

Forested wetlands in a protected area and the adjacent working landscape provide complementary biodiversity value based on breeding birds: A case study from Nova Scotia, Canada

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Abstract

Protected areas (PAs) are a key component of most conservation strategies because they are thought to enhance biodiversity value relative to similar habitats in working landscapes. To examine whether PAs in Nova Scotia are functioning to enhance the biodiversity value of the landscapes in which they are embedded, we surveyed breeding bird communities in forested wetlands inside and outside of a large PA during 2018 and 2019. We found significantly higher species richness and diversity at sites in the working landscape relative to those inside the PA. Bird communities from different wetland types inside the PA were distinct from each other and those outside the PA, whereas bird communities at outside sites were homogenized and comprised of more early-successional species. There were numerous species of conservation concern at both inside and outside sites, indicating that both types of sites are playing important conservation roles. Abundances of these key species were driven by a combination of local (e.g., water table depth, herb, and shrub cover) and landscape scale factors (e.g., edge density and human disturbance). The higher abundance of long-distance migrants and insectivores at inside sites suggests PAs are providing critical additional support to key guilds that are in steep decline.

Key words: protected areas, biodiversity value, effectiveness monitoring, forested wetlands, conservation, working landscapes, bird communities, human disturbance

Introduction

One of the primary responses to the global decline in biodiversity in recent decades is the expansion of protected area (PA) networks. Targets developed under the post-2020 Global Biodiversity Framework have promoted a substantial increase in this expansion. One key target in this framework is to “protect and conserve through well connected and effective system of PAs and other effective area-based conservation measures at least 30 per cent of the planet with the focus on areas particularly important for biodiversity” (Convention on Biological Diversity 2020). Canada has committed to this target as part of the High Ambition Coalition for Nature and People to “address the dual crises of biodiversity loss and climate change” (Environment and Climate Change Canada 2021a). However, as of the end of

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2020, Canada had only conserved about 12% of its land and freshwaters in formally designated PAs ([Environment and Climate Change Canada 2021b](#)).

PA networks are often established to maintain important components of biodiversity in a region (e.g., [Beazley et al. 2005](#); [Deguise and Kerr 2005](#); [Dudley 2012](#); [Watson et al. 2014](#)). It is generally agreed that designated PAs should be a key component of most conservation strategies because they can enhance biodiversity value relative to similar habitats in the working landscape (e.g., [Myers et al. 2000](#); [Jackson et al. 2009](#); [Kukkala and Moilanen 2013](#)), with working landscapes being the area outside of PAs where forest harvesting and other human activities such as farming and ranching are permitted and ongoing ([Garibaldi et al. 2021](#)). Although there have been numerous studies examining biodiversity in PAs compared to working landscapes, the results vary widely, with different studies finding both higher and lower biodiversity values across areas ([Gaston et al. 2008](#); [Geldmann et al. 2013](#); [Coetzee et al. 2014](#); [Rayner et al. 2014](#); [Zlonis and Niemi 2014](#); [Gray et al. 2016](#)). This ambiguity in biodiversity response contributes to difficulties in assessing PA effectiveness.

In addition to ambiguities in biodiversity response, there are other factors that make it difficult to draw firm conclusions about whether a particular PA is meeting conservation expectations. Often, no explicit conservation targets or indicators to assess progress have been identified or the identification process was not sufficiently precise (e.g., SMART – specific, measurable, ambitious, realistic, and time-bound) to allow for a meaningful evaluation ([Green et al. 2019](#); [Visconti et al. 2019](#)). Because monitoring the effectiveness of PA management is critical to conserving biodiversity ([Graham et al. 2021](#)), there has been a recent call to track progress in a more highly structured and defensible manner ([Adams et al. 2021](#)).

Few efforts of this nature have been completed in Canada, although ongoing ecological condition monitoring in Canadian national parks is an important exception ([Woodley 2020](#)). In addition, [Deguise and Kerr \(2006\)](#) demonstrated that existing reserve networks in Canada rarely performed better than randomly selected areas and several included fewer endangered species than expected by chance. [Kerr and Cihlar \(2004\)](#) proposed that one of the main reasons for this sort of result is that PAs in Canada have often not been established to protect biodiversity. They have in many cases been established for recreational benefits and the enjoyment of people and are often embedded in vast tracts of surrounding wilderness where threats to biodiversity are lower. However, this does not seem to be the case in Nova Scotia, with 71% of land in private ownership ([Government of Nova Scotia 2021](#)) and a higher degree of landscape fragmentation than in many other parts of Canada. The more fragmented landscapes in Nova Scotia and the potential influence on successful biodiversity conservation likely heighten the importance of specific site selection choices for new PA designations relative to those in less developed parts of Canada.

There are no published studies that evaluate the biodiversity value of PAs relative to similar sites in the working landscape in Nova Scotia. However, recent unpublished studies suggest relative population declines in two flycatchers were less severe in PAs than in the broader landscape and that several classes of upland forest plants (e.g., orchids, sedges, and geophytes) are more likely to occur in PAs than in the surrounding working landscape (Robert Cameron, Dalhousie University, personal communication).

Nearly 13% of terrestrial lands have already been protected in Nova Scotia ([Environment and Climate Change Canada 2021a, 2021b](#)), including more than 160 formally designated sites, and the Province has committed to protecting 20% of its terrestrial lands by 2030 as a target within the Environmental Goals and Climate Change Reduction Act of 2021 ([nslegislature.ca/legc/bills/64th_1st/1st_read/b057.htm](https://www.nslegislature.ca/legc/bills/64th_1st/1st_read/b057.htm)). Because of limited effort to compare relative biodiversity value inside and outside of PAs in Nova Scotia and the current push for more quantitative evaluation of PAs from

a biodiversity perspective (e.g., [Adams et al. 2021](#)), we undertook a study to examine the relative biodiversity value of sites inside and outside of Cloud Lake Wilderness Area (CLWA), one of the larger, formally designated PAs in Nova Scotia.

We chose to focus on biodiversity in forested wetlands because they are a common feature in the landscape in this region ([Brazner and Achenbach 2020](#)) and globally (e.g., [Calhoun 1999](#)) and although there has been a considerable amount of work on their ecology in eastern Canada (e.g., [Cameron 2009](#); [Padgett 2019](#); [Brazner and Achenbach 2020](#); [Harper et al. 2021](#); [Kendall et al. 2021](#)), no studies have examined the relative contributions of forested wetlands to biodiversity inside and outside of PAs. It has been suggested for some time that forested wetlands are biodiversity hot spots (e.g., [Sjöberg and Ericson 1997](#); [Hörnberg et al. 1998](#)) and this is supported by recent studies in Atlantic Canada ([Brazner and MacKinnon 2020](#); [Brooks and Nocera 2020](#); [Cameron and Bayne 2020](#); [Padgett and Wiersma 2020](#)). Additionally, forested wetlands are commonly threatened by human development and forest harvesting in Nova Scotia ([Brazner and Mackinnon 2020](#)) despite the important ecosystem services, such as carbon storage (e.g., [Temmink et al. 2022](#)), that are impacted by these activities.

We selected birds as our focal biotic community to assess relative biodiversity values because forested wetlands support a rich diversity of avian species that occupy a wide variety of niches (e.g., [Smith 1977](#); [Golet et al. 1993](#); [Morrissette et al. 2013](#); [Brazner and Achenbach 2020](#)) and birds have long been known to be good indicators of forest condition (e.g., [Welsh 1987](#); [Canterbury et al. 2000](#)), including forested wetland–riparian condition (e.g., [Croonquist and Brooks 1991](#); [Bryce et al. 2002](#)). In addition, the home ranges of most forest songbirds (passerines) are well within 500 m of the nesting area (e.g., [Mace and Harvey 1983](#); [Gnass-Giese et al. 2015](#)), so the species we focus on here should be good indicators of relatively local forest conditions during the breeding season. However, birds do respond to habitat conditions at a variety of spatial scales (e.g., [Mensing et al. 1998](#); [Crozier and Niemi 2003](#); [Cunningham and Johnson 2016](#)), so also reflect conditions in the surrounding landscape. Birds are relatively easy to sample reliably during the breeding season in forested habitats (e.g., [Howe et al. 1997](#)) and there are many species with rapidly declining populations that are of special concern provincially ([Stewart et al. 2015](#)), nationally ([Government of Canada 2022](#)), and internationally ([Billerman et al. 2020](#)).

Our main objective for this study was to begin examining whether PAs in Nova Scotia are functioning to enhance the biodiversity value of forested wetland bird communities relative to those in the nearby working landscape using a large PA in the province and its associated surrounding landscape as an initial proxy for PAs elsewhere in the province. We evaluated biodiversity value using the approach described by [Brazner and MacKinnon \(2020\)](#) where sites with higher richness and abundance of birds were considered to have higher biodiversity value, along with those that contained higher abundances or proportions of species of conservation concern (SOCC) and guilds of conservation concern (GOCC). Secondary objectives were to determine if the bird communities inside and outside of the PA were ecologically distinct, and which habitat and landscape factors were the best predictors of bird community characters and abundances across all sites.

Methods

Study area

The study took place within the Western Ecoregion of Nova Scotia, known as the Kespukwitiq region of Mi'kma'ki by the Mi'kmaw people, with all study sites either in or within 15 km of CLWA. All but two of the sites (including all sites within CLWA) are in the South Mountain Ecodistrict (SME), and the other two are in the LaHave Drumlins Ecodistrict (LDE) immediately to the south and east of

SME. The two sites in LDE are just outside of the boundary of the SME and the character of the landscape is similar to that of the other study sites. A granitic formation known as the South Mountain Batholith underlies 95% of the complex rolling plain typical of SME. PAs comprise 24% of SME and 8% of LDE. The surficial geology is dominated by a thin stony till cover with bedrock often exposed at surface (Bush and Baldo 2019). Soils are shallow and acidic and there is extensive wetland and lake cover, including large areas of forested wetlands, typically dominated by stunted black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in peatlands and mature red maple (*Acer rubrum*) and black spruce in swamps (Neily et al. 2017). Recent estimates suggest that about 7% of the forest in our study area is forested wetland (Brazner and Mackinnon 2020). Upland forest cover is a mosaic of mixedwood, deciduous, and coniferous stands, comprised mainly of red spruce (*Picea rubens*), red (*Pinus resinosa*) and white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), white birch (*Betula papyrifera*), and red and sugar maple (*Acer saccharinum*) (Nova Scotia Department of Environment and Labour 2002; Bush and Baldo 2019).

Study sites

To examine differences in bird communities inside and outside of the PA, we selected half our 24 study sites within CLWA and half in the adjacent working landscape. At 15,802 ha, CLWA is one of the largest designated Wilderness Areas in the province. CLWA includes parts of the LaHave and Nictaux river watersheds and is characterized by mature forests, large interconnected lakes, meandering streams with adjoining fens, and a variety of other wetlands and landforms characteristic of the rest of the ecodistrict (Cameron 2004; novascotia.ca/nse/protectedareas/wa_cloudlake.asp). It was formally designated as a Wilderness Area by the Province of Nova Scotia in 1998 and expanded in 2012 and 2015.

We used the Nova Scotia Wetland Inventory, aerial imagery from Google Earth, swamps included in the Nova Scotia Topographic Database from the Nova Scotia Geomatics Centre (nsgi.novascotia.ca/gdd/), and field reconnaissance to identify potential forested wetlands in and around CLWA to include in the study using the methods detailed in Brazner and Achenbach (2020). We selected four sites of each of the three focal wetland types (shrub swamps, treed swamps, and wooded peatlands) both inside and outside of CLWA (Figs. 1 and 2). Our goal was to select “outside” sites that were close to CLWA (within 15 km) to limit landscape character differences besides those typically associated with human disturbance in working landscapes (e.g., forest harvesting) and “inside” sites that were relatively accessible on foot (within ~ 1 km of the PA boundary) and far enough from the PA boundary (~250 m) to minimize potential edge effects (Parker et al. 2005; Manolis et al. 2002; Chizinski et al. 2011). We were limited by the natural distribution of our focal ecosystem types across the landscape, but only one of our sites did not meet these criteria (one “inside” shrub swamp was only 135 m from the CLWA boundary). However, the forest outside CLWA adjacent to this site was a mature mixedwood stand similar to the adjacent forest inside CLWA, so we presume any edge effects were minimal. To provide perspective on site proximity to the CLWA boundary, sites outside CLWA were on average 8.1 km from the Wilderness Area boundary (range = 1.8–13.2 km) and sites inside CLWA were on average 611 m inside the wilderness boundary (range = 135–1690 m).

Bird surveys

All sites were surveyed with automated recording units (ARU) with two built-in omnidirectional microphones (Wildlife Acoustics SM4 Song Meters; signal-to-noise ratio 80 dB at 1kHz and a sensitivity of -35 ± 4 dB; 24 kHz/16 bit sampling rate; 16 dB gain; 26 dB preamplifier gain) located centrally in each wetland to maximize distance from the edge of the focal habitat. Six sites were surveyed in 2018 and 18 sites were surveyed in 2019, evenly distributed within years among both focal wetland type and whether they were inside or outside of CLWA. ARUs were deployed during the last

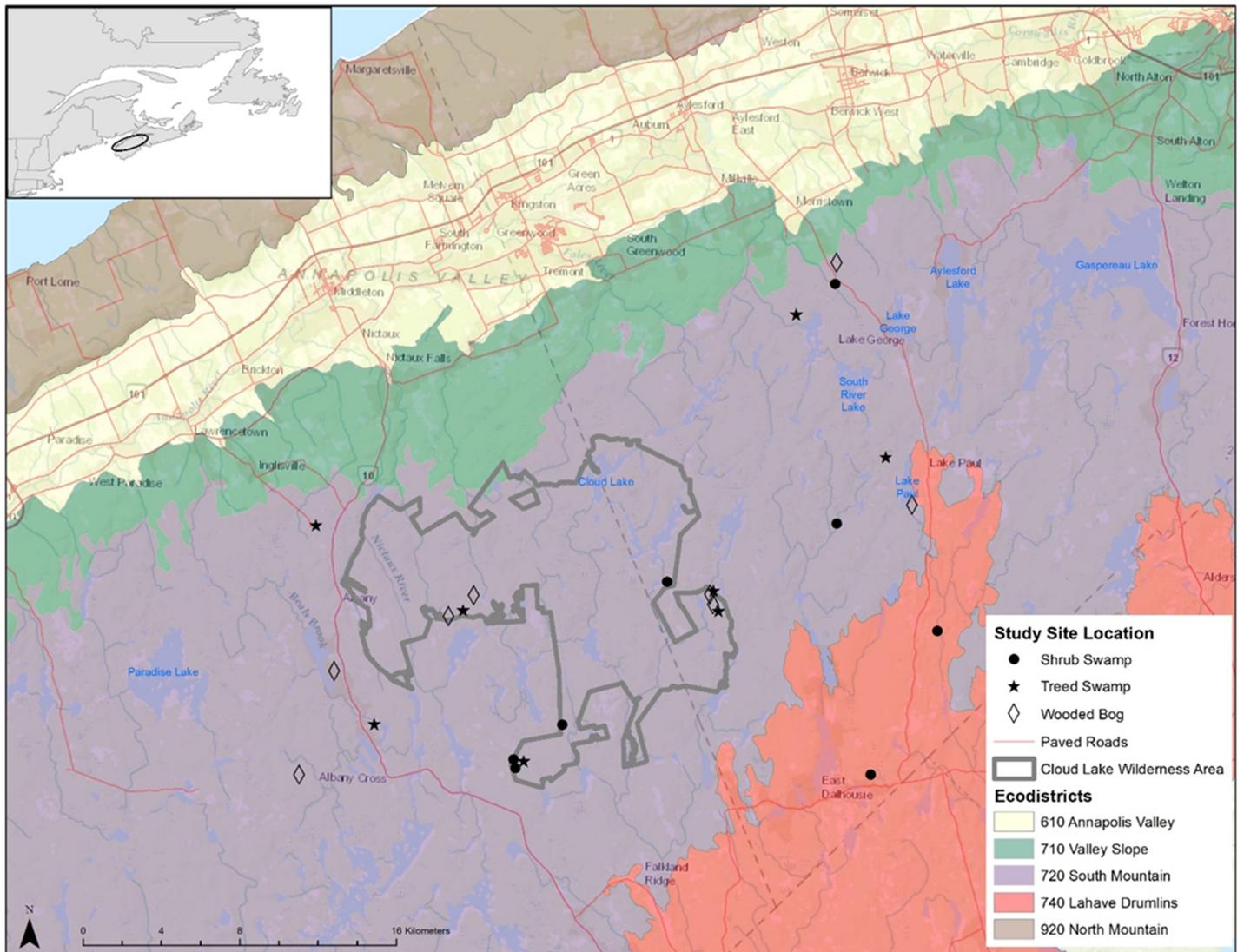


Fig. 1. Location of sites surveyed in western Nova Scotia for this study (● = shrub swamps ★ = tree swamps, and ◇ = wooded bogs; inset map shows study area in regional context). The map was constructed using ArcGIS version 10.5.1 (Esri, Redlands, Calif., USA) using a NAD83 projection and a UTM coordinate system; the base map was sourced from the Nova Scotia Department of Natural Resources and Renewables Ecological Land Classification 2015; the inset map was sourced from Esri (North America States provinces).

week of May after being programmed to record for 10 min at 0500, 0600, 0700, 2200, 2300, and 0000 each day. Once recordings were downloaded at the end of the breeding season, we randomly selected two days from among all those with appropriate weather/sound conditions (e.g., light or no wind, no audible rain, limited background noise) both early (25 May to 15 June) and late (16 June to 5 July) in the breeding season to analyze for bird songs. Experience has shown there are greatly diminishing returns in terms of new species detected beyond the level of subsampling effort we employed here (Brazner unpublished; Gautreau 2022).

Recordings were imported into Raven Pro 1.4 software (<https://ravensoundsoftware.com/>) and played with spectrograms visible while listening through circumaural headphones (Sennheiser HD 280) at

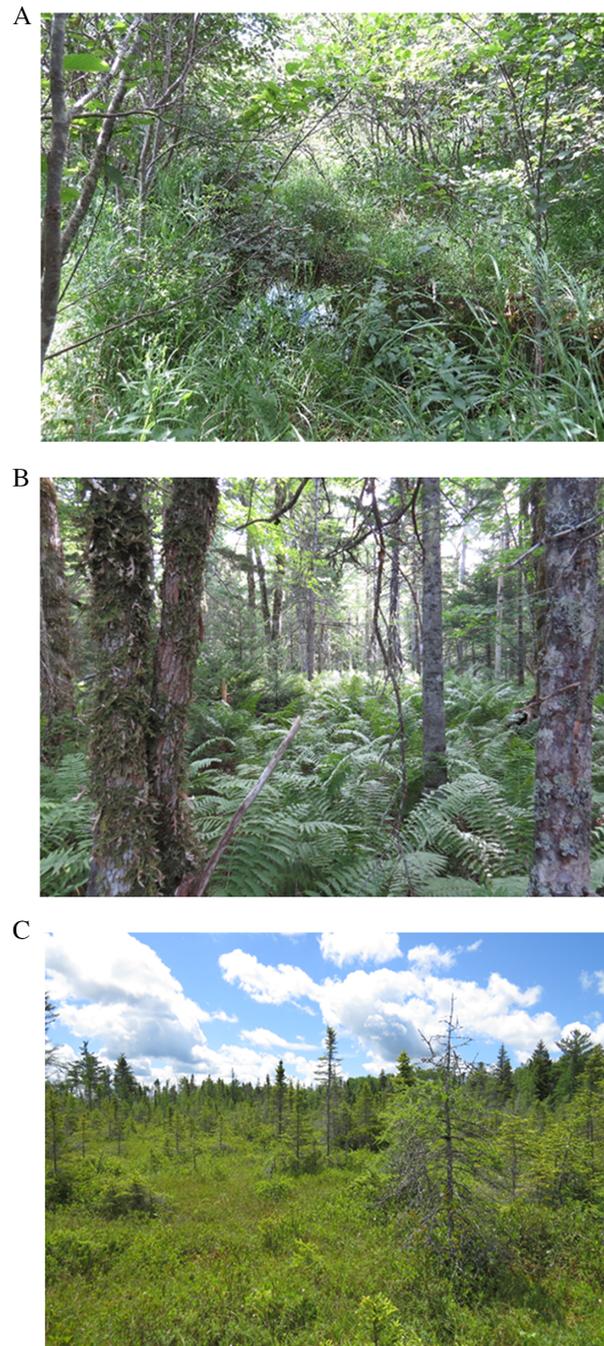


Fig. 2. Photos of representative shrub swamp (A), treed swamp (B), and wooded peatland (C) study sites used for this study (photo credits – John Brazner).

the maximum tolerable volume. Each individual of each species detected was recorded as a separate row in the database. Based on the intensity of the vocalization (decibel level) and the clarity of the spectrogram, we assigned a value of 1, 2, or 3 as a proxy for distance from the microphone for each individual where “1” represented a distinct, loud vocalization that was deemed close to the ARU,

“2” represented vocalizations that were more moderate in volume and clarity and deemed to be at an intermediate distance from the ARU, and “3” represented vocalizations that were faint and deemed distant from the ARU. While we do not have data that allow determination of precise distances for these proximity values, based on experience with song and call volumes in the field and experience using these ARUs in previous studies, we estimate that birds at Distance 1 were likely within 50 m of the ARU, Distance 2 birds were likely between 50 and 150 m from the ARU, and Distance 3 birds were likely greater than 150 m from the ARU. We felt it was important to estimate proximity because we are confident that a substantial portion of “Distance 3” birds with very loud songs/calls (e.g., olive-sided flycatcher, barred owl, common raven) were singing from beyond the boundaries of our study wetlands from other habitats and we did not want to include those detections as part of the final count at a site. As a result, to be precautionary, we removed all Distance 3 detections from our final data set before analysis.

Individual species abundances at each site were based on Distance 1 and 2 detections summarized as the maximum number of individuals of each species summed across proximity categories that were detected during any 10 min survey period for that site. Birds deemed to be flyovers or known to not use the focal habitat (e.g., common loons, *Gavia immer*) were excluded, but these comprised only a small fraction (<1%) of our counts. Because our counts could not be distance-corrected, they should be interpreted as indices of relative abundance among sites rather than absolute abundances or densities (e.g., [Ralph et al. 1995](#); [Dunn et al. 2006](#)).

From the overall bird community matrix, eleven SOCC were identified ([Table 1](#)) using the approach described in [Brazner and Mackinnon \(2020\)](#) based on current threat and at-risk assessments ([Table S1](#)). We also examined patterns in four specific GOCC (long-distance migrants, cavity and ground nesters, insectivores) that are deemed to be at higher risk from human disturbance (e.g., [Flather and Sauer 1996](#); [Nebel et al. 2010](#)) and one habitat guild (early successional-edge dwellers) that often responds positively to human disturbance (e.g., [Rodewald and Yahner 2001](#); [Miller et al. 2007](#); [Gnass-Giese et al. 2015](#)). The rationale for selecting long-distance migrants and insectivores has already been detailed elsewhere ([Brazner and Mackinnon 2020](#)) but was primarily due to population declines observed in these guilds worldwide (e.g., [Gilroy et al. 2016](#); [Rosenberg et al. 2019](#)). Cavity and ground nesters were examined because they are known to be particularly susceptible to forest harvesting ([Czeszczewik and Walankiewicz 2006](#); [Lammertink et al. 2009](#)) and recreational activity ([Mallord et al. 2007](#)), respectively – both activities that are prevalent in our study area. Finally, patterns in early successional-edge dwellers were examined because we expected fragmentation around sites in the working landscape to have an important influence on this group of birds (e.g., [Kroodsmma 1984](#); [Halstead et al. 2019](#)). Guild assignments for each bird species were based on a number of relevant bird life history summaries: migration strategy guilds were based on [Billerman et al. \(2020\)](#); trophic and nesting guilds were based primarily on [DeGraaf and Rudis \(1987\)](#) and [Niemi et al. \(2016\)](#); and the habitat guilds were based on [Stewart et al. \(2015\)](#) and [Niemi et al. \(2016\)](#).

Habitat and landscape characterization

Because we were interested in estimating the relative importance of local habitat and landscape condition on bird community and individual species responses, we measured a variety of habitat variables within the boundaries of each of our study sites and landscape characters in 1000 m buffers immediately surrounding the boundaries of our study sites.

The habitat assessment approach detailed by [Brazner and Mackinnon \(2020\)](#) was used to quantify differences in the structural character of each forested wetland. The variables we measured ([Table 2](#)) were all thought to have potentially important influences on bird communities (e.g., [Schwab et al. 2006](#); [Millington et al. 2011](#); [Fuller and Rothery 2013](#); [Stirnemann et al. 2015](#);

Table 1. Mean abundance (se = standard error) of bird community characteristics and species of conservation concern (only species detected at ≥ 2 sites included) at different site types (Bog = wooded bog, ShSw = shrub swamp, TrSw = treed swamp, In = inside protected area, Out = outside protected area) based on the maximum number of individuals detected during all survey periods.

Bird Community Characteristic, Species or Guild	Site Type									
	Bog		ShSw		TrSw		In		Out	
Community Characteristics	Mean	se	Mean	se	Mean	se	Mean	se	Mean	se
Species richness	35.38	0.93	35.5	1.88	34.87	1.14	32.92a	0.95	37.58b	0.73
Shannon's diversity index (H')	3.45	0.03	3.48	0.06	3.47	0.04	3.39a	0.03	3.55b	0.02
Number of individuals	55.25	4.71	48.25	2.43	47.38	2.43	48.67	3.03	51.92	3.28
Species										
American bittern (<i>Botaurus lentiginosus</i>)	0.00	0.00	0.13	0.13	0.13	0.13	0.00	0.00	0.17	0.11
American woodcock (<i>Scolopax minor</i>)	0.25	0.17	0.38	0.18	0.13	0.13	0.08	0.08	0.42	0.15
Canada jay (<i>Perisoreus canadensis</i>)	1.00a	0.19	0.25b	0.17	0.50ab	0.27	0.67	0.19	0.50	0.20
Canada warbler (<i>Cardellina canadensis</i>)	0.63a	0.26	0.75a	0.25	1.75b	0.37	1.33	0.26	0.75	0.28
Chestnut-sided warbler (<i>Setophaga pensylvanica</i>)	0.25	0.17	0.63	0.38	0.25	0.17	0.33	0.14	0.42	0.26
Common nighthawk (<i>Chordeiles minor</i>)	1.00	0.27	0.50	0.27	0.25	0.17	0.42	0.19	0.75	0.22
Eastern wood-pewee (<i>Contopus virens</i>)	0.13	0.13	0.13	0.13	0.13	0.13	0.00	0.00	0.25	0.13
Olive-sided flycatcher (<i>Contopus cooperi</i>)	0.88	0.35	0.50	0.19	0.88	0.35	0.75	0.25	0.75	0.25
Pine siskin (<i>Spinus pinus</i>)	0.25	0.17	0.13	0.13	0.13	0.13	0.08	0.08	0.25	0.13
Red-breasted nuthatch (<i>Sitta canadensis</i>)	1.50	0.38	0.63	0.19	1.13	0.13	1.17	0.21	1.00	0.24
Veery (<i>Catharus fuscescens</i>)	0.13	0.13	0.63	0.38	0.13	0.13	0.17	0.11	0.41	0.26
Guild										
Long-distance migrants (%)	0.41	0.02	0.45	0.03	0.45	0.03	0.48a	0.02	0.40b	0.01
Ground nesters (%)	0.41	0.03	0.37	0.02	0.42	0.01	0.41	0.02	0.39	0.02
Cavity nesters (%)	0.12	0.02	0.14	0.02	0.13	0.01	0.13	0.02	0.13	0.01
Early successional/forest edge dwellers (%)	0.17	0.02	0.17	0.02	0.14	0.02	0.12a	0.01	0.19b	0.01
Insectivores (%)	0.66	0.02	0.67	0.03	0.71	0.03	0.72a	0.02	0.64b	0.02
Birds of conservation concern (%) ¹	0.12	0.01	0.10	0.01	0.12	0.01	0.10	0.01	0.12	0.01

Note: Guilds of conservation concern analyzed as the mean percentage of the total number of birds detected at the different site types. Site types with no letters in common for each species or guild were significantly different ($p \leq 0.05$) among wetland types or between sites inside and outside of the protected area based on two-way nonparametric ANOVA tests with pairwise comparisons for differences among wetland types ($n = 8$ for each of the 3 forested wetland types) and between sites inside and outside of the protected area (12 sites inside and 12 sites outside). All models included a wetland type by in-out interaction term, but none were significant ($p > 0.20$), so interaction results have been omitted. Comparisons where mean differences were marginally significant ($0.05 < p \leq 0.10$) are in bold.

Mahon et al. 2016). Total percent cover for five vegetation strata (canopy, tall shrub, low shrub, herb, and sphagnum moss layers), as well as for ferns, graminoid plants, exposed rock and soil, and surface water (>2 cm depth), was visually estimated within a 10 m radius plot centered at the ARU locations. Total cover was calculated as the sum of canopy, tall shrub, low shrub, fern, graminoid, and sphagnum cover to provide an index of overall structural complexity (McElhinny et al. 2005). The number of dead snags ≥ 10 cm diameter at breast height (breast height = 1.30 m) and ≥ 3 m height was also counted within each plot. ArcGIS was used to calculate stream length through each wetland based on water features included in the Nova Scotia Topographic Database – Water Features

Table 2. Mean habitat and landscape characteristics (se = standard error) at different site types (Bog = wooded bog, ShSw = shrub swamp, TrSw = treed swamp, In = inside protected area, Out = outside protected area).

Habitat Variable	Site Type									
	Bog		ShSw		TrSw		In		Out	
<i>Site Cover Characteristics</i>	Mean	se	Mean	se	Mean	se	Mean	se	Mean	se
% Canopy Cover	0.8a	0.4	2.9a	2.1	45.0b	4.8	14.1	5.1	18.4	7.7
% Tall Shrub Cover	10.3a	2.9	70.0b	8.0	29.7c	4.5	32.7	7.5	40.6	9.6
% Low Shrub Cover	76.3a	4.5	20.0b	4.7	20.3b	3.0	41.9	8.4	35.8	8.7
% Herb Cover	11.2a	5.7	60.6b	5.6	47.5b	9.6	42.2	10.1	37.4	6.5
% Sphagnum Cover	70.6a	8.7	15.6b	10.3	63.3a	11.1	56.7	10.1	43.0	11.3
% Fern Cover	0.8a	0.4	10.4ab	8.0	31.9b	12.0	20.3	9.7	8.4	4.2
% Graminoid Cover	9.0a	5.9	47.8b	8.8	15.6a	6.0	20.4	8.2	27.9	6.8
% Mud/Bare Cover	0.0a	0.0	6.4b	2.3	1.8c	0.4	1.9	1.0	3.5	1.6
% All Cover ¹	98.6a	4.8	153.6b	10.6	142.5b	7.3	130.9	11.0	132.2	7.8
% Surface Water Cover	0.3a	0.2	8.3b	4.7	3.9a	2.9	1.8	0.6	6.4	3.5
<i>Other site habitat characteristics</i>										
# Dead Snags	2.9ab	1.3	0.8a	0.8	6.8b	1.1	3.3	1.0	3.4	1.2
Stream length through wetland (m)	8.9a	5.9	941.0b	235.6	271.5c	146.6	189.8a	182.9	624.4b	203.7
Depth to water table (~cm)	51.4a	7.5	48.0a	7.5	91.9b	15.6	72.7	12.8	54.8	6.7
Wetland perimeter to area ratio	0.024	0.003	0.022	0.003	0.017	0.002	0.022	0.002	0.020	0.003
Wetland Area (ha)	6.6a	1.4	12.0ab	3.1	13.9b	3.8	7.1a	1.5	14.6b	2.8
<i>Landscape cover in 1000 m buffer</i>										
% Mature Forest (>40 yr old)	67.0	7.0	70.1	6.3	72.9	5.7	83.1a	1.7	56.9b	4.7
% Establishment Forest (≤25 yr old)	11.8	4.8	12.5	4.0	12.4	4.9	3.2a	1.1	21.2b	3.3
% Young Forest (26-40 yr old)	7.2	2.0	6.5	2.6	4.0	1.4	3.9	0.7	7.9	2.1
% Wetland	5.7	0.9	7.2	1.5	5.3	0.6	6.8	0.8	5.3	0.8
% Water (lakes and rivers)	6.0	2.6	1.1	0.6	3.8	1.2	1.9	0.6	5.3	1.9
% Developed	1.7	0.8	0.4	0.3	0.9	0.6	0.03a	0.01	2.0b	0.6
% Human Disturbed	14.1	5.3	13.8	4.7	13.3	5.2	3.3a	1.1	24.3b	3.3
Road density (m/m ²)	0.002	0.000	0.001	0.000	0.002	0.000	0.001a	0.000	0.002b	0.000
Distance to nearest road (m)	1750	1027	1466	607	1275	817	2885a	737	110b	35
Mean patch size	4.8	0.5	5.2	0.7	5.0	0.6	6.1a	0.3	3.9b	0.3
Edge density	256.7	9.0	236.5	14.4	248.3	10.8	231.1a	6.9	263.2b	9.5
Patch diversity index	2.014	0.115	2.145	0.113	2.032	0.098	1.877a	0.047	2.251b	0.079

Note: Site types with no letters in common for each characteristic were significantly different ($p \leq 0.05$) among wetland types or between sites inside and outside of the protected area based on permutation-based two-way nonparametric ANOVA tests with pairwise comparisons for differences among wetland types ($n = 8$ for each of the 3 forested wetland types) and between sites inside and outside of the protected area (12 sites inside and 12 sites outside). All models included a wetland type by in-out interaction term; however, only the one for the Canopy Cover model was significant ($p \leq 0.05$), so the other results for interaction terms have been omitted.

(nsgi.novascotia.ca/gdd/). Wetland area for individual study sites was estimated by delineating approximate boundaries from Google Earth Imagery informed by reconnaissance done at each site during site selection and ARU deployment. Wetland perimeter to area ratio was calculated using Patch Analyst extension for ArcMap, version 5.2.0.16 (Rempel et al. 2012), as a surrogate for site habitat complexity (e.g., Helzer and Jelinski 1999). Depth to water table was estimated using the Wet Areas Mapping data set (novascotia.ca/natr/forestry/gis/wamdownload.asp) to provide an index of wetness at each site (e.g., Westwood et al. 2019).

Given that we selected our focal ecosystems to have a similar character both inside and outside of CLWA, we expected that landscape context would have an important influence on species richness, diversity, and abundance as well as on individual species (e.g., Howell et al. 2000; Galitsky and Lawler 2015; Basile et al. 2021). We quantified 12 land-use/land cover variables in the 1000 m buffer surrounding each of our study wetlands (Table 2) that could be calculated with available data and were considered likely to influence bird communities at these sites based on previous studies (e.g., Kroodsma 1984; Villard et al. 1999; Gnass-Giese et al. 2015; Halstead et al. 2019; Westwood et al. 2019). These included % mature forest (>40 yr old), % establishment forest (≤ 25 yr old), % young forest (26–40 yr old), % wetland, % water (lakes, ponds, rivers, and streams), % developed (all urban, suburban, commercial and industrial patches, and road corridors), % human disturbed (included all developed, agricultural, and establishment forest patches), road density (included all road types), and distance to the nearest road (measured from the study site boundary using the Near Tool in ArcMap) based on roads in the Nova Scotia Topographic Database. The other variables were calculated using information in the Nova Scotia Forest Inventory (novascotia.ca/natr/forestry/gis/forest-inventory.asp). Patch metrics were based on 24 unique patch classes based on land cover categories and maturity classes (Table S2). We calculated mean patch size (total area in the buffer divided by the number of patches), edge density (amount of edge relative to the buffer area), and a patch diversity index (Shannon's diversity index [Shannon and Weaver 1949]) as a relative measure of patch diversity in the buffer) with the Patch Analyst tool in ArcGIS. Technical details associated with GIS layers (e.g., ownership, resolution, year) are presented in Table S3.

Data analysis

We used permutation-based two-way nonparametric analysis of variance (npANOVA) with pairwise comparisons for differences among wetland types ($n = 8$ for each of the 3 forested wetland types) and between sites inside and outside of the PA (12 sites inside and 12 sites outside) to examine differences in mean habitat and landscape characteristics (McCune and Mefford 2009). All models included a wetland type by location (inside vs outside) interaction term. The same npANOVA methodology was also used to characterize site differences in species richness, Shannon's diversity index (H' ; Shannon and Weaver 1949), bird abundance, as well as the abundance of SOCC and GOCC.

Nonmetric multidimensional scaling (NMDS; Clarke 1993) was used to ordinate study wetlands based on untransformed abundances of all bird counts (PC-ORD version 7; McCune and Mefford 2016) to see whether patterns in overall community composition were related to forested wetland type or whether sites were inside or outside of CLWA. The methods employed for NMDS and related analyses were the same as those described in Brazner and Achenbach (2020), so are only reiterated briefly here. The method used a steepest-descent minimization algorithm and a Monte Carlo randomization technique to determine the optimal number of axes. The percentage of variance in the original data matrix explained by each axis in the ordination was calculated as the coefficient of determination (R^2) between distances among sites in the ordination space and distances in the original matrix (McCune and Mefford 2016). We used npMANOVA to test for differences in the centroids of site distributions among forested wetland types and site location relative to the CLWA boundary (inside vs outside) in the final NMDS result to characterize overall patterns in community

composition. To examine the relationship between species abundances as well as habitat and landscape conditions and NMDS axes, we plotted joint-plot vectors (McCune and Mefford 2016) radiating from the ordination centroid based on the combined correlation (r) between each variable and the axes. The angle and length of the vectors reflect the strength of the correlations (only species with $r \geq 0.4$ included).

We also wanted to determine which local habitat and adjacent landscape characteristics in the 1000 m buffer around each site were the most important drivers for key community characteristics and key SOCC and GOCC. When we examined three-dimensional plots of our habitat and landscape predictors with response variables, it was clear that non-linear and interactive relationships were common, so we used nonparametric multiplicative regression (NPMR implemented in HyperNiche version 2.30; McCune and Mefford 2009) to quantify these relationships. A key advantage to using NPMR for this type of habitat modeling is that the approach is easily extended to many dimensions (predictors) and the multidimensionality is provided multiplicatively. This automatically accommodates the complex interactions that are typical among predictors in species distribution modeling and the overall form of the response surface need not be specified (McCune 2006).

We used a local multiplicative smoothing function with leave-one-out cross-validation to estimate the importance of the predictor variable. We used a Gaussian weighting function with a local mean estimator in a forward stepwise regression of community, species, or guild variables to gauge response to predictors and expressed the fit as a cross-validated R^2 (xR^2). This is based on the size of the cross-validated residual sum of squares in relation to the total sum of squares (Guisan and Zimmermann 2000; Antoine and McCune 2004). We used a sensitivity analysis to evaluate the relative importance of predictors included in the final model by assessing the proportional change in response variables to proportional changes in predictors so that sensitivity is independent of the units of the variables (McCune 2006). To control for overfitting, in addition to cross-validation, only predictors that provided at least a 0.05 improvement in the xR^2 were retained in the final model. We also limited the number of predictors to 3 for any given model based on guidance from Harrell et al. (1996) on the ratio of study sites to predictors and set the minimum acceptable average neighborhood size to 1.2 as recommended by McCune (2006).

Before developing our NPMR models, we calculated cross-correlation matrices (Table S4) for the habitat and landscape variables to reduce the number of predictors in Table 2 to 8 habitat (% Canopy Cover, % Shrub Cover, % Herb Cover, % Sphagnum Cover, # Dead Snags, Stream Length, Depth to Water Table, and Wetland Perimeter to Area Ratio) and 8 landscape variables (% Mature Forest, % Establishment Forest, % Wetland and Water, % Developed, % Human Disturbed, Road density, Distance to Nearest Road, and Edge Density). We retained all variables that were relatively uncorrelated ($|r| \leq 0.70$; Dormann et al. 2013) as well as all landscape variables directly tied to human disturbance to examine a representative cross-section of the local habitat and landscape conditions in our study area. Shrub cover in these analyses represents a summation of our original tall and low shrub cover variables. Wetland and Water cover were combined in a similar fashion. Percent cover variables were arcsine square-root transformed and Wetland Stream Length and Distance to the Nearest Road were \log_{10} -transformed.

Results

Differences in habitat characteristics

Structural characteristics of our study sites varied significantly among the three wetland types, but differences among sites based on whether they were inside or outside of CLWA were minimal (Table 2). All but one of the treed swamps had red maple and black spruce as dominant species

(one site was dominated by red maple with tamarack as the subdominant), and typically had Canada holly (*Ilex verticillata*) and speckled alder (*Alnus incana*) as shrub dominants and cinnamon fern (*Osmundastrum cinnamomeum*) and *Carex* spp. as dominant species in the herb layer. Tree canopy and fern cover were significantly higher in treed swamps than other wetland types and had the highest mean number of dead snags and lowest mean depth to the water table (Table 2).

Six of our eight shrub swamps were dominated exclusively by speckled alder and two were dominated by Canada holly with speckled alder as the subdominant species. Shrub swamps were mainly tree free and dominated by *Carex* spp. and blue-joint grass in the herb layer. These sites had the highest tall shrub, graminoid, mud/bare and surface water cover, the longest mean stream length, and the lowest Sphagnum cover of the three wetland types.

There were few trees above 7 m tall in our wooded bogs (< 1% cover on average) but stunted black spruce and tamarack (*Larix laricina*; ~3–6 m tall) were the dominant tree species at these sites. The dominant shrubs were lambkill (*Kalmia angustifolia*) and rhodora (*Rhododendron canadense*) and *Carex* spp., cottongrass (*Eriophorum* spp.) and three-leaved false Solomon's seal (*Maianthemum trifolium*) were the dominants in the sparse herb layer. Bogs had the highest low shrub and Sphagnum spp. cover and the lowest tall shrub, herb, mud/bare, and overall cover (Table 2).

Differences in landscape characteristics

The main differences in landscape cover in the 1000 m buffer adjacent to our study sites were between sites inside CLWA and those outside CLWA in the working landscape. There were no significant differences in any of our landscape cover variables associated with the different wetland types (Table 2). Mature forest cover, distance to the nearest road, and mean patch size were significantly higher at sites inside CLWA, while establishment forest cover, developed area, and human-disturbed cover along with road density, edge density, and patch diversity were all lowest at these sites. Forest harvesting, based on establishment forest cover, was the dominant human disturbance in these landscapes.

Differences in bird community characteristics and SOCC and GOCC

Based on the maximum number of individuals of each species recorded during any survey period for each site, we estimated there were a total of 1207 unique individual birds from 79 species detected on the ARU recordings (a total of 5739 detections across all survey periods). We detected a mean of 50.3 birds (range = 33–79) and 35.2 species (range = 25–42) per site. The most common species based on overall number detected were hermit thrush (*Catharus guttatus*), common yellowthroat (*Geothlypis trichas*), and palm warbler (*Setophaga palmarum*). Each was detected at all 24 sites, as was ovenbird (*Seiurus aurocapilla*), black and white warbler (*Mniotilta varia*), and yellow-rumped warbler (*Setophaga coronata*) (Table S5). Hermit thrush was also the most common species detected at treed swamps, and across all inside and outside sites, while the most common species at wooded bogs and shrub swamps were palm warbler and swamp sparrow (*Melospiza georgiana*), respectively (Table S5).

Of species that were detected at 2 or more sites, there were 11 species (e.g., American crow, *Corvus brachyrhynchos*; tree swallow, *Tachycineta bicolor*; white-breasted nuthatch, *Sitta carolinensis*) that were only detected outside of CLWA and only one (downy woodpecker, *Picoides pubescens*) that was exclusively detected inside CLWA (Table S5). There were also 17 prevalent species that had abundances or frequency of occurrence (# of sites detected) that were $\geq 50\%$ higher at sites outside CLWA (e.g., American crow; American woodcock, *Scolopax minor*; blue jay, *Cyanocitta cristata*; common grackle, *Quiscalus quiscula*; common raven, *Corvus corax*; mourning dove, *Zenaidura macroura*), including three SOCC (e.g., American bittern, *Botaurus lentiginosus*; common nighthawk, *Chordeiles minor*; eastern wood-pewee, *Contopus virens*). This was only the case for 11 prevalent

species at inside sites, but included the Endangered Canada warbler, *Cardellina canadensis* (Table S5). Of the 79 species we detected, 73 were observed in sites outside CLWA while only 66 species were observed inside.

Based on two-way npANOVA, we found no differences in mean species richness, diversity, or number of individuals detected among wetland types, but species richness and diversity were significantly higher at sites outside of CLWA than those inside (Table 1, Fig. 3). Greater frequency of occurrence of early successional-edge dwelling species such as blue jay, common grackle, and mourning dove at outside sites (Table S5) contributed to these richness and diversity differences, but there were other relatively common species that were either unique to or occurred more frequently at outside sites that were not part of this early successional-edge dwelling guild (e.g., hairy woodpecker, *Leuconotopicus villosus*; pileated woodpecker, *Hylatomus pileatus*; red-eyed vireo, *Vireo olivaceus*). Differences in overall abundance of individuals between inside and outside sites were minimal and not statistically distinct.

Based on the npANOVA results, patterns in abundances of SOCC varied mainly by wetland type. Canada jay (*Perisoreus canadensis*) were significantly more abundant in bogs than in shrub swamps and Canada warbler (*Cardellina canadensis*) had the highest abundance in treed swamps (Table 1). There were also a number of other SOCC that were marginally more abundant ($p < 0.10$) in shrub swamps (chestnut-sided warbler, *Setophaga pensylvanica*, and veery, *Catharus fuscescens*) and wooded bogs (common nighthawk, *Chordeiles minor*, and red-breasted nuthatch, *Sitta canadensis*). There were no statistically clear differences in SOCC mean abundances between sites inside and outside of CLWA, but Canada warbler abundances were marginally higher at inside sites while American woodcock (*Scolopax minor*) were marginally higher at outside sites ($p < 0.10$; Table 1, Fig. 3).

While there were no significant differences in GOCC detected among wetland types, we did find some key differences in GOCC mean abundances between inside and outside sites. The mean proportion of long-distance migrants and insectivores were both significantly higher at sites inside CLWA, while early successional-edge dwellers were significantly more prevalent at outside sites (Fig. 3). We detected no difference in the proportion of the total number of birds of conservation concern either among wetland types or between inside and outside sites (Table 1).

Bird community patterns, species, and habitat associations detected with NMDS ordinations

Ordinations demonstrated that there are significant differences in the bird communities inside and outside of PAs. The optimal solution provided by the NMDS was three dimensional, statistically clear ($p < 0.01$), and accounted for 80% of total variation in the original data matrix (axis 1 = 45%; axis 2 = 25%; axis 3 = 10%). Visual examination of the convex hulls associated with each site type (Fig. 4) as well as statistical analysis of the differences in the site type centroids using one-way npMANOVA revealed an overall difference among the six site types ($p < 0.01$) and considerable overlap among the bird communities from the three wetland types outside CLWA. Axis 1 primarily separated the different wetland types inside CLWA from each other. Axis 2 mainly separated sites inside CLWA from those outside CLWA. More specifically, the npMANOVA analysis identified that the key differences in the bird communities associated with inside and outside sites were that bogs inside CLWA were distinct from shrub swamps ($p < 0.03$) and treed swamps ($p < 0.03$) outside, treed swamps inside CLWA were distinct from shrub swamps outside ($p = 0.03$), and shrub swamps inside CLWA were distinct from shrub swamps outside ($p < 0.03$). In addition, bird communities associated with shrub swamps inside CLWA were statistically distinct from the other inside types (bogs inside – $p = 0.03$; treed swamps inside – $p = 0.05$).

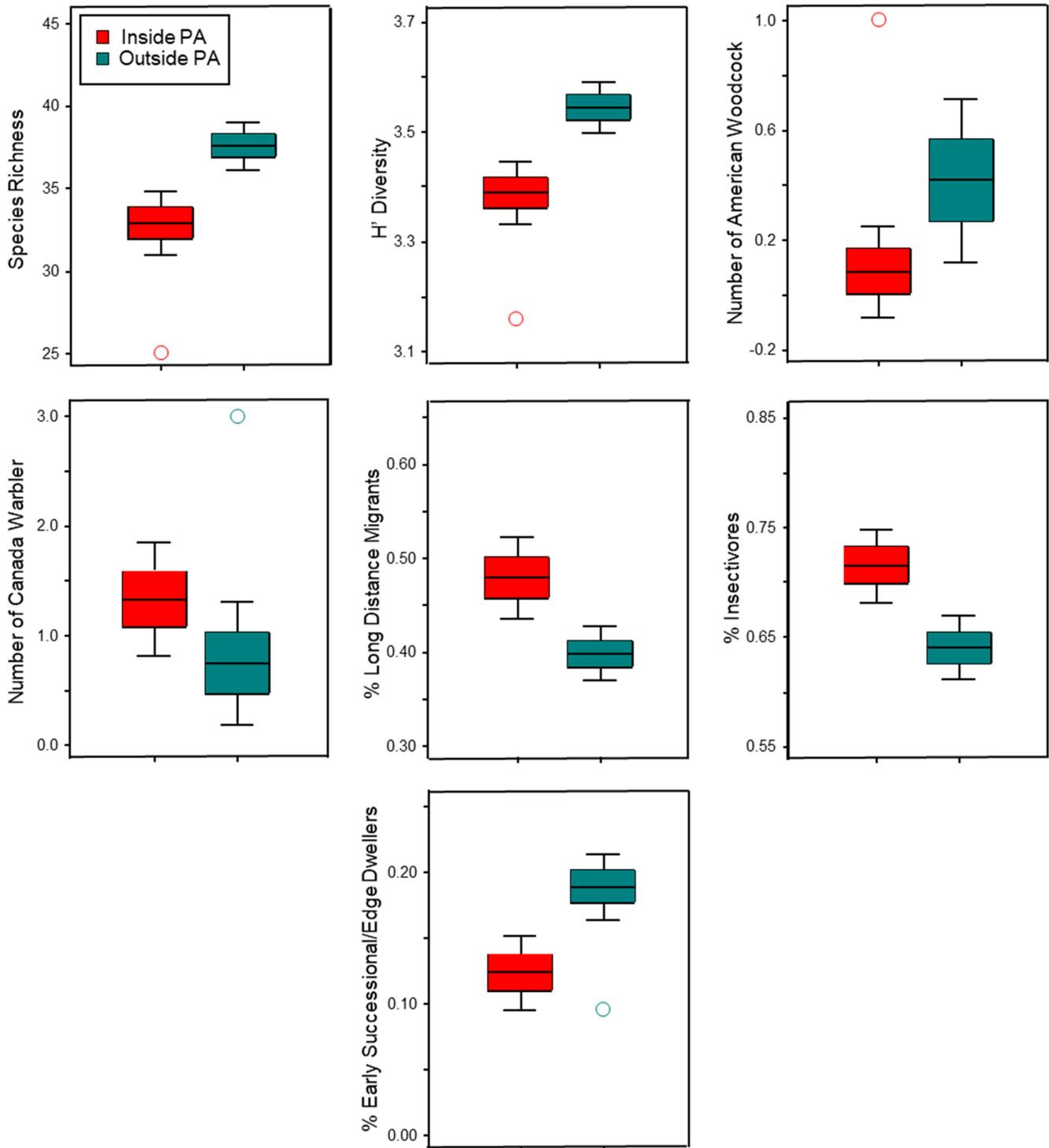


Fig. 3. Box plots of select bird community characteristics, species, and guilds from **Table 1** where differences between inside and outside the protected area were clearest (box length represents one standard error above and below the mean; whiskers represent plus or minus two standard errors; outliers plotted exceed two standard deviations; significance of differences shown in **Table 1**).

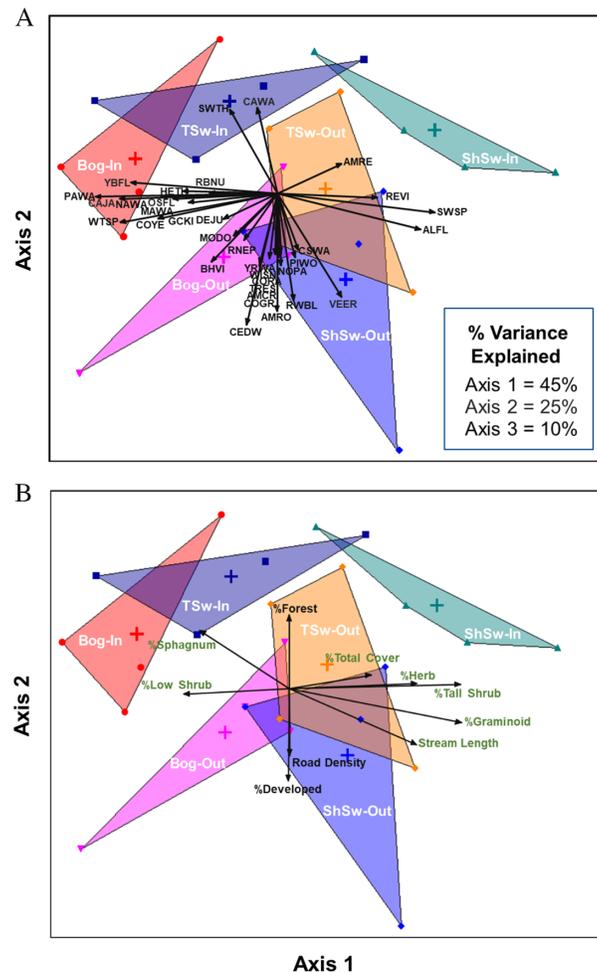


Fig. 4. Non-metric multidimensional scaling ordination plot of surveyed sites based on maximum abundance of each bird species detected during all survey periods. Colored polygons (convex hulls) outline the outermost points of each site type (centroids for each group denoted by “+”). The angle and length of bird species (Panel A; 4 letter species codes defined in [Table S1](#)) and habitat/landscape variables (Panel B) joint-plot vectors radiating from ordination centroid reflect the strength of the combined correlation (r) of each species site abundances with NMDS axes 1 and 2 (only vectors with $r \geq 0.4$ included; habitat variables labeled in green, landscape variables in black in Panel B).

Examination of the joint-plot vectors associated with individual bird species presented as overlays on the ordination ([Fig. 4A](#)) suggests that more species are strongly associated with bogs inside the PA compared with other wetland types, including four SOCC (Canada jay, olive-sided flycatcher, *Contopus cooperi*, yellow-bellied flycatcher, *Empidonax flaviventris*, and red-breasted nuthatch). Canada warbler was also strongly associated with inside sites but with treed swamps rather than bogs. There were also many species with strong associations with outside sites in general and these were mainly early successional-edge dwelling species (e.g., American robin, *Turdus migratorius*, red-winged blackbird, *Agelaius phoeniceus*, cedar waxwing, *Bombycilla cedrorum*, common grackle, *Quiscalus quiscula*, American crow, *Corvus brachyrhynchos*). However, veery was one exception as a SOCC mainly associated with outside shrub swamps. Alder flycatcher (*Empidonax alnorum*) and

swamp sparrow (*Melospiza georgiana*) had a general association with shrub swamps, regardless of whether they were inside or outside of CLWA.

Examination of the joint plot vectors associated with local habitat and landscape variables highlighted many of the same patterns we noted with our npANOVA analyses of these factors (Fig. 4B). Low shrub cover was most positively associated with bogs, especially bogs inside CLWA, while sphagnum was most positively associated with a combination of bogs and treed swamps inside CLWA. High forest cover in the 1000 m buffer was generally associated with sites inside CLWA, while high cover of developed land and road density in the 1000 m buffer were most strongly associated with sites outside CLWA. Shrub density, tall shrub, herb, and graminoid cover as well as total cover were all positively associated with shrub swamps along Axis 1, whereas the length of streams was more generally associated with swamps (both treed and shrub-dominated).

Key habitat and landscape drivers of bird community characters and SOCC and GOCC abundances

NMPPR analyses of bird species richness, diversity, and abundance responses to habitat and landscape drivers suggest that landscape predictors had the strongest influence on these characters (Table 3), but the overall relationships were not statistically clear (p -values associated with $xR^2 > 0.18$). Based on the sensitivity analyses, mature forest cover had the strongest influence on both bird species richness and diversity, while distance to the nearest road was most predictive of total abundance. Shrub cover was the only important local habitat predictor for these community characteristics, being positively related to total abundance.

The most influential factors in the best models for the at-risk bird species were a mixture of local and landscape variables. Both Canada warbler and common nighthawk abundance were most positively associated with edge density followed by tree (Canada warbler) and shrub (common nighthawk) cover. The Canada warbler model was statistically clear ($p = 0.05$), while the common nighthawk model was only marginally significant ($p = 0.08$). The relationship between eastern wood-pewee (*Contopus virens*) and both distance to the nearest road and the proportion of developed cover was strongly negative ($p < 0.01$), suggesting landscape condition was the most important factor driving their abundance. Interestingly, the three most influential predictors for olive-sided flycatcher (*Contopus cooperi*) were all local habitat variables (water table depth, herb, and shrub cover), but the best model was only marginally significant ($p = 0.10$). The two GOCC (proportion of long-distance migrants and insectivores) we examined with NMPPR modeling were influenced by a combination of local habitat and landscape characteristics with both peaking in abundance at intermediate levels of shrub cover (Table 3). They were also each negatively related to human disturbance. The overall xR^2 associated with these models was statistically clear ($p \leq 0.04$).

Discussion

Our study reaffirms the idea that forested wetlands are diversity hotspots for breeding birds in Nova Scotia (Brazner and MacKinnon 2020), with 79 species detected overall, including 12 SOCC and 4 species listed as at-risk either provincially or federally. The 79 species we observed are similar to richness levels reported by other studies of bird communities associated with forested wetlands in eastern Canada (Brazner and Mackinnon 2020; Calmé et al. 2002 – 102 species in 112 bogs in Quebec) and are notably higher than the bird species richness observed in similar studies further west in Canada and the northern United States (Swift et al. 1984 – 46 species in 8 swamps; Riffell et al. 2006 – 55 species in 25 swamps; Morissette et al. 2013 – 55 species in 41 swamps and peatlands). As noted by Brazner and Mackinnon (2020), it is difficult to make direct comparisons of species richness differences among studies due to design and effort disparities, but these results suggest forested

Table 3. Relationship among bird species richness, abundance, and key species and guilds of conservation concern and habitat and landscape characters associated with each study wetland and the 1000 m wetland buffer based on nonparametric multiplicative regression analyses.

Bird Community Characteristic, Species or Guild	Best Predictor Variables	S	N*	xR ²
<i>Community characteristics</i>				
Species richness	%Mature Forest (i–)	1.07	1.4	0.36 ^{.346}
	%Human Disturb. (+)	0.32		
Shannon’s diversity index (H')	%Mature Forest (i–)	0.48	2.0	0.34 ^{.188}
	Dist. Nearest Rd. (i+)	0.25		
Number of individuals	Dist. Nearest Rd. (i–)	0.25	1.2	0.44 ^{.277}
	%Shrub Cover (+)	0.20		
	Edge Density (i–)	0.14		
<i>Species-at-risk</i>				
Canada warbler (<i>Cardellina canadensis</i>)	Edge Density (i+)	0.71	1.5	0.71 ^{.047}
	%Tree Cover (+)	0.27		
Common nighthawk (<i>Chordeiles minor</i>)	Edge Density (+)	0.55	1.3	0.55 ^{.079}
	%Shrub Cover (+)	0.36		
	%Wetland-Water (i–)	0.11		
Eastern wood-pewee (<i>Contopus virens</i>)	Dist. Nearest Rd. (–)	0.08	2.0	0.83 ^{.009}
	%Developed (–)	0.07		
Olive-sided flycatcher (<i>Contopus cooperi</i>)	Water Table Dep. (bi)	0.88	1.2	0.57 ^{.099}
	%Herb Cover (–)	0.25		
	%Shrub Cover (+)	0.09		
<i>Guilds of conservation concern</i>				
Long-distance migrants (%)	%Shrub Cover (i+)	0.27	1.3	0.69 ^{.029}
	%Human Disturb. (–)	0.22		
	Water Table Dep. (–)	0.10		
Insectivores (%)	%Shrub Cover (i+)	0.90	1.2	0.60 ^{.039}
	Road Density (–)	0.19		
	%Human Disturb. (–)	0.06		

Note: Predictor variables ordered by explanatory power for each response variable based on sensitivity values (S) and only included when they provided an increase in variance explained that was ≥ 0.05 and met or exceeded the average neighborhood size criteria (N*) of 1.2. Primary direction of response to predictors based on examination of three-dimensional projections included parenthetically (+ = positive; – = negative; i+ = highest at intermediate levels; i– = lowest at intermediate levels; bi = bimodal). Percent cover variables were arcsine square-root transformed and wetland stream length and distance to nearest road were log₁₀-transformed. Significance of full models included here denoted in superscripts of xR² values based on randomization tests.

wetlands in eastern Canada have atypically rich bird communities, and therefore may have heightened importance as avian diversity hotspots. It may be that the character (e.g., size, density, type, total area) of forested wetlands or the forest in general in eastern Canada is somehow different than those elsewhere (e.g., ecotonal between temperate and boreal landscapes), and as a result support greater

avian species richness. Broad scale, comparative studies across North America would be required to definitively answer this question.

Another important finding was that the bird communities associated with forested wetlands inside and outside of CLWA were ecologically distinct, but differences among wetland types were only clear for sites inside CLWA. The fact that sites from different forested wetland types outside CLWA had large overlaps in ordination space suggests there has been a homogenization of these bird communities relative to those in minimally disturbed areas. Homogenization of biotic communities has been linked to landscape disturbance by numerous studies (e.g., Devictor et al. 2008; Karp et al. 2018; Liang et al. 2019), so the result is not surprising here given the differences in landscape character that were apparent between sites inside and outside of CLWA (e.g., higher development, road density, and recently cut forest in the working landscape).

However, given the biotic homogenization we observed, it was surprising that sites outside CLWA had higher species richness and diversity than inside sites. Results from other studies comparing species richness and diversity among sites inside and outside of PAs have not revealed a consistent pattern (e.g., Deguise and Kerr 2006; Gaston et al. 2008; Laurance et al. 2012; Geldmann et al. 2013), but some of the more recent analyses strongly suggest that local biodiversity is typically higher inside terrestrial PAs worldwide (Coetzee et al. 2014) even though neither rarefaction-based richness nor endemism appears to differ significantly in many cases (Gray et al. 2016). In some studies where sites inside PAs had the greatest species diversity, the distinctiveness and richness of species in sites outside of PAs were still found to contribute substantially to regional avifaunal diversity because they supported a complementary assemblage (Gardiner et al. 2007; Dahal et al. 2014; Mönkkönen et al. 2014). We observed this sort of complementarity in our study as well, with 10 of 11 species that were only found in either inside or outside sites being found at outside sites. Our npANOVA results and biases in the frequency of detection (Table S5) also reflect complementarity with respect to SOCC in that six SOCC were notably more abundant at outside sites (American bittern, American woodcock, common nighthawk, eastern wood-pewee, pine siskin, and veery) and our ordination results suggest that four other SOCC (Canada jay, Canada warbler, olive-sided flycatcher, and red-breasted nuthatch) were most strongly associated with inside sites.

It is important to consider the landscape context when trying to interpret the species richness and diversity patterns we observed. There have been many studies designed to determine the importance of landscape relative to local habitat context (e.g., Villard et al. 1999; Driscoll et al. 2013; Galitsky and Lawler 2015; Häkkinen et al. 2018; Basile et al. 2021; Ramirez-Delgado et al. 2022) since Franklin (1993) first proposed it as a key need for biodiversity conservation across landscapes. The results, although mixed, are directly relevant to understanding the biodiversity differences that were apparent in our study. Given the high proportion of early successional-edge dwelling birds and community homogenization, the forested wetland bird communities we sampled outside of CLWA clearly reflect disturbance in the working landscape. Nevertheless, the high numbers of species we found in the working landscape overall and the presence of many SOCC suggest these sites may serve as important reservoirs of biodiversity and act as important refugia for many bird species. However, birds and other biota in disturbed or fragmented areas may experience reduced reproductive success (Villard et al. 2012; Betts et al. 2019) and increased risk of extirpation (e.g., Donovan et al. 1995; Robinson et al. 1995; Ramirez-Delgado et al. 2022), so more work would be needed to determine if these areas are acting as effective long-term refugia.

Although the association of early successional-edge dwelling species with disturbance and fragmentation is well established (e.g., Rodewald and Yahner 2001; Miller et al. 2007; Gnass Giese et al. 2015), increased richness and diversity under these conditions are not. Greater bird species richness and diversity at sites in fragmented landscapes outside of PAs were observed in a study comparing

fragmented to large contiguous forest patches in Missouri (Howell et al. 2000). They attributed this to increased area of non-forested and edge habitats in fragmented landscapes that supported more early-successional and non-migratory and short-distance migrant species (similar to the pattern we observed in our study), suggesting disturbance and fragmentation may increase local species diversity in some circumstances (e.g., Noss 1983). However, Halstead et al. (2019) caution that these sorts of results may be dependent on the landscape characterization approach. Their examination of the relative importance of habitat fragmentation and habitat loss on species richness found that a species-centered approach identified habitat configuration relationships obscured by land-cover based approaches, suggesting positive relationships between species richness and fragmentation may be an artifact of some study designs.

We do not think that is the case with our study, as we used similar patch and landscape metrics to those used by Halstead et al. (2019) to assess landscape versus local habitat effects with our NPMR models. Their results suggest it was a combination of landscape and local habitat factors that were most important in driving differences in bird communities. In our study, community characteristics were mainly driven by landscape condition (e.g., mature forest cover and human disturbance factors such as distance to the nearest road and overall human disturbance), whereas SOCC abundances and GOCC proportions were driven by a combination of landscape and local habitat predictors. Landscape factors tended to be most important for SOCC (e.g., edge density and distance to the nearest road), but the response was highly species dependent. For example, olive-sided flycatcher abundance was strictly driven by local habitat factors (e.g., water table depth, herb, and shrub cover). With respect to GOCC, local habitat character (particularly shrub cover) had the strongest influence. Some recent studies (e.g., Lorenzón et al. 2016; Halstead et al. 2019) have found local habitat to be most influential, but Galitsky and Lawler (2015) found that the response was highly context specific with some species and guilds much more responsive to landscape factors and others to local factors. In contrast to our results related to bird diversity, Galitsky and Lawler (2015) found that local factors explained four times more variance than landscape factors for overall species diversity. Other studies (e.g., Mazerolle and Villard 1999; Häkkinen et al. 2018; Basile et al. 2021) have found similarly context-dependent importance of local habitat and landscape matrix influences on bird community richness and diversity suggesting there is still much to be learned about what tips the balance in one direction or the other.

In direct comparisons of biodiversity inside and outside PAs, increased species richness and diversity are not typical of the sites outside PAs, but there are some notable exceptions, particularly in studies of marine PAs (e.g., Edgar et al. 2004; Ashworth and Ormond 2005; Monaco et al. 2007). One notable exception in relation to terrestrial PAs reported higher bird species richness at woodland sites outside of PAs compared to comparably structured sites inside of designated reserves in a long-term study in Australia (Rayner et al. 2014). They concluded that both PAs and off-reserve conservation schemes have important roles to play in securing species populations and suggested that the conservation value of PAs is strongly influenced by the physical characteristics, as well as the landscape context, and can diminish with changes in surrounding land use over time. Gardiner et al. (2007) in studies of multiple taxa (e.g., small mammals, birds, amphibians, butterflies) across a gradient of human disturbance from PAs to areas dominated by low intensity agriculture in East Africa found that species richness remained about the same across the gradient, but that there were distinctly different species in each taxon in the areas under different management regimes. This reinforces the idea of complementarity of species assemblages in working landscapes relative to those in PAs and highlights the importance of developing landscape-scale conservation strategies and a broader taxonomic or as Caro et al. (2009) suggest, a functional approach to assessing changes over time.

Studies that have taken a more functional approach to assessing bird community responses to fragmentation (e.g., Flather and Sauer 1996; Howell et al. 2000; Keller and Yahner 2007;

[Brown et al. 2019](#)) report a higher percentage of long-distance migrants in large contiguous forest patches, just as insectivores seem to be more common ([Greve et al. 2011](#); [Timmers et al. 2022](#)) in PAs compared to those in more fragmented landscapes. Large contiguous forest patches, even if outside of a formally designated PA, can function in a similar manner to those typical of PAs like CLWA in our study and may explain why we found higher proportions of both long-distance migrants and insectivorous birds at sites inside CLWA. In their meta-analysis of a global data set including 2000 bird species in 741 forest fragments that varied in size and protection status, [Timmers et al. \(2022\)](#) found that the occurrence of all bird foraging guilds strongly declines with decreasing fragment size (particularly below 50 ha) and that declines were especially pronounced for forest-dependent species, insectivores, carnivores, and more dispersive species. In a long-term study at a 26 ha temperate forest in a highly fragmented New Jersey, USA landscape, [Brown et al. \(2019\)](#) found that nearly half the species found in the forest at the time of initial protection 40 years ago are now extirpated and that long-distance migrants and ground nesters were most likely to be extirpated. Both the [Timmers et al.](#) and [Brown et al.](#) studies indicate that PAs are effective for maintaining bird species if they are larger and highlight the importance of large intact forests for conserving avian diversity. These results also support the conclusion of [Gray et al. \(2016\)](#) that the positive effects of protection are strongly attributable to differences in land use between protected and unprotected sites, but [Gray et al.](#) also noted that protection does not consistently benefit all species or guilds (e.g., low mobility guilds) or increase the variety of ecological niches for functional groups to exploit. Our study provides support for the idea that certain species and guilds (e.g., Canada warbler and long-distance migrants) will benefit from being in PAs, while other species, like woodcock, benefit from intact wetlands within a matrix of other habitat types – landscape context is clearly important. Our study also highlights the importance of broadening the focus to habitats and landscapes outside of PAs to provide more effective and comprehensive conservation for many avian species.

Management implications and conclusions

Although our study was limited in scope and should only be considered a necessary first step in testing the effectiveness of PAs throughout the province for conserving biodiversity, it does highlight the fact that there are many aspects of biodiversity conservation in PAs that we still do not fully understand. Why, in some instances, biodiversity is lower in PAs than in similar habitats in the working landscape is an important question that deserves greater attention. Based on their meta-analyses, [Gaston et al. \(2008\)](#) suggested that greater richness or abundance outside rather than within PAs could arise because PAs were originally designated in areas of lower richness or abundance, because of competing interests for resource exploitation (e.g., forest harvesting), insufficient consideration of biological criteria as part of formal designation, or if there were significant spatial mismatches in the richness and abundance of features for which the protected places were primarily designated. It might also be due to expanding human land use on lands surrounding PAs, resulting in changes in ecological function and biodiversity within PAs (e.g., [Hansen and DeFries 2007](#); [Rayner et al. 2014](#); [Mönkkönen et al. 2014](#); [Betts et al. 2019](#)). Determining whether the intensity of harvesting or other development is substantially higher in the boundary immediately adjacent to CLWA relative to the landscape in general would be one way of investigating this possibility in relation to our study. However, the results we observed may also be at least partially due to the effects of the “ghost of land-use past” ([Harding et al. 1998](#)). The area within CLWA may still be recovering from historic land use in the study area (e.g., forest harvesting and agriculture) or past large-scale disturbances (e.g., wildfire or blowdowns) that continue to affect species richness and abundance ([Bernes et al. 2015](#)). Regardless of the specific reason, it has become increasingly clear that additional research and better monitoring are required to improve our understanding of factors affecting the capacity of PAs for maintaining biodiversity through time and whether PAs are meeting conservation expectations and targets ([Adams et al. 2021](#); [Graham et al. 2021](#)).

The fact that bird species richness and the abundance of SOCC in forested wetlands inside CLWA were lower than at sites in the working landscape outside CLWA suggests that forested wetlands outside CLWA may be acting as important refugia for birds despite the higher intensity of human disturbance adjacent to these sites. Our results also support the idea that these ecosystems merit special protection provided by the new silvicultural guidelines which prescribe no harvesting of trees in wet deciduous, wet coniferous, and floodplain forests on Crown lands in Nova Scotia (McGrath et al. 2021). In addition, our results also suggest that there is potential for biodiversity gains through investments in conservation schemes outside of PAs and on private lands (e.g., Lindenmayer and Franklin 2002; Cox and Underwood 2011) and highlights the need for working lands conservation. The challenge of shifting from managing working lands solely for profit to conservation of working lands is substantial, but there are clear paths toward larger-scale integration of this approach (Kremen and Merenlender 2018). Only time will tell, but the recommended move toward ecological forestry in Nova Scotia (Lahey 2018), which prioritizes biodiversity conservation over other forest values, seems like a sensible first step in that direction and worth careful evaluation in the coming years.

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Author contributions

JB, FM, and RC conceived and designed the study. JB, JW, and FM performed the experiments/collected the data. JB, JW, FM, and RC analyzed and interpreted the data. JB, FM, and RC contributed resources. JB, JW, FM, and RC drafted or revised the manuscript.

Competing interests statement

The authors declare there are no competing interests.

Data availability statement

Data generated or analyzed during this study are available from the Atlantic Canada Conservation Data Centre – accdc.com/. Data generated or analyzed during this study are also available from the corresponding author upon request.

Supplementary material

The following Supplementary Material is available with the article through the journal website at doi:[10.1139/facets-2022-0161](https://doi.org/10.1139/facets-2022-0161).

Supplementary Material 1

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