *Bombycilla cedrorum* Vieillot; Common Nighthawk, *Chordeiles minor* Forster; Black-capped Chickadee, *Poecile atricapillus* L.; Slate-colored Junco, *Junco hyemalis* L.; Hermit Thrush; *Catharus guttatus* Pallas) avoided YOUNG habitat and used only in KW and OLD habitats combined (Table 1).

Seven bird species (12%) were ubiquitously observed in ≥ 10% of point counts in all three habitat types: Northern Flicker, *Colaptes auratus* L.; Nashville Warbler, *Vermivora ruficapilla* Wilson; Chipping Sparrow, *Spizella passerine* Bechstein; Blue Jay, *Cyanocitta cristata* L.; Common Grackle, *Quiscalus quiscula* L.; Common Raven, *Corvus corax* L.; and Mourning Dove, *Zenaida macroura* L. Five bird species (Song Sparrow, Melospiza melodia Wison; Alder Flycatcher, *Empidonax alnorum* Brewster; American Crow, *Corvus brachyrhynchos* Brehm; Eastern Bluebird, *Sialia sialis* L.; Indigo Bunting, *Passerina cyanea* L.) were observed only in YOUNG habitat. Six bird species (Kirtland's Warbler, Common Yellowthroat, *Geothlypis trichas* L.; American Goldfinch, *Carduelis tristis* L.; Eastern Towhee, *Pipilo erythrophthalmus* L.; White-throated Sparrow, *Zonotrichia albicollis* Gmelin; Red-tailed Hawk, *Buteo jamaicensis* Gmelin) were observed only in KW habitat. Nine bird species (Rose-breasted Grosbeak, *Pheucticus ludovicianus* L.; Eastern Wood-Pewee, *Contopus virens* L.; Great Crested Flycatcher, *Myiarchus crinitus* L.; Ovenbird, *Seiurus aurocapilla* L.; Scarlet Tanager, *Piranga olivacea* Gmelin; Blue-headed Vireo, *Vireo solitarius* Wilson; Red-eyed Vireo, *Vireo olivaceus* L.; White-breasted Nuthatch, *Sitta carolinensis* Latham; Red-breasted Nuthatch, *Sitta vireo* L.) were observed only in OLD habitat.

The five most frequently documented species across all point counts were Blue Jay, Nashville Warbler, Hermit Thrush, Common Raven, and Mourning Dove (Table 1). Field Sparrow, Brown Thrasher, Common Raven, and Vesper Sparrow exceeded 80% registration frequency in YOUNG habitat. In KW habitat, Blue Jay, Field Sparrow, Hermit Thrush, Kirtland's Warbler, and Nashville Warbler were all recorded in over 80% of points. In OLD habitat, only Blue Jay and Hermit Thrush exceeded the 80% registration frequency level. For those species observed in two or more of the habitat types at a registration frequency of ≥ 10%, six species became more common from YOUNG to OLD (Cedar Waxwing, Common Nighthawk, Black-capped Chickadee, Chipping Sparrow, Slate-colored Junco, Blue Jay) and eight species became less common (Black-billed Cuckoo, Field Sparrow, Northern Flicker, Brown Thrasher, Vesper Sparrow, Upland Sandpiper, Clay-colored Sparrow, Common Raven).

In YOUNG habitat, Field Sparrow was the most abundant species at an average of 1.73 males per point count. Blue Jay, Brown Thrasher, Common Raven, and Lincoln's Sparrow were also observed on average with > 1 individual per point in YOUNG habitat. In KW habitat, 2.80 Kirtland's Warblers were observed on average per point count, the highest level of single-species abundance within any of the three jack pine habitat types. Blue Jay, Field Sparrow, Hermit Thrush, and Nashville Warbler were all also observed on average with > 1 individual per point in KW habitat. The Hermit Thrush was the most abundant species in OLD habitat at 1.83 birds on average per point count,

with Blue Jay, Chipping Sparrow, Nashville Warbler, and Ovenbird also observed on average with > 1 individual per point (Table 2).

Five USFWS Regional Conservation Priority species were observed: Black-billed Cuckoo, Field Sparrow, Kirtland's Warbler, Northern Flicker, and Upland Sandpiper. Kirtland's Warbler was observed in 90% (27 of 30) of the KW habitat patches. The other four Priority species all had their highest registration frequencies in YOUNG habitat, suggesting a relatively high conservation value for this habitat type. Three of the 60 bird species had no PIF score: Upland Sandpiper, Spotted Sandpiper, *Actitis macularius* L., and Wilson's Snipe, *Gallinago delicata* Ord. Consequently, to conduct further analyses, each received the mean (± 1SD) combined score of 11.7 (± 2.6) of the other 57 bird species (range of PIF scores 6 to 22). Based on species lists per habitat type, the average PIF conservation score did not differ significantly among the three habitat patch types (ANOVA, df = 2, F = 0.79, P = 0.46): YOUNG 11.29 (± 2.45), KW 12.15 (± 3.09), and OLD 11.32 (± 2.32). Excluding Kirtland's Warbler, the range of PIF scores for all three habitat patch types was also the same (6 to 16). When we weighted pooled conservations scores for habitat patch type by the registration frequencies of the included bird species, the average conservation score also did not differ significantly among the three habitat types (ANOVA, df = 2, F = 0.18, P = 0.83): YOUNG 5.17 (± 3.52), KW 5.40 (± 4.61), and OLD 4.73 (± 2.91).

Functional groupings based on published nest location, nest type, and foraging technique for the pooled list of species across habitat types illustrated how habitat patch structure is important for many bird species (Figure 3). For instance, trees and snags accounted for 44% to 78% of all nest locations among YOUNG, KW, and OLD habitat types. Cavities, which can occur in live trees or in snags, were an especially important nest type in OLD habitat, while far fewer species in OLD habitat utilized platforms. Interestingly, KW habitat (which is the densest and most shrub-dominated habitat) had the most foliage-foraging

Table 1. Sixty bird species at Kirtland's Warbler Wildlife Management Area listed in ranked order by Partners in Flight (PIF) conservation score, their registration frequencies (shown as a percentage) among three jack pine habitat types, and the P-value of the Chi-square test for association. Maximum registration frequency among habitat types is shown in bold. An * denotes bird species with expected counts < 5 in one or more habitat types. U.S. Fish and Wildlife Service Regional Conservation Priority species are in italics.

Common name	YOUNG	KW	OLD	Overall	*P* -Value
Kirtland's Warbler	9.5	90	-	29.9	0
Black-billed Cuckoo	28.6	10	4.3	11.3	0.01*
Field Sparrow	85.7	83.3	6.5	47.4	0
Mourning Warbler	-	-	2.2	1	-
Rose-breasted Grosbeak	4.8	3.3	50	25.8	0
Northern Flicker	42.9	40	23.9	33	0.19
Brown Thrasher	85.7	70	6.5	43.3	0
Common Yellowthroat	9.5	16.7	8.7	11.3	0.54*
Least Flycatcher	-	-	2.2	1	-
Yellow-bellied Sapsucker	-	-	2.2	1	-
American Goldfinch	-	10	2.2	4.1	-
Cedar Waxwing	-	13.3	15.2	11.3	0.17*
Common Nighthawk	-	10	10.9	8.2	0.30*
Eastern Kingbird	4.8	3.3	-	2.1	-
Eastern Towhee	4.8	33.3	2.2	12.4	0.00*
Eastern Wood-Pewee	-	-	30.4	14.4	0.00*
Great Crested Flycatcher	-	6.7	15.2	9.3	0.12*
Nashville Warbler	28.6	96.7	71.7	70.1	0
Ovenbird	4.8	6.7	78.3	40.2	0
Scarlet Tanager	-	-	23.9	11.3	0.00*
Tree Swallow	-	6.7	2.2	3.1	-
American Redstart	-	-	2.2	1	-
Brown-headed Cowbird	-	3.3	2.2	2.1	-
Clay-colored Sparrow	42.9	43.3	-	22.7	0.00*
Golden-crowned Kinglet	-	-	2.2	1	-
Song Sparrow	23.8	6.7	4.3	9.3	0.03*
Vesper Sparrow	81	63.3	-	37.1	0
White-throated Sparrow	-	13.3	2.2	5.2	0.05*
Upland Sandpiper	52.4	13.3	-	15.5	0.00*
Spotted Sandpiper	-	-	2.2	1	-
Wilson's Snipe	-	-	6.5	3.1	-
Alder Flycatcher	23.8	-	-	5.2	0.00*
Black-capped Chickadee	4.8	40	58.7	41.2	0
Blue-headed Vireo	-	-	13	6.2	0.03*
Brown Creeper	-	-	6.5	3.1	-

Continued

Table 1. (Cont'd) Sixty bird species at Kirtland's Warbler Wildlife Management Area listed in ranked order by Partners in Flight (PIF) conservation score, their registration frequencies (shown as a percentage) among three jack pine habitat types, and the P-value of the Chi-square test for association. Maximum registration frequency among habitat types is shown in bold. An * denotes bird species with expected counts < 5 in one or more habitat types. U.S. Fish and Wildlife Service Regional Conservation Priority species are in italics.

Common name	YOUNG	KW	OLD	Overall	*P*-Value
Chipping Sparrow	14.3	60	69.6	54.6	0
Hairy Woodpecker	-	3.3	8.7	5.2	0.28*
Red-eyed Vireo	-	3.3	34.8	17.5	0.00*
Slate-colored Junco	-	16.7	37	22.7	0.00*
White-breasted Nuthatch	-	3.3	30.4	15.5	0.00*
American Crow	14.3	-	6.5	6.2	0.11*
Barred Owl	-	-	2.2	1	-
Blue Jay	71.4	86.7	87	83.5	0.24*
Eastern Bluebird	23.8	-	-	5.2	0.00*
Eastern Phoebe	-	-	2.2	1	-
House Wren	-	-	4.3	2.1	-
Indigo Bunting	57.1	3.3	8.7	17.5	0.00*
Lincoln's Sparrow	76.2	43.3	8.7	34	0
Pine Warbler	-	-	2.2	1	-
American Robin	14.3	3.3	13	10.3	0.32*
Common Grackle	19	10	10.9	12.4	0.57*
Common Raven	81	70	41.3	58.8	0
Hermit Thrush	9.5	86.7	84.8	69.1	0
Red-breasted Nuthatch	-	-	41.3	19.6	0.00*
Red-tailed Hawk	-	10	6.5	6.2	0.34*
Red-winged Blackbird	-	3.3	4.3	3.1	-
Wild Turkey	9.5	-	-	2.1	-
Yellow-rumped Warbler	-	6.7	2.2	3.1	-
Turkey Vulture	-	3.3	-	1	-
Mourning Dove	19	66.7	65.2	55.7	0

species, underscoring the importance of shrubbery within this habitat type. Not surprisingly, as jack pine habitat patches developed from predominately open YOUNG areas to close-canopy OLD areas, the number of ground-foraging bird species decreased (Figure 3). Our analysis of the pooled PIF conservation scores based on functional groups showed no significant difference among them based on nest location (ANOVA, df = 2, F = 0.64, P = 0.59) or nest type (df = 2, F = 0.41, P = 0.67). Significant differences were noted, however, in foraging techniques, with species that forage amongst foliage carrying a greater average PIF score (df = 2, F = 3.61, P = 0.04) (Figure 4).

Habitat Patch Composition and Structure

Seventeen overstory (stems >10.0 cm dbh) species were sampled, with jack pine, red pine (*P. resinosa* Soland), scarlet oak (*Quercus coccinea* Muenchh.), trembling aspen (*Populus tremuloides* Michx.), black cherry (*Prunus serotina* Ehrh.), black oak (*Quercus velutina* Lam.), northern red oak (*Quercus rubra* L.), and bigtooth aspen (*Populus grandidentata* Michx.) being common. The YOUNG habitat patches were dominated by several species, including jack pine, trembling aspen, and black cherry, while the KW habitat patches were dominated by jack pine. The OLD habitat patches (> 23 years old) had variable composition, but for the most part were dominated by mature jack pine.

Twenty three understory (stems < 10.0 cm dbh and >2.54 cm dbh) species were sampled, including jack pine, red pine, white pine (*Pinus strobus* L.), black cherry, pin cherry (*Prunus pennsylvanica* L.), white oak (*Quercus alba* L.), scarlet oak, northern pin oak (*Q. ellipsoidalis* Hill), northern red oak, black oak, trembling aspen, and bigtooth aspen. Jack pine was the most common understory tree sampled, and was characteristic of the understory in all three habitat types. Black cherry, trembling aspen, and northern red oak were also common, especially within YOUNG and KW habitat patches.

The seedling layer (stems < 2.5 cm dbh) was characterized by 29 woody plants, including jack pine, red pine, eastern white pine, bigtooth aspen, trembling aspen, white oak, scarlet oak, northern pin oak, northern red oak, black oak, black cherry, pin cherry, choke cherry (*Prunus virginiana* L.), red maple (*Acer rubrum* L.), green ash (*Fraxinus pennsylvanica* Marsh), black ash (*F. nigra* Marsh), American basswood (*Tilia americana* L.), balsam fir (*Abies balsamea* L.), witch-hazel (*Hamamelis virginiana* L.), serviceberry (*Amelanchier* spp.), alternate-leaf dogwood (*Cornus alternifolia* L. f.), dogwood (*Cornus* spp.), hawthorne (*Crataegus* spp.), eastern hophornbeam (*Ostrya virginiana* (P. Mill.) K. Koch), willow (*Salix* spp.), honeysuckle (*Lonicera* spp.), currant or gooseberry (*Ribes* spp.), and two unknown species.

There was also considerable variability in overstory and understory stem density within each habitat patch type, especially within the YOUNG patches. This trend is largely due to the range of conditions associated with recent management activities wherein portions of the patches may not have been harvested. Of greatest relevance

Table 2. Abundance by jack pine habitat type for 40 bird species found at ≥ 10% registration frequency in at least one habitat type at Kirtland's Warbler Wildlife Management Area. Species are listed in decreasing ranked order by Partners in Flight (PIF) conservation score. U.S. Fish and Wildlife Service Regional Conservation Priority species are in italics.

Symbol	Mean number of individuals detected during point counts
	>1.26
	1.01 – 1.25
	0.76 – 1.00
	0.51 – 0.75
	0.26 – 0.50
	0.10 – 0.25
	<0.10

Common name	Habitat patch type			
	YOUNG	KW	OLD	Overall
Kirtland's Warbler				
Black-billed Cuckoo				
Field Sparrow				
Rose-breasted Grosbeak				
Northern Flicker				
Brown Thrasher				
Common Yellowthroat				
American Goldfinch				
Cedar Waxwing				
Common Nighthawk				
Eastern Towhee				
Eastern Wood-Pewee				
Great Crested Flycatcher				
Nashville Warbler				
Ovenbird				
Scarlet Tanager				
Clay-colored Sparrow				
Song Sparrow				
Vesper Sparrow				
White-throated Sparrow				
Upland Sandpiper				
Alder Flycatcher				
Black-capped Chickadee				
Blue-headed Vireo				
Chipping Sparrow				
Red-eyed Vireo				
Slate-colored Junco				
White-breasted Nuthatch				
American Crow				
Blue Jay				
Eastern Bluebird				
Indigo Bunting				
Lincoln's Sparrow				
American Robin				

Continued

Table 2. (Cont'd) Abundance by jack pine habitat type for 40 bird species found at ≥ 10% registration frequency in at least one habitat type at Kirtland's Warbler Wildlife Management Area. Species are listed in decreasing ranked order by Partners in Flight (PIF) conservation score. U.S. Fish and Wildlife Service Regional Conservation Priority species are in italics.

Symbol	Mean number of individuals detected during point counts
	>1.26
	1.01 – 1.25
	0.76 – 1.00
	0.51 – 0.75
	0.26 – 0.50
	0.10 – 0.25
	<0.10

Common name	Habitat patch type			
	YOUNG	KW	OLD	Overall
Common Grackle				
Common Raven				
Hermit Thrush				
Red-breasted Nuthatch				
Red-tailed Hawk				
Mourning Dove				

to Kirtland's Warbler usage, mean (± 1SD) total stem density in the KW patches was low, with an average of 180.7 (± 26.7) stems ha^{-1} compared to 822.8 (± 35.8) stems ha^{-1} in the OLD habitat. Similarly, jack pine densities in the KW habitat have on average 30.8 (±12.8) stems ha^{-1} and 60.1 (± 6.2) stems ha-1 for a total average of 91.8 (± 15.0) stems ha^{-1}. While these estimates are indicative of under-stocking in these patches relative to most Kirtland's Warbler habitat guidelines, it is important to point out that the variability within a tract may "depress" these estimates when mean values are calculated.

As with overstory and understory stem density values, seedling densities were also quite variable among habitat patch types. We found an average of 4395 (± 745) seedlings ha^{-1} in the YOUNG habitat patches, 6210 (± 384) seedlings ha-1 in the KW habitat patches, and 6927 (± 515) seedlings ha^{-1} in the OLD habitat patches. Jack pine seedling densities were considerably lower, comprising less than 25% of the total seedling community in all three habitat patch types, indicating the difficulty in regenerating this species without planting at Kirtland's Warbler WMA.

Relationship between Bird Communities and Habitat Patch Attributes

MRPP suggested that there are significant differences in bird assemblages among the three habitat types (T = -43.28, A = 0.192, P < 0.0001). The strong chance-corrected within-group agreement (A) and test statistic (T) indicate that groups occupy different regions of species space, suggesting significant differences in the overall assemblage of species. Five indicator species were associated with YOUNG and KW habitat types, while nine species were indicative of the OLD habitat type (Table 3).

The ordination of bird abundance as related to habitat composition and structure—with sample plots arranged by habitat type and structural characteristics along the first canonical axis—suggested a significant relationship (P < 0.01, eigenvalue = 0.368) (Figure 5). The density of jack pine seedlings was associated with the YOUNG and KW habitat types, and was negatively related to the density of jack pine in the overstory, which itself was positively associated with the OLD habitat. The CCA also confirms the MRPP and Indicator Analyses. For example, Kirtland's Warbler, Nashville Warbler, Eastern Towhee, and Alder Flycatcher were associated with KW habitat with higher jack pine seedling densities and shorter jack pine canopies. The CCA also suggests that the variation in bird assemblages was greater in the OLD habitat than in the YOUNG or KW habitats, as evidenced by the large spread of sample points on the right side of the ordination. This variation in bird assemblages is likely influenced by differences in habitat patch structural characteristics. For example, Ovenbird, Red-eyed Vireo, Eastern Wood-Pewee, and Rose-breasted Grosbeak tended to be associated with habitat patches that had higher densities of jack pine in the overstory (Figure 5).

DISCUSSION

Our findings quantify for the first time the bird community structure and associated conservation scenarios across jack pine habitat types typically encountered during intensive, multi-agency management of jack pine plantations for Kirtland's Warbler. Besides documenting how recovery efforts have been successful at producing warblers (e.g., 90% occupancy rate of KW habitat and, on average, three singing male Kirtland's Warbler per point count), our data suggest that each jack pine habitat type

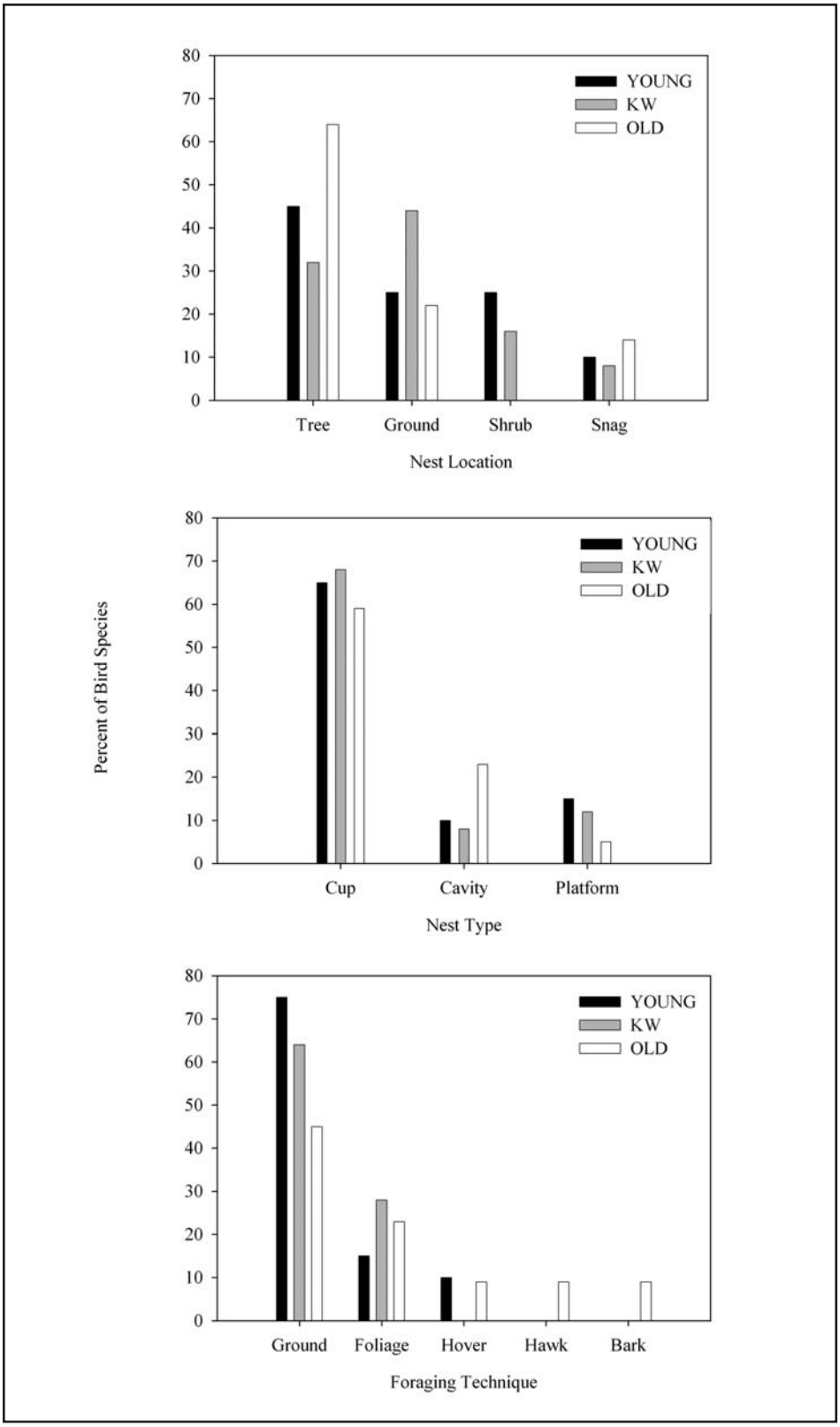

Figure 3. Percent of 40 bird species observed in three jack pine habitat types based on nest location, nest type, and foraging technique. Only bird species observed in ≥ 10% of point counts in a given habitat type are included. Functional groups comprising ≤ 5% of the species list per habitat type are not shown.

(recent clear cuts, dense jack pine plantations, and mature jack pine stands) has a unique assemblage of bird species that respond to different structural variables. For instance, jack pine stem density has long been known to influence Kirtland's Warbler occupancy rates (Probst 1986, 1988), but our findings suggest similar responses by other species, such as Eastern Towhee, Nashville Warbler, and Alder Flycatcher (albeit this species is often considered a wetland-obligate). Conversely, the greater structural heterogeneity found in OLD habitat leads to an increased list of indicator species that seem to respond to more structural variables, a finding supportive of Vernier and Pearce (2005) who worked with bird communities and jack pine successional stages in Canada. However, as Kirtland's Warbler continues to expand its breeding distribution into other states and ecoregions of the Upper Midwest (Probst et al. 2003), conservationists trying to promote warbler habitat should view our results with caution. Geographic variability in community structure, species presence, relative abundance, and habitat affinity can make extrapolation of such findings difficult at best (Theobald et al. 2000; Harding et al. 2001).

In Michigan, our findings support and enhance previous broad-scale conservation assessments that suggested the prioritization of the northern Lower Peninsula ecoregion for species such as Black-billed Cuckoo, Brown Thrasher, Field Sparrow, and Eastern Towhee based upon state-wide geographic distribution and registration frequency patterns (Corace 2007). In particular, our study indicates specific stages of jack pine that would benefit other bird species presently found on the 52,600 ha dedicated to Kirtland's Warbler management (USFWS 2005). For instance, the area historically devoted to the more open jack pine barrens has declined since the implementation of plantation management for Kirtland's Warbler (Houseman and Anderson 2002). Our findings suggest, however, that recent clearcuts provide habitat for a suite of species of relatively high conservation priority and may be an important, yet underappreciated, breeding habitat in the Upper Midwest for species such as Upland Sandpiper (Vickery et al.

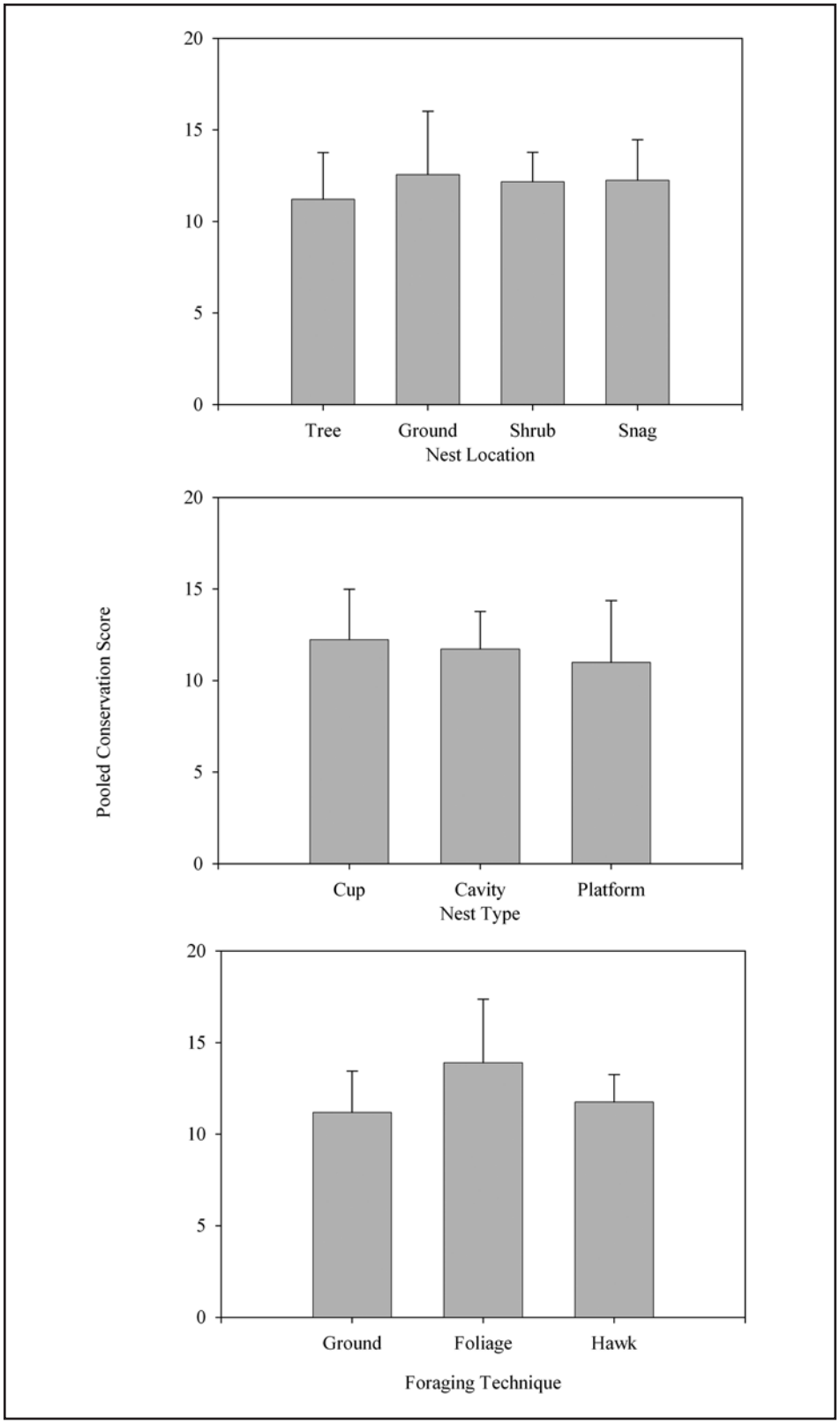

Figure 4. Average (± 1 SD) Partners in Flight (PIF) conservation score for 40 bird species observed in ≥ 10% of point counts in at least one jack pine habitat type by nest location, nest type, and foraging technique. Functional groups comprising ≤ 10% of the species list per habitat type are not shown.

2008). We suggest that land managers consider delaying the replanting of clear cuts for Kirtland's Warbler habitat, especially in larger openings that are preferred by openland flora and fauna of conservation priority, or integrate barrens restoration more broadly into Kirtland's Warbler habitat management (Appendix).

For conservationists working in ecoregions recently colonized by Kirtland's Warbler, we suggest that future habitat management consider more than just Kirtland's Warbler and jack pine plantations. Instead, we suggest that land managers consider habitat management based on an ecological framework (Franklin et al. 2007) that incorporates ecoregional disturbance history and resulting compositional and structural patterns (Drobyshev et al. 2008a,b). The natural jack pine disturbance agent (wildfire) produces a large volume of snags and coarse woody debris (Goff and Sirois 2004; Spaulding and Rothstein 2009), with much of this structure maintained for 50 years or more (Metsaranta et al. 2008). Unfortunately, existing plantation management for Kirtland's Warbler poorly emulates these structural patterns (Spaulding and Rothstein 2009). Thus, ecological management of jack pine should consider structural heterogeneity across habitat types. Because many of the bird species we documented in this study rely on snags for nest placement, management should incorporate the enhancement of these important structural features in future stand treatments (Corace et al, in press. Figure 6).

Intensive management of jack pine plantations on state and federally-owned lands has been instrumental in the recovery of Kirtland's Warbler. Although in many instances Kirtland's Warbler habitat management will still involve plantations, we believe that our findings provide a baseline for those wishing to shift to a more ecologically-based approach to jack pine management (Corace et al. 2009). Scott et al. (2005) recommended that future endangered species recovery efforts consider cooperative relationships for management that maintains recovered species above listing thresholds. We suggest that extensive, more ecologically-based management that considers the dynamic nature of ecosystems

Table 3. Bird species significantly associated with three jack pine habitat types at Kirtland's Warbler Wildlife Management Area. Common names of U. S. Fish and Wildlife Service Regional Conservation Priority species are in italics.

Habitat type		
YOUNG	KW	OLD
(< 5 years old)	(5-23 years old)	(> 23 years old)
Indigo Bunting***	*Kirtland's Warbler* ***	Eastern Wood-Pewee***
Eastern Bluebird***	Nashville Warbler***	Hermit Thrush***
Field Sparrow ***	Eastern Towhee***	Ovenbird***
Lincoln's Sparrow***	Brown Thrasher**	Rose-breasted Grosbeak***
Black-billed Cuckoo *	Alder Flycatcher**	Red-breasted Nuthatch***
		Red-eyed Vireo***
		Black-capped Chickadee**
		Chipping Sparrow**
		Mourning Dove*

MRPP P-values (see text): *P ≤ 0.05; ** P ≤ 0.01; *** $P < 0.001$.

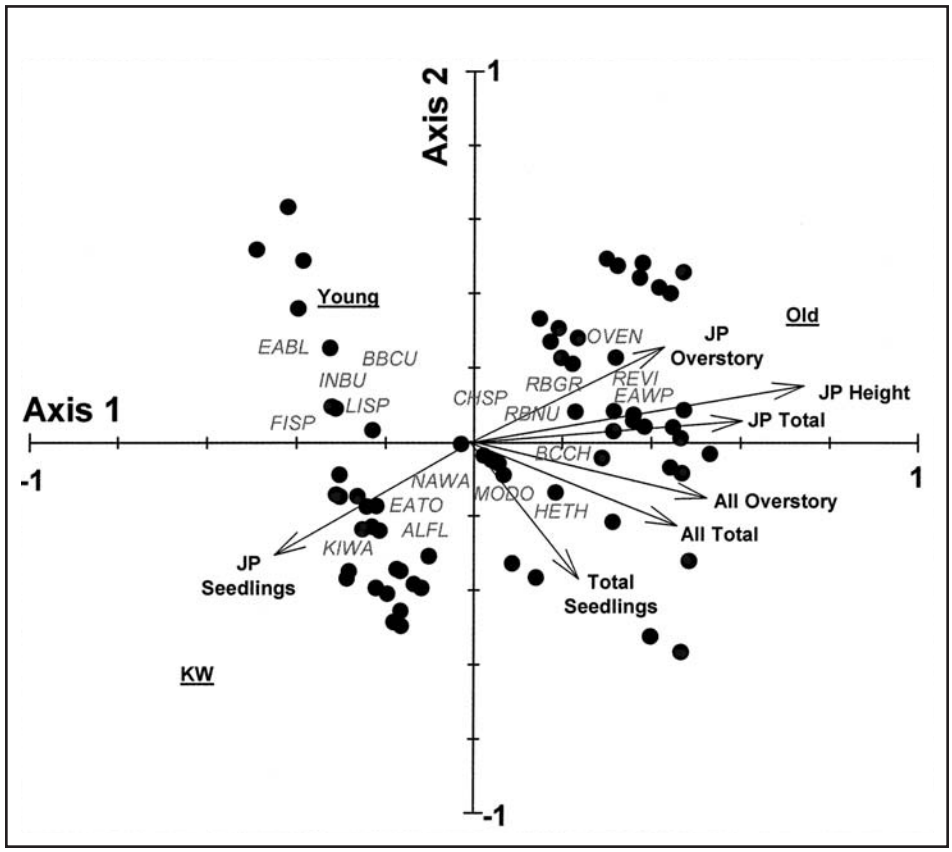

Figure 5. CCA triplot relating bird species abundance with habitat patch vegetation structural characteristics. See Appendix for species codes.

and species occurrence and abundance patterns also be integrated into recovery efforts of threatened and endangered species.

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Figure 6. Wildfire-generated Kirtland's Warbler habitat. Note the biological legacies and structural complexity.

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Appendix. Sixty bird species observed at Kirtland's Warbler Wildlife Management Area, their Partners in Flight (PIF) conservation scores, and natural history attributes. Bird species are listed in ranked order by PIF conservation score. U. S. Fish and Wildlife Service Regional Conservation Priority species are shown in italics. Three species (Upland Sandpiper, Wilson's Snipe, and Alder Flycatcher) did not have an assigned PIF score and instead were given the mean score for the other 57 species (11.7).

Species code	Common name	Scientific name	PIF score[a]	Nest location[b]	Nest type[c]	Foraging technique[d]
KIWA	*Kirtland's Warbler*	*Dendroica kirtlandii* Baird	22	GR	C	F
BBCU	*Black-billed Cuckoo*	*Coccyzus erythropthalmus* Wilson	16	T	P	F
FISP	*Field Sparrow*	*Spizella pusilla* Wilson	15	GR	C	G
MOWA	Mourning Warbler	*Oporornis Philadelphia* Wilson	16	GR	C	F
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus* L.	16	T	C	F
NOFL	*Northern Flicker*	*Colaptes auratus* L.	15	SN	CA	G
BRTH	Brown Thrasher	*Toxostoma rufum* L.	14	SH	C	G
COYE	Common Yellowthroat	*Geothlypis trichas* L.	14	SH	C	F
LEFL	Least Flycatcher	*Empidonax minimus* Baird and Baird	14	T	C	H
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius* L.	14	SN	CA	B
AMGO	American Goldfinch	*Carduelis tristis* L.	13	SH	C	F
CEDW	Cedar Waxwing	*Bombycilla cedrorum* Vieillot	13	T	C	F
CONI	Common Nighthawk	*Chordeiles minor* Forster	13	GR	None	A
EAKI	Eastern Kingbird	*Tyrannus tyrannus* L.	13	T	C	HA
EATO	Eastern Towhee	*Pipilo erythrophthalmus* L.	13	GR	C	G
EAWP	Eastern Wood-Pewee	*Contopus virens* L.	13	T	C	HA
GCFL	Great Crested Flycatcher	*Myiarchus crinitus* L.	13	SN	CA	HA
NAWA	Nashville Warbler	*Vermivora ruficapilla* Wilson	13	T	C	F
OVEN	Ovenbird	*Seiurus aurocapilla* L.	13	GR	O	G
SCTA	Scarlet Tanager	*Piranga olivacea* Gmelin	13	T	S	H
TRES	Tree Swallow	*Tachycineta bicolor* Vieillot	13	T	CA	A
AMRE	American Redstart	*Setophaga ruticilla* L.	12	T	C	H

Continued

Appendix. (Cont'd) Sixty bird species observed at Kirtland's Warbler Wildlife Management Area, their Partners in Flight (PIF) conservation scores, and natural history attributes. Bird species are listed in ranked order by PIF conservation score. U. S. Fish and Wildlife Service Regional Conservation Priority species are shown in italics. Three species (Upland Sandpiper, Wilson's Snipe, and Alder Flycatcher) did not have an assigned PIF score and instead were given the mean score for the other 57 species (11.7).

Species code	Common name	Scientific name	PIF score[a]	Nest location[b]	Nest type[c]	Foraging technique[d]
BHCO	Brown-headed Cowbird	*Molothrus ater* Boddaert	12	SH	PA	G
CCSP	Clay-colored Sparrow	*Spizella pallida* Swainson	12	SH	C	G
GCKI	Golden-crowned Kinglet	*Regulus satrapa* Lichtenstein	12	T	PE	F
SOSP	Song Sparrow	*Melospiza melodia* Wison	12	T	C	G
VESP	Vesper Sparrow	*Pooecetes gramineus* Gmelin	12	GR	C	G
WTSP	White-throated Sparrow	*Zonotrichia albicollis* Gmelin	12	GR	C	G
UPSA	*Upland Sandpiper*	*Bartramia longicauda* Bechstein	11.7	GR	SC	G
SPSA	Spotted Sandpiper	*Actitis macularius* L.	11.7	GR	SC	G
COSN	Wilson's Snipe	*Gallinago delicata* Ord	11.7	GR	SC	P
ALFL	Alder Flycatcher	*Empidonax alnorum* Brewster	11	SH	C	HA
BCCH	Black-capped Chickadee	*Poecile atricapillus* L.	11	SN	CA	F
SOVI	Blue-headed Vireo	*Vireo solitarius* Wilson	11	T	C	F
BRCR	Brown Creeper	*Certhia americana* Bonaparte	11	T	B	B
CHSP	Chipping Sparrow	*Spizella passerine* Bechstein	11	T	C	G
HAWO	Hairy Woodpecker	*Picoides villosus* L.	11	SN	CA	B
REVI	Red-eyed Vireo	*Vireo olivaceus* L.	11	T	C	H
SCJU	Slate-colored Junco	*Junco hyemalis* L.	11	GR	C	G
WBNU	White-breasted Nuthatch	*Sitta carolinensis* Latham	11	T	CA	B
AMCR	American Crow	*Corvus brachyrhynchos* Brehm	10	T	P	G
BDOW	Barred Owl	*Strix varia* Barton	10	T	CA	LP
BLJA	Blue Jay	*Cyanocitta cristata* L.	10	T	C	G
EABL	Eastern Bluebird	*Sialia sialis* L.	10	SN	CA	HA
EAPH	Eastern Phoebe	*Sayornis phoebe* Latham	10	BR	C	HA

Continued

Appendix. (Cont'd) Sixty bird species observed at Kirtland's Warbler Wildlife Management Area, their Partners in Flight (PIF) conservation scores, and natural history attributes. Bird species are listed in ranked order by PIF conservation score. U. S. Fish and Wildlife Service Regional Conservation Priority species are shown in italics. Three species (Upland Sandpiper, Wilson's Snipe, and Alder Flycatcher) did not have an assigned PIF score and instead were given the mean score for the other 57 species (11.7).

Species code	Common name	Scientific name	PIF score[a]	Nest location[b]	Nest type[c]	Foraging technique[d]
HOWR	House Wren	*Troglodytes aedon*	10	SN	CA	G
INBU	Indigo Bunting	*Passerina cyanea* L.	10	SH	C	F
LISP	Lincoln's Sparrow	*Melospiza lincolnii* Audubon	10	GR	C	G
PIWA	Pine Warbler	*Dendroica pinus* Wilson	10	GR	C	B
AMRO	American Robin	*Turdus migratorius* L.	9	T	C	G
COGR	Common Grackle	*Quiscalus quiscula* L.	9	GR	C	G
CORA	Common Raven	*Corvus corax* L.	9	T	P	G
HETH	Hermit Thrush	*Catharus guttatus* Pallas	9	GR	C	G
RBNU	Red-breasted Nuthatch	*Sitta vireo* L.	9	T	CA	B
RTHA	Red-tailed Hawk	*Buteo jamaicensis* Gmelin	9	T	P	HP
RWBL	Red-winged Blackbird	*Agelaius phoeniceus* L.	9	SH	C	G
WITU	Wild Turkey	*Meleagris gallopavo* L.	9	T	SC	G
MYWA	Yellow-rumped Warbler	*Dendroica coronata* L.	9	GR	C	F
TUVU	Turkey Vulture	*Cathartes aura* L.	8	GR	None	HP
MODO	Mourning Dove	*Zenaida macroura* L.	6	T	S	G

[a]See PIF (2006).

[b]See Ehrlich et al. (1988): BR, bridge; CL, cliff; GR, ground; SH, shrub; SN, snag; T, tree (coniferous or deciduous).

[c]See Ehrlich et al. (1988): B, under bark; C, cup; CA, cavity; O, oven; P, platform; PA, parasite; PE, pendulant; S, saucer; SC, scrape.

[d]See Ehrlich et al. (1988): A, aerial; B, bark; F, foliage; G, ground; H, hover; HA, hawks; HP, high patrol; LP, low patrol; P, probes.

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