Do Breeding Bird Communities or Conservation Value Differ Among Forested Wetland Types or Ecoregions in Nova Scotia?

John Brazner[1] · Laura Achenbach[2]

Abstract

Forested wetlands are being lost to development at a higher rate than other wetland types in Nova Scotia despite limited understanding about the ecology of these ecosystems. To examine differences in community composition or conservation value among forested wetland types (peatlands, treed and shrub swamps) or ecoregions (Western, Valley, Fundy Shore), we surveyed breeding birds at 229 sites in western Nova Scotia in 2015 and 2016. We observed 95 species (46% of Nova Scotia's breeding bird species) and 8971 individuals across all sites. In addition, 5 of 13 (38%) inland (noncoastal) bird species that are listed as at-risk in Nova Scotia were detected. There were more distinct differences in communities among wetland types than ecoregions, shrub swamps and peatlands had significantly more species and higher mean abundances than treed swamps, and Valley Ecoregion sites had the highest species richness and abundance. We also found strong wetland type and ecoregion affinities for particular species. Our results indicate that shrub swamps, particularly in the Valley Ecoregion, have high conservation value and are acting as important refugia for birds in this highly-fragmented landscape. The conservation value of peatlands and treed swamps is also high, partly owing to the at-risk species they support.

Keywords Avian community · Biodiversity · Bog · Fen · Species at risk · NMDS ordination

Introduction

Forested wetlands (FW) are estimated to comprise about 2% of global land area and 60% of all wetlands (Matthews and Fung 1987). Trends in the loss of FWs reflect the loss in global forest cover (Frelich 1995; Williams 2002; Dahl 2011), but global losses of FWs are difficult to quantify due to insufficient data in many parts of the world (Davidson 2014). Nevertheless, loss appears to have been high wherever FWs are common landscape features (Calhoun 1999; Dahl 2011). In the United States where FW loss has been relatively well-characterized, loss estimates for northeastern states ranged from 64% in Maine to 87% in New York through the late 1990s (Dahl and Zoltai 1997). This historic loss pattern was likely similar in parts of southeastern Canada, where loss of freshwater wetlands was estimated at around 70% (Snell 1987; Ducks Unlimited Canada 2010), but data specific to FW loss is lacking. There is also no reason to believe the more recently noted accelerated loss pattern for FWs in the United States (Dahl 2011) and more widely (Tockner and Stanford 2002; Davidson 2014) is any different in Canada.

The biodiversity ramifications of FW loss have not been well-documented, but there was considerable focus on FW ecology during the 1980s and 90s (e.g., Lugo et al. 1990; Trettin et al. 1997; Calhoun 1999), and renewed interest more recently (e.g., Remm 2015), particularly in relation to their importance to birds (e.g., Zlonis et al. 2017; Morissette et al. 2018). Although the prevalence of FWs in Nova Scotia's forested landscapes is uncertain, they are presumed to have high conservation value relative to other forested habitats (Cameron 2009; Hill and Garbary 2011). The extent of some FW types (e.g., peatlands) are represented relatively accurately in the Nova Scotia wetland inventory (https://novascotia.ca/natr/wildlife/habitats/wetlands.asp), but other types, such as

✉ John Brazner
john.brazner@novascotia.ca

1 Department of Lands and Forestry – Wildlife Division, 136 Exhibition St., Kentville, Nova Scotia B4N 4E5, Canada

2 Canadian Wildlife Service, Environment and Climate Change Canada, 45 Alderney Dr., Dartmouth, Nova Scotia B2Y 2N6, Canada

treed swamps, are substantially underrepresented (Jahncke et al. 2018). This makes it difficult to assess their importance relative to other forest types, but a recent estimate suggests that about 7.5% (~330,000 ha) of all forest in the province is FW (Frances MacKinnon, Nova Scotia Department of Lands and Forestry, pers. comm.).[1]

Despite the substantial area they occupy and the ecosystem services and biodiversity values FWs provide (e.g., Trettin et al. 1997; Calhoun 1999), only a few studies have focused on their ecology in the Canadian Maritimes (Damman and Dowhan 1981; Comeau and Bellamy 1986; Cameron 2009; Hill and Garbary 2011), or the northeastern United States (e.g., Golet et al. 1993; Anderson and Davis 1997; Rheinhardt 2007; Yu and Ehrenfeld 2010). At the same time, FWs are being converted to other uses at a higher rate in Nova Scotia than other wetland types. Estimates of loss are between 80 and 100 ha per year over the last five years, primarily due to urbanization and large industrial development in rural areas (Jeremy Higgins, Nova Scotia Environment 2011). The area and frequency of alteration of FW by timber harvesting activities in Nova Scotia has not been quantified, but there is a keen interest by the forest industry in harvesting in these forest types (John Gilbert, J.D. Irving Corporation, pers. communication) despite uncertainty about regeneration potential after harvest (Roy et al. 2000; Moreno-Mateos et al. 2012; Diamond et al. 2018).

Given concerns about loss and limited understanding of the conservation value of FWs, our first objective was to examine differences in the avian communities among the different FW types in Nova Scotia. Previous studies (Hoffman and Mossman 1993; Sallabanks et al. 2000; Morissette et al. 2013; Zlonis et al. 2017) suggested there would be substantive differences in bird community composition among FW types. Based on the well-established premise that habitats with greater vertical structural complexity support greater bird diversity (e.g., MacArthur and MacArthur 1961; Hunter 1999), we expected treed swamps would have higher species richness and abundance than peatlands or shrub swamps.

Our second objective was to determine whether any differences apparent among FW types varied by ecoregion, to help guide the design of future studies in these habitats. Assessments to characterize differences in bird species composition among ecoregions have been limited (e.g., McDonald et al. 2005; Hanowski et al. 2007) but sometimes incorporated

for conservation planning purposes (e.g., Roca et al. 1996; Ricketts et al. 1999; Olson et al. 2001). Because ecoregional boundaries were developed to reflect broad differences in physical and biotic factors such as climate, geology, soils, and vegetation (e.g., Bailey et al. 1985; Wiken 1986; Omernik 1987), and these factors affect important components of bird habitats (Lovette and Fitzpatrick 2016), it seemed likely that ecoregion would influence some of the differences we would observe. The high mobility of birds in combination with the limited geographic scope of our study was expected to limit ecoregion-associated differences in species composition (e.g., Hanowski et al. 2007) to less than those among FW types.

Our final objective was to assess whether there were differences in conservation value among FW types or ecoregions to help set provincial priorities for the management and possibly restoration of these ecosystems. Site types that supported higher species richness and abundance overall or had higher numbers of individual species of conservation concern were deemed to have the highest conservation value. We hypothesized that treed swamps would have the highest conservation value for birds among the three FW types examined for this study for two reasons: 1) species richness and total abundance of birds were expected to be highest in treed swamps; and, 2) although data are equivocal, indications are that several "at-risk" species including Olive-sided Flycatcher (*Contopus cooperi*), Canada Warbler (*Cardellina canadensis*), Rusty Blackbird (*Euphagus carolinus*), and Eastern Wood-pewee (*Contopus virens*) (https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry.html) may rely more on treed swamps for breeding than other FW types (Stewart et al. 2015; Westwood 2016; Bale 2017).

Methods

Study Area

The study was conducted in an area of about 21,000 km^2 in western Nova Scotia that encompassed most of three ecoregions (Fig. 1) including the Western, Valley and Central (Valley), and Fundy Shore (Fundy) Ecoregions. Differences in the character of each ecoregion are described by Neily et al. (2017) so are reiterated only briefly here. Western is the largest (nearly 17,000 km^2), with stands of red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) common. Wetland and lake cover are extensive, including large areas of FWs dominated by stunted black spruce (*Picea mariana*) and tamarack (*Larix larcina*) in peatlands and mature red maple (*Acer rubrum*) in swamps. The most distinguishing features of the Valley (~ 2500 km^2) are the predominance of sheltered fertile lowlands,

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[1] Estimates for swamps were obtained by using the totals for treed and shrub swamps from the wetland inventory and then adding stands from the forest inventory (https://novascotia.ca/natr/forestry/gis/forest-inventory.asp) that had depth to water table less than 0.5 m (https://novascotia.ca/natr/forestry/gis/wamdownload.asp), on poorly or imperfectly drained soils and on slopes that were less than or equal to 2% to the treed swamp class if they were dominated by pole-sized or larger black spruce, tamarack or red maple, and to the shrub swamp class if they were dominated by alder (*Alnus* spp.) or other tall shrub species (designated as "brush" in the forest inventory). Peatland area was taken directly from the wetland inventory.
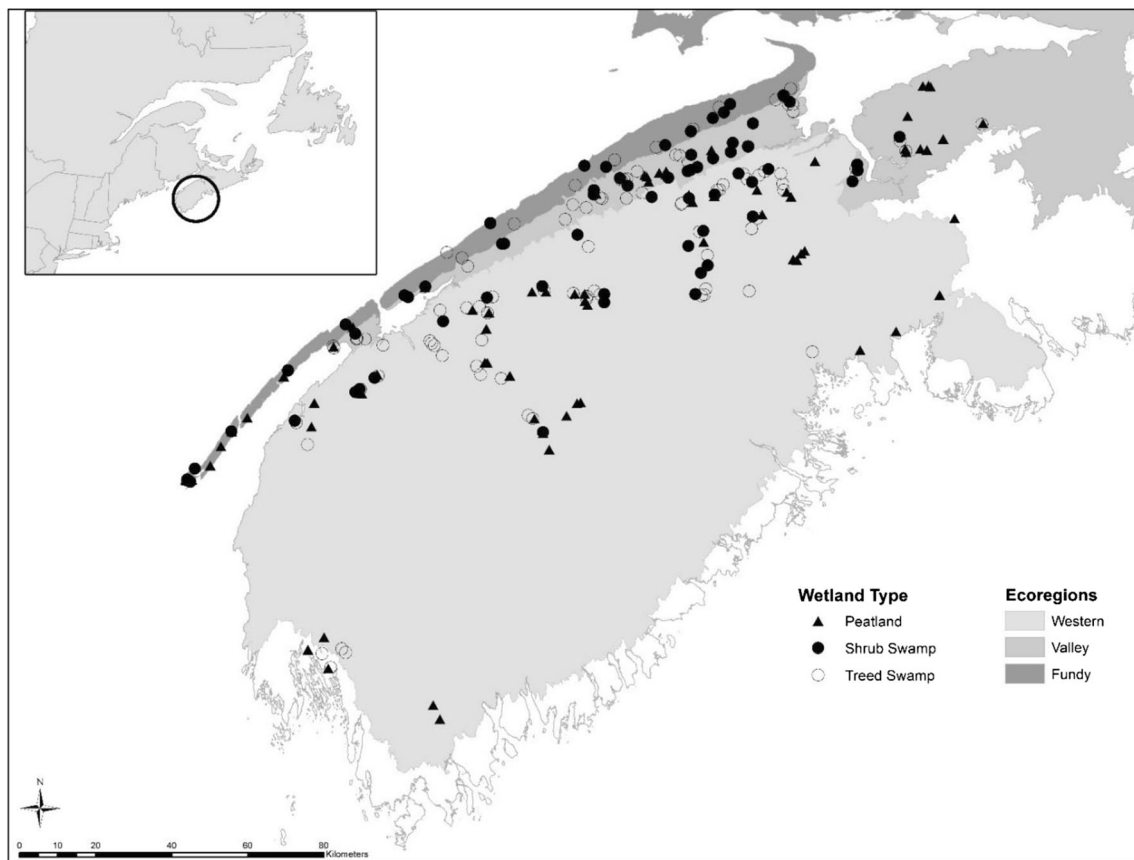
Fig. 1 Location of FWs surveyed in western Nova Scotia for this study (shades of grey denote different ecoregions, symbols denote different wetland types; inset map shows study area in regional context)

warm summer temperatures and extensive farmlands. Shade tolerant hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and beech (*Fagus grandifolia*) are common in the uplands. Lowlands with poorly drained soils are dominated by trees such as red maple and black spruce, and shrubs such as speckled alder (*Alnus incana*) and false holly (*Ilex mucronata*) at wetter sites. Fundy is a small ecoregion (~1200 km²) separated from the Valley by a 225 m volcanic ridge (North Mountain). Fundy has cool, foggy summers, and milder winters than more interior regions. Much of the coastal forest consists of stunted black and white spruce (*Picea glauca*) while mixed forests of balsam fir (*Abies balsamea*), red spruce, red maple, yellow and white birch (*Betula papyrifera*) dominate inland areas. Extensive peatlands are common on fine-textured, imperfectly-drained soils.

Forested Wetland Classification

The four main types of FWs in Nova Scotia are classified as treed bogs and fens, shrub swamps and treed swamps by the Canadian Wetland Classification System (CWCS) (National Wetlands Working Group 1997). Consistent with the CWCS, any sites that had 30% or more cover of woody species 2 m or taller were considered swamps. We used a compromise between the CWCS and the Forest Ecosystem Classification methodology for Nova Scotia (Keys et al. 2007) for distinguishing shrubby from treed sites that better reflected natural breaks in the height structure we observed in the field (2–7 m = tall shrub swamp, > 7 m = treed swamps). Due to similarity in vegetation structure among most forested bogs and fens we encountered, we combined these two types into a single forested peatland class. We followed the CWCS approach of classifying peatlands as sites with ≥40 cm of deep peat (assessed with a standard soil auger) and less than 30% cover in tall woody species. We set an arbitrary lower threshold for tall woody species cover at greater than or equal to 5% in keeping with the study focus on "forested" wetlands. The CWCS does not provide criteria to make such a distinction.

Site Selection

We used the Nova Scotia Wetland Inventory, historic aerial imagery from Google Earth, swamps included in the Nova Scotia Topographic Database from the Nova Scotia Geomatics Centre (https://nsgi.novascotia.ca/gdd/) and on-the-ground reconnaissance to identify potential FWs to include in the study. We looked for sites in one of our three

target FW classes that had an estimated size of 3 ha or larger, and ideally, were 100 m or more in width and within 1 km of a road for ease of access. *A priori* random selection of sites was not possible due to incomplete knowledge of FW locations across western Nova Scotia. Our goal was to sample a broad cross section of FWs. We selected 80 sites that met or approximated our selection criteria out of over 130 that were examined in 2015 and 149 out of 211 in 2016. Treed swamps ($n = 92$) and sites in Western were the most commonly surveyed ($n = 117$) while shrub swamps ($n = 63$) and sites in Fundy ($n = 39$) were surveyed the least (Table 1).

The mean size of our FWs estimated from aerial photographs was 16.5 ha (std. error = 1.3 ha), with a range from 2 to 137 ha. Shrub swamps had the smallest mean size (8.7 ha, std. error = 2.3 ha) and peatlands the largest (20.9 ha, std. error = 2.5 ha). Sites in the Fundy Ecoregion (mean = 8.9 ha, std. error = 2.9 ha) tended to be smaller than sites in the other two ecoregions and shrub swamps in the Fundy Ecoregion were typically smaller than other FW type by ecoregion classes. Despite this large range in sizes of FWs surveyed, we did not detect any relationship between species richness or abundance and wetland size with a simple regression analysis ($r^2_{spp\,rich} = 0.03$, $p = 0.70$; $r^2_{abun} = 0.01$, $p = 0.11$), suggesting that the point count method we used, and the abundance indices derived from those counts were relatively independent of wetland size.

Bird Surveys

All sites were surveyed with unlimited distance, 10-min bird point counts based on well-established methods (Ralph et al. 1995; Howe et al. 1997). Each FW was surveyed at two points during a single visit to optimize information gained while maximizing the number of sites sampled (Hanowski and Niemi 1995), between May 31 and July 6 in either 2015 or 2016. Points were placed in habitat that was representative of overall site conditions, 100 m from the edge of the FW and at least 250 m apart whenever site geomorphology allowed. In the few instances when these conditions could not be fully realized (e.g., FWs were elongated and narrow or less than 3 ha in size), distances were maximized given site constraints and effort was made to avoid double counting between points. We used a precautionary approach by excluding birds when we could not be certain that birds were heard from within the study wetland. However, birds judged to be near the edge (within 20 m of wetland boundaries) were recorded under the presumption that birds occupying the edges were likely using both habitats.

Counts for each FW were analyzed as all birds per 20 min (total per 2, 10 min point counts). We did not correct for variation in detectability among species and habitat classes because the number of detections was often too low (< 10 per species) to allow effective distance sampling (Nichols et al. 2000), and each site was visited only once (Hutto 2016) at only two survey locations (MacKenzie et al. 2006; Niemi et al. 2016). However, we reduced variation in detectability as much as possible by conducting surveys only on days with optimal conditions (e.g., no rain, no heavy fog, wind speeds below 20 km/h) to avoid bias associated with inclement conditions or noise from wind (Ralph et al. 1995). In addition, sites had similar structure in that they were all "forested" which should have limited variability in detection associated with larger habitat differences (Nichols et al. 2000; Johnson 2008) and we did not conduct surveys until one-half hour after sunrise or after 9:30 am to avoid potential bias associated with increased song activity during the dawn chorus and decreased song activity later in the day (Farnsworth et al. 2002; Foote et al. 2017). The authors performed all point counts, except for those completed by citizen scientists at 10 sites in 2015 and 6 sites in 2016, and 2 sites surveyed by the Provincial Wetland Specialist in 2016. All of the additional surveyors had been previously trained and conducted point counts for the most recent Maritime Breeding Bird Atlas (Stewart et al. 2015).

Since the counts were not distance-corrected, they should be treated as indices of abundance or relative abundance among sites rather than absolute abundance or densities (e.g., Ralph et al. 1995; Dunn et al. 2006). They are sometimes referred to as abundances in the text as a simplification. Although corrections are often applied to point count data to account for differences in detectability among species or habitats (e.g., Nichols et al. 2000, Alldredge et al. 2007), these sorts of adjustments have been described as problematic and unnecessary for many multi-species monitoring surveys (Johnson 2008, Etterson et al. 2009; Hutto 2016). Assumptions about accurate distance estimation by observers, differences in detection probability among observers and rates of movement into or out of habitats which are essential to

Table 1 Distribution of sites among forested wetland types and ecoregions (numbers of each site type surveyed in 2015, 2016 in parentheses)

Wetland type	Valley and Central Ecoregion	Western Ecoregion	Fundy Shore Ecoregion	Total
Bog/Fen	20 (8, 12)	43 (12, 31)	11 (5, 6)	74
Shrub Swamp	26 (12, 14)	22 (6, 16)	15 (6, 9)	63
Treed Swamp	27 (12, 15)	52 (16, 36)	13 (3, 10)	92
Total	73	117	39	229

making meaningful corrections are difficult to ensure and often introduce error (Alldredge et al. 2007, Etterson et al. 2009; Hutto 2016).

Conservation Status Assignments

Conservation status of each species was based on a number of ranking schemes relevant to birds in Atlantic Canada (Appendix 1). When evaluating conservation value we focused on "at-risk" (Endangered, Threatened or Vulnerable) species listed under the Nova Scotia Endangered Species Act (NSESA) (https://novascotia.ca/just/regulations/regs/eslist.htm), and those with CCS_{max} scores of 11 or above in the Partners in Flight (PIF) Conservation Scoring System (CCS_{max}; 5 = lowest concern, 20 = highest concern; Panjabi et al. 2017), that were ranked S1, S2 or S3 (Critically Imperiled, Imperiled, or Vulnerable) in the Atlantic Canada Conservation Data Centre "S-ranks" scheme (http://accdc.com/en/ranks.html).

General Site Habitat Characterization

Although we completed a rapid assessment of a wide range of habitat variables to characterize local habitat at each site, we included only a few of those here to provide a general sense of the main habitat differences among the FW types surveyed for this study. The total percentage cover in six vegetation strata (canopy, tall shrub, low shrub, herb, fern and moss layers) was visually estimated within a 10 m radius plot around the center of one of the two bird survey locations at each study wetland or at a point between those locations deemed most representative of habitat conditions at that site.

Data Analysis

General Site Habitat Characterization

One-way analysis of variance (ANOVA) was used (SYSTAT Ver. 11.0) to characterize differences in the primary vegetation structures among FW types. All data met homogeneity and normality assumptions without transformation. Tukey's HSD was used to assess all pairwise differences among FW type means.

Differences in Bird Community Characteristics, Abundant Species and Conservation Status

Two-way ANOVA was employed using a general linear model approach (SYSTAT Ver. 11.0) to characterize differences in species richness (total number of species per site) or relative abundance among different FW types or ecoregions based on all species encountered across all sites (complete species list in Appendix 1). We included a FW type by ecoregion interaction term because we were interested in whether any apparent differences detected might be associated with a particular FW type by ecoregion class. It was necessary to log-transform total abundance to meet homogeneity and normality assumptions. Because individual species abundance data distributions were not normal or homogeneous we used the nonparametric multiple response permutation procedure (MRPP; Mielke and Berry 2001) to examine differences in individual species of highest conservation concern and a grouping of individuals from species with high CCS_{max} scores (CCS_{max} 12–14) among FW type by ecoregion classes. MRPP tests the null hypothesis of no difference between two or more groups of entities and is not limited by data distribution assumptions that are seldom met with species or community data (McCune and Grace 2002). The chance-corrected within group agreement (A = 1 − (observed distance/expected distance)) describes within group homogeneity, compared to random expectation that it is independent of sample size. All p values obtained from MRPP analyses were corrected to keep the experiment-wide error rate at $p \leq 0.05$ (McCune and Mefford 2011).

Differences in Bird Community Patterns

We used nonmetric multidimensional scaling (NMDS; Clarke 1993) to ordinate study wetlands based on untransformed abundances of all bird counts (PC-Ord Ver. 6; McCune and Mefford 2011) to see whether patterns in overall community composition were related to FW type or ecoregion. NMDS is an iterative technique that is effective at preserving the original rank similarities among samples in the final solution and is more robust to highly heterogenous data sets than other ordination techniques (Faith et al. 1987; Clarke 1993). We used the Sørensen distance measure to define our sample ranks, a random starting configuration and 250 Monte Carlo randomization runs to determine the optimal solution. The number of axes in the final solution was determined by choosing solutions where dissimilarity in the original data matrix relative to distance in the ordination space ("final stress") was minimized and the p value in the randomization tests was ≤0.05.

To evaluate the percentage of variance in the original data matrix explained by each axis in the ordination, we calculated the coefficient of determination (r^2) between distances among sites in the ordination space and distances in the original matrix (McCune and Mefford 2011). To examine the relationship between individual bird species and site locations in the NMDS ordination, we included a "joint-plot". The angle and length of vectors radiating from centroid of the ordination reflect the correlation (only species with r ≥ 0.30 plotted) between ordination scores and bird species abundances – the stronger the combined correlation with the two axes plotted, the longer the vector in the joint-plot (McCune and Mefford 2011). In addition, the MRPP method we used to characterize differences in individual species abundances was also used to

characterize differences in overall community composition among FW types and ecoregions in the final NMDS ordination solution.

Species Associations with Forested Wetland types and Ecoregions

Indicator-species analysis (ISA; Dufrêne and Legendre 1997) was used to evaluate the degree to which a species was associated with a particular FW type or ecoregion (PC-Ord Ver 6; McCune and Mefford 2011). The method combines information on the concentration of species abundance and the faithfulness of occurrence of a species in a particular group (e.g., FW type or ecoregion). It produces indicator values (IV) for each species in each group that range from 0 (no affinity for a particular group) to 100 (highest affinity/perfect indication). A Monte Carlo randomization test was used to evaluate the strength of the maximum indicator value (IV_{max}) recorded for a given species. As recommended by Dufrêne and Legendre (1997), only species with an $IV_{max} > 25$ and a p value less than 0.05 in the Monte Carlo test for a particular FW type or ecoregion were considered to have an ecologically important IV_{max}.

Results

General Site Characteristics

General site characterization supported the classification of sites into three FW types. As expected, treed swamps had higher tree cover, shrub swamps had higher tall shrub cover and peatlands had higher low shrub and sphagnum cover (Fig. 2; $p \leq 0.008$). In addition, treed swamps had generally higher, although more variable, fern cover and peatlands significantly lower herbaceous cover (Fig. 2; $p \leq 0.008$).

Peatlands were typically dominated by a variety of low woody shrub species such as lambkill (*Kalmia angustifolia*), leatherleaf (*Chamaedaphne calyculata*) and rhodora (*Rhododendron canadense*), but also sparse cover (5–20%) in stunted black spruce and tamarack, and occasionally shrubby (0–5 m) red maple, Canada holly and alder. The ground layer in peatlands was almost always dominated by *Sphagnum* spp. (80–90% cover), and sparse (< 5%) cover in pitcher plants (*Sarracenia purpurea*), cottongrass (*Eriophorum* spp.), *Carex* spp. and a variety of orchids (e.g., *Arethusa bulbosa*).

The majority of the 92 treed swamps we surveyed were either red maple-dominated (50%) or mixed red maple and black spruce (36%); only 6 (6.5%) were black spruce-dominated despite a concerted effort to find more of these wetlands. Understory shrub species in red maple or mixed swamps were typically speckled alder, false

holly/Canada holly, balsam fir, and young red maple in the 20–40% cover range with species such as cinnamon fern (*Osmundastrum cinnamomeum*), *Carex* spp., and bluejoint grass (*Calamagrostis canadensis*) dominating the herbaceous layer (50–70% cover) and moderate sphagnum cover on the forest floor. Black spruce swamps tended to be more sparsely covered in all non-tree layers with light speckled alder, false holly/Canada holly, and lambkill cover, little herbaceous cover (spotty cover in goldthread, *Coptis trifolia*, bunchberry, *Cornus canadensis*, and *Maianthemum* spp. were typical) and a forest floor dominated by sphagnum and moderate (30–60% cover) cinnamon fern.

Shrub swamps were most typically dominated by speckled alder (50–80%), but some sites, especially in the Western and Fundy Ecoregions, were dominated by false holly/Canada holly, and many sites had a minor *Salix* spp. component. The herbaceous/low shrub layer at these sites was typically quite diverse with light cover in species such as sensitive fern (*Onoclea sensibilis*), *Aster* spp., goldenrod (*Solidago* spp.), *Glyceria* spp., jewelweed (*Impatiens capensis*), meadow rue (*Thalictrum pubescens*), steeplebush (*Spiraea* spp.) and dense cover of graminoids such as bluejoint, or reed canary (*Phalaris arundinacea*) grass or *Carex* spp. (30–50%).

Differences in Overall Richness, Relative Abundance and Common Species

We recorded 8971 individuals from 95 different bird species during surveys across all sites during 2015 and 2016. The mean number of individuals per site was 38.3 (std. error = 0.9) and the mean number of species per site was 16.4 (std. error = 0.3). Species richness and relative abundance were higher in peatlands and shrub swamps than in treed swamps ($p < 0.001$). Relative abundance was also higher in the Valley than in other ecoregions (p < 0.001), but for richness, Valley sites were only clearly higher than those in Fundy ($p = 0.042$; Fig. 3). The five most common species (top 5) overall were Common Yellowthroat (*Geothlypis trichas*), Ovenbird (*Seiurus aurocapillus*), Swamp Sparrow (*Melospiza georgiana*), American Goldfinch (*Spinus tristis*), and Alder Flycatcher (*Empidonax alnorum*) (Appendix 2).

Of the species of highest conservation concern, two species (Canada Jay *Perisoreus canadensis* and Canada Warbler *Cardellina canadensis*) were most common in treed swamps and peatlands (Canada Jay was never detected in shrub swamps), but only Canada Warbler relative abundances had clear statistical differences in the MRPP analyses (p < 0.001; Table 2). Mean relative abundance of Canada Warblers was particularly high in Fundy treed swamps and low in shrub swamps in all ecoregions. Eastern Wood-pewee (*Contopus virens*) was the only
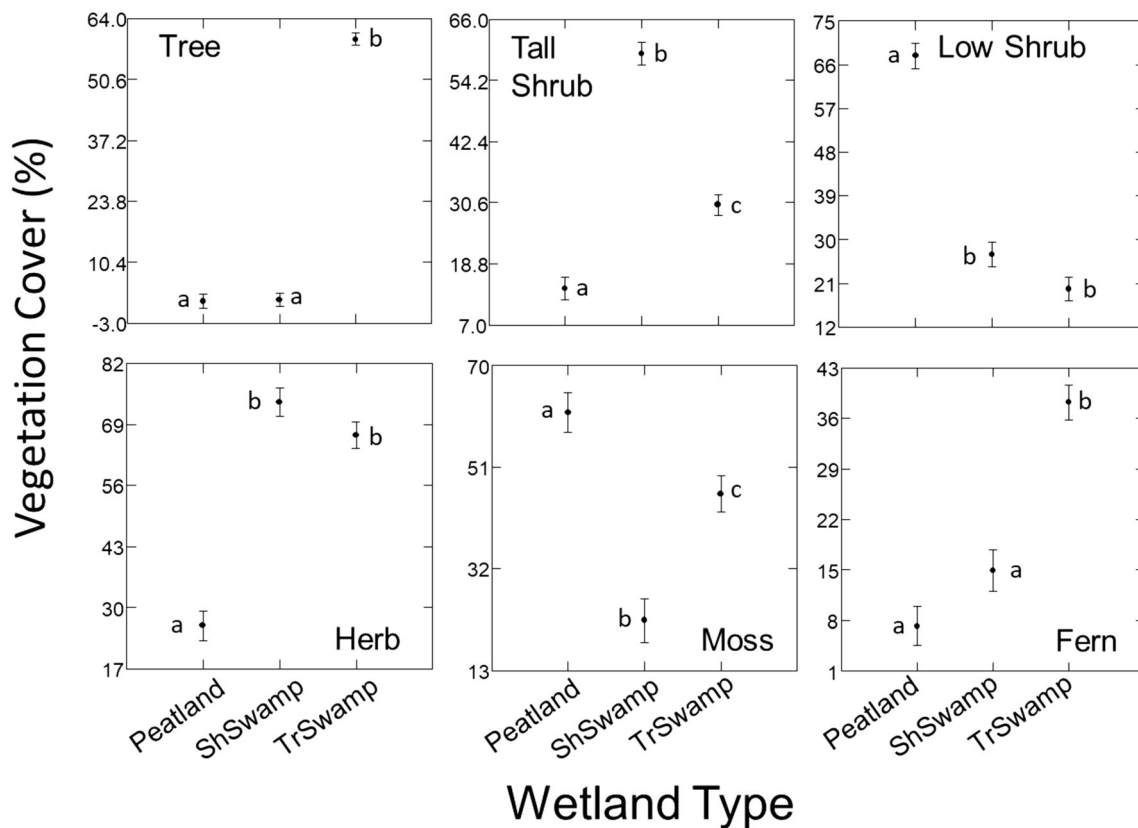
Fig. 2 Mean vegetation cover (%) by wetland type (tree cover = total canopy cover of woody species ≥7 m tall; tall shrub cover is total cover in woody species ≥2 and < 7 m tall; low shrub cover = total cover in woody species <2 m tall; herb cover = total cover in all herbaceous species except mosses and ferns; moss cover = total cover in *Sphagnum* spp.; fern cover = total cover in all fern species). Means (and associated standard errors) are least squares values from one-way ANOVAs. Wetland types with no letters in common for each variable were significantly different, p < 0.01)

species that was most common in treed swamps, particularly treed swamps in the Valley where it was more abundant than all other site-types ($p \leq 0.01$). There were three species (Chestnut-sided Warbler *Setophaga pensylvanica*, Gray Catbird *Dumetella carolinensis* and Rose-breasted Grosbeak *Pheucticus ludovicianus*) that were more common in shrub swamps. All three species were most common in Valley shrub swamps, but the ecoregion difference was only significant for Chestnut-sided Warblers and Rose-breasted Grosbeaks ($p \leq 0.007_{CSWA}$, $p \leq 0.03_{RBGB}$; Table 2). Rusty Blackbird (*Euphagus carolinus*) and Veery (*Catharus fuscescens*) were most common in shrub swamps with Veery significantly more abundant in Valley shrub swamps ($p \leq 0.03$; Table 2). Olive-sided Flycatchers were uncommon and detected at all three FW types (9 peatlands, 6 treed swamps, 4 shrub swamps), but were most commonly detected along the edges of peatlands and in the Western Ecoregion although differences were not statistically clear ($p > 0.1$). Birds with high PIF CCS_{max} scores were most common in the Valley and Fundy Ecoregions with Valley shrub swamps and Fundy treed swamps having the highest relative abundances of species of conservation concern ($p \leq 0.02$; Table 2).

Differences in Bird Community Patterns

Our MRPP comparisons on NMDS results revealed clear differences in community-wide patterns among FW types, with less variation apparent among ecoregions (Fig. 4). The optimal solution provided by the NMDS was three dimensional, statistically clear ($p = 0.004$) and accounted for 66% of total variation in the original data matrix (Axis 1 = 25%, Axis 2 = 23%, Axis 3 = 18%). Community differences among FW types were clear along both Axis 1 and 2. There was separation between treed and shrub swamps along Axis 1, while Axis 2 mainly separated swamps from peatlands (Fig. 4a). MRPP results revealed these differences were statistically clear among each pair of FW types (A = 0.046, $p < 0.0001$). Joint-plot vectors overlaid on the ordination indicated that Veery, Song Sparrow (*Melospiza melodia*), Yellow Warbler (*Setophaga petechia*) and Alder Flycatcher were most strongly associated with shrub swamps, Common Yellowthroat, Palm Warbler (*Setophaga palmarum*) and Hermit Thrush (*Catharus guttatus*) were most strongly peatland-associated, and Ovenbird, Northern Waterthrush (*Parkesia noveboracensis*) and Golden-crowned Kinglet (*Regulus satrapa*) most strongly associated with treed swamps (Fig. 4a).

Fig. 3 Least-squares means (± se) from two-way ANOVA results for species richness and total abundance by wetland type and ecoregion. Within each panel, means with no letters in common were significantly different (p ≤ 0.05; interactions were not significant for either response variable)
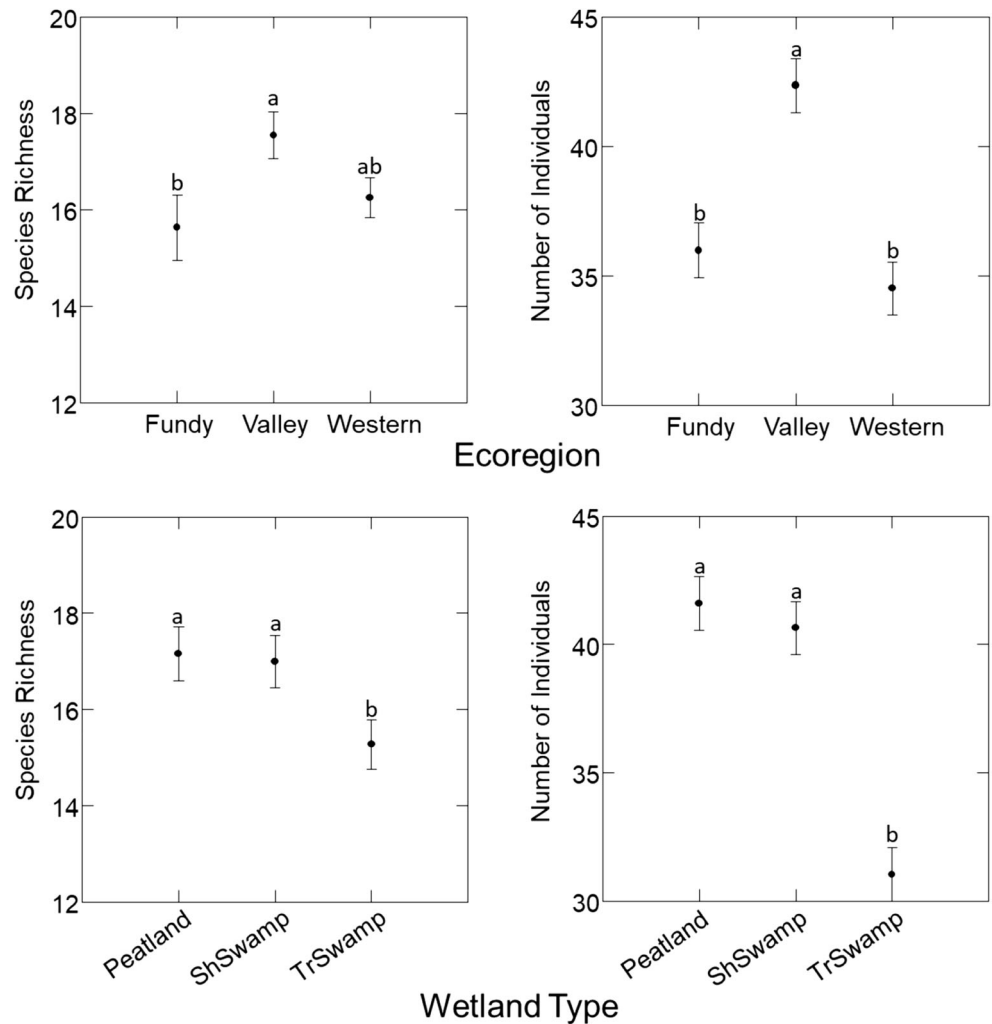
Differences in bird communities among ecoregions were less clear than those apparent among FW types. Distinctions among sites from different ecoregions were harder to visually

detect along the primary axes in the ordination with sites from each ecoregion spread more broadly across the ordination space (Fig. 4b), particularly for sites in the Fundy

Table 2 Mean abundances (standard error parenthetic) of nine species of conservation concern and for all individuals from species with high (12–14) PIF CCS$_{max}$ scores. Site-types (ShSwamp = shrub swamp,

TrSwamp = treed swamp) with no letters in common in their superscripts were significantly different ($p \leq 0.05$) in multi-response permutation procedure (MRPP) tests

Species	Ecoregion and Wetland type								
	Western			Valley			Fundy		
	Peatland	ShSwamp	TrSwamp	Peatland	ShSwamp	TrSwamp	Peatland	ShSwamp	TrSwamp
Canada Jay	0.19(0.13)	0.00(0.00)	0.04(0.03)	0.00(0.00)	0.00(0.00)	0.04(0.04)	0.09(0.09)	0.00(0.00)	0.31(0.31)
Canada Warbler	0.65(0.16)[ac]	0.36(0.19)[bc]	0.73(0.19)[ac]	0.55(0.29)[abc]	0.04(0.04)[b]	0.19(0.09)[bc]	0.82(0.40)[ac]	0.27(0.21)[bc]	1.85(0.48)[a]
Chestnut-sided Warbler	0.07(0.05)[b]	0.50(0.27)[bc]	0.23(0.09)[b]	0.35(0.15)[bc]	1.31(0.35)[ac]	0.15(0.09)[b]	0.09(0.09)[bc]	0.80(0.42)[bc]	0.23(0.17)[bc]
Eastern Wood-pewee	0.05(0.03)[b]	0.05(0.05)[b]	0.29(0.10)[b]	0.30(0.13)[b]	0.19(0.08)[b]	1.15(0.25)[a]	0.00(0.00)[b]	0.00(0.00)[b]	0.08(0.08)[b]
Gray Catbird	0.05(0.03)	0.05(0.05)	0.00(0.00)	0.05(0.05)	0.46(0.25)	0.22(0.13)	0.09(0.09)	0.07(0.07)	0.00(0.00)
Olive-sided Flycatcher	0.33(0.14)	0.23(0.13)	0.13(0.06)	0.05(0.05)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.07(0.07)	0.00(0.00)
Rose-breasted Grosbeak	0.00(0.00)	0.23(0.16)	0.00(0.00)	0.00(0.00)	0.81(0.21)	0.11(0.06)	0.00(0.00)	0.60(0.34)	0.08(0.08)
Rusty Blackbird	0.00(0.00)	0.05(0.05)	0.04(0.04)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)
Veery	0.02(0.02)[b]	0.36(0.19)[acd]	0.19(0.09)[bd]	0.30(0.16)[bcd]	2.58(0.42)[a]	1.59(0.42)[ac]	0.18(0.12)[bcd]	1.00(0.40)[ac]	0.77(0.34)[cd]
PIF CCS_12–14	1.07(0.25)[b]	1.50(0.36)[bc]	1.46(0.28)[bc]	1.25(0.46)[bc]	4.00(0.54)[a]	1.96(0.43)[ab]	1.18(0.48)[bc]	2.13(0.64)[ab]	2.85(0.59)[ac]

Ecoregion. MRPP analysis revealed that differences were only about half as large as observed for FW types ($T = -44.4_{WetType}$ and $-25.2_{Ecoregion}$; $A = 0.046_{WetType}$ and $0.026_{Ecoregion}$).

Species Associations with Forested Wetland types and Ecoregions

In the ISAs, there were more species with strong affinities for shrub swamps ($n = 10$) and peatlands ($n = 8$) than treed swamps ($n = 2$) and more species with strong affinities for sites in the Valley ($n = 7$) than Western or Fundy ($n = 3$ for each; Fig. 5). The total number of species with strong affinities for a particular FW type ($n = 20$) was 42% higher than those with strong affinities for a particular ecoregion ($n = 13$). In addition, several of the species with the highest IV_{max} values for particular FW types were the same as those with the strongest associations with the ordination axes (e.g., Palm Warbler, Common Yellowthroat, Yellow Warbler and Ovenbird). Almost all (14 of 17) of the species (e.g., American Goldfinch, Veery, American Redstart (*Setophaga ruticilla*), Song Sparrow, American Crow (*Corvus brachyrhynchos*)) with significant IV_{max} values for shrub swamps or the Valley were species that are known to thrive along forest edges, regenerating openings or in areas disturbed by humans (Niemi et al. 2016).

Discussion

Overall, we found that FWs in western Nova Scotia supported a rich community of breeding birds. Of the 208 documented breeding bird species in Nova Scotia (Stewart et al. 2015), we found evidence (mainly singing males) that 95 (46%) were breeding in the 229 FWs we surveyed. Given that our surveys were restricted to a single visit at only two points within each wetland, this is no doubt a conservative estimate of the diversity of breeding birds that are using these habitats. In addition, 5 of 13 (38%) inland (noncoastal) bird species listed as at-risk in Nova Scotia (Appendix 1) were detected at our study sites with Canada Warbler, Eastern Wood-pewee and Olive-sided Flycatcher observed relatively frequently considering their status. These results and other studies suggest that a large number of bird species depend on or at least utilize FWs in Nova Scotia during the breeding season and that they may play important roles in the conservation of several at-risk species (Darlington-Moore 2014; Westwood 2016; Bale 2017).

We found distinct differences in the bird communities associated with different FW types and these differences were more distinct than those observed among ecoregions. Species like Palm Warbler, Dark-Eyed Junco (*Junco hyemalis*) and Common Yellowthroat (most abundant in peatlands), Yellow Warbler, Song Sparrow and Alder Flycatcher (most abundant in shrub swamps), and Ovenbird, Northern Waterthrush, and
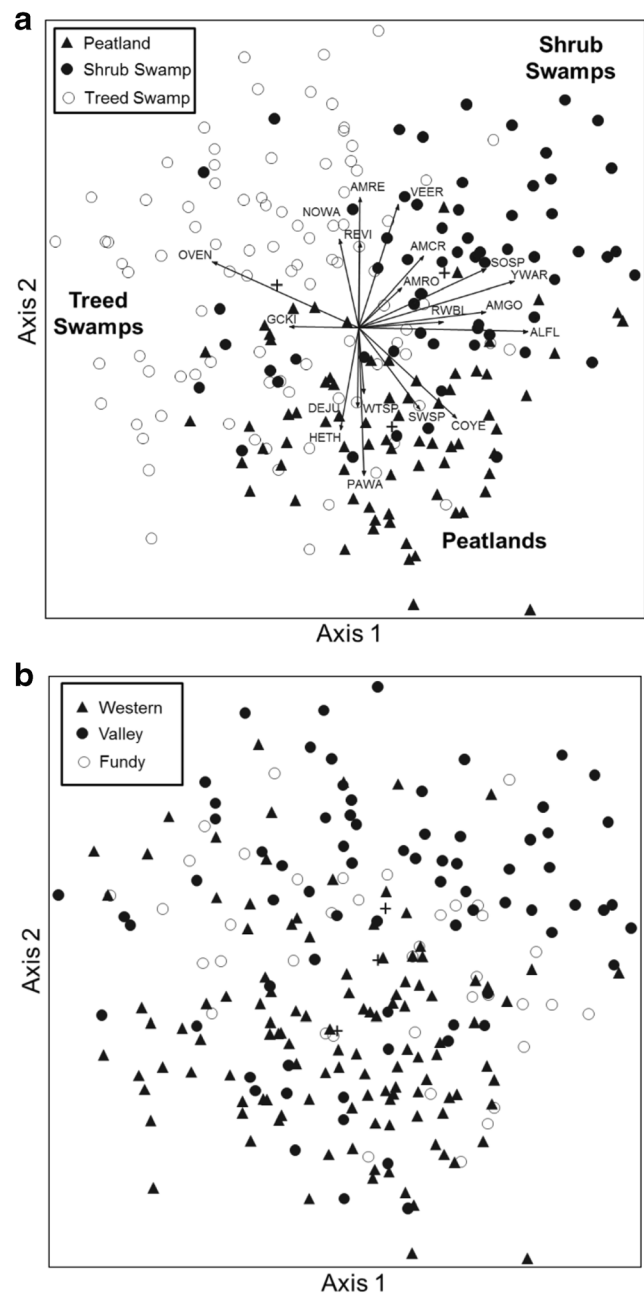

Fig. 4 Non-metric multidimensional scaling ordination of FW sites based on bird species composition with wetland type (Panel A) and ecoregion (Panel B) affiliation of each site denoted symbolically. Angle and length of vectors radiating from the centroid reflect the correlation (r > 0.30) of bird abundances with ordination axes. Four letter codes and scientific names of bird species detailed in Appendix 1

Eastern Wood-pewee (most abundant in treed swamps) were key species driving differences among FW types. Swamp Sparrows (most abundant in Western), American Goldfinch (most abundant in Valley) and Black-throated Green Warblers ((*Setophaga virens*; most abundant in Fundy) were primary drivers of differences among ecoregions.

Many of the same species we found to be strongly associated with different FW types were also found to be associated

Fig. 5 Significant indicator species ($p < 0.01$ and $IV_{max} \geq 25$) by wetland type and ecoregion (significance based on Monte Carlo randomization test; four letter species codes defined in Appendix 1)
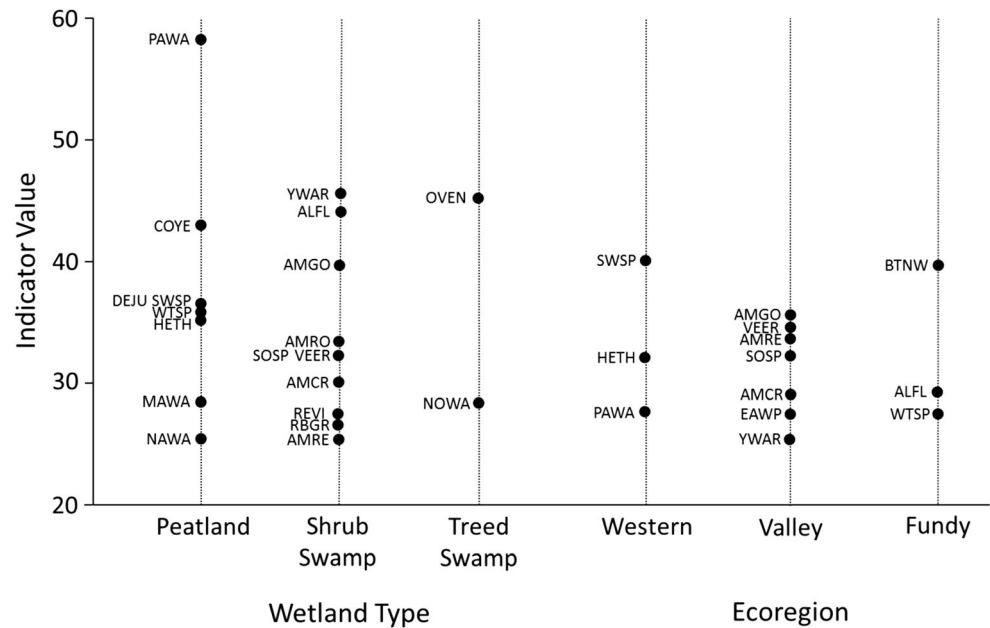
with similar FW types elsewhere in Canada (e.g., Erskine 1977; LaRue et al. 1995; Calme et al. 2002; Morissette et al. 2013) and the northern United States (Swift et al. 1984; Merrow 1990; Wilson et al. 1998; Niemi et al. 2016; Zlonis et al. 2017). Direct comparisons are difficult since most studies were focused on only one wetland type, but Morissette et al. (2013) and Niemi et al. (2016) are exceptions. Both report a similar suite of species that have strong associations with the three FW types we focused on here, although there were some notable differences (e.g., Common Yellowthroat and Northern Waterthrush were shrub swamp species in the Morrissette et al. study, but peatland and treed swamp species, respectively, in our study; Veery were a mature hardwood swamp species in Niemi et al., but a shrub swamp species in our study).

Although we found there were fairly distinct differences in bird communities among different FW types, it was also clear that certain FW type by ecoregion combinations were driving many of the differences we observed, particularly Valley shrub swamps. This result, at least as it pertains to high richness and relative abundance in shrub swamps, runs counter to expectations about vertical structural complexity and bird community structure in forested landscapes (e.g., MacArthur and MacArthur 1961; Hunter 1999). However, the high stem density, complex tangled structure under the canopy and interspersed patches of dense graminoids associated with shrub swamps provides high horizontal complexity and may at least partially explain the pattern we observed (MacArthur et al. 1962; Roth 1976; LaRue et al. 1995).

We could find little data on bird communities associated with shrub swamps to corroborate our findings, but there is one study of bird richness and abundance in seven New England FWs that included one shrub swamp (Swift et al. 1984). Species richness and abundance in this shrub swamp was higher than in all the other red maple swamps that were surveyed. In addition, LaRue et al. (1995) highlighted the important contribution of alder-grass edge swamps to the high bird species richness they observed in boreal riparian forests and Niemi and Hanowski (1984) found generally higher species richness and abundance in tall shrub swamps compared to treed swamps and forested peatlands in a boreal peatland complex.

High richness and relative abundance in shrub swamps across all ecoregions may reflect generally higher productivity relative to the other two FW types. Nutrient richness, and associated higher productivity, was positively correlated with bird diversity and abundance in northern Ontario (Welsh and Lougheed 1996). We did not measure primary productivity for this study but have measured high conductivity of surface water in some of these shrub swamps (Brazner in review), which suggests higher productivity (Dodds 2002). Differences in wetness among FW types may have also contributed in that moisture gradients have been shown to structure FW avian communities in other studies (e.g. Kirk et al. 1996) with wetter sites having generally higher species richness and abundance (Odum 1950; Smith 1977; Swift et al. 1984). Preliminary evidence from western Nova Scotia suggests shrub swamps are wetter than treed swamps with higher peak water levels and less extreme drawdowns (Brazner et al. 2007).

Other factors may have contributed to the high richness and relative abundance patterns we observed specifically in Valley shrub swamps and other FW types in the Valley. One is that the Valley landscape has only small fragments of forest cover

remaining, due primarily to dense agricultural development. Forty-four percent of the central part of the Valley is actively farmed and another 13% is urbanized; a much higher degree of developed landscape than anywhere else in our study area (Neily et al. 2017). As a result of this fragmentation and because they are hard to farm or build on without drainage, the wetlands we surveyed are some of the last relatively intact habitat patches in the Valley and appear to be acting as habitat refugia, concentrating species with a variety of life history strategies (Kirk et al. 1996; Burivalova et al. 2014). In addition, soil fertility in the Valley is high (Neily et al. 2017) which may transfer up the food chain promoting higher avian diversity (Welsh and Lougheed 1996).

Management Implications

The result with the most important management implications is that FWs support a rich avifauna, that includes a number of uncommon and at-risk species. As such, alteration of FWs will have a high probability of negatively impacting species of conservation concern, at a local habitat scale if not more broadly. Our results suggest species that are most likely to be affected will depend on the FW type and ecoregion, but overall loss/displacement of species and individuals is likely to be high regardless because all the FW types we examined in all three ecoregions supported high bird diversity. The fact that our study and others (e.g., Westwood 2016; Bale 2017) demonstrate the importance of treed swamps to a number of at-risk species (Canada Warbler, Olive-sided Flycatcher, Eastern Wood-peewee, Rusty Blackbirds) suggests a reexamination of what activities are considered appropriate in and around forested wetlands would be prudent.

Although our results strongly suggest that FWs have high biodiversity value, to better inform management decisions it will be important to determine their biodiversity value relative to other forested habitats. There is some evidence that FWs are used as breeding habitats for many birds that are rarely found in upland forests (e.g., Inman et al. 2002) and generally have higher species richness and abundance than upland habitats (e.g., McKinney et al. 2011; Zlonis and Niemi 2014; Morissette et al. 2018). However, systematic studies comparing various aspects of biodiversity in wetland and upland forests are scarce. Additional comparative habitat studies could help inform the design of a more prescriptive monitoring approach relevant to conservation decision-making in a variety of actively managed landscapes.

Another result with important management implications, particularly for farmers, is that shrub swamps have high biodiversity value. Farmers in Nova Scotia generally perceive shrub swamps to be nuisance habitats and spend considerable effort trying to convert them to productive agriculture (MacDonnell 2001), often without success (Reg Newell,

Nova Scotia Department of Lands and Forestry – retired, pers. comm.). This suggests outreach to farmers about the ecological significance of these habitats might be beneficial, particularly in the Valley where farming is most prevalent and where the biodiversity value of shrub swamps was especially high.

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