RESEARCH ARTICLE

Beaver activity and red squirrel presence predict bird assemblages in boreal Canada

Mariano J. Feldman[1], Marc J. Mazerolle[2], Louis Imbeau[1], and Nicole J. Fenton[1]

[1]Institut de Recherche sur les Forêts (IRF), Chaire industrielle CRSNG-UQAT sur la biodiversité en contexte minier, Centre d'étude de la forêt, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boulevard de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada

[2]Centre d'étude de la forêt, Département des sciences du bois et de la forêt, Faculté de foresterie, de géographie et de géomatique, Centre d'étude de la forêt, Université Laval, QC, Canada

* Corresponding author. E-mail: marianojavier.feldman@uqat.ca

ABSTRACT

Wetlands and predation in boreal ecosystems play essential roles throughout the breeding season for bird assemblages. We found a positive association of beaver activity and a negative influence of American red squirrels (*Tamiasciurus hudsonicus*) on bird assemblages. We used a multispecies hierarchical model to investigate whether bird communities differ between two major wetland habitats in boreal Canada: beaver ponds and peatland ponds. In addition to including variables such as forest cover and latitude, we adopted a structural equation model approach to estimate the occupancy of American red squirrels and its potential influence on bird communities. Using automated recording stations deployed at 50 ponds, we detected 96 bird species in 2018 and 2019. Bird species were grouped into four taxonomic guilds according to their habitat successional requirements: early successional species, late successional species, generalists, and wetland species. Beaver ponds harbored higher species richness, a pattern driven primarily by early successional species. The occupancy of almost a quarter of the species was lower in the presence of red squirrels. Late successional species responded positively to the cover of forest surrounding the pond. Our results highlight the value of considering acoustic data of red squirrels to quantify habitat quality in boreal forests. We conclude that beaver activity shapes bird assemblages through modification of their habitat, and that some bird guilds are associated negatively with the presence of American red squirrels.

Keywords: Beaver activity, red squirrels, bird assemblages, boreal ecosystems, automated recordings, multispecies hierarchical model.

RÉSUME

Les milieux humides et la prédation dans les écosystèmes boréaux jouent des rôles essentiels tout au long de la saison de reproduction pour les assemblages d'oiseaux. Nous avons trouvé une association positive entre les assemblages d'oiseaux et l'activité des castors, mais une association négative entre les assemblages d'oiseaux et la présence des écureuils roux d'Amérique (*Tamiasciurus hudsonicus*). Nous avons utilisé un modèle hiérarchique multi-espèces pour étudier si les communautés d'oiseaux diffèrent entre deux importants types de milieux humides du Canada boréal : les étangs de castors et les étangs de tourbières. Au-delà de l'inclusion de variables telles que le couvert forestier et la latitude, nous avons adopté une approche de modèle d'équation structurelle pour estimer l'occupation de l'écureuil roux d'Amérique et son influence potentielle sur les communautés d'oiseaux. En utilisant des stations d'enregistrement automatisées déployées sur 50 étangs, nous avons détecté 96 espèces d'oiseaux en 2018 et 2019. Les espèces des oiseaux ont été regroupées en quatre guildes taxonomiques en fonction de leurs exigences en matière de succession de l'habitat : espèces de début de succession, espèces de fin de succession, généralistes et espèces des milieux humides. Les étangs de castors abritaient une plus grande richesse d'espèces et une composition d'espèces différente de celle des étangs de tourbières, une tendance principalement liée aux espèces de début de succession. L'occupation de près d'un quart des espèces était plus faible en présence de l'écureuil roux. Les espèces de fin de succession ont répondu positivement à la couverture de la forêt entourant l'étang. Nos résultats soulignent l'intérêt de considérer les données acoustiques de l'écureuil roux pour quantifier la qualité de l'habitat dans les forêts boréales. Nous concluons que l'activité des castors façonne les assemblages d'oiseaux en modifiant leur habitat et que certaines guildes d'oiseaux sont associées négativement à la présence de l'écureuil roux d'Amérique.

Mots clés : Activité du castor, écureuil roux, assemblages d'oiseaux, écosystèmes boréaux, enregistrements automatiques, modèle hiérarchique multi-espèces

LAY SUMMARY

- Studies of bird assemblages and their responses to local and landscape factors in boreal landscapes can inform wetland conservation.
- The aim of our study was to assess how bird occupancy differed between two major pond types and responded to habitat, landscape factors, and potential predators in boreal assemblages in northeastern Canada.

- We detected 96 species using automated recorders deployed at 50 ponds in 2018 and 2019.
- Species richness was higher in beaver ponds than peatland ponds. Species richness was lower in the presence of red squirrel, a potential nest predator, and decreased with increasing latitude.
- Our results highlight the importance of beavers and factors associated with red squirrel presence in shaping bird assemblages in boreal landscapes.

INTRODUCTION

Wetland ecosystems are high quality habitats for a wide range of wildlife species (Weller 1999, Hansson et al. 2005, Lesbarrères et al. 2014), but are suffering from global impacts due to human land conversion and climate change pressures (Gibbs 2000, Tarnocai 2009, Davidson 2014). Wetland loss and degradation have contributed to the global decline of wetland-dwelling birds (Quesnelle et al. 2015, Davidson 2018). Wetlands with permanent and seasonal water bodies and adjacent inland terrestrial environments play a key role throughout the breeding season for bird assemblages (Kantrud and Stewart 1984, Naugle et al. 2001, Desgranges et al. 2006). For example, these wetlands attract several species associated with aquatic habitats, such as waterfowl (Lemelin et al. 2010), and are important for long-distance migratory species that benefit from adjacent habitats (Junk et al. 2006). This indivisible complex of aquatic and terrestrial habitats usually entails a greater diversity and richness than those formed exclusively by water (i.e. ponds or lakes) or by uplands habitats such as forest patches (e.g., Gutzwiller and Anderson 1987, Drapeau et al. 2000, Gopal 2009). Therefore, determining the relationships between bird assemblages and wetland habitat characteristics is of paramount importance for management and conservation decisions.

Wetlands in boreal landscapes are largely intact, but anthropogenic activities, including forestry, mining and energy resource extraction, are important and growing stressors that can reduce the quality of breeding habitats and modify forest vegetation composition (Poulin et al. 2004, Foote and Krogman 2006, Wetlands International 2022). However, we lack basic ecological information regarding species-habitat associations for wetland-dwelling species beyond the northern limit of commercial forest harvesting. For instance, boreal landscapes of northern Canada are home to different types of wetlands, although peatlands comprise most of the wetlands in this region (Payette and Rochefort 2001, Pellerin and Poulin 2013). Fens and bogs represent the two main types of peatlands. Minerotrophic or fen peatlands are mainly fed by rain and flow from adjacent aquatic environments previously exposed to mineral soils, and consequently the pH typically varies from 5.5 to 7.5 (Zoltai and Vitt 1995, Payette and Rochefort 2001, Leboeuf et al. 2012b). In contrast, water and nutrients in ombrotrophic peatlands or bogs come mostly from atmospheric sources and have a pH ranging from approximately 4.0 to 5.5 (Payette and Rochefort 2001). To date, relatively few bird species, including migratory birds, have been reported in Canadian peatlands (Calmé and Desrochers 2000, Desrochers 2001, Junk et al. 2006). Given the dominance of peatlands in many boreal regions and increasing pressures from anthropogenic activities such as forestry and mining, there is a need to characterize the assemblage of bird species associated with structurally diverse peatlands.

Bird species assemblages in peatlands are likely to differ from those found in less acidic ponds, such as ponds modified by North American beavers (*Castor canadensis*). Beavers have a substantial impact on wetland dynamics that positively affects overall bird diversity (Grover and

Baldasarre 1995, Lemelin et al. 2010, Nummi and Holopainen 2014). Beaver activities change the water level, which stimulates plant growth and increases invertebrate production (McKinstry et al. 2001), thus increasing food sources for a variety of waterfowl species and their broods (Nummi 1992, McCall et al. 1996, Nummi and Hahtola 2008). Beaver dams increase shallow water areas that can enhance nest concealment and reduce predation (Brown et al. 1996). Newly modified habitats provide snags and flooded trees, which attract birds like woodpeckers for nesting and feeding (Grover and Baldasarre 1995). Indeed, Aznar and Desrochers (2008) reported higher levels of songbird biodiversity in abandoned beaver ponds than in adjacent riparian habitats. Beaver ponds may therefore increase regional avian diversity. Yet, we are aware of only a few studies comparing bird assemblages in ponds that are influenced or unaffected by beaver activity in North American boreal forest (e.g., McKinstry et al. 2001, Aznar and Desrochers 2008, Desjardins et al. 2021). To our knowledge, no previous study has investigated the relative importance of beaver ponds and peatland ponds for habitat use by boreal birds. Increased knowledge of these habitats could contribute to the conservation of these species in their northern breeding habitats.

During the breeding period, nesting success is a critical stage that can influence the viability of bird populations (Vickery et al. 1992, Hoekman et al. 2002, Smith et al. 2011). Nest predation is typically the dominant cause of nest failure in birds (Martin and Li 1992, Sherry and Holmes 1992, Martin 1993). Hence, predation risk structures breeding bird assemblages by conditioning nest site selection and limiting breeding success (Martin and Roper 1988, Sieving and Willson 1998, Martin and Joron 2003). Direct encounters with predators may discourage the choice of a bird from using nesting sites (Dinkins et al. 2012). Among nest predators, American red squirrels (*Tamiasciurus hudsonicus*) are recognized as dominant passerine nest predators in mature coniferous boreal forest of North America (Darveau et al. 1997, Bayne and Hobson 2002). Bird nesting success decreases in forests where red squirrels are present (Darveau et al. 1997, Martin and Joron 2003). Moreover, densities of ground and shrub-nesting birds decrease with increasing abundance of red squirrels (Sieving and Willson 1998, Willson et al. 2003). These studies suggest that red squirrel occurrence influences both habitat selection and structure of bird assemblages (Darveau et al. 1997, Willson et al. 2003), although the effects may vary among prey species (Martin and Joron 2003). However, current knowledge of red squirrel predation is mostly based on artificial nests, which are more conspicuous, smell differently, and lack parental protection, possibly leading to an overestimation of predation levels (Willson et al. 1998, Buler and Hamilton 2000, Rangen et al. 2000). This gap highlights the need to formally quantify predation by squirrels in future studies, particularly in forests where the species is abundant.

In addition to local effects, researchers have sought to explain processes operating at the landscape level by considering the amount of surrounding habitat on species abundance and distribution (Fahrig 2001, Prugh et al. 2008, De Camargo et al. 2018). Both local habitat conditions and landscape characteristics adjacent to wetlands may also determine the structure of bird assemblages in boreal landscapes (Sedgwick and Knopf 1990, Strong and Bock 1990, Froneman et al. 2001). Indeed, the extent and structure of the surrounding forest often has a dominant influence on passerine presence and abundance in boreal ecosystems (Hobson and Schieck 1999, Saab 1999, Drapeau et al. 2000). Similarly, boreal species of woodpeckers vary with decreasing cover of old-growth coniferous forest in a landscape (Imbeau and Desrochers 2002, Hutto and Gallo 2006, Koivula and Schmiegelow 2007).

In this paper, our objectives were to assess the response of bird assemblages in wetlands to local-scale habitat and landscape factors in boreal regions. Specifically, we determined whether species occupancy and richness differed between two pond types, namely peatland ponds and beaver ponds. We also quantified the response of bird assemblages at these wetlands to the presence of a nest predator, as well as to latitude and the surrounding forest cover. We hypothesized that species occupancy varies with pond type, but depends on species habitat preferences (Calmé and Desrochers 1999, Desgranges et al. 2006, Alza 2014). Beavers may create favorable habitat for certain groups such as waterfowl or cavity-nesting birds. Therefore, we predicted that beaver ponds have a higher bird species richness and different bird assemblages than peatland ponds. We also hypothesized that occupancy of bird species decreases in the presence of American red squirrels, a known nest predator for most boreal species. Because of the various factors that operate across large geographical areas (Soininen et al. 2007), we expected species richness to decrease with increasing latitude. Finally, we expected differences in occupancy as a function of surrounding forest cover. Late successional species may react positively to increases in forest cover because they rely on tree substrates for breeding and feeding. As terminology in community ecology is ambiguous, we use here the terms "assemblage" *sensu* Fauth et al. (1996) when referring to a phylogenetic subgroup of species of a community (i.e. bird assemblage) and "taxonomic guild" *sensu* Stroud et al., (2015) to refer to a group of taxonomically related species that exploit the same class of resources in a similar way (i.e. early successional species, late successional species).

METHODS

Study Area

We conducted the study in the Eeyou Istchee James Bay region of northwestern Quebec (Canada) between the latitudes of 49º and 53º N, encompassing an area of about 400,000 km^2. The study area experiences a subpolar and subhumid climate with a short growing season, decreasing in days with latitude from south to north (Lord and Robitaille 2013). Mean annual temperatures range from -0.5 ºC to -4 ºC, decreasing gradually from south to north and also with elevation. The typical mean temperatures during the field work were 9 °C in May, 14 °C in June, 16 °C in July, and 17 °C in August (WorldWeatherOnline 2021). The annual mean amount of precipitation in the region ranges from 700 to 900 mm. Most of the snow falls generally from August to April (WorldWeatherOnline 2021).

The study region is distributed across three ecozones, including the Hudson Plains, the Boreal Shield, and the Taiga Shield (Lord and Robitaille 2013, Environment Canada 2015). The Hudson Plains comprise the southern portion of the study area and contain one of the highest density of wetlands in the world (Fraser and Keddy 2005). This landscape is characterized by a mosaic of forest mainly dominated by black spruce (*Picea mariana*) stands. The Boreal Shield portion is characterized by rocky hills mostly covered by coniferous forests of spruce-moss stands and abundant small to medium-sized lakes with peatlands (Environment Canada 2013a). The northernmost portion of the study region extends into the Taiga Shield ecozone (Ducruc et al. 1976, Lord and Robitaille 2013) with an undergrowth dominated by lichens of *Cladonia* spp. (Environment Canada 2013b). Spruce-lichen woodlands are prevalent in this forest where black spruce occurs at lower density than in spruce-moss woodlands (Environment Canada 2013b). The entire study area features numerous lakes and rivers and different types of wetlands, the latter are dominated by a complex mosaic of peatlands. Beavers are ubiquitous within the study region, although their abundance is higher in the southwestern sites and decreases along the northeast gradient.

We randomly selected 50 ponds in all three ecozones. To do so, we identified three sectors. The most southern sector (Casa Berardi) is encompassed by the Hudson Plains and located within commercial forests. The central sector (Whabouchi) is found in the Boreal Shield and the most northern sector (Renard) is within the Taiga Shield (Figure 1). Sixteen ponds were located in the vicinity of the Casa Berardi site, and 17 in each area surrounding Whabouchi and Renard sectors (Figure 1). Ponds were selected based on the criteria of accessibility (<1 km from the road), size (<2 ha), and habitat type (peatland or beaver pond). We retained 38 peatland ponds and 12 beaver ponds with similar size and depth (peatland ponds: 0.11–1.84 ha, 26.58–69.55 cm, beaver ponds: 0.14–1.87 ha, 29.55–176.52 cm). We maintained at least 800 m between two ponds to ensure independence of our observations. The inclusion of the peatland type was not possible because some peatlands included areas that were ombrotrophic and others that were minerotrophic (Bourgeau-Chavez et al. 2017).

Sampling with Passive Acoustic Surveys

We sampled the 50 ponds during the 2018 and 2019 breeding seasons. Each pond was visited during two periods in each year of study: between May 19 and August 12, 2018, and between May 16 and July 21, 2019. Pond visits during a given year were separated by 5–7 weeks. During a given visit, we deployed an autonomous recording unit (ARU). We used a SM4 Song meter (Wildlife Acoustics Incorporation, Concord, Massachusetts, USA) at each pond to record bird and squirrel vocalizations. Certain species such as ducks, herons, and raptor species are underrepresented in our assessment of bird communities because these species rarely vocalize and were unlikely to be detected by ARUs. At each pond, the ARU was positioned 2–10 m from the water's edge and fastened to a tree or wooden stake at a height of 1.5 m. We removed branches around the unit to reduce wind noise. During a given sampling period, ARUs were set with both microphones facing upward for four consecutive days to record a 5-min sample at 00600 h, at which time most of the singing birds are expected to peak (Robbins 1981, Wimmer et al. 2013). Previous studies showed that more than 70% of the species can be detected within the first 5-min of recording (Fuller and Langslow 1984, Sólymos et al. 2018). Each file was encoded at a sampling rate of 44.1 kHz and a 16-bit resolution.

Each pond was sampled for four consecutive days during two periods in both years, yielding an average of 80 minutes per pond. Due to technical limitations, a total of 92 failures occurred out of 800 (11.5%) planned recording periods, producing a total of 708 five-minute recording fragments. All recording data were analyzed by an ornithologist with extensive field experience in the study region (L. Imbeau) to identify species based on their vocalizations or other aural cue (i.e. wing noise, woodpecker drumming). Species were categorized into four taxonomic guilds based on their requirements for various successional stages of black spruce following Imbeau et al. (2003) and Drapeau et al. (2000): (1) early successional species, associated with open areas of low-vegetation such as young forests or regenerating shrublands; (2) late-successional species preferring older forest stands; (3) generalists, consisting of species that use a wide range of successional stages; and (4) wetland and aquatic species. In addition to birds, we identified the vocalizations of the American red squirrel from recordings, as suggested by Chavel et al. (2017), for use in occupancy analysis.

Site and Survey Covariates

We included four candidate variables as potential predictors of boreal bird occupancy. We used pond type to distinguish between beaver ponds and peatland ponds. To account for a possible effect of predation on bird occupancy, we considered American red squirrel occupancy, because this species is assumed to be a major nest predator of a wide range of birds in both coniferous and adjacent deciduous stands (Darveau et al. 1997, Sieving and Willson 1998, Willson et al. 2003). We also assessed the proportion of forest cover of all forest types over 2 m (deciduous, mixed, and coniferous forest) within circular buffers of 1000 m centered on acoustic recorder locations (Leboeuf et al. 2012a, Berger and Leboeuf 2015). This buffer area roughly corresponded or exceeded the sizes of territories of most bird species expected to occur in the study area (Gauthier and Aubry 1996). We included latitude to reflect habitat changes given that peatland ponds were more abundant in northern sites and beaver ponds were concentrated in the lower latitudes of the study area.

We considered two parameters that potentially influenced detection probability during acoustic surveys: the quality of the recording and the number of days after snowmelt. Recording quality was classified as bad in cases of high-volume saturation, rain or moderate to strong wind, otherwise quality was classified as good. We used the number of days elapsed since snowmelt to reflect potential differences in the phenology of vocal behaviors of species across our latitudinal gradient (Furnas and Callas 2015). We defined the date of snowmelt as the first day of a series of 7 consecutive days during which minimum temperatures were above 0 ºC.

Data Processing and Analysis

We investigated occupancy patterns of the American red squirrel, and occupancy of each bird species detected at least once in our recordings. We prepared detection histories for each species at each pond, where we indicated detection (1) or non-detection (0) in each recording of the two periods of four consecutive days in each year. Each pond in each year was considered as an independent site and we included a fixed year effect as well as a site random effect to account for potential differences in occupancy between years (Kéry and Royle 2020). Thus, detection histories for a given species were arranged in a matrix of 100 rows (50 sites x 2 years) and 8 columns (4 recordings x 2 periods).

We estimated bird occupancy and richness with a multispecies site-occupancy model (Dorazio and Royle 2005, Royle and Dorazio 2008, Zipkin et al. 2010). This hierarchical model approach can include rare or discrete species, by sharing information from species that are more common (Zipkin et al. 2009). We adapted a structural equation strategy to our multispecies occupancy model (Grace et al. 2010, Cubaynes et al. 2012; Figure 2). Specifically, one component of our model estimated the occupancy of American red squirrels (a potential nest predator) as a function of different explanatory variables, and then used the latent squirrel occupancy as an explanatory variable in the multispecies occupancy model for individual bird species and richness. This approach allowed us to simultaneously propagate the errors associated with the estimation of the squirrel latent occupancy state directly into the multispecies model. We estimated the occupancy probability of American red squirrel ($\psi_{\text{Squirrel}, ik}$) at site i in year k and associated latent occupancy state ($z_{\text{Squirrel}, ik}$):

$$\text{logit}(\psi_{\text{Squirrel},ik}) = \delta_0 + \delta_{\text{TypeBeaver}} * \text{TypeBeaver}_i + \delta_{\text{Forest}} * \text{Forest}_i +$$

$$\delta_{\text{Year2019}} * \text{Year2019}_{ik} + \delta_{\text{Latitude}} * \text{Latitude}_{i}$$

$$z_{\text{Squirrel},ik} \sim Bernoulli(\psi_{\text{Squirrel},ik})$$

where δ_0 corresponds to the intercept and other δ denote the slopes of explanatory variables on squirrel occupancy and where the latent occupancy state $z_{\text{Squirrel},\,ik}$ is drawn from a Bernoulli distribution with probability $\psi_{\text{Squirrel},\,ik}$. Detection probability of American red squirrel at site *i* on visit *j* in year *k* was estimated as:

$$\text{logit}(p_{\text{Squirrel},ijk}) = \gamma_0 + \gamma_{\text{QualityBad}} * \text{QualityBad}_{ijk} + \gamma_{\text{Thaw}} * \text{Thaw}_{ijk}$$

where γ denotes parameters associated with a given explanatory variable on squirrel detection probability.

The occupancy (ψ_{ikl}) of bird species *l* at site *i* in year *k* was modeled with effects of pond type, forest cover, year, latitude, and squirrel latent occupancy state:

$$\text{logit}(\psi_{ikl}) = \phi_{0,1} + \beta_{\text{TypeBeaver},l} * \text{TypeBeaver}_{i} + \beta_{\text{Forest},l} * \text{Forest}_{i} +$$

$$\beta_{\text{Year2019},l} * \text{Year2019}_{ik} + \beta_{\text{Latitude},l} * \text{Latitude}_{i} + \beta_{zSquirrel,l} * z_{Squirrel,ik} + \upsilon_{i}$$

$$z_{ikl} \sim Bernoulli(\psi_{ikl})$$

where $\phi_{0,l}$ is the average occupancy of species *l*, whereas β_l denotes the slopes of a given explanatory variable for species *l*. Because species from the same guild may respond similarly to habitat characteristics, we drew average occupancy as well as the slopes of pond type and forest cover for each species from a normal distribution specific to each guild g, e.g., $\beta_{\text{TypeBeaver},\,l} \sim N(\mu_{\beta\text{TypeBeaver},g}, \sigma^2_{\beta TypeBeaver,\,g})$. Here, $\mu_{\beta\ \text{Beaver},\,g}$ and $\sigma^2_{\beta Beaver,\,g}$denote the mean slope and variance of β_{Beaver} for guild g, respectively. In contrast, slopes for year, latitude, and squirrel occupancy state were drawn for each species *l* without reference to guild, e.g., $\beta_{\text{Year2019},\, l} \sim N$ ($\mu_{\beta\text{Year2019}}$, $\sigma^2_{\beta Year2019}$). The random effect υ of site *i* was drawn from N (0, σ^2_{Site}).

We allowed the detection probability of species *l* to vary with the recording quality and the number of days after snowmelt:

$$\text{logit}(p_{ijkl}) = \eta_{0,1} + \theta_{\text{QualityBad},l} * \text{QualityBad}_{ijk} + \theta_{\text{Thaw},l} * \text{Thaw}_{ijk}$$

Where $\eta_{0,1}$ corresponds to average detection probability of species *l*, and θ_l denotes the random slope associated with a given explanatory variable for species *l*, drawn from a normal distribution, e.g., $\theta_{\text{Thaw},\, l} \sim N$ ($\mu_{\theta\text{ Thaw}}$, $\sigma^2_{\theta Thaw}$).

Model parameters were estimated in a Bayesian framework with Markov chain Monte Carlo (MCMC) using five chains in JAGS 4.3.0 within R 4.1.2 using the jagsUI package (Plummer et al. 2006, Lunn et al. 2013, Kellner 2019, R Core Team 2021). Each chain consisted of 500 000 iterations with a thinning rate of 25 and we used the first 250 000 iterations as burn-in. We used vague prior distributions for all parameters. Specifically, we considered normal priors with N ($\mu = 0$, $\sigma^2 = 100$) for the β parameters and uniform priors U (0, 10) for the standard deviation of random intercepts and random slopes. Model structure and priors are reported in Feldman et al. 2022. We used trace plots, posterior density plots, and the Brooks-Gelman-Rubin statistic to assess chain convergence, where values < 1.05 of the latter metric suggested different chains stabilized to similar estimates (Lunn et al. 2013). Model fit was assessed with posterior predictive checks based on a Pearson chi-square aggregated over rows and columns (Kéry and Royle 2020). We also estimated the area under the receiver operating characteristic (ROC) curve as a measure of predictive ability (Zipkin et al. 2012). We used the multispecies model to derive the species richness from the posterior distribution of the true occurrence of each species at each site, expressed as the mean of the posterior distribution (Tingley et al. 2020). We investigated the relationship between species richness at site *i* in year *k* against the explanatory variables pond type, forest cover, latitude, and the posterior mean of the squirrel occupancy state in a linear mixed effect model:

$$\mu_{ik} = \alpha_{\text{i}} + \beta_0 + \beta_{\text{TypeBeaver}} * \text{TypeBeaver}_i + \beta_{\text{Forest}} * \text{Forest}_i +$$

$$\beta_{\text{Year2019}} * \text{Year2019}_{ik} + \beta_{\text{Latitude}} * \text{Latitude}_i + \beta_{zSquirrel} * z_{Squirrel,ik}$$

$$S_{jk} \sim N(\mu_{jk}, \sigma^2_{posterior})$$

where α_j denotes the random deviation of the intercept of site *i* with distribution *N* (0, σ^2_{Site}) and S_{ik} is drawn from a normal distribution with mean μ_{ik} and variance $\sigma^2_{posterior}$. Here, we used the variance of the posterior distribution ($\sigma^2_{posterior}$) of the species richness from the multispecies model above to propagate the errors into the linear mixed model (McCarthy and Masters 2005, Kéry and Royle 2020). We estimated the parameters using MCMC with five chains each of 75 000 iterations with a thinning rate of 25 and a burn-in of 40 000 iterations. Again, we used vague prior distributions for each parameter. In addition to the posterior diagnostics, we ensured that the normality and homoscedasticity assumptions were met.

RESULTS

A total of 708 five-minute recordings were analyzed and 99.1% of these recordings contained bird vocalizations. We detected a total of 96 bird species from 31 families and 12 orders at beaver and peatland ponds in 2018 and 2019. The most represented families were Parulidae (18 species), Passerellidae (9 species), Picidae (7 species), Fringillidae (6 species), Scolopacidae (5 species), and Tyrannidae (5 species). A total of 88 species were identified in 2018 and 86 species in 2019. Fourteen species were detected exclusively at each pond type, and 68 species were commonly found in both pond types. The most frequently detected species were the Hermit Thrush (*Catharus guttatus*), White-throated Sparrow (*Zonotrichia albicollis*), and Yellow-rumped Warbler (*Setophaga coronata*). In contrast, 13 species were detected only once. Wetland species were the most commonly encountered (33%) followed by late-successional species (27%), generalists (23%), and early successional species (17%). Among the 96 species detected at our sites with ARUs, only five species do not breed in our study area (Horned Lark, Least Sandpiper, American Pipit, Lapland Longspur, and Semipalmated Plover; Robert 2019).

Red Squirrel Occupancy and Bird Assemblage Response

Trace plots and other diagnostics for the multispecies single-season occupancy model suggested that chains mixed well and were of sufficient length. The posterior predictive check based on the aggregated columns suggested mild lack-of-fit ($\chi^2_{\text{columns}} = 908.76$, $P = 0.02$), whereas the check based on the aggregated rows suggested adequate fit ($\chi^2_{\text{rows}} = 13170.95$, $P = 0.80$). The area under the receiver operating characteristic (ROC) curve was 0.91 (95% CRI: [0.87, 0.93]), suggesting high predictive ability of the model.

The occupancy of American red squirrel did not vary with any of the explanatory variables (Table S2). However, the detection probability of red squirrels was greater in recordings of good quality and increased with days elapsed since snowmelt (Table S2). The occupancy of 11 bird species varied with pond type, all with higher occupancy in beaver ponds than in peatland ponds (Figure 3A). This preference was particularly marked among seven early successional species (Table S3). Twenty-four species (25%) varied with the presence of American red squirrels (Figure 3B). The occupancy of 20 species was lower in the presence of squirrels, whereas four species responded positively to squirrel presence (Figure 3B). Overall, our analyses revealed that the occupancy of 27 species (28,12%) responded to forest cover within 1000-m surrounding the pond (Figure 3C, Table S1). For most late-successional species (21 of 26 species, 80.8%), the occupancy probability increased with the proportion of forest cover (Table S3). Species of the remaining three guilds responded to a lesser degree, with the occupancy of one early successional species and five wetland species decreasing with increasing forest cover (Figure 3C, Table S1). The occupancy of several species varied with latitude, increasing for 12 species (12.5%), whereas it decreased for 29 species (30.2%; Figure 3d). The occupancy of only eight of the 96 species varied among years (Figure 3E). The occupancy of five species was greater in 2019 than 2018, whereas three species had a lower occupancy in 2019 than 2018 (Table S1).

Detection probability varied among bird species, but all bird species were more likely to be detected in recordings of good quality than those of low quality (Figure 4A). Furthermore, detection probability varied with days elapsed since snowmelt for 29 species among the 96 species (30.2%; Figure 4B). Twenty species were more likely to be detected earlier than later in the season, whereas nine species were more likely to be detected as the season progressed.

Species Richness and Structure of Bird Assemblages

Trace plots and MCMC diagnostics of the linear mixed model suggested that chains mixed well and that the assumptions of residual normality and homoscedasticity were met. Beaver ponds had an average of 4.9 species (95% CRI: [2.37, 7.46]) greater than peatland ponds (Figure 5A). Bird species richness was lower in the presence of American red squirrel than at sites without this potential predator (β_{Squirrel} = -3.97, 95% CRI: [-7.52, -0.36]; Figure 5b, Table S4). Species richness decreased with increasing latitude (β_{Latitude} = -3.89, 95% CRI: [-5.00, -2.78]), leading to fewer species in the northernmost sites (Figure 5C, Table S4).

DISCUSSION

The aim of the present study was to assess how bird assemblages responded to habitat and landscape factors at the local scale in an understudied boreal region of northern Quebec. By using a multispecies occupancy model, we estimated baseline occupancy for 96 bird species including two species of conservation concern at a national scale (Olive-sided Flycatcher and Rusty Blackbird). Overall, beaver ponds harbored a higher bird species richness and different assemblages than peatland ponds, a pattern driven primarily by early successional species. Another novel aspect of our work was to model squirrel occupancy, and include it as an explanatory variable on bird species occupancy, using a structural equation model approach. We showed that bird species richness and the occupancy of several species in the bird assemblages were lower in the presence of red squirrels.

Beaver Activity Shaping Avian Assemblages

We expected that bird assemblages would differ between beaver ponds and peatland ponds. Our study supports this hypothesis and shows that beaver ponds contain a higher bird species richness than peatland ponds. This finding is in general agreement with previous research that has compared bird diversity in beaver ponds to non-flooded wetlands (Longcore et al. 2006, Aznar and Desrochers 2008). Aznar and Desrochers (2008) found that abandoned beaver ponds supported higher numbers of songbirds compared to all other adjacent riparian habitats. Although we did not consider beaver ponds along a successional gradient in our study due to a limited number of ponds, various mechanisms may explain the greater species richness we observed in these habitats. For instance, beaver-flooded wetlands increase habitat complexity and provide a greater diversity of habitats that favor birds for brood rearing, foraging, and predation avoidance (e.g., Grover and Baldasarre 1995, Nummi and Holopainen 2014).

While no species preferred peatland ponds in our study, 11 species increased significantly in beaver ponds, primarily early successional species. This group consisted of sparrows and warblers that usually nest close to the shore and feed on or near the ground in open grassy or shrubby habitats. These species presumably benefit by increased vegetation cover in beaver ponds (Stoffyn-Egli and Willison 2011, Alza 2014). Through dam construction, beavers alter water hydrology and create areas of open water with inundated trees and snags. The subsequent denser understories and greater amounts of emergent herbaceous vegetation generated at beaver sites may increase the availability of insects (Reese and Hair 1976), which is the main diet of these species, and therefore render beaver ponds a more suitable foraging habitat for early successional species (Askins et al. 2007, Chandler et al. 2009, Alza 2014). The effects of habitat modification through beaver disturbance also influence the stage of vegetation succession. Once beavers abandon the site, beaver ponds drain and form patches with a variety of grasses and shrub species, known as beaver meadows (Naiman et al. 1988). Abandoned beaver ponds limit the progress of forest succession, due to prolonged flooding and anaerobic conditions, and promotes the regrowth of early successional plant species that support many shrubland bird species (Terwilliger and Pastor 1999, Wright et al. 2002, Chandler et al. 2009). As a result, beavers potentially create high quality habitat for early successional species in boreal forest that may persist in the landscape for many decades after abandonment (Barnes and Dibble 1988, Terwilliger and Pastor 1999, McMaster and McMaster 2000).

Red Squirrel Presence and possible influence

While the effects of beaver activity on bird assemblages are clearly evident, the effects of red squirrel presence are less clear. The red squirrel may have a direct effect on birds through nest predation (Reitsma et al. 1990, Bayne and Hobson 2002). Our results show that the occupancy of 20 species was lower in the presence of red squirrels, of which early successional species showed the strongest decrease (10 of 16 species, Figure 2A). Several studies have reported a decline in nesting success of bird species in the presence of red squirrels based on artificial nests (Darveau et al. 1997, Sieving and Willson 1998, Jobin and Picman 2002) and natural nests (Martin et al. 2003). Our results are consistent with these patterns. However, our observational study cannot identify the mechanisms behind these patterns or rule out that they were caused by other predators such as corvids, mustelids, or short-tailed shrew (Reitsma et al. 1990, Sieving and Willson 1998, Dyson et al. 2020). We did not find a negative relationship of red squirrels on late successional species. This is in line with reports of late successional species nesting in the upper levels of trees while squirrels prefer to predate bird nests in the understory (Sieving and Willson 1998). However, it is more difficult to explain the positive association between red squirrel presence and four species: Canada Jay, Olive-sided Flycatcher, Yellow-bellied Flycatcher, and Ruby-crowned Kinglet. The Canada Jay is a direct competitor of red squirrel for bird nests, as it can attack as many nests as red squirrels (Boulet et al. 2000). Hence, our data are consistent with Canadian boreal studies that report a high predation pressure and joint dominance of nest predation by red squirrels and Canada Jays (Boulet et al. 2000, 2003; Sieving and Willson 1998). The Canada Jay and Olive-sided Flycatcher are larger species potentially less vulnerable to nest predation by American red squirrels. Nonetheless, this explanation does not hold for the other two species that had higher occupancy in the presence of squirrels. Because red squirrels are the main source of nest mortality for many bird species (Martin 1993, Rodewald and Yahner 2001), we recommend recording detections of red squirrel when sampling bird occupancy using acoustic methods (Chavel et al. 2017). Acoustic methods for detecting territorial behaviors displayed by squirrels are equally reliable as live trapping, which is more invasive and requires a greater sampling effort (Chavel et al. 2017).

The association between the presence of red squirrels and bird assemblages we observed may also reflect unmeasured variables. For example, an alternative explanation of the association between red squirrel presence and that of early successional species could be related to stand age. Forest stand age plays an important role in driving bird assemblages (Schieck et al. 1995, Stelfox 1995, Imbeau et al. 2001). Squirrels in the boreal region feed mostly on seeds of black spruce and these trees start producing seeds at about 30 years of age (Viglas et al. 2013). Conifer seed production may be related to the presence of squirrels, as squirrel density decreases with lower seed availability (Rusch and Reeder 1978, Gurnell 1984). Furthermore, red squirrels typically respond positively to habitat characteristics associated with stand age and cone production that can fluctuate between years (Gurnell 1983). Addressing the relative importance of red squirrels in structuring boreal avian community will require shedding light on the mechanisms at play among squirrels, nesting bird success, and temporal variations related to cone production and stand age.

Amount of Forest and Latitudinal Gradient

The bird assemblages in the boreal wetland landscapes of our study responded differentially to forest cover. The occupancy of late-successional species increased with the forest cover. Our results support the idea that late-successional species are more likely to be negatively affected by habitat loss or fragmentation, mainly because they have large area requirements (e.g., Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Venier et al. 2014). This result is not surprising, given that old-growth forest specialists prefer interior forest environments for nesting (Huhta et al. 1999) and because cavity-nesting species included in late-successional guilds generally feed on saproxylic insects (Nappi et al. 2003, Saint-Germain et al. 2007). A reduction in forest cover may lead to decreased availability of insect prey and to the loss of specialized microhabitats for foraging and breeding substrates (Stratford and Stouffer 2015). Beyond the clear pattern between forest cover and occupancy of species in the late-successional guild, effects of forest cover were inherent to individual species in other guilds. The amount of habitat, measured here as forest cover, is one of the most important landscape determinants of bird biodiversity (Drolet et al. 1999, Trzcinski et al. 1999, Harrison et al. 2005), though other metrics merit investigation. Forest type, forest age, and disturbance type also influence forest bird assemblages (Saab 1999, Mitchell et al. 2001, Venier et al. 2014), but such variables were not available for our whole study area. These variables could be considered in future investigations of bird assemblages in boreal wetlands.

We believe that the latitudinal patterns detected here are not caused by latitude per se, but rather driven by biotic and abiotic forces (Rohde 1992). Bird species richness generally decreases moving north (Kouki 1999). However, latitude in our case reflected a decrease in habitat heterogeneity, as beaver ponds were absent at the northern sites, whereas peatland ponds were well represented throughout the region. In addition to latitude, another potential bias in our study was the sampling year. We found that occupancy of certain species varied with years, reflecting potential differences in abundance across years. We included latitude and year as explanatory variables on occupancy to reflect potential differences related to these spatial and temporal effects, although they were not the primary focus of our study. These variables allowed us to estimate the effects of the variables of interest, notably pond type, squirrel occupancy, and forest cover.

Detection Probability and Sampling Covariates

Our study highlights the importance of including temporal and sound quality variables when modeling detection probability of birds within wetlands. Species responded differently to the number of days since snowmelt. Of the 96 species studied, 20 species were most active early in the season, whereas 9 species were least active early in the season. Detection probability varied with the breeding song phenology of each species. This result is directly associated with the phase of the reproductive cycle of resident species (Wilson and Bart 1985) and the timing of arrival or passage of short and long-distance migrants (Furnas and McGrann 2018). The inclusion of the number of days elapsed since snowmelt also accounted for important differences in locations and spring weather patterns in our study area that spanned 400 000 km^2. Indeed, using such an approach is beneficial where the expected timing of the breeding season is affected by spatial locations and the timing of surveys (Sólymos et al. 2018).

The detection of birds relied on vocalizations in audio recordings. Unsurprisingly, the quality of the recording was an important predictor of detection probability of all species. Our results concur with previous studies using acoustic surveys (Acevedo and Villanueva-Rivera

2006, Celis-Murillo et al. 2009, Swiston and Mennill 2009). Sound quality decreases with background noise such as rain or wind in passive field recordings. Further refinements of filters to remove background noise or to identify recording quality (several species vocalizing simultaneously) will prove useful in automating species identification.

Overall, we estimated the composition and structure of bird assemblages in boreal wetlands and quantified their relationship with habitat and landscape patterns across a broad geographic region. Our results highlight the benefits of beaver ponds for bird assemblages, in agreement with studies indicating positive effects of beaver activities on boreal communities. These positive impacts should be considered in the context of beaver management practices. Our results suggest drawbacks of red squirrel presence, probably caused by nest predation or through an indirect influence of stand age. We hypothesize that nest predation pressure is high in our study area and is mainly driven by red squirrel. Climate change, by modifying the distribution of these two rodents, has the potential to indirect impact bird species assemblages found in northern Quebec. These trade-offs could be investigated in further studies which will contribute to prioritize regional wetland conservation in a landscape with increasing rates of wetland loss and degradation.

ACKNOWLEDGMENTS

We wish to thank M. Desrochers for providing valuable assistance to extract spatial data in a georeferenced information system. Special thanks to J. Arsenault and R. Chevalier for their assistance in fieldwork who were instrumental in field deployment and logistical support. We appreciate the insightful comments and feedback on previous drafts by A. Pietrek, M. Darveau and reviewers from @Corrige-moi students group including M. Arsenault and N. Chabaud of the

Université du Québec en Abitibi-Témiscamingue (UQAT). We thank M. A. Young for identifying Red Crossbill types based on our recordings added to eBird checklists. We thank J. Morarin for the artistic illustrations of the graphical abstract. We thank Hydro-Quebec and FaunENord for providing weather data throughout James Bay region. We also thank Hecla mining (Casa Berardi mine), Nemaska Lithium (Whabouchi mine) and Stornoway Diamonds (Renard mine) for project support and access to study sites. We also thank the associate editor and two anonymous referees for their precious comments on previous versions of this manuscript.

Funding statement: This project was funded by the Natural Sciences and Engineering Research Council (NSERC) of Canada—Université du Québec en Abitibi-Témiscamingue (UQAT) industrial research chair on northern biodiversity in a mining context.

Ethics statement: No animals were handled as part of this research.

Author contributions: L.I conceived the idea; M.J.F. developed, designed, and led the fieldwork supervised by L.I. and M.J.M. L.I. interpreted recordings to identify species through acoustic detection. M.J.M. designed the statistical methods and analyzed the data. M.J.F. and M.J.M. wrote the paper. All authors contributed to editing the manuscript and approved the submitted version. N.J.F. secured funding.

Data depository: Analyses reported in this article can be reproduced using the data provided by Feldman et al. (2022).

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Figure Captions

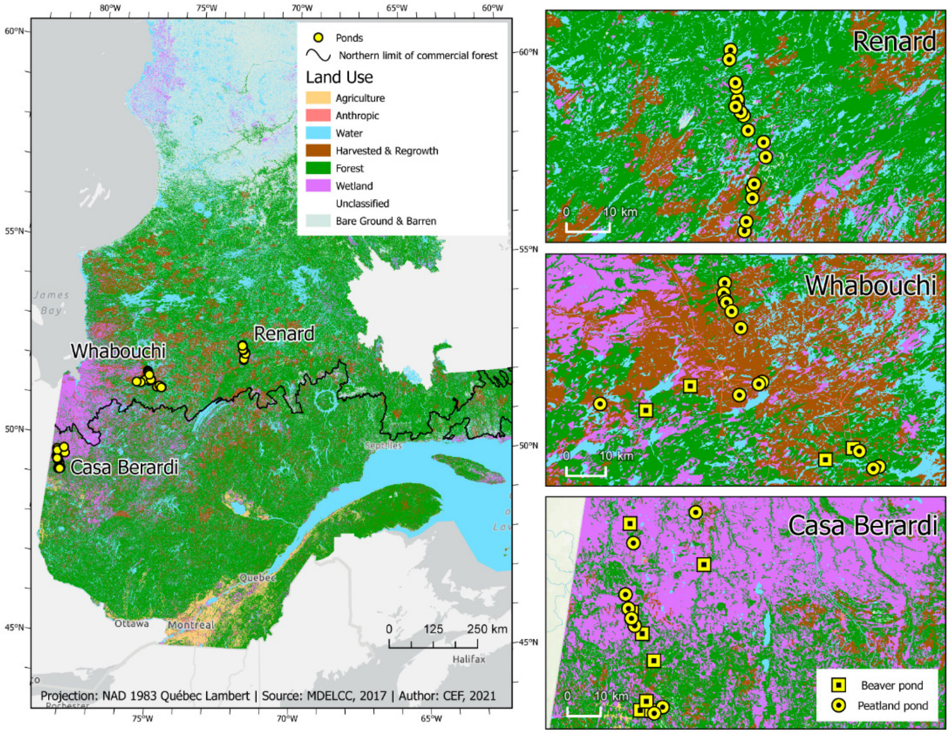


Figure 1. Study area with the distribution of ponds sampled in three sectors in 2018 and 2019 in Northern Quebec (Canada) using passive acoustic surveys.

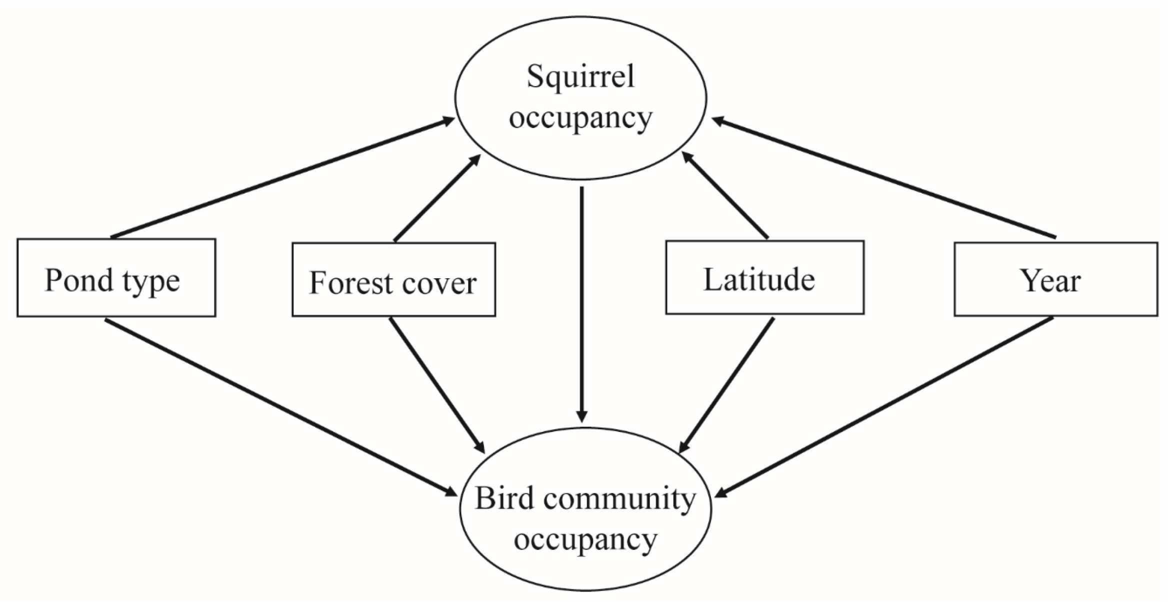
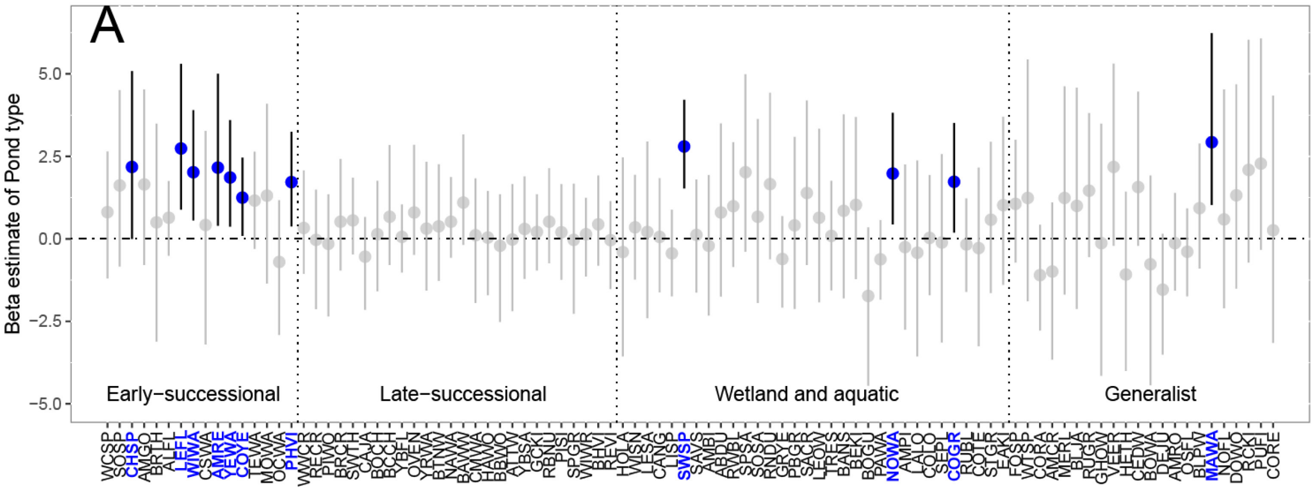


Figure 2. Structural equation model showing the hypothesized links between variables and bird community occupancy from the acoustic data recorded at beaver ponds and peatland ponds during the breeding season of 2018 and 2019 in northern Quebec. Explanatory variables are shown in boxes. Arrows link these explanatory variables to the biological parameters of interest (squirrel occupancy, occupancy of different bird species). Note that one component of the model estimates the influence of pond type, forest cover, latitude, and year on the occupancy of American red squirrel. This latent occupancy state for squirrel was then used as a predictor in the final component of the multispecies bird occupancy model, along with the pond type, forest cover, latitude, and year.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0.0
−2.5
−5.0
Early−successional
Late−successional
Wetland and aquatic
Generalist
WCSP
SOSP
CHSP
AMGO
BRTH
ALFL
LEFL
WIWA
CSWA
AMRE
YEWA
COYE
TEWA
MOWA
OCWA
PHVI
WWCR
RECR
PIWO
BRCR
SWTH
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BOCH
BCCH
YBFL
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HAWO
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BEKI
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NOWA
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COLO
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RUGR
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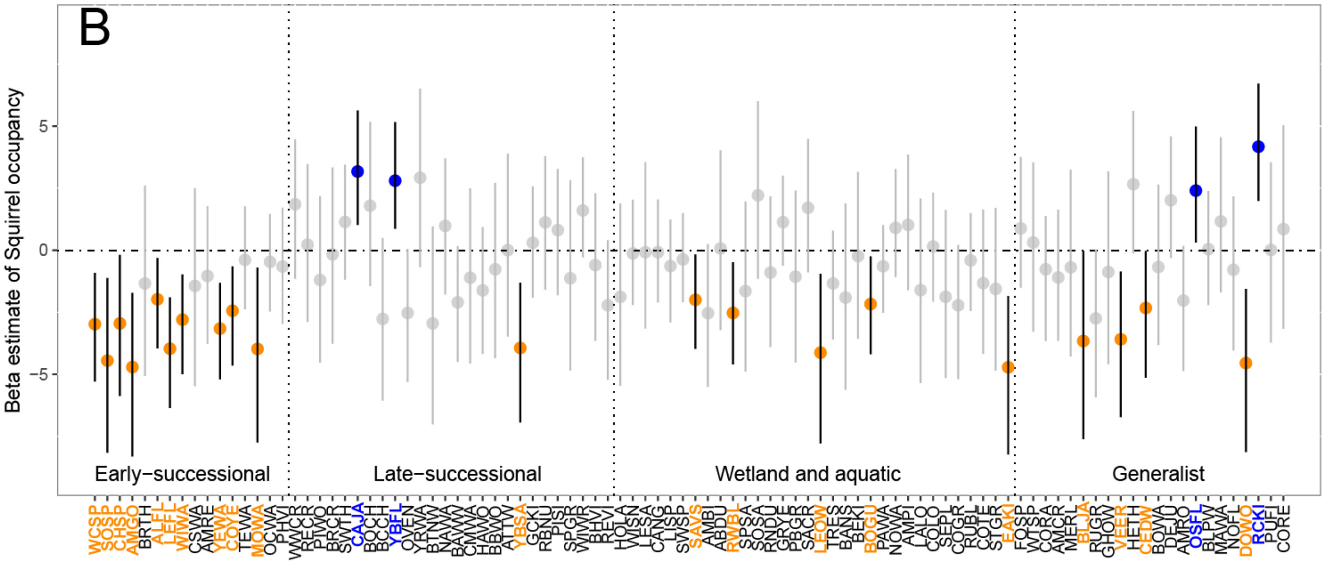
B
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Early−successional
Late−successional
Wetland and aquatic
Generalist
WCSP
SOSP
CHSP
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BRTH
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LEFL
WIWA
CSWA
AMRE
YEWA
COYE
TEWA
MOWA
OCWA
PHVI
WWCR
RECR
PIWO
BRCR
SWTH
CAJA
BOCH
BCCH
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OVEN
YRWA
BTNW
NAWA
BAWW
CMWA
HAWO
BBWO
ATTW
YBSA
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RBNU
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SPGR
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REVI
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CANG
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SAVS
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ABDU
RWBL
SPSA
SOSA
RNDU
GRYE
PBGR
SACR
LEOW
TRES
BANS
BEKI
BOGU
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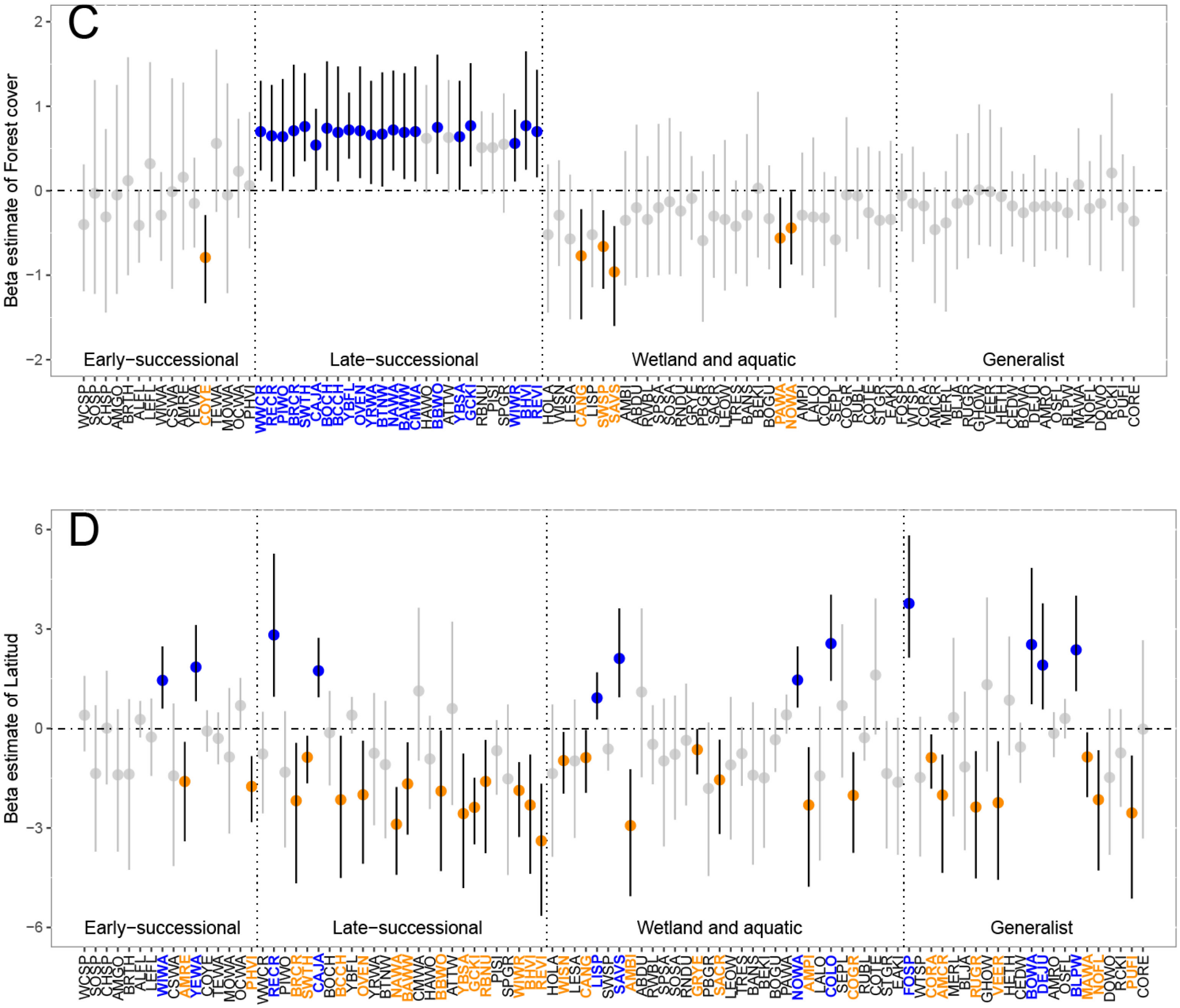
C
Beta estimate of Forest cover
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Early−successional
Late−successional
Wetland and aquatic
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Late−successional
Wetland and aquatic
Generalist

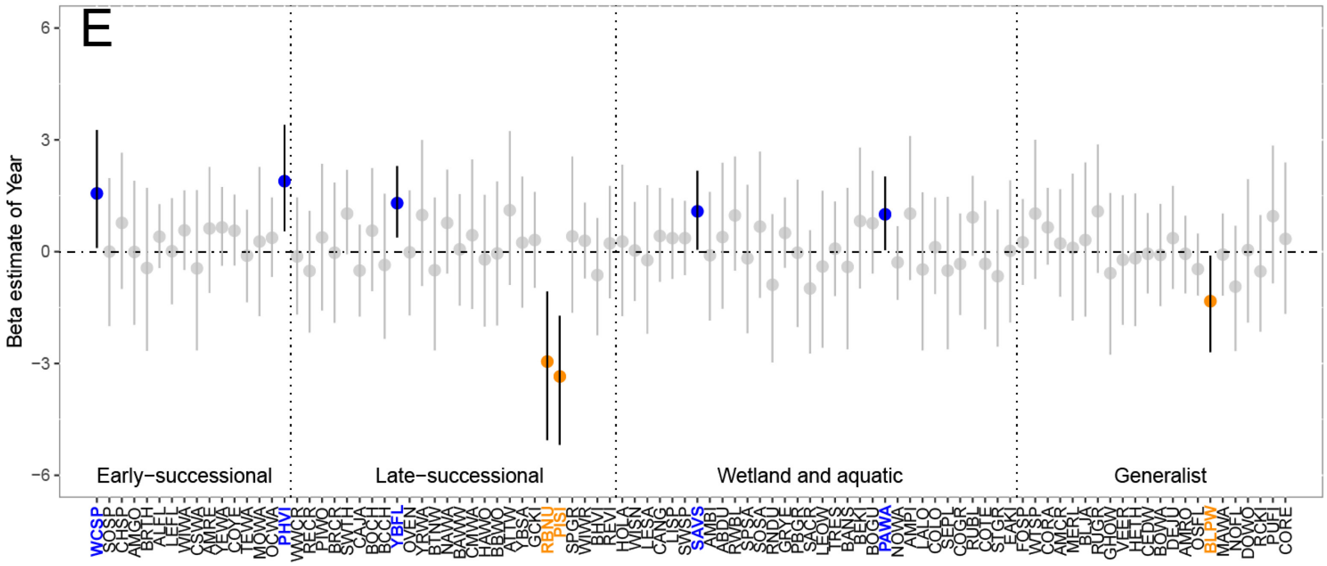

Figure 3. Bird community analysis based on acoustic data at beaver and peatland ponds in Northern Quebec in 2018 and 2019 for 96 species. Species-specific beta estimates on occupancy are presented for (**A**) pond type (beaver as reference level), (**B**) squirrel latent occupancy state, (**C**) forest cover, (**D**) latitude, and (**E**) year (2019 as reference level). Vertical lines represent the 95% Bayesian credible intervals around estimates obtained from MCMC. Orange points denote species that varied negatively, and blue points and denote species that varied positively with a given parameter. Complete species names and species-specific results are presented in Table S1.

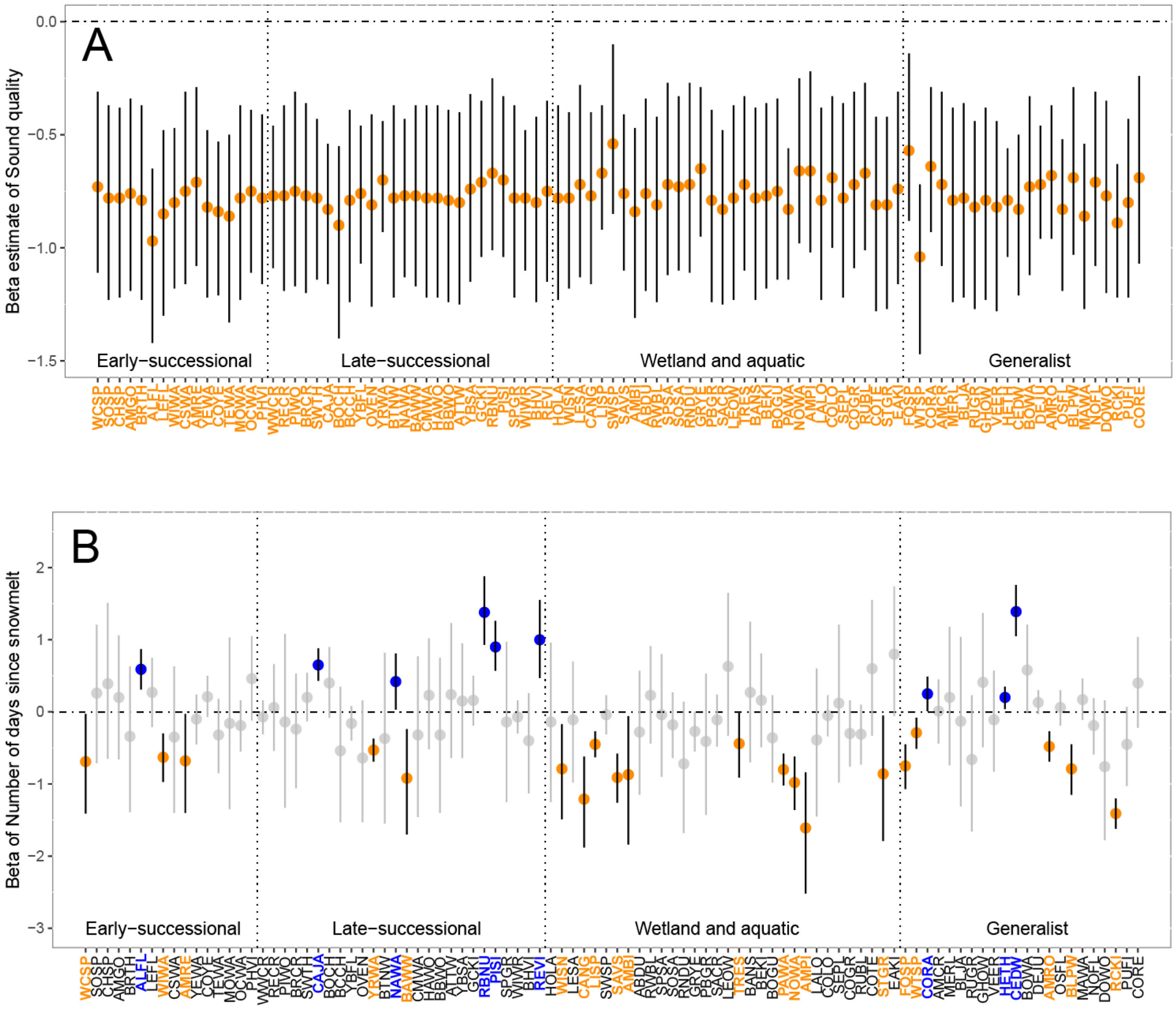

Figure 4. Detection probabilities for 5-minute surveys conducted with automated recorders in northern Quebec, 2018–2019. Species level responses to (**A**) sound quality (bad vs good as reference level), (**B**) and number of days since snowmelt. Vertical lines represent the 95% CRI around estimates. Orange points denote species that varied negatively, and blue points and denote species that varied positively with a given parameter as the estimated coefficients differ significantly from zero. Complete species names and species-specific results are presented in Table S1.

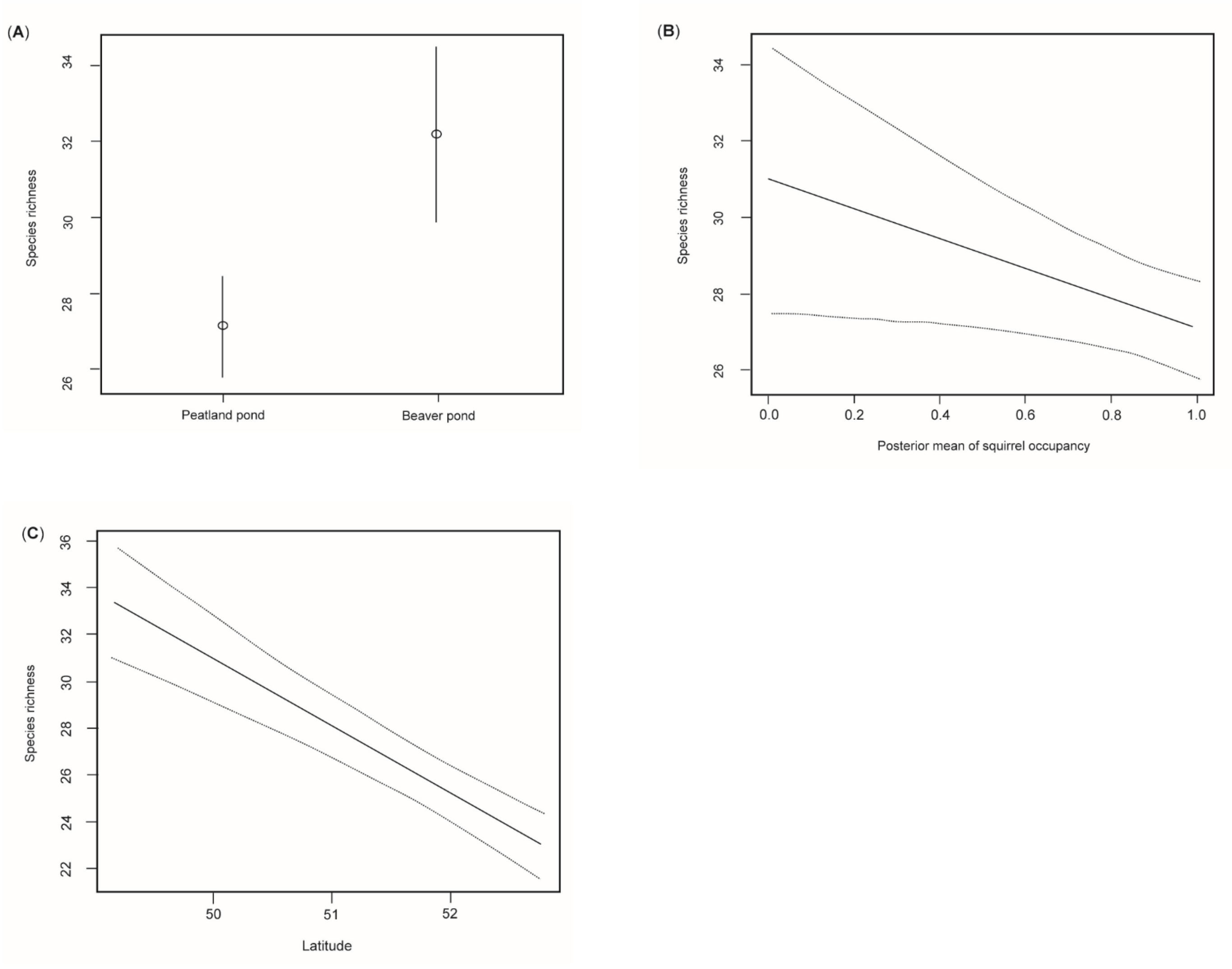

Figure 5. Estimated species richness of bird assemblages across A- Pond type, B- Squirrel occupancy state, and C- Latitude in Northern Quebec, Canada. Predictions and their 95% credible intervals are shown by holding the other explanatory variables at their mean values.

Figure caption for Graphical abstract. Using acoustic recording, we detected 96 bird species in 50 ponds in Northern Quebec, Canada. Our analysis revealed that species richness was higher in beaver ponds compared to peatland ponds, and lower in the presence of red squirrel, a potential nest predator. For illustrative purposes, we show here three early successional species affected by both major drivers, namely Wilson's Warbler, Common Yellowthroat, and Yellow Warbler. We analyze and discuss the effects of local and landscape factors on different levels of boreal bird assemblages.