

Limited evidence for the influence of the physical structure and floristics of habitat on a boreal forest bird community

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Abstract

Studies conducted at regional and continental scales show that avian richness, community composition, and abundance are associated with variation in the vegetation physical structure and community composition (floristics) within broad habitat types. The relative contributions of physical structure and floristics are contested, and relationships are often taxon-specific. We used 110 microphone arrays deployed across 90 sampling locations and two breeding seasons to survey an avian community in the boreal forest in Labrador, Canada. Our objectives were (1) to describe the avian community of an underrepresented portion of the boreal forest, (2) to estimate the relationships between avian species richness and habitat characteristics, (3) to estimate if species detection at a given location was related to local habitat characteristics, and (4) to investigate the spatial and temporal patterns of the avian community composition. We detected 32 species at our sampling locations; physical structure and floristics were not related to avian species richness, although estimates of richness were higher on warmer days and lower on windier days. Habitat characteristics were associated with the detection of Boreal Chickadee (*Poecile hudsonicus*), Yellow-rumped Warbler (*Setophaga coronata*), American Robin (*Turdus migratorius*), and Black-throated Green Warbler (*Setophaga virens*). Finally, avian community composition was only moderately consistent among three categorical forest types and between audio sampling periods in two consecutive breeding seasons. Overall, we show that the structural and floristic traits measured at our study site are not related to the detection of most avian species or to species richness.

Key words: Behaviour; boreal forest; conservation; habitat selection

Introduction

Avian community characteristics, such as species diversity and community composition, are influenced by several environmental factors. Changes in avian community composition, species abundance, and presence/absence patterns across a landscape have been correlated with aspects of the physical structure of the habitat, including foliage height diversity, mean tree height, stem density, and canopy cover (MacArthur *et al.* 1962; Lee and Rotenberry 2005; McElhinny *et al.* 2005; Lemaître *et al.* 2012), as well as with aspects of the community composition of vegetative species (i.e., floristics), including the richness and diversity of vegetative species (Gillespie and Walter 2001; Poulsen 2002; Lee and Rotenberry 2005) and the densities of particular tree species (Willson and Comet 1996; Thompson *et al.* 1999). These relationships are often complex and

the direction of any correlation is often specific to an avian species, population, or foraging guild. Avian communities also are influenced by abiotic factors, such as local weather conditions. For example, inter-annual variation in avian abundance and community composition during the breeding season is related to variation in temperature and rainfall, which affects the distribution and availability of food, resources, and shelter across the landscape (Şekercioğlu *et al.* 2012; Zellweger *et al.* 2016; Grima *et al.* 2017; Bradley *et al.* 2022). It is therefore important to consider not only the relationship between habitat and avian communities, but also how the communities change over time and in relation to abiotic factors such as weather (Sparks *et al.* 2002).

Many bird-habitat relationships that incorporate physical structure and floristics of habitat are conducted at large spatial scales that include several

environmental gradients throughout North America (MacArthur *et al.* 1962; Willson and Comet 1996; Thompson *et al.* 1999; Lee and Rotenberry 2005; Lemaître *et al.* 2012) and Europe (Poulsen 2002; Honkanen *et al.* 2010). Relatively few studies have investigated if the bird-habitat relationships observed at large-scales are consistent at the local or stand scale (Rotenberry 1985; Berg 1997; Seavy and Alexander 2011), or how local weather conditions might influence these relationships. The Boreal Shield Ecozone in Canada is an important breeding location for more than 240 North American bird species (Blancher and Wells 2005; Downes *et al.* 2011), yet most surveys in this ecozone have been conducted in southern Ontario and Quebec, with poor coverage outside these regions in areas such as Labrador (Downes *et al.* 2011). We used acoustic surveys to study bird-habitat relationships across two breeding seasons and multiple locations at a local scale in Labrador, Canada. Because each bird species produces a unique vocalization and vocalizes regularly throughout the breeding season, acoustic surveys can be a reliable method of determining which species are present at a given location (Blumstein *et al.* 2011; Shonfield and Bayne 2017). Compared to point counts that are conducted by human listeners and often last only minutes, acoustic surveys can record continuously for hours or days and thus detect species that vocalize infrequently or at unusual times, such as at night (e.g., owls) when human point counts are rarely conducted (Shonfield and Bayne 2017). A concern with acoustic surveys, however, is that multiple factors affect the range over which vocalizations can be heard, including weather, species, and an individual's behaviour (Hobson *et al.* 2002; Blumstein *et al.* 2011). Using a single audio recorder or human listener to conduct acoustic surveys can thus confound the probability of detecting a species with the audible range of that species' vocalizations. Microphone arrays resolve this issue because they allow researchers to localize vocalizing birds in two- or three-dimensional space and therefore to standardize the area sampled at each location (Stevenson *et al.* 2015; Pérez-Granados and Traba 2021). The method is tantamount to using a fixed-radius point count, but with the added benefit of allowing users to determine objectively if birds are located within the fixed radius of the sampling location (Stevenson *et al.* 2015; Pérez-Granados and Traba 2021). By surveying birds with microphone arrays, we correlated species richness and presence, as inferred through acoustic detection, with the physical structure and floristics of the habitat at each sampling location.

We had four objectives. First, we described the avian community of Labrador, an underrepresented portion of the boreal forest in avian ecological

studies. Second, we determined the relationships between avian species richness and three environmental factors, including weather and the physical structure and floristics of the habitat. Consistent with previous studies, we hypothesized that local avian species richness would increase with greater diameter at breast height (DBH; McCarthy and Weetman 2006; Klein *et al.* 2020) and greater vegetative species richness (Gahbauer and Rashleigh 2021). We also hypothesized that avian species richness would increase at later dates in the breeding season and on warmer days (DesGranges and LeBlanc 2012). Third, we tested whether the detection of individual species was related to either the physical structure or floristics of a location. Based on previous findings in the boreal forest (Seavy and Alexander 2011; Lemaître *et al.* 2012; Ralston *et al.* 2019) and the expectation that each bird species differs in its food and shelter requirements (Johnson 1980), we hypothesized that any associations between habitat characteristics and if a species was detected would vary among species. Fourth, we compared the avian community composition between two consecutive breeding seasons and among three categorical forest types identified at the study site. Because many bird species show site fidelity to breeding locations (Schlossberg 2009), we predicted that the avian community composition would not be significantly different between breeding seasons unless a dramatic change such as a Spruce Budworm (*Choristoneura fumiferana*) infestation occurred between seasons. Conversely, we predicted that avian community composition would differ among forest types, because each type differs in physical structure and floristics.

Methods

Study area

Boreal forest bird communities are underrepresented in bird-habitat studies, and Labrador, Canada in particular is understudied (Lewis and Starzomski 2015). The current study focussed on an $\sim 50 \times 50$ km area (250 000 ha; centred at 666550 m E, 5921190 m N, UTM Zone 20U [53.413°N, 60.494°W]) within the Lake Melville Ecoregion in Labrador, Canada (Riley *et al.* 2013; Figure 1). Houses and cottages are distributed sparsely throughout the entire area, but most of the human population is concentrated in the towns of Happy Valley-Goose Bay to the south, and North West River and Sheshatshiu to the north. This region is relatively unpopulated compared to other portions of Canada, with an estimated human population of 8040 in Happy Valley-Goose Bay as of the 2021 census (Statistics Canada 2022). The study area falls within the provincial Forest Management District 19A, which is ~ 2.27 million ha (Forsyth *et al.*

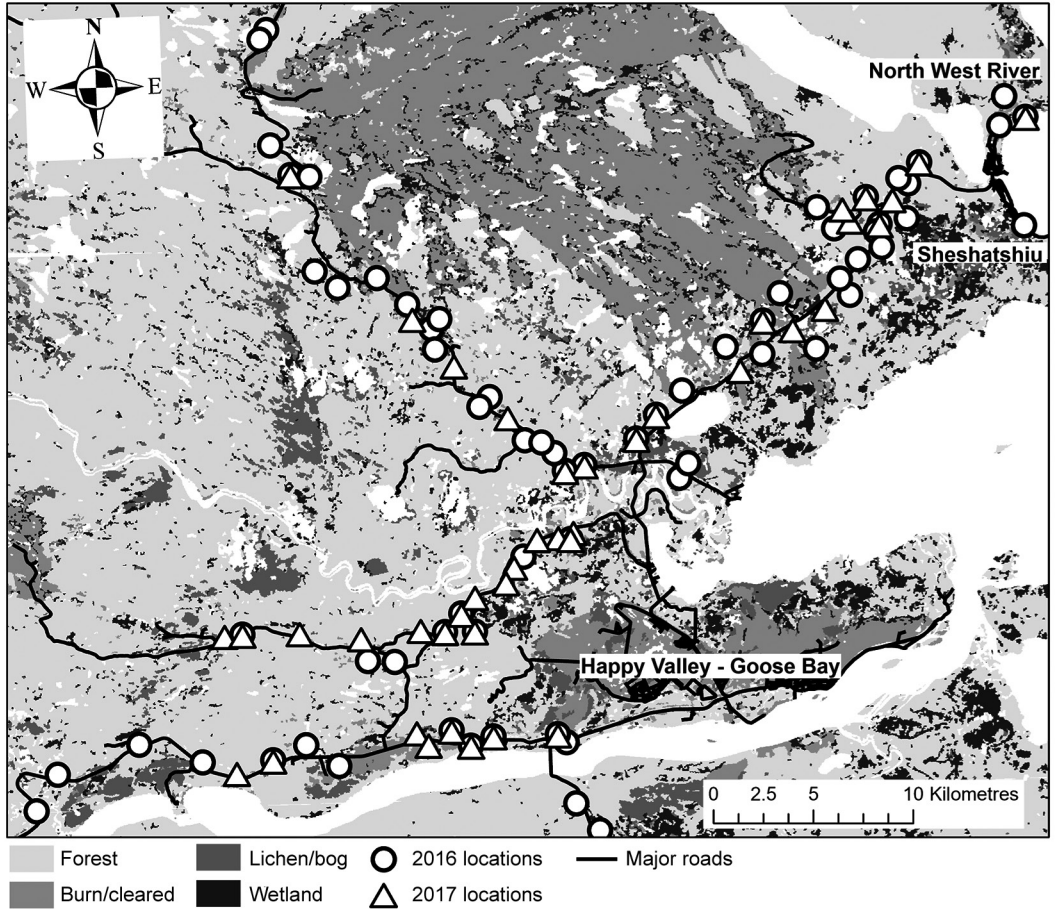


FIGURE 1. Map of locations sampled in District 19A in Labrador, Canada, where aspects of the avian community were compared to the physical structure and floristics of the habitat. Sites were sampled during the avian breeding season (May–July) in 2016 ($n = 68$) and 2017 ($n = 42$). Note: some points overlap because 20 locations from 2016 were resampled in 2017. The large area identified as “Burn/cleared” represents the 1985 wildfire that destroyed 340 km² of forest. Base map and 2017 land cover dataset (10 m resolution) provided by Impact Observatory and ESRI (Karra *et al.* 2020).

2003), or ~0.4% of the 552 million ha boreal forest in Canada. The area has a history of forest harvesting and other disturbances, including natural wildfire, drought, and disease. The most recent large-scale burns occurred in 1972, 1985, and 1994 (Simon and Schwab 2005). Most notably, a large portion of the study area (~34 000 ha or 13.6%) was burned by wildfire in 1985 (Notzl *et al.* 2013). During the same years, several portions of the forest were clearcut (Simon and Schwab 2005).

Forest stands in the area are dominated by Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) and Balsam Fir (*Abies balsamea* (L.) Miller). Other species in the upper canopy, in order of decreasing prevalence within study locations, are

Tamarack (*Larix laricina* (Du Roi) K. Koch), White Birch (*Betula papyrifera* Marshall), Heart-leaved Birch (*Betula cordifolia* Regel), and Trembling Aspen (*Populus tremuloides* Michaux). The woody vegetation in the understorey includes Speckled Alder (*Alnus incana* (Du Roi) R.T. Clausen), American Mountain-ash (*Sorbus americana* Marshall), Squashberry (*Viburnum edule* (Michaux) Rafinesque), willow (*Salix* spp.), serviceberry (*Amelanchier* spp.), and Skunk Currant (*Ribes glandulosum* Grauer). The most common ericaceous species in the understorey are Labrador Tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), Sheep Laurel (*Kalmia angustifolia* L.), Swamp Laurel (*Kalmia polifolia* Wengenheimer), and Leatherleaf (*Chamaedaphne calyculata*

(L.) Moench). Vegetation layers below the canopy layer were largely homogenous, with all stands being dominated by lichen in the ground cover layer, Labrador Tea in the herbaceous layer, and Speckled Alder in the shrub/understorey layer.

Microphone arrays

Between 16 May and 10 July of the 2016 avian breeding season, we deployed microphone arrays at 68 locations for a minimum of 24 h each. During the 2017 avian breeding season, we deployed microphone arrays between 17 May and 30 June at 42 locations, including 22 new locations and 20 locations sampled during 2016 to allow for analyses of temporal species similarity. All locations that were resampled in 2017 were sampled within three days of the year of when they were sampled in 2016. We chose to conduct our study over this wide range of dates to maximize our sample size and to capture the breeding seasons and periods of peak vocal activity of diverse avian species. In some species, such as Ruby-crowned Kinglet (*Regulus calendula*), vocal activity peaks as early as mid-May and decays precipitously thereafter (Fahmy and Wilson 2020). In other species, such as Swainson's Thrush (*Catharus ustulatus*) and Tennessee Warbler (*Leiothlypis peregrina*), individuals do not even arrive at our study site until mid-June (e-bird [ebird.org] checklist data for the Happy Valley-Goose Bay area). There are no known publications on arrival dates in these remote regions; however, several experts of the Newfoundland and Labrador birding community based in Happy Valley-Goose Bay regularly post to eBird.

Array locations were selected at random, but with the constraints that they were within 1 km of road access (either a two-lane highway or a gravel road) and a minimum distance of 500 m from each other. We chose a maximum distance from road access of 1 km because hiking beyond this distance through dense forest while carrying a microphone array would have been difficult and would have reduced our sample size. We chose to separate array locations by a minimum of 500 m because this reduced the risk of detecting the same birds at multiple locations (Wilson and Mennill 2011). Global positioning system (GPS) coordinates for locations were generated using a random integer set generator that creates non-repeating integers within confined boundaries (RANDOM.org). These random coordinates were then plotted on 1:50 000 scale topographic maps (National Topographic System, Series A771, Edition 4 MCE, Map 13 F/7 – 13 F/10) and discarded if they violated the inclusion criteria or were within a delineated swamp, bog, or water body based on provincial forest inventory maps. We chose to randomly select locations to sample rather than intentionally sample locations of

high species richness identified by previous researchers and birders. Random sampling produces unbiased estimates of the probability of detecting a given species at a given location, which can then be used in future research to model species richness and species occupancy throughout the general study area. We navigated to array locations using a survey-grade global navigation satellite systems (GNSS) unit with 10 cm accuracy (model: Geo7X; Trimble, Sunnyvale, California, USA).

Each array was left recording for 24 h, beginning two hours after setup to minimize potential disturbance effects associated with setup. An array consisted of four autonomous recorders (SongMeter 3; Wildlife Acoustics, Concord, Massachusetts, USA) placed at the corners of an ~40 m × 40 m square that was centred on a predetermined array location. Each recorder had two channels: one built-in omnidirectional microphone (frequency response: 20–20 000 Hz ± 10 dB) was positioned ~1 m above the ground, and a second external omnidirectional microphone (model: SMM-A2; frequency response: 20–20 000 Hz ± 10 dB; Wildlife Acoustics, Concord, Massachusetts, USA) was positioned in the understorey or lower canopy ~2–3 m above the first. All microphones were pointed towards the centre of the array, and their exact positions were determined with the survey-grade GNSS described above. Each recorder was programmed to record continuously and to produce a new stereo audio file every two hours (WAVE format, 24 kHz sampling rate, 16 bit amplitude encoding). In 2016, we had enough recorders to construct two arrays per day (i.e., eight recorders). We therefore deployed these arrays at two of our randomly determined locations, left them to record for at least 24 h, then redeployed them at two different locations the next day. Given the logistical challenges of accessing many of our array locations, the two arrays deployed on the same day were deployed at locations that were within a few kilometers of each other (1–4 km). In 2017, we only had enough recorders to construct one array per day (i.e., four recorders).

We recorded weather variables by placing a portable weather station (Kestrel 5500; Kestrel Instruments, Boothwyn, Pennsylvania, USA) 0.5–1.0 m above the ground in the middle of every second array during 2016 and at every array during 2017. Arrays were always deployed in pairs within a few kilometers (1–4 km) of each other during 2016, so weather conditions should have been sufficiently similar between the locations to justify obtaining weather data from only one of them. The weather station provided data at 20 min intervals throughout the 24 h recording period, including temperature (± 0.1°C), wind speed (± 0.1 km/h), relative humidity

($\pm 0.1\%$), and barometric pressure (± 0.1 mb). Temperature, in particular, affects the speed of sound and was required for the sound localization process. Wind can also affect the signal-to-noise ratio of audio recordings and thus the probability of detecting distant signals. However, wind speed, as measured with the portable weather stations, was always low (mean \pm SD = 0.7 ± 1.0 km/h; range 0.0–4.6 km/h) and thus was not considered further. We note, however, that wind speeds in and above the canopy were likely higher than those measured at ground-level by our portable weather stations. We therefore obtained hourly wind speeds measured throughout the 24 h recording period by Environment and Climate Change Canada (ECCC) in an open environment at the nearby Canadian Forces Base in Goose Bay (671845 m E, 5910973 m N, UTM Zone 20U [53.320°N, 60.420°W]; elevation 49 m), and used these in all subsequent analyses. The Canadian Forces Base in Goose Bay was a mean (\pm SD) distance of 17.3 ± 8.1 km from array locations. Because precipitation can affect avian vocal activity and the signal-to-noise ratio on recordings, we obtained precipitation data for Happy Valley-Goose Bay, Labrador from ECCC. If the first 24 h of recording included more than 10 mm of rain, we left the array recording until at least 24 h after the rainfall had decreased to below the threshold, and then used only the audio recordings from the final 24 h period in subsequent acoustic analyses. Only 23 arrays had any precipitation during their recording period and the mean (\pm SD) rainfall among them was only 2.8 ± 2.0 mm over 24 h (range 0.6–8.4 mm). We therefore did not consider precipitation in subsequent analyses.

General habitat characterization

The general habitat was characterized at each array by assessing vegetation cover at five standardized habitat sampling points, including midway between each pair of recorders and in the centre of the array. At each point, we measured canopy cover (%) with a spherical densiometer held pointing north. We determined stem density by holding a 2 m pole horizontally by one end at breast height (1.4 m) and then counting the number of trees touched by the pole while making a full rotation (i.e., a circle with a radius of 2 m; Avery and Burkhart 2015). The standard definition of a tree in monitoring protocols is any woody species with a height exceeding 2 m and a diameter at breast height (DBH) exceeding 4 cm (EMAN 2004). However, with several locations being dominated by wetlands with stunted tree growth, we defined a “tree” as any woody species with a minimum height of 1.5 m and a minimum DBH of 1 cm. The number of trees was divided by the area of the circle (12.57 m^2) to determine stem density in trees/ m^2 (Avery and

Burkhart 2015). Using a standard diameter tape, we measured the DBH of the three trees nearest to the sampling point. We determined vegetative species richness within the array by recording the total number of species of trees, shrubs, and ericaceous plants encountered within 1 m of the observer while walking slowly along the perimeter of the array, then from the SW corner to the NE corner of the array, and then from the NW corner to the SE corner of the array (~ 1 h of effort). We found that the ground layer among arrays was consistently a combination of *Sphagnum* moss and lichen, and thus omitted it from further consideration. Using the data from the five habitat sampling points, we calculated the mean value/array for stem density and canopy cover and the maximum value/array for DBH. We calculated maximum DBH instead of mean DBH because we expected that the presence of birds would be influenced more by a few large trees than by many trees of average size (Kebrle *et al.* 2021).

Although all locations were dominated by Black Spruce and Balsam Fir, we identified three distinct forest types within the general coniferous forest habitat type on the basis of species that were secondarily dominant. Although we did not quantify the prevalence of each tree species, these three forest types appeared to us to be discrete in nature. The “spruce/fir type” contained only Black Spruce and Balsam Fir in the canopy layer, or also contained a smaller portion (we estimate $\leq 20\%$ of stems) of Jack Pine (*Pinus banksiana* Lambert). The “birch/poplar type” was distinguished by the secondary prominence (we estimate 5–50% of stems) of birch and/or poplar species in the canopy layer. The “tamarack type” was distinguished by secondary prominence (we estimate 5–50% of stems) of Tamarack in the canopy layer and greater ericaceous plant species richness.

Acoustic analysis

We used Kaleidoscope software (Version 4.3.2, Wildlife Acoustics, Maynard, Massachusetts, USA, <https://www.wildlifeacoustics.com>) to automatically detect avian vocalizations and to group them into clusters of similar sounds. The settings used in the program included: maximum distance from the cluster centre = 2.0, fast-Fourier transform size = 256 points (5.33 ms), maximum number of states = 12, maximum distance to cluster centre for building clusters = 0.5, and maximum clusters created = 500. These settings ensure that all detections are assigned to a cluster. The clusters approximate species, but, sometimes, multiple clusters were associated with a single species. We therefore inspected sample detections from each cluster and manually renamed clusters according to the species they represented. Species identities were determined by listening to recordings

of vocalizations and reviewing their associated spectrograms and comparing these to the species accounts on the Birds of North America (Rodewald 2015), Xeno-Canto (www.xeno-canto.org), and Macaulay Library (<https://www.macaulaylibrary.org>) websites. Detected vocalizations were localized using a custom MATLAB program (details of the localization algorithm are in Ethier and Wilson 2019; Hennigar *et al.* 2019; Fahmy and Wilson 2020). The program uses waveform cross-correlation to measure the latencies of when a vocalization reaches each microphone in the array, relative to when that same vocalization reaches the closest microphone in the array (speed of sound through air is approximately 343 m/s). Separate sets of theoretical latencies are then calculated for all possible origins in the array and the origin that produces theoretical latencies closest to the observed latencies is selected as the most likely origin of the vocalization. The program produces UTM coordinates in two- and three-dimensions, and a localization error value that reflects the certainty of the estimated location.

We applied several exclusion criteria to the initial vocalization dataset. Previous studies (e.g., Mennill *et al.* 2012; Wilson *et al.* 2014) demonstrated that localization becomes less reliable when analysing sounds produced outside the array. Additionally, we wanted to limit the sampling area to that which was assessed for general habitat characteristics and to an area that was small enough to ensure that quieter species would still be within the detection range of the microphones. Using the “rgeos” package (Bivand and Rundel 2017) in R (Version 3.0.1; R Core Team 2017), we created a 2-dimensional spatial polygon of the array based on the UTM coordinates of the array microphones. We then determined the minimum distance of each localized vocalization from the edge of the polygon (0 m if inside the polygon). The list of vocalizations was reduced to include only those that originated from inside the microphone array or from within 5 m of its edge. This filtering step reduced the number of vocalizations considered for statistical analysis by ~60%, from 4879 624 to 1 928 312 vocalizations. This reduction is substantial, but not surprising. Based on localization estimates in our study, and on previous research (e.g., Dawson and Efford 2009), microphones can detect some birds that are up to 90 m away. Therefore, the vast majority of the active “listening” space of the array fell outside the target area.

We further reduced the vocalization dataset to include only those vocalizations that occurred during the targeted 24 h period of the recordings and that had a localization error value of 0.02 or less, which reduced the dataset from 1 928 312 to 470 761 vocalizations (i.e., to 10% of the original). We considered

these localizations to be accurate because, based on a “ground-truthing” speaker playback experiment, 90% of vocalizations with an error value ≤ 0.02 are within 3.55 m of their true locations (Ethier 2018). This error value strikes a balance between including vocalizations that are localized with a relatively high accuracy and retaining a large enough dataset that still reflects the local avian community. Next, although the localization procedure relies on vocalizations being detected in multiple channels, it is necessary to remove duplicate detections when counting the number of vocalizations produced. Whenever the same species was detected in multiple channels within 250 ms of each other, we retained only the first instance of the vocalization. This reduced the dataset from 470 761 to 89 242 unique vocalizations (i.e., to 2% of the original). Finally, we excluded vocalizations produced by non-target sources, such as Red Squirrel (*Tamiasciurus hudsonicus*) and humans, which reduced the dataset from 89 242 to 49 155 vocalizations (i.e., to 1% of the original). The remaining 49 155 vocalizations were manually reviewed in Kaleidoscope using visual scanning and by listening to audio clips to confirm species identity. This step was important because vocalizations from the same species were sometimes incorrectly assigned by the software to other species.

Statistical analysis

All statistical analyses were performed in R (Version 4.2.1; R Core Team, Boston, Massachusetts, USA). For all analyses, data from the 2016 and 2017 breeding seasons were combined. After applying the exclusion criteria described above, two array locations from the 2017 breeding season yielded no detections, and thus were removed from analysis. For locations that were sampled in both years, only data from 2017 were included in statistical models, to yield a similar number of samples from each year (2016 = 48 locations, 2017 = 40 locations). All descriptive statistics are mean \pm (SD), unless stated otherwise. Taxonomy follows the American Ornithological Society’s checklist (Chesser *et al.* 2021; Table 1). We provide our R script (R script 1) and two data files (Data file 1 and Data file 2) as supplemental material.

Species richness—Species richness was the total number of species detected at a location during the 24 h sampling period. First, we used a general linear model (GLM) to determine if species richness was related to habitat characteristics and abiotic factors. Predictor variables were three physical structure variables: mean canopy cover (%), mean stem density (stems/m²), and maximum DBH (cm); two floristic variables: vegetative species richness and forest type; and three abiotic variables: mean daily temperature, day within year, and mean daily wind speed. For

TABLE 1. Family, scientific name, common name, and nomenclature authority of avian species detected in Labrador, Canada. Taxonomy follows the American Ornithological Society's checklist (Chesser *et al.* 2021).

Family	Scientific name	Common name	Authority
Anatidae	<i>Branta canadensis</i>	Canada Goose	Linnaeus, 1758
Scolopacidae	<i>Gallinago delicata</i>	Wilson's Snipe*	Ord, 1825
Gaviidae	<i>Gavia immer</i>	Common Loon	Brünnich, 1764
Caprimulgidae	<i>Chordeiles minor</i>	Common Nighthawk	Forster JR, 1771
Picidae		Woodpecker sp.*†	
Tyrannidae	<i>Empidonax flaviventri</i>	Yellow-bellied Flycatcher	Baird and Baird, 1843
Vireonidae	<i>Empidonax alnorum</i>	Alder Flycatcher	Brewster, 1895
Corvidae	<i>Vireo philadelphicus</i>	Philadelphia Vireo*	Cassin, 1851
	<i>Perisoreus canadensis</i>	Canada Jay	Linnaeus, 1766
	<i>Corvus brachyrhynchos</i>	American Crow	Brehm, 1822
	<i>Corvus corax</i>	Common Raven	Linnaeus, 1758
Paridae	<i>Poecile hudsonicus</i>	Boreal Chickadee	Forster JR, 1772
Regulidae	<i>Regulus calendula</i>	Ruby-crowned Kinglet	Linnaeus, 1766
	<i>Regulus satrapa</i>	Golden-crowned Kinglet*	Lichtenstein MHC, 1823
Bombycillidae	<i>Bombycilla garrulus</i>	Bohemian Waxwing	Linnaeus, 1758
Sittidae	<i>Sitta canadensis</i>	Red-breasted Nuthatch	Linnaeus, 1766
Certhiidae	<i>Certhia americana</i>	Brown Creeper	Bonaparte, 1838
Troglodytidae	<i>Troglodytes hiemalis</i>	Winter Wren	Vieillot, 1819
Turdidae	<i>Catharus ustulatus</i>	Swainson's Thrush	Nuttall, 1840
	<i>Catharus guttatus</i>	Hermit Thrush	Pallas, 1811
	<i>Turdus migratorius</i>	American Robin	Linnaeus, 1766
Fringillidae	<i>Pinicola enucleator</i>	Pine Grosbeak	Linnaeus, 1758
	<i>Acanthis flammea</i>	Common Redpoll*	Linnaeus, 1758
	<i>Spinus pinus</i>	Pine Siskin	Wilson A, 1810
Passerellidae	<i>Passerella iliaca</i>	Fox Sparrow	Merrem, 1786
	<i>Junco hyemalis</i>	Dark-eyed Junco	Linnaeus, 1758
	<i>Melospiza lincolnii</i>	Lincoln's Sparrow	Audubon, 1834
	<i>Zonotrichia leucophrys</i>	White-crowned Sparrow*	Forster JR, 1772
	<i>Zonotrichia albicollis</i>	White-throated Sparrow	Gmelin JF, 1789
Parulidae	<i>Parkesia novaboracensis</i>	Northern Waterthrush	Gmelin JF, 1789
	<i>Leiothlypis peregrina</i>	Tennessee Warbler	Wilson, 1811
	<i>Oreothlypis celata</i>	Orange-crowned Warbler	Say, 1822
	<i>Setophaga ruticilla</i>	American Redstart	Linnaeus, 1758
	<i>Setophaga tigrina</i>	Cape May Warbler	Gmelin JF, 1789
	<i>Setophaga magnolia</i>	Magnolia Warbler	Wilson A, 1811
	<i>Setophaga striata</i>	Blackpoll Warbler	Forster JR, 1772
	<i>Setophaga palmarum</i>	Palm Warbler*	Gmelin JF, 1789
	<i>Setophaga coronata</i>	Yellow-rumped Warbler	Townsend, 1837
	<i>Setophaga virens</i>	Black-throated Green Warbler	Gmelin JF, 1789
	<i>Cardellina pusilla</i>	Wilson's Warbler*	Wilson A, 1811

*Detected by one or more audio recorders but fell outside the boundary of the microphone array(s) and thus was not included in formal analyses.

†Species identity could not be determined with certainty.

each location, mean daily temperature was calculated by averaging values recorded by the portable weather station at 20 min intervals across the 24 h recording

session; mean daily wind speed was calculated by averaging hourly measurements from the weather station at Goose Bay for the same period. The statistical

significance of individual predictor variables and the statistical significance and adjusted R^2 of the overall model were assessed using the summary function in base R. Variance inflation factors (VIF) >5 indicate potential problems associated with collinearity (Quinn and Keough 2002); our greatest VIF was 2.73, so all variables remained in the model. Second, we calculated the intraclass correlation coefficient (ICC) to test if species richness was repeatable between the 2016 and 2017 breeding seasons across the 20 locations that were sampled in both years (Wolak *et al.* 2012; Koo and Li 2016). The ICC was calculated with a 95% CI in the R package “irr” using a two-way consistency type model (Gamer *et al.* 2019).

Species-specific detection—We used GLM (family = binomial, link = logit) to test for relationships between habitat characteristics, abiotic factors, and the presence/absence of each species that was detected in at least 10% of the array locations (i.e., $\geq 9/88$ locations) to have sufficient sample size for statistical analysis. As predictor variables, we included three physical structure variables (mean canopy cover, mean stem density, and maximum DBH), two floristic variables (vegetative species richness and forest type), and three abiotic factors (mean daily temperature, day of the year, and mean daily wind speed). The statistical significance of individual predictor variables was assessed using the “summary” function of base R, and *post-hoc* pairwise comparisons between forest types were conducted using a Tukey procedure in the “multcomp” package (Hothorn *et al.* 2008). Regression coefficients were calculated using the “summary” function in base R, adjusted odds ratios and their 95% CI were estimated using the “logistic.display” function in the “epiDisplay” package (Chongsuvivatwong 2022), and pseudo R^2 was calculated according to McFadden (1974) in the “pscl” package (Jackman 2020).

Spatial and temporal consistency in avian community composition—We used the Sorensen index (C_s), which is widely used in pairwise comparisons (Sorensen 1948; Southwood and Henderson 2000; Lennon *et al.* 2001; Magurran 2004) to compare the avian community composition in a given location from one forest type to the avian community composition in a given location from another forest type (spatial species similarity). We limited this analysis to species that were detected in at least 10% of the array locations (i.e., $\geq 9/88$ locations). The index is defined as:

$$C_s = \frac{2a}{2a + b + c}$$

where a is the number species found at both locations, b is the number of species found at the first location and not the second, and c is the number of species found at the second location but not the first. C_s values

near one indicate that the two locations are very similar in community composition, whereas C_s values near zero indicate that the two locations are very different. To compare the average similarities in avian community composition among the birch/poplar, spruce/fir, and Tamarack forest types, we calculated C_s between all possible combinations of array locations for each pair of forest types. For example, we compared each of the 34 locations of the birch/poplar type to each of the 24 locations of the Tamarack type, which resulted in 816 C_s values. We then calculated the mean of these C_s values to quantify the average (\pm SD) similarity for the two forest types. We also calculated the average (\pm SD) C_s between all possible pairwise combinations of array locations within a given forest type as a way of assessing if avian community composition differed more between forest types than within forest types. Rather than using a different index, we adjusted the variables of the Sorensen index to calculate temporal species similarity (C_t) for each of the 20 arrays that were deployed in the same locations in both 2016 and 2017. Temporal species similarity at a given location was defined as the proportion of species that were detected at the location at both time points (Magurran 2004):

$$C_t = \frac{2a}{2a + b + c}$$

where a = number of species found at both points in time, b = number of species at time point 1 but not time point 2, and c = number of species at time point 2 but not time point 1. C_t was calculated separately for each of the 20 array locations sampled in both 2016 and 2017, and then averaged among the 20 locations. Again, we limited this analysis to species that were detected in at least 10% of the array locations (i.e., $\geq 9/88$ locations) to have sufficient sample size for statistical analysis.

Results

Based on the 49 155 detections composing our final dataset, we detected 32 species across the 88 microphone array locations (Table 1, Figure 1). The three most common species, as determined by the proportion of locations in which they were detected, were Ruby-crowned Kinglet, Dark-eyed Junco (*Junco hyemalis*), and Yellow-rumped Warbler (*Setophaga coronata*; Figure 2). Most species (26/32, or 81%) were detected at fewer than half of the locations. Common Nighthawk (*Chordeiles minor*) was detected at a single location and is the only federally or provincially listed species-at-risk (SARA Public Registry 2023; <https://www.gov.nl.ca/ffa/wildlife/endangeredspecies/birds/>) we detected. Although not considered forest birds, Canada Goose (*Branta canadensis*) and Common Loon (*Gavia immer*) were

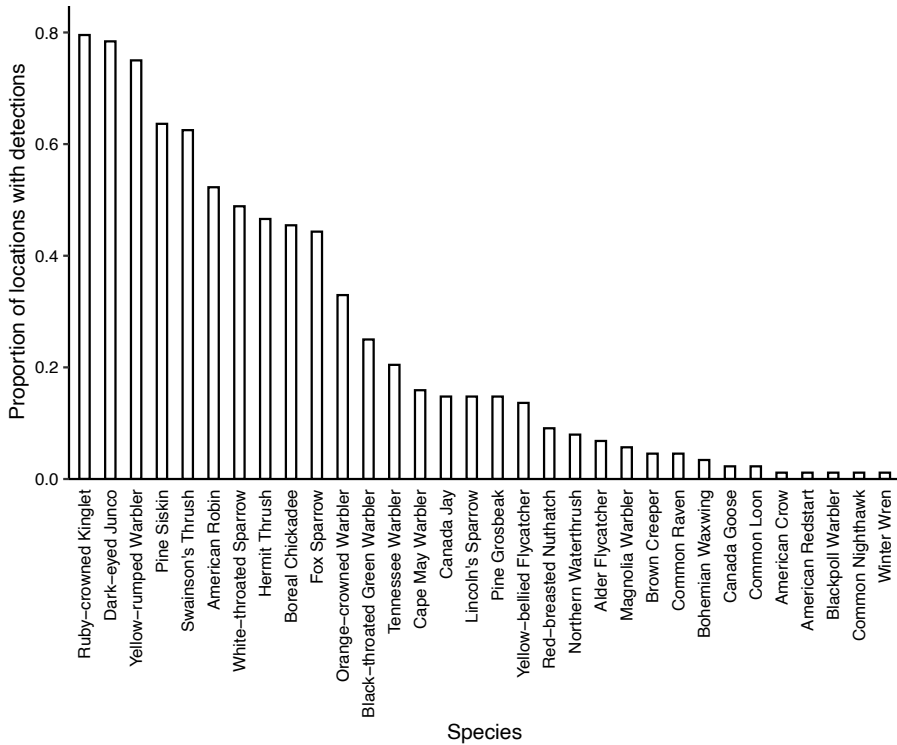


FIGURE 2. The proportion of 88 locations sampled in Labrador, Canada where bird species were detected. Locations were sampled during the 2016 ($n = 48$) and 2017 ($n = 40$) avian breeding seasons. See Table 1 for common name, scientific name, and nomenclature authority for listed species.

detected at two locations that included a small pond/lake edge within the boundaries of the array. Finally, we note that our recorders detected 40 species during the 2016 and 2017 breeding seasons, but that eight species did not meet our inclusion criteria and were thus excluded from statistical analyses. We include those eight species in Table 1 to provide a more comprehensive description of the species present at our overall study site.

Among the 88 microphone array locations, we detected an average (\pm SD) of 8.0 ± 3.3 avian species/location (range 1–17). The locations had an average mean canopy cover of $48.1 \pm 23.9\%$ (0.2–91.5%), average mean stem density of 0.8 ± 0.4 trees/m² (0.0–2.3 trees/m²), average maximum DBH of 13.2 ± 7.3 cm (1.0–41.0 cm), and an average vegetative species richness of 4.8 ± 1.4 species (2–10 species). On average, arrays were set up 160.1 ± 14.0 days after the start of the year (136–188 days). The average mean daily temperature was $10.0 \pm 4.6^\circ\text{C}$ (0.9–20.7°C) and the average mean daily wind speed was 15.6 ± 5.4 km/h (6.2–35.2 km/h).

Species richness

Avian species richness was predicted by the model

containing habitat characteristics, including mean canopy cover, mean stem density, maximum DBH, vegetative species richness, and forest type, and abiotic factors, including mean daily temperature, day of the year, and mean daily wind speed ($F_{9,78} = 3.31$, $P = 0.002$, adjusted $R^2 = 0.19$; Table 2). However, the only significant variables in the model were mean daily temperature and mean daily wind speed (Figure 3). On average, species richness (model coefficient \pm SE) increased by 0.2 ± 0.1 species/ 1°C increase in temperature and decreased by 0.1 ± 0.1 species/1 km/h increase in wind speed (Table 2, Figure 3).

Species richness was compared among 20 locations sampled in both 2016 and 2017 (Table S1). Among those 20 locations, avian species richness was 9.1 ± 2.3 species (range 5–14 species) in 2016, and 6.5 ± 3.7 species (range 0–15) in 2017. Species richness among locations was moderately consistent between years, with an intraclass correlation coefficient of 0.559 (95% CI of ICC = 0.17–0.80; $F_{19,19} = 3.53$, $P = 0.004$; Table S1).

Species-specific detection

We tested the relationship between the detection of a given species at a location and the habitat

TABLE 2. Summary of the general linear model of avian species richness regressed against mean canopy cover (%), mean stem density (trees/m²), maximum diameter at breast height (DBH [cm]), vegetation species richness, forest type (spruce/fir, birch/poplar, Tamarack), mean daily temperature (°C), day of the year, and mean daily wind speed (km/h) across 88 locations in Labrador, Canada during the 2016 and 2017 avian breeding seasons. Statistically significant ($\alpha = 0.05$) variables are shown in bold. The reference level for forest type is “birch/poplar”.

Variable	Coefficient	SE	<i>t</i> value	<i>P</i> -value
Intercept	4.26	4.69	0.91	0.367
Mean canopy cover	-0.03	0.02	-1.27	0.209
Mean stem density	1.45	1.05	1.39	0.169
Max DBH	0.07	0.06	1.07	0.289
Vegetation species richness	0.06	0.28	0.22	0.827
Mean daily temperature	0.20	0.10	2.10	0.039
Day of the year	0.02	0.03	0.74	0.464
Wind speed	-0.14	0.06	-2.37	0.020
Forest type (birch/poplar)				
Tamarack	-1.30	0.90	-1.45	0.152
Spruce/fir	-1.57	0.85	-1.84	0.069

Overall model: $F_{9,78} = 3.31$, $P = 0.002$, adjusted $R^2 = 0.19$.

characteristics and abiotic factors at that location for the 18 species that occurred in at least 10% of locations (Table 3). General habitat characteristics were significantly associated with species detection for 4/18 species (22%). Boreal Chickadee (*Poecile hudsonicus*) was more likely to be detected at array locations with greater stem density (adjusted odds ratio [OR] and 95% CI = 6.01 [1.03–34.97]) and Yellow-rumped Warbler was more likely to be detected at locations with larger diameter trees (OR = 1.27 [1.05–1.53]) and less canopy cover (OR = 0.95 [0.91–1.00]; Table 3). American Robin (*Turdus migratorius*) was less likely to be detected in the spruce/fir forest type than in the birch/poplar forest type (OR = 0.13 [0.04–0.48]), and Black-throated Green Warbler (*Setophaga virens*) was less likely to be detected in either the spruce/fir (OR = 0.06 [0.01–0.40]) or Tamarack forest types (OR = 0.05 [0.01–0.49]) than in the birch/poplar forest type (Table 3, Table S2). Abiotic factors were significantly associated with species detection for 9/18 species (50%; Table 3). Warmer days were associated with a greater probability of detecting Boreal Chickadee (OR = 1.25 [1.06–1.48]), Ruby-crowned Kinglet (OR = 1.28 [1.021–1.59]), Pine Siskin (*Spinus pinus*, OR = 1.23 [1.03–1.48]), Orange-crowned Warbler (*Oreothlypis celata*, OR = 1.22 [1.04–1.45]), and Yellow-rumped Warbler (OR = 1.45 [1.10–1.91]), whereas cooler days were associated with a greater probability of detecting Pine Grosbeak (*Pinicola enucleator*, OR = 0.72 [0.54–0.97]; Table 3). Boreal Chickadee and Ruby-crowned Kinglet were more likely to be detected earlier in the season (Boreal Chickadee, OR = 0.90 [0.85–0.96];

Ruby-crowned Kinglet, OR = 0.91 [0.85–0.98]), whereas Swainson’s Thrush (OR = 1.08 [1.02–1.14]) and Tennessee Warbler (OR = 1.10 [1.03–1.18]) were more likely to be detected later in the season (Table 3). Lincoln’s Sparrow (*Melospiza lincolni*, OR = 0.80 [0.65–0.97]) and Tennessee Warbler (OR = 0.84 [0.72–0.98]) were less likely to be detected on windier days.

Spatial and temporal consistency in avian community composition

Based on the 18 species that were detected in at least 10% of locations, we found that avian community composition was moderately consistent among the three forest types: birch/poplar and Tamarack: mean $C_s = 0.496 \pm 0.183$, birch/poplar and spruce/fir: mean $C_s = 0.487 \pm 0.203$, Tamarack and spruce/fir: mean $C_s = 0.495 \pm 0.192$. The degree of similarity in avian community composition among the three forest types is comparable (within 1 SD) to the degree of similarity in avian community composition among locations within forest types (birch/poplar: mean $C_s = 0.534 \pm 0.209$, spruce/fir: mean $C_s = 0.485 \pm 0.208$, Tamarack: mean $C_s = 0.556 \pm 0.184$). These values indicate a moderate level of similarity within and among forest types, with ~50% of species being found in both forest types on average in pairwise comparisons. Avian community composition was also moderately consistent between 2016 and 2017 (mean $\pm C_t = 0.543 \pm 0.244$; range 0.000–0.889; Table S1), with the community composition ranging among locations from very similar between years to complete species replacement. The temporal species similarity at a given site was not related to the day of

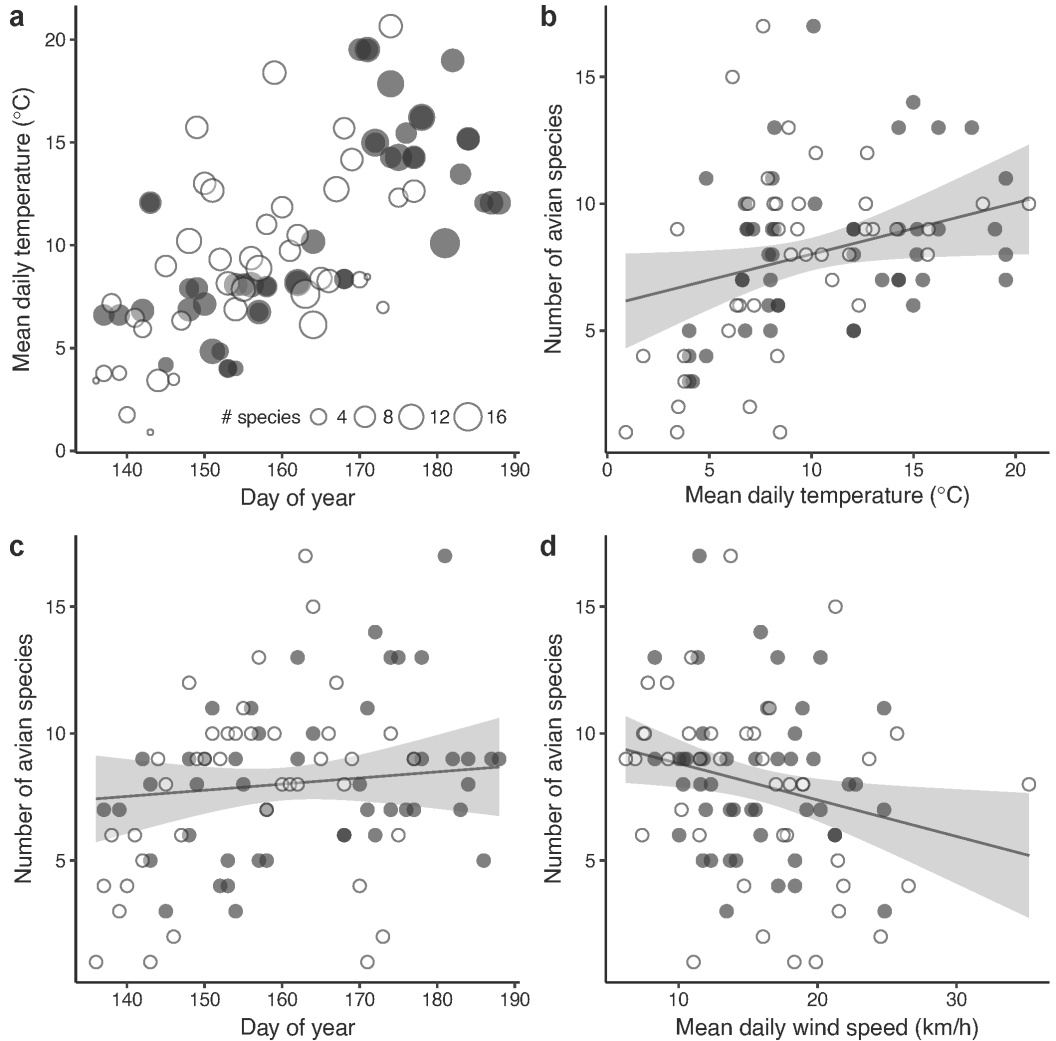


FIGURE 3. Abiotic predictors of avian species richness. Mean daily temperature and day of the year were positively correlated with each other (a) but mean daily temperature (b) was also correlated with the number of avian species detected on a given day, whereas day of the year (c) was not. The number of avian species detected was negatively associated with mean daily wind speed (d). Data points represent 24 h recording periods at 88 array locations in 2016 (filled circles, $n = 48$) or 2017 (open circles, $n = 40$) in Labrador Canada. The number of avian species detected during the 24-hour recording period are depicted by the size of the data points in a and on the y-axis in b–d. Regression lines and their 95% CI (grey shading) are based on estimated marginal means derived from the statistical model described in the text.

the year when the site was sampled (linear regression: $F_{1,18} = 0.27$, $P = 0.608$, $R^2 = 0.01$).

Discussion

Species richness

Several studies have shown a relationship between avian species richness at different sampling locations within a single forested habitat type and the DBH, stem density, and canopy cover at those locations (i.e.,

Berg 1997; Warren *et al.* 2005; Deppe and Rotenberry 2008; Lemaître *et al.* 2012). However, those studies were conducted in more heterogeneous habitats and across larger spatial extents (i.e., $\geq 100 \times 100$ km). At the smaller spatial scale used in our study (50×50 km or 250 000 ha), DBH, tree height, and stem density were not significantly associated with avian species richness, which is consistent with previous studies that found that physical structure characteristics better explain differences in avian assemblages

TABLE 3. Regression coefficients and pseudo R^2 of logistic regression models comparing presence/absence versus habitat characteristics and abiotic factors for 18 bird species across 88 locations in Labrador, Canada during the 2016 and 2017 avian breeding seasons. Coefficients represent the change, per one-unit increase in the predictor variable, in the log odds of the species being present (versus absent). Only those species that were present in at least 10% of the locations (i.e., $\geq 9/88$ sites) were analysed. Pseudo R^2 was calculated using McFadden (1974). Coefficients of statistically significant continuous predictors are in bold ($\alpha = 0.05$). For the categorical variable forest type, only statistically significant pairwise comparisons are shown (e.g., BIR>TAM indicates that the probability of a species being present is higher in the birch/poplar compared to the Tamarack forest type). Order of species reflects taxonomy according to the American Ornithological Society's checklist (Chesser *et al.* 2021).

Species	Intercept	Mean canopy cover	Mean stem density	Max DBH	Vegetative species richness	Mean temp	Day of year	Wind speed	Forest type*	Pseudo R^2
Yellow-bellied Flycatcher	-11.75	-0.01	0.11	0.01	0.25	0.08	0.05	0.06	.	0.23
Canada Jay	-10.79	-0.03	1.61	0.04	0.01	0.03	0.05	0.01	.	0.17
Boreal Chickadee	12.99	-0.01	1.79	0.04	-0.09	0.23	-0.10	0.02	.	0.22
Ruby-crowned Kinglet	14.40	0.01	0.08	0.09	-0.17	0.24	-0.09	-0.04	.	0.21
Swainson's Thrush	-11.43	-0.01	1.10	0.04	-0.01	0.05	0.07	-0.04	.	0.23
Hermit Thrush	3.23	-0.03	1.30	-0.03	-0.14	0.09	-0.02	-0.02	.	0.12
American Robin	8.58	-0.01	-1.12	-0.04	-0.21	0.08	-0.03	-0.09	BIR > SPF	0.16
Pine Grosbeak	-11.63	0.03	0.28	-0.03	0.37	-0.33	0.07	-0.10	.	0.15
Pine Siskin	-4.86	0.00	1.38	0.03	-0.16	0.21	0.02	-0.04	.	0.21
Fox Sparrow	1.57	-0.01	1.04	0.02	0.02	0.05	-0.01	-0.08	.	0.07
Dark-eyed Junco	-3.27	-0.01	-0.43	-0.03	0.15	0.19	0.02	-0.03	.	0.18
Lincoln's Sparrow	2.38	0.02	-2.78	-0.20	0.12	0.05	0.01	-0.23	.	0.31
White-throated Sparrow	-3.17	-0.03	-0.52	-0.04	-0.08	0.01	0.03	0.00	.	0.21
Tennessee Warbler	-15.20	0.02	0.01	0.00	0.12	-0.04	0.09	-0.17	.	0.28
Orange-crowned Warbler	1.88	-0.01	-1.61	-0.01	0.23	0.20	-0.03	-0.02	.	0.25
Cape May Warbler	1.15	0.04	1.06	-0.09	-0.25	-0.04	-0.01	-0.03	.	0.29
Yellow-rumped Warbler	-3.06	-0.05	2.31	0.24	-0.21	0.37	0.00	-0.04	.	0.35
Black-throated Green Warbler	-4.23	-0.01	2.00	0.10	0.25	0.04	0.00	-0.04	BIR > (SPF, TAM)	0.38

*Forest type codes: BIR = birch/poplar, TAM = Tamarack, SPF = spruce/fir.

between, rather than within, broad habitat classifications (Rotenberry 1985; Lee and Rotenberry 2005). A possible explanation for the lack of relationships between avian species richness and habitat structure at the smaller spatial scales used in our study is that the three physical structure characteristics that we considered (DBH, stem density, and canopy cover) are closely related to stand age. Stand age correlates with the number of avian species in the boreal forest region (Thompson *et al.* 1999; McCarthy and Weetman 2006) yet appeared to us to be homogeneous throughout our study site, perhaps owing to recent burns and harvesting activity. Limited variation in stand age therefore may have resulted in limited variation in the structural traits measured and, in turn, a lack of relationship between habitat structure and avian species richness.

Previous studies have shown that habitat floristics can affect avian assemblages at various scales (Hewson *et al.* 2011; DesGranges and LeBlanc 2012; Lemaître *et al.* 2012; Gahbauer and Rashleigh 2021) and that this is especially true when comparing assemblages within a single, broad habitat type. A strong, positive correlation between vegetative species richness and avian species richness has been demonstrated previously at the landscape scale (i.e., James and Wamer 1982; Currie 1991; Tews *et al.* 2004). Even at finer spatial scales, a greater diversity of tree species increases the number of niches that different species can exploit for foraging, nesting, and shelter (Lee and Rotenberry 2005). For example, within 1 km² plots, Gillespie and Walter (2001) and Poulsen (2002) both found that the number of bird species and the number of individuals of each

species were positively correlated with the number of tree species. However, these studies were conducted in areas of high avian and vegetative species richness and diversity. In Gillespie and Walter (2001), for example, mean forest bird richness was 22 ± 8.4 species (range 12–35) and mean woody vegetation richness was 41 ± 9.2 species (range 27–54). In our study, vegetative species richness was not significantly associated with avian species richness, which may be due to the limited variation in vegetative species richness among the locations where our arrays were deployed (mean vegetative richness = 5 ± 1.4 species; range 2–10 species).

In our study, mean daily temperature was significantly associated with avian species richness after controlling for all other variables in the model (Table 2, Figure 3). DesGranges and LeBlanc (2012) conducted a similar study in the Quebec-Labrador Peninsula region of the Canadian boreal forest and similarly found that species richness was significantly and positively correlated with temperature. One explanation for this relationship is that some avian species were present but remained silent and undetected on cooler days. Indeed, Wiley and Richards (1982) found positive correlations among temperature, the number of vocalizations produced, and the detectability of birds. An alternative explanation is that the relationship between temperature and avian species richness is due to variation in the arrival dates of the various bird species, because departure and arrival dates are known to be affected by weather variables such as precipitation, wind, and temperature (Sparks *et al.* 2002; Deppe *et al.* 2015). In particular, Sparks *et al.* (2002) showed that migratory species arrive on breeding grounds earlier when spring temperatures are warmer. Because our models included day of year, any effect of temperature is in addition to seasonal effects that influence arrival date and the total number of species that are present in the general area on a given date. The positive correlation between avian species richness and temperature in our study might therefore be driven by migratory species that had not yet arrived in early spring when temperatures were cold, but which had arrived days or weeks later when temperatures had increased. Although temperature and day of year are generally positively correlated, exceptions do occur that could explain why temperature but not day of year predicted species richness. In 2016, for example, temperature remained consistently low for the first half of the sampling period but then increased suddenly and remained consistently high for the remainder of the sampling period (Figure 3a). Future research involving longer sampling periods that span a mixture of cooler and warmer days would help determine whether the observed relationship

between avian species richness and temperature is due to some species being present but silent on cooler days or to them not arriving on the breeding grounds until temperatures warm.

Avian species richness was moderately consistent between consecutive years among the 20 locations that were sampled in both years (intraclass correlation coefficient of 0.559, 95% CI of ICC 0.166–0.798), suggesting that it may have been influenced by some combination of abiotic and biotic environmental variables that were consistently associated with each location. Given that the physical structure and floristic variables measured in our study were poorly correlated with avian species richness, it is likely that other habitat variables, or perhaps stable microgeographic variation in weather, influence the consistency of species richness. On the other hand, because avian species richness was positively correlated with mean daily temperature, any differences in temperature at a given array location between years may have reduced our estimate of inter-annual consistency. It is also important to note that repeatability in species richness does not necessarily mean that the same species returned to each location the following year, only that a similar number of species returned. We discuss temporal consistency in avian community composition below.

Species-specific detection

For most species (14/18 species that were detected in at least 10% of array locations), the physical structure and floristics of the habitat were not significantly associated with their detection. This is consistent with previous studies (i.e., Rotenberry 1985; Lee and Rotenberry 2005; Seavy and Alexander 2011; Lemaître *et al.* 2012; Ralston *et al.* 2019) that found both the physical structure and floristics of a habitat are potentially important when considering species individually, but that each species responds differently to variation in habitat characteristics, with some species showing little or no response to variation in physical structure and floristics.

Temperature and day of year were significantly associated with species detection for 6/18 species and 4/18 species, respectively. For Ruby-crowned Kinglet, Swainson's Thrush, Pine Siskin, Tennessee Warbler, Orange-crowned Warbler, and Yellow-rumped Warbler, which are migratory at our study site, the patterns are consistent with previous research showing that migrants are more likely to arrive on the breeding grounds during warmer weather, which tends to occur later in the year (Sparks *et al.* 2002). Because we used audio recorders to estimate species presence, relationships between species detection and temperature and date may also have been driven by seasonal and temperature-related variation in vocal activity.

For example, Wiley and Richards (1982) showed that birds produce more vocalizations and are more likely to be detected on warmer days, which could explain why five species were more likely to be detected on warmer days. Interestingly, Boreal Chickadee and Ruby-crowned Kinglet were both more likely to be detected on warmer days earlier in the season. In a study conducted at the same time and location as ours, Fahmy and Wilson (2020) found that Ruby-crowned Kinglet had an early breeding season and was most vocal in early June (2016) and late May (2017), which could explain why we were more likely to detect them earlier within our sampling period (16 May to 10 July). However, there are exceptions. Pine Grosbeak were less likely to be detected on warmer days. Pine Grosbeak call throughout the day, from dawn to dusk, but less often during the warmest parts of the day (1000–1600), suggesting a negative relationship between vocal activity and temperature in this species (Young and Adkisson 2020). Finally, wind speed affected the detection of 2/18 species, with Lincoln's Sparrow and Tennessee Warbler both less likely to be detected on windier days. High wind speeds are known to reduce the ability of recorders to detect birds (Thomas *et al.* 2020) but it is unclear why this occurred only for Lincoln's Sparrow and Tennessee Warbler.

The relationship between forest type and detection was also species-specific. American Robin was detected in a higher proportion of birch/poplar stands versus spruce/fir stands, and Black-throated Green Warbler was detected in a higher proportion of birch/poplar stands versus any other forest type. Our findings are consistent with Gahbauer and Rashleigh (2021), who found that Black-throated Green Warbler is associated with hardwood forest in Labrador. The apparent preference for birch/poplar by these species might be explained by previous research conducted in Alberta, Canada, which shows that an increasing deciduous/hardwood component is associated with increased diversity of food resources and potential nest sites in forests previously harvested for timber (Work *et al.* 2004; Buddle *et al.* 2006). Yet, more abundant resources in forests with hardwood tree species does not explain why these patterns emerged for American Robin and Black-throated Green Warbler and not for other bird species. Gahbauer and Rashleigh (2021) suggested that the increased presence of Black-throated Green Warbler in mixed or hardwood stands was associated with their preference for large-diameter trees, but maximum DBH was not significantly associated with the detection of either Black-throated Green Warbler or American Robin in our study, although it was significantly and positively associated with the presence of Yellow-rumped Warbler.

Overall, our findings suggest that, at the local scale used in our study, the composition of avian assemblages is influenced predominantly by factors other than the habitat characteristics measured. Several non-habitat factors affect habitat selection in birds, including competition (Jaakkonen *et al.* 2015), conspecific and heterospecific attraction (Forsman *et al.* 1998; Parejo *et al.* 2005; Campomizzi *et al.* 2008), and physiological constraints (Block and Brennan 1993; Jones 2001). Alternatively, it may be that, as Niemi *et al.* (1998) state, there is an “overabundance of suitable sites” in our study area. Those authors speculated that, while some locations are avoided, the majority of habitat is perceived as being of comparable quality and thus equally exploited.

Spatial and temporal consistency in avian community composition

Avian community composition was moderately consistent among the three forest types categorized in our study (~49% similarity) and was only slightly lower between forest types than within forest types (~53% similarity). Many migratory bird species that depend on boreal forests for breeding tend to have similar requirements (Schmiegelow and Mönkkönen 2002), likely contributing to the comparable results observed among versus within forest types.

Avian community composition among the 20 locations sampled in 2016 and 2017 was moderately consistent between years (mean \pm SD C_i : 0.54 ± 0.24 ; range 0–0.89), suggesting that individuals and species do not always occupy particular patches or territories within the overall area between consecutive years. The moderate C_i values might be attributed to the observation that species richness at these locations was generally lower during 2017 (mean \pm SD: 6.5 ± 3.7 species; range 0–15) in comparison to 2016 (9.1 ± 2.3 ; range 5–14; Table S1). If a small number of species present in the first year do not return the next year, this will increase the temporal species turnover, even if there are no new species that are present only in the second year. Another possible explanation for the moderate C_i values is that individuals may have returned in 2017 to similar locations but just outside the small target area of the array. Whatever the reason, our results are consistent with the meta-analysis by Schlossberg (2009), which found that 64% of adult migratory forest birds do not return to the same location between breeding seasons. Finally, although C_i values varied among the 20 locations, we did not find evidence that they were related to the day of the year when the locations were sampled, suggesting that low C_i values were not an artifact of sampling a particular location early in the season before all the migrants had arrived.

Differences in weather patterns and the arrival dates of individual species potentially influenced the differences in avian community composition observed between years. We also observed that snow in the forest persisted on the ground for a longer period into the breeding season in 2017, and that the daily mean temperature (averaged over 24 h) in 2017 was 3.5°C (\pm 4.8°C) cooler compared to 2016 when comparing the same dates between years. It is possible that migration in 2017 was delayed one or two weeks. E-bird checklists (ebird.org) for Happy Valley-Goose Bay for these years support this argument. Several migratory warbler species (e.g., Black-throated Green Warbler, Magnolia Warbler [*Setophaga magnolia*], Orange-crowned Warbler, Tennessee Warbler) were first recorded on the checklist approximately one week later in 2017, as compared to 2016. Because locations were sampled within a few days (day of the year) of each other in 2016 and 2017, daily temperature, through its effects on arrival dates, is likely the primary cause for differences in community composition between breeding seasons.

Considerations and implications

We acknowledge the clustering algorithm used by Kaleidoscope is imperfect and its accuracy varies by species. Sometimes, multiple clusters were created for each species (e.g., based on different song types) or vocalizations from the same species were distributed across clusters belonging to two or three different species; our manually reviewing the spectrograms and listening to the sounds resolved these issues. Woodpeckers were the only group for which we did not have the expertise to confidently distinguish among related species based on drumming patterns. Although we did not quantify the rate of correct assignments, we estimate that it ranged from ~40% for species with variable sounds or sounds that are similar to other species, to over 80% for species with simple or stereotyped song structure. The reasonable clustering accuracy made the manual review process much more efficient than it otherwise would have been.

Similarly, we can never be completely confident that our 24 h recording at each site was sufficient to detect every species present. The duration of the monitoring period must always be balanced with the number of sampling locations. The 24 h of continuous recordings allowed us to deploy 110 arrays across two seasons and diverse habitat. For comparison, most conventional point counts used for surveying birds last only 10 min per location and rely on human auditory detection. We doubt that the temperature effect influenced the analysis of the relationship between species richness and habitat because each habitat type was sampled evenly throughout the season and because

both temperature and habitat were included in the model (see Table 2). It is possible, however, that inter-annual variation in temperature affected our estimate of the consistency of avian species richness between years. Given that temperature correlated with our estimate of richness, any difference in temperature at a given array location between the two years could have reduced our consistency estimate.

There also are limitations to the scope of our study. Our findings are likely only applicable to the general area in which the study took place (i.e., the boreal forest of Labrador), because wildlife-habitat relationships inferred from relatively small spatial extents have limited transferability (Tuanmu *et al.* 2011). Regardless, such relationships are important for making local land-use decisions and are often necessary for establishing conservation efforts to protect habitat critical for survival and reproduction (Morrison *et al.* 2006). Furthermore, in our study, inferences based on statistical analysis could only be made for species that were adequately abundant. However, the most common species are generally those with the fewest constraints on habitat selectivity, such as generalists, which are the least likely to show a relationship between presence and habitat characteristics. This presents a potential problem, because those species that are of the greatest interest to conservation efforts are usually uncommon or rare (Cunningham and Lindenmayer 2005).

We only considered a small subset of physical structure and floristic variables that have previously been used to study bird-habitat relationships. Other commonly used variables include percent cover of each vegetative species (Gillespie and Walter 2001; Poulsen 2002; Lee and Rotenberry 2005; DesGranges and LeBlanc 2012), the number and percent cover of vegetative strata/height classes (Hobson and Schieck 1999; Deppe and Rotenberry 2008), total vegetative volume (Lewis and Starzomski 2015), and the number and DBH of snags/standing dead trees and downed woody debris (Imbeau *et al.* 1999; Drapeau *et al.* 2000). Incorporating these habitat variables may explain more variation in species richness and species-specific detection but would also take more time to measure and may thus limit sample size. However, our study was able to produce avian species richness and species-specific models with high adjusted R^2 values (>0.20) with relatively few physical structure and floristic variables. Changes in food abundance and pest infestations, such as Spruce Budworm, could also have drastic effects on the presence and abundance of avian species (Venier and Holmes 2010). Pest infestations often occur in 10–15 year cycles and their impact on avian composition is unlikely to be captured in shorter duration surveys such as our two-year

study. Future studies should also include distances to landscape features such as wetlands, waterbodies, and anthropogenic structures (e.g., roads, powerlines), because these features have the potential to significantly influence avian assemblages (e.g., Summers *et al.* 2011; Zlonis *et al.* 2017).

It is important to collect data about habitat selection by common species, because many rare species were once abundant. Indeed, conservation organizations, such as Partners in Flight, emphasize that prevention is more feasible and affordable than recovery (Rosenberg *et al.* 2016), and consequently stress the importance of studying and monitoring all species to keep “common birds common”. Overall, our data show that the structural and floristic traits measured at our study site in the boreal forest in Labrador, Canada are not related to the detection of most avian species or to species richness.

Author Contributions

Conceptualization: J.E. and D.W.; Investigation: J.E. and D.W.; Formal Analysis: J.E. and D.W.; Writing – Original Draft: J.E.; Writing – Review & Editing: J.E. and D.W.; Supervision: D.W.; Funding Acquisition: D.W.

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SUPPLEMENTARY MATERIAL:

R SCRIPT 1. The R script for statistical analysis and creation of figures.

DATA FILE 1. Data used to model the relationships between avian species richness and three environmental factors, including weather and the physical structure and floristics of the habitat and to produce species-specific models.

DATA FILE 2. Data used to calculate ICC values for avian richness in 2016 and 2017 to determine the consistency in richness between years.

TABLE S1. Avian species that were detected in 2016 and 2017 for 20 arrays sampled in both years in Labrador, Canada.

TABLE S2. The number of array locations, sampled from each forest type, where a given species was detected.