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Avian Behavior, Ecology, and Evolution

Associations between elevation, introduced red squirrels, and boreal bird distributions on Newfoundland

Asociaciones entre la elevación, la introducción de ardillas rojas y la distribución de aves boreales en Newfoundland

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ABSTRACT. Elevational gradients in boreal forest songbird assemblages have received limited attention but may have important conservation implications in the face of climate change–induced habitat alteration and shifts in predator communities. Red squirrels (*Tamiasciurus hudsonicus*), introduced to Newfoundland in the 1960s and limited to lower elevations of the island, are important nest predators in boreal forests and influence bird assemblages where they are present. Our objectives were (1) to examine the role that elevation plays in the distribution of individual species, (2) to identify bird species for which occupancy rate was correlated with squirrel probability of occurrence, and (3) to investigate the influence of elevation and red squirrel occurrence on the species richness of different nesting guilds. We completed 1960 point count surveys for birds and red squirrels over two years across a 257 km² study area in western Newfoundland, Canada, which spanned southern boreal to northern boreal bioclimatic zones (75–610 m elevation). Among 28 species, eight had greater occupancy at higher elevations, 11 had decreasing occupancy with elevation, and nine showed no relationship. The relationship between red squirrel predicted occurrence and elevation was strongly negative. However, relationships between squirrel predicted occurrence and songbird occupancy varied by species, with occupancy for ten species being negatively related to squirrel probability of occurrence, and nine having squirrel occurrence as a better predictor of distribution than elevation. Richness of ground nesting species was best predicted by squirrel occupancy, but richness of above-ground and cavity-nesting species was best predicted by elevation. Populations of boreal birds in mountainous areas such as western Newfoundland are likely to show significant change and re-distribution in response to climate change as a function of altered forest composition and upslope expansion of red squirrels. Targeted monitoring of montane portions of the boreal forest is needed to assess responses to climate change by boreal songbirds.

RESUMEN. Los gradientes de elevación en las asociaciones de aves canoras del bosque boreal han sido poco estudiados, a pesar de sus posibles implicaciones para la conservación ante la alteración del hábitat inducida por el cambio climático y los cambios en las comunidades de depredadores. Las ardillas rojas (*Tamiasciurus hudsonicus*), introducidas en Terranova en la década de 1960 y restringidas a las elevaciones más bajas de la isla, son importantes depredadores de nidos en los bosques boreales e influyen en las asociaciones de aves donde están presentes. Nuestros objetivos fueron: (1) examinar el papel de la elevación en la distribución de especies individuales, (2) identificar las especies de aves cuya tasa de ocupación se correlaciona con la probabilidad de presencia de ardillas, y (3) investigar la influencia de la elevación y la presencia de ardillas rojas en la riqueza de especies de diferentes grupos de nidificación. Realizamos 1960 censos de puntos de aves y ardillas rojas durante dos años en un área de estudio de 257 km² en el oeste de Terranova, Canadá, que abarca zonas bioclimáticas boreales del sur al norte (75–610 m de elevación). De 28 especies, ocho mostraron mayor ocupación en elevaciones más altas, 11 una ocupación decreciente con la elevación y nueve no presentaron relación. La relación entre la probabilidad de presencia de ardillas rojas y la elevación fue fuertemente negativa. Sin embargo, las relaciones entre la probabilidad de presencia de ardillas y la ocupación de aves canoras variaron según la especie: diez especies mostraron una relación negativa con la probabilidad de presencia de ardillas, y en nueve la presencia de ardillas fue un mejor predictor de la distribución que la elevación. La riqueza de especies que anidan en el suelo fue mejor predicha por la ocupación de ardillas, mientras que la riqueza de especies que anidan sobre el suelo y en cavidades fue mejor predicha por la elevación. Es probable que las poblaciones de aves boreales en áreas montañosas como el oeste de Terranova experimenten cambios y redistribuciones significativas en respuesta al cambio climático, debido a la alteración de la composición del bosque y la expansión altitudinal de las ardillas rojas. Se requiere un monitoreo dirigido de las zonas montanas del bosque boreal para evaluar las respuestas de las aves canoras boreales al cambio climático.

Key Words: *assemblages; boreal songbirds; distribution; elevation; Newfoundland; red squirrels*

INTRODUCTION

Latitudinal patterns in the composition of boreal forest vegetation communities are relatively well understood (Brandt 2009) and in large part reflect the bioclimatic gradients that led to the development of southern, mid, and northern boreal (taiga) zones in post-Pleistocene North America (Rowe 1972). These gradients also influence bird distributions, as reflected in the delineation of North American Bird Conservation Regions (NABCI 2000) and the affiliations of birds with specific forest types and seral stages within those forests (Schieck and Song 2006). However, topography can also structure vegetation and bird assemblages along elevational bioclimatic gradients, creating zonation and "habitat islands" within avifaunal assemblages (e.g., Lewis and Starzomski 2015, Mizel et al. 2016, Ralston and DeLuca

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2020). These "habitat islands" may be found across eastern North America, including in Newfoundland and southern Labrador, eastern Quebec, and the Maritime provinces of Canada, as well as the mountains of New York, Vermont, and New Hampshire in the United States (Damman 1983, Jones and Willey 2012, Anderson et al. 2013, Ralston and DeLuca 2020). Additional heterogeneity in the associated bird assemblages of these regions may arise as species move into newly developing habitat and/or are pushed out of former locations at different rates in response to shifting habitat structure caused by climate change (Auer and King 2014, Mizel et al. 2023). The range shifts that have occurred over recent decades have been documented in a growing body of work associated with southern-periphery eastern boreal bird assemblages, along with the modeling of projected responses by species to climate change (Ralston and Kirchman 2013, DeLuca and King 2017, Kirchman and Van Keuren 2017). Commonly discussed outcomes of climate change in these montane bird assemblages include species hybridization, increased competition among historically allopatric species, range expansions and contractions, and range shifts of nest predators (Ralston and DeLuca 2020). None of these phenomena can be quantified and assessed without baseline knowledge of the contemporary elevational distributions of individual species.

Within eastern North America, the songbird avifauna of insular Newfoundland shows high levels of overlap with that of continental southern boreal forest communities but also has some unique features. Populations of several species on the island are either currently (Northern Waterthrush, scientific names of birds provided in Appendix Table S1; Whitaker and Eaton 2020) or were historically (Gray-cheeked Thrush; Whitaker et al. 2015) unusually abundant, and many bird species are genetically distinct from mainland populations (e.g., Lait and Burg 2013, Fitzgerald et al. 2017, Wilson et al. 2021). This endemism may have arisen in a disjunct forested Atlantic shelf refugium during the Pleistocene, while the contemporary oceanic barrier has limited subsequent gene flow (Ralston and Kirchman 2012, Ralston and DeLuca 2020). Loss of these genetically distinct populations or subspecies from Newfoundland would exacerbate any climate change–driven erosion of genetic diversity across the broader ranges of these species (Ralston and Kirchman 2013) and reflects concerns regarding biodiversity losses more generally in the context of climate change (Lees et al. 2022, Miller et al. 2024). Understanding the nature of threats to Newfoundland songbird populations is constrained by limited knowledge of long-term population dynamics, reflecting a problem common to the avifauna of other boreal regions (but see DeSante et al. 2015). Limited documentation of historical distributions for forest bird species makes it difficult to assess contemporary changes in elevation range distribution (Robineau-Charette et al. 2023), or to forecast the potential impact of climate change on future population status (but see Bateman et al. 2020 for examples of forecasting for some boreal forest species). Breeding Bird Survey (BBS) data offer broad-scale information on species distributions, but as with other regions of the boreal forest in North America, there are gaps in coverage across the Newfoundland landscape, especially at higher elevations, and BBS effort has varied over time (e.g., Pardieck et al. 2016, Robineau-Charette et al. 2023). Additionally, studies on the elevation distribution of bird communities in Newfoundland are limited. Notable exceptions were that the density of Canada Jays was unrelated to elevation (Thompson et al. 2008), whereas the Gray-cheeked Thrush is now most abundant in high elevation areas but rare at lower elevations where they were historically common (Whitaker et al. 2015, McDermott et al. 2023). Ralston et al. (2019) also described Blackpoll Warblers, Fox Sparrows, and Gray-cheeked Thrushes as being associated with colder sites, which they infer are higher elevation sites; Olive-sided Flycatchers with lower-elevation sites; and Magnolia Warblers and Yellow-bellied Flycatchers with both low- and high-elevation sites. Local knowledge and eBird records can likely fill in some gaps, but a rigorous, quantitative assessment of the elevation distribution of boreal birds on Newfoundland is lacking.

Expansion or shift of nest predator range is among the potential changes in broader community composition and distribution as a response to climate change (Mainwaring et al. 2017). Because such predators are the primary cause of nest failure in birds (Martin and Li 1992, Martin 1995), this may also alter songbird distributions and assemblage structure. These latter responses may arise as a reaction to both perceived risk and direct encounters with predators that influence avian distributions across a range of landscape scales (Lima 2009, Morosinotto et al. 2010). The North American red squirrel (*Tamiasciurus hudsonicus*; hereafter red squirrel or squirrel) is an important predator of boreal songbird eggs and young (Darveau et al. 1997, Bayne and Hobson 2002, Haché et al. 2014). Red squirrels were introduced to Newfoundland in the 1960s and are now widespread and abundant at lower elevations (Whitaker 2015). Squirrels decrease in abundance with increasing elevation on Newfoundland and reach an altitudinal limit at ~500 m but could potentially expand their range upslope in response to climate or land use–driven changes in forest composition and structure (McDermott et al. 2020). Squirrels adversely affect nesting success for forest songbirds (McFarland et al. 2008, Poulin et al. 2010, Sherry et al. 2015), negatively influence site occupancy by boreal birds (Feldman et al. 2023), and are thought to have played a key role in the decline of the Newfoundland subspecies of Gray-cheeked Thrush (*Catharus minimus mimimus*) which is now largely restricted to coastal islands and high elevation areas of Newfoundland's Long Range Mountains (Whitaker et al. 2015, Fitzgerald et al. 2017, COSEWIC 2024). Impacts of red squirrels are so pervasive that they can dramatically alter the population dynamics and potentially the structure of boreal forest songbird assemblages at a landscape scale (Siepielski 2006, Feldman et al. 2023, Hallworth et al. 2024). The vulnerability of bird species to nest predation by red squirrels is affected by life history traits such as nest site selection, and is typically cited as lowest for cavity-nesters, with different degrees of increased vulnerability for ground, shrub, and tree nesters depending on the study (Martin and Joron 2003, Lewis 2004, Fontaine et al. 2007). Consequently, information on the distribution of bird species categorized into these nesting guilds would be useful to assess the potential impacts of red squirrels on bird assemblage structure.

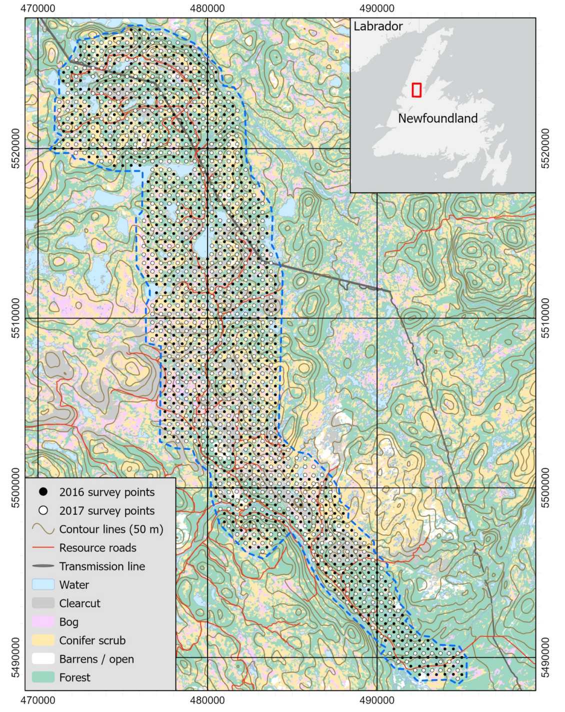
This study describes the contemporary distributions of individual bird species and patterns in assemblage structure across a montane landscape in western Newfoundland. Our first objective was to examine the role of elevation in these patterns, because it reflects changes in forest composition and structure. Although the relationship between species diversity and elevation in montane systems may not be linear across all fauna and flora (Rahbek 1995), diverse taxonomic groups (Pecl et al. 2017) and birds in particular (Blake and Loiselle 2000, McCain 2009) display an overall pattern of decreased diversity and abundance with increasing elevation. Elevation has a strong influence on many parameters of ecological interest, reflecting sometimes sharp contrasts in environment over short geographical distances (Körner 2007), including the tendency for temperatures to drop by 0.65° C for every 100 m increase in elevation (Barry 2008) and a general shift toward greater wind exposure and harsher and more variable conditions at higher elevations (Robertson 1993, McCain 2009). Thus, elevation can serve as a proxy reflecting changes in abiotic and resulting biotic conditions that occur across the gradient. Because individual bird species vary in their bioclimatic and habitat requirements, we predicted that the association between occupancy and elevation would vary across species. Specifically, we expected that southern boreal species would have higher occupancy at lower elevations, that species having northern boreal distributions would have higher occupancy at higher elevations, and that the occupancy of species having broad latitudinal distributions would be unrelated to elevation. Our second objective was to identify bird species for which occupancy was correlated with squirrel probability of occurrence, which might reflect impacts of this introduced species on the distributions of those bird species. Prior research (McDermott et al. 2020, 2023, COSEWIC 2024) suggested that introduced red squirrels may be acting at a landscape scale (i.e., across geospatial gradients) to restrict the distribution of Gray-cheeked Thrush. Extension of these analyses to the broader forest bird community of our montane system is warranted given the apparent impact we observed for Gray-cheeked Thrush in this study system. Because squirrels are important predators of the eggs and young of many open cup–nesting boreal birds, we predicted that occupancy of these species would be negatively related to squirrel probability of occurrence. Our third objective was to investigate the influence of elevation and predicted red squirrel occurrence on the species richness of different nesting guilds. Based on the assumption that the impact of red squirrel nest predation on bird species on Newfoundland is similar to patterns reported for continental boreal bird populations, we predicted that species richness for ground nesters and above-ground nesters should be lowest at low elevations, where squirrels are most abundant (McDermott et al. 2020), whereas cavity-nesting species should have a similar richness across all elevations. Because our study was observational, findings reported here require experimental studies to conclusively demonstrate causal impacts.

METHODS

Study area

We conducted our surveys in a 257 km² area of the upper Humber River and Main River watersheds in the Long Range Mountains of western Newfoundland, Canada (from 75 to 608 m elevation; centered at 49.66° N, 57.27° W; Whitaker et al. 2015, McDermott et al. 2020, 2023 provide detailed descriptions of the study area; Fig. 1). Broadly, this is a wet boreal landscape consisting of a natural matrix of openings (bogs and barrens), water bodies (streams, rivers, ponds, and lakes), and forest. Forest stands are primarily composed of balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*), with some white spruce (*Picea glauca*), tamarack (*Larix laricina*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), pin cherry (*Prunus pensylvanica*), and mountain ash (*Sorbus* spp.; Damman 1983, McCarthy and Weetman 2006). Bioclimatic zonation in this region is compressed by proximity to cold ocean waters on both sides of the Great Northern Peninsula. Thus, this mountainous area spans eastern boreal up to eastern alpine tundra bioclimatic zones (Baldwin et al. 2019) including vegetation communities dominated by Arctic-alpine barrens and windswept krummholz (Damman 1983). Above 450 m, open areas and unproductive conifer-dominated scrub forest become increasingly prevalent because of increased wind exposure, deep snow cover that persists into June, low nutrient availability, and shallow saturated soils (Damman 1983). Forests below 450 m and in deep valleys are characterized by a matrix of mixed and single species stands of biologically productive forest dominated by balsam fir or black spruce along with bogs, heaths, rock barrens, and other natural openings (Damman 1983, McCarthy and Weetman 2006). Vegetation surveys in our study area (McDermott et al. 2020) revealed higher elevation sites with different tree and shrub species composition than lower elevation sites. For example, shrub species such as alder (*Alnus* spp.), mountain-ash, and pin cherry were less common from 275 to 449 m than at lower elevations and absent above 450 m. Likewise, white spruce, white birch, and tamarack declined as elevation increased, whereas a higher proportion of points above 450 m had standing dead trees and open habitat. Because abiotic and biotic conditions shift predictably from low to high elevation, we used elevation as a proxy that reflects and integrates environmental variability across our study area.

Fig. 1. Study area in the Long Range Mountains of Newfoundland, Canada. The study area boundary is illustrated with a dashed blue line and a 10 km Universal Transverse Mercator map grid is shown for scale (UTM zone 21N, WGS84 coordinate system).



Fire is largely absent in this landscape, so infrequent outbreaks of defoliating insects are the primary form of stand-level natural disturbance in the region but seldom occur above 400 m because of climate constraints (McCarthy and Weetman 2006, Arsenault et al. 2016). Timber harvesting between 1990 and 2004 led to 21% of forest between 300 and 550 m being cleared with a mean harvest block size of 13.0 ha (median = 5.2, range 0.05 to 197.5). Additionally, in 2016 and 2017, a 60-m-wide electricity transmission corridor was created through the north-eastern corner of the survey area. The diversity of potential nest predators in the study area is limited. Along with red squirrels, Canada Jays and small mammals (i.e., *Microtus* spp. and *Peromyscus* spp.) are the most common nest predators in the study area; snakes, skunks, and racoons are absent, whereas marten and foxes occur at low densities (Thompson et al. 2008). Thus, nest predation is dominated by red squirrels with no compensatory predation occurring when red squirrels are removed (Lewis 2004), a phenomenon that has been found in other parts of the boreal forest (Bayne and Hobson 2002).

Data collection

Unlimited distance point count surveys were completed between 0500 h and 1400 h during the local breeding season from 8 June to 17 July 2016 and 11 June to 15 July 2017 (McDermott et al. 2023). Points were spaced 500 m apart in a grid pattern with 991 visited during 2016; the grid was shifted 250 m north and east in 2017, such that the 969 survey points visited during the second year of surveys fell midway between the 2016 locations (Fig. 1). This study design provided a systematic survey with balanced effort across the entire landscape that was proportional to fine-scale habitat availability, allowing us to assess the distributions of boreal birds across a >500 m elevation gradient. Each point was surveyed once by a solitary observer (four individuals during 2016, five individuals during 2017; one common to both years). The survey protocol was conceived for a separate study on Gray-cheeked Thrush, and included three 2-min silent listening periods (the basis for the current analyses; see below), followed by 2 min of Gray-cheeked Thrush song and call broadcast, 1 min of silent listening, 1 min of red squirrel call broadcast, and a final 1-min silent listening period (McDermott et al. 2023). Auditory and visual detections of red squirrels and all bird species were recorded in each time block. Site and survey information that could affect detection was also recorded, including date, time, observer, cloud cover (categories from 0 [no clouds] to 5 [complete cloud cover]), precipitation (categories of none, fog, drizzle, rain, snow), and wind speed (measured on the Beaufort scale). Surveys were not completed when precipitation or wind would strongly affect bird activity or detection (sustained rain, wind >5 Beaufort scale; 29 km/h). Other data for this study included red squirrel predicted occupancy, and elevation. The value for red squirrel predicted occupancy was taken from a previous analysis of this dataset and based on a model that best described squirrel occurrence in relation to landcover (McDermott et al. 2020). The model reflected negative associations between squirrels and water, coniferous scrub, and 10- to 30-year-old fir-spruce cover within 52.3 m of each sample point, as well as positive associations with the presence of 30- to 70-year-old fir-spruce and >70-year-old fir cover (McDermott et al. 2020). McDermott et al. (2020) found a strong negative trend in the probability of a red squirrel being present with increasing elevation, so our analyses below did not incorporate both variables in the same model. Note that although we collected squirrel observations in 2016 and 2017, squirrels were ~4 times more abundant in 2016 because of the high cone crop in the region during winter 2015–2016. For the analysis here we modeled squirrel predicted occupancy based solely on the 2016 data, which predicted much higher occupancy rates, because we feel that this better reflected the level of squirrel exposure that would have the greatest effect on bird distributions. That is, if a bird species is strongly affected by squirrels we do not expect the population to redistribute across the landscape each spring based on current squirrel numbers, but rather to have distributions that reflect the impacts of the high squirrel populations that would occur every 2-4 years in response to conifer masting. Elevation for each survey point was extracted from a digital elevation model from Natural Resources Canada's CanVec geospatial database (available under the Government of Canada's Open Government License [https://open.canada.ca/en]).

Data analysis

Individual species occupancy as a function of elevation and red squirrels

Data for all analyses were limited to the three 2-min silent listening periods at the beginning of the point counts to avoid potential positive or negative reactions of different bird species to the Gray-cheeked Thrush and red squirrel vocalization broadcasts. Time blocks were treated as independent visits (Manson et al. 2020, Eyster et al. 2024) in single season occupancy models using the *unmarked* package in R (Fiske and Chandler 2011). Observation covariates used to account for imperfect detection included: ordinal date (i.e., day of the year), time, observer, wind, cloud, precipitation, and elevation, as well as additive models, including date and time (to account for seasonal shifts in activity through the day), date and observer (to account for any potential differences among observers in learning across the season), plus date and elevation (to account for differences linked to heavier snow pack one year that limited access to higher elevation sites early in the season). Site was included in all models as a random effect to account for correlations in detections arising from visits occurring in sequence (three 2-min listening periods). Red squirrel predicted occupancy, year, and elevation were used as site covariates to assess their relations with the occupancy of each bird species analyzed. Continuous variables (time, red squirrel occupancy, and elevation) were standardized to have a mean of zero and a standard deviation of one. Occupancy analyses were limited to passerine and woodpecker species that were detected at >1.5% of points (i.e., at least 30 detections; total of 28 species), because fewer detections than this resulted in model convergence errors and unreliable parameter estimates.

Modeling followed a two-stage process. First, for each bird species, a series of 11 occupancy models was fit to identify the best detectability model for each species. These included a null model and ten models that each contained 1 or 2 observation covariates (as listed above). These models were compared using Akaike's Information Criterion corrected for small sample sizes (AICc), where the best model is the one with the lowest AICc and models within ΔAICc <2 are considered competing models (i.e., the "best model set"; Burnham and Anderson 2002). In cases where the null model fell within the best model set, it was chosen as the best detectability model. In cases where the best model was

>2 AICc better than the second-ranked model, it was chosen as the best detectability model. Where the best model set included more than one model, a new additive model that included both observation covariates was compared to the univariate models, and if it improved the AICc, then the additive model was chosen as the best detectability model.

Following this step, the observation covariate(s) present in the best detectability model for each species was used as the observation covariate(s) when fitting a set of occupancy models. A set of six models was fit for each species; a null model that only contained the chosen observation covariate(s) and no site covariates, and five models that contained the chosen observation covariate(s) and a subset of the site covariates: (1) year, (2) elevation, (3) elevation + year, (4) red squirrel, and (5) red squirrel + year. As noted above, the strong correlation between elevation and red squirrel occupancy negated our ability to include these covariates in the same model. These fitted models were then compared using AICc to assess the explanatory value of each term relative to the null model. Predicted occupancy plots for each bird species were created to visualize the relationship between bird species occurrence and their elevation distribution, as well as with respect to the predicted occupancy of red squirrels.

Species richness as a function of elevation and red squirrels

Avian species richness at each survey point was calculated for ground-nesting species, cavity-nesting species, and above-ground-nesting species (i.e., nesting in shrubs or trees above ground level, but not in a cavity), based on information in Billerman et al. (2020) and also reflecting guild placement by Thompson et al. (1999). These guilds were chosen because of differences in their susceptibility to nest predation by red squirrels (Martin 1995, Lewis 2004, Fontaine et al. 2007). Only passerines and woodpeckers were included in the species richness calculation for the nesting guilds (53 species). Other bird groups (an additional 19 species), such as gulls, raptors, waders, and waterfowl, were excluded because they are not reliably detected during point count surveys. Generalized additive models (GAMs) were then fit for each nesting guild, with species richness at each survey point as the response variable and a Poisson error distribution (R package *mgcv* 1.8–34; Wood 2011). For each species group we fit a null model and the same set of five explanatory models as for the single species analyses: (1) year, (2) elevation, (3) elevation + year, (4) red squirrel, and (5) red squirrel + year. Elevation and squirrel predicted occupancy were fit as continuous explanatory variables with smoothed nonparametric splines to allow for non-linear relationships. Predicted values of species richness were calculated on the basis of the GAMs and used to visualize the relationship of species richness with elevation and squirrel occupancy for each of the three nesting guilds. In some models (ground-nesting vs. elevation; cavity-nesting species vs. squirrel; and above-ground nesting species vs. squirrel) the value of *k* for the splined term was restricted to three to avoid overfitting and yield a biologically interpretable result. Models for each species group were compared and ranked by using AICc.

RESULTS

In 2016 and 2017 we surveyed a total of 1960 point locations and detected 72 bird species. Individual species were detected at as few as one survey point, and as many as 1682 (85.8% of) points (Appendix Table S1). Passerines and woodpeckers accounted for 53 of the species detected. Of these, 11 species were cavity nesters, 17 were ground nesters, and 25 were above-ground nesters (Appendix Table S1).

For the individual species occupancy analyses focusing on the 28 species of passerines and woodpeckers for which we had sufficient data, the null model was the best model or within 2 AICc of the best model for five species (Table 1), indicating that neither elevation nor red squirrel predicted occupancy was more informative in predicting the occupancy of these species. Elevation or elevation + year were the clear best models for 11 species (Table 1) and red squirrel or red squirrel + year were the clear best model for nine species (Table 1). Three species analyses produced results either with both elevation and red squirrel included in the best model set (Savannah Sparrow and Yellow-rumped Warbler) or with year as the best model (Black-and-white Warbler). Of the 28 species, there were 20 for which elevation (as either elevation or elevation + year) had more explanatory power than the null (i.e., performed better than the null by >2 AICc), even when they were not necessarily the best model, and for 17 of these, the univariate elevation model was better than the null, though not necessarily the best model (Appendix Table S2). The relationship between elevation and occupancy varied among species, where eight species had higher occupancy rates at higher elevations (Fig. 2), 11 species had lower occupancy as elevation increased (Fig.3), and the occupancy rates of nine species were unrelated to elevation (Canada Jay, Common Yellowthroat, Hermit Thrush, Northern Waterthrush, Pine Siskin, Rusty Blackbird, Tree Swallow, Winter Wren, and Yellow-rumped Warbler).

Red squirrel predicted occupancy had more explanatory power than the null (i.e., performed better than the null by >2 AICc) for 16 of 28 species (Appendix Table S2) and red squirrel + year had more explanatory power than the null for 19 species (Appendix Table S2). Species often responded inversely to elevation versus red squirrel occurrence with respect to expected occupancy probability, and in total nine species exhibited a positive relationship with squirrel occurrence (Fig. 4; American Robin and Yellow-bellied Flycatcher expected here because of negative relationship with elevation, but had no directional relationship with red squirrel occurrence) and ten species had a negative relationship with expected squirrel predicted occupancy (Fig. 5; including Hermit Thrush and Rusty Blackbird, which were neutral with respect to elevation but displayed directionality with respect to red squirrel occupancy).

For all three guilds considered in our species richness analyses, the candidate models were better than the null model, and in all cases the additive models including both elevation + year or red squirrel predicted occupancy + year were the two highest ranked models (Table 2). The output from the GAM analyses suggested curvilinear relationships with both elevation and squirrel occupancy (Figs. 6 and 7). Ground-nesting species richness was best predicted by the additive model that included predicted squirrel occupancy + year. The models suggested significant approximately linear relations with squirrel predicted occupancy, where richness decreased from ~3 to ~2 ground-nesting species per point as squirrel occupancy increased.

Table 1. Occupancy model comparisons grouped by best explanatory model for individual species relationships (passerines and woodpeckers) with elevation (elev), red squirrels (resq), and year on Newfoundland, Canada (2016 and 2017). Only best models (ΔAICc < 2) are presented (see Appendix Table S2 for full results). Each model contains a detection term(s) that was previously determined to be the best fit (all include site as a random effect), and an a priori set of occupancy terms. Species included were detected at > 1.5% of survey points.

Species	Detection structure	Occupancy structure	K	AICc	ΔAICc	ω	Log likelihood
Null model							
Canada Jay	cloud	null	8	1782.52	0.00	1.00	−883.22
Downy Woodpecker	cloud	null	8	173.81	0.00	1.00	−78.87
Northern Waterthrush	observer + day	null	11	4331.95	0.00	0.39	−2154.91
	observer + day	resq	12	4333.33	1.38	0.2	−2154.58
	observer + day	year	12	4333.91	1.96	0.14	−2154.88
Rusty Blackbird	wind	null	8	1572.90	0.00	1.00	−778.41
Winter Wren	day + time + elev	year	7	981.30	0.00	0.32	−483.62
	day + time + elev	resq + year	8	981.98	0.67	0.23	−482.95
	day + time + elev	null	6	982.84	1.53	0.15	−485.40
	day + time + elev	elev + year	8	983.14	1.84	0.13	−483.53
	day + time + elev	resq	7	983.23	1.93	0.12	−484.59
Elevation (+ year)							
American Robin	observer + day	elev	12	3201.51	0.00	0.41	−1588.68
	observer + day	elev + year	13	3202.30	0.79	0.27	−1588.06
Boreal Chickadee	observer + day	elev + year	12	1189.45	0.00	0.83	−582.64
Fox Sparrow	observer + day	elev + year	13	6479.19	0.00	1.00	−3226.50
Gray-cheeked Thrush	day + elev	elev	6	1543.60	0.00	0.62	−765.78
	day + elev	elev + year	7	1544.56	0.96	0.38	−765.25
Magnolia Warbler	observer + day	elev	12	1531.40	0.00	0.72	−753.62
	observer + day	elev + year	13	1533.28	1.88	0.28	−753.55
Olive-sided Flycatcher	observer	elev + year	12	766.34	0.00	1.00	−371.09
Pine Grosbeak	precipitation	elev + year	8	2428.65	0.00	0.69	−1206.29
Ruby-crowned Kinglet	observer + day	elev + year	13	6503.72	0.00	1	−3238.76
Tree Swallow	day + elev	year	6	699.26	0.00	0.69	−343.61
	day + elev	elev + year	7	701.24	1.99	0.26	−343.59
Wilson's Warbler	observer + day + time	elev	13	475.77	0.00	0.71	−224.79
	observer + day + time	elev + year	14	477.74	1.96	0.27	−224.76
Yellow-bellied Flycatcher	time	elev + year	6	5109.16	0.00	0.93	−2548.56
Red squirrel (+ year)							
Blackpoll Warbler	observer + day	resq	12	4970.08	0.00	0.65	−2472.96
	observer + day	resq + year	13	4971.38	1.30	0.34	−2472.60
Black-throated Green Warbler	observer + day	resq	12	421.11	0.00	0.50	−198.48
	observer + day	resq + year	13	421.90	0.79	0.34	−197.86
Common Yellowthroat	wind	resq + year	10	718.92	0.00	1.00	−349.40
Dark-eyed Junco	day + time + observer	resq + year	14	4473.36	0.00	0.86	−2222.57
Hermit Thrush	observer + day	resq	12	4586.20	0.00	0.52	−2281.02
	observer + day	resq + year	13	4586.78	0.58	0.39	−2280.30
Lincoln's Sparrow	observer + day	resq + year	13	3641.95	0.00	0.98	−1807.88
Pine Siskin	time	resq + year	6	445.90	0.00	1.00	−216.93
Swainson's Thrush	wind	resq	9	4094.82	0.00	0.64	−2038.37
	wind	resq + year	10	4096.62	1.79	0.26	−2038.25
White-throated Sparrow	observer + day	resq + year	13	5877.51	0.00	1	−2925.66
Other results							
Black-and-white Warbler	observer + day	year	12	1770.79	0.00	1.00	−873.31
Savannah Sparrow	cloud	elev	9	521.91	0.00	0.42	−251.91
	cloud	resq	9	523.26	1.35	0.22	−252.58
	cloud	elev + year	10	523.54	1.63	0.19	−251.72
Yellow-rumped Warbler	observer + day	elev + year	13	6078.59	0.00	0.39	−3026.20
	observer + day	year	12	6078.79	0.20	0.35	−3027.32
	observer + day	resq + year	13	6080.23	1.64	0.17	−3027.02

Richness of both cavity-nesting species and above-ground nesting species were both best predicted by the additive model that included elevation + year. For cavity-nesting species, richness was lower than one species per point throughout the elevation gradient and was highest at low elevations and decreased as elevation increased (Fig. 7). Above-ground nesting species richness decreased steadily with increasing elevation and averaged around 2.5 species per point. In contrast, for this guild the model with red squirrels suggested a curvilinear relation, where richness was highest at intermediate predicted squirrel occupancy rates.

DISCUSSION

Elevational gradients in boreal forest breeding songbird assemblages have received limited attention until relatively recent examinations of the impact of climate change at southern (e.g., Ralston and Kirchman 2013, Stralberg et al. 2015, Kirchman and Van Keuren 2017) and northern treeline (e.g., Lewis and Starzomski 2015, Mizel et al. 2023, Raymundo et al. 2024) peripheries. Information from databases such as the British Columbia Breeding Bird Atlas (Davidson et al. 2015) also shows the importance of elevation in structuring boreal bird

Fig. 2. Bird species that had a positive expected occupancy probability with increasing elevation in 2016 and 2017 in the Long Range Mountains, Newfoundland, Canada. Plots present expected occupancy probability (dark line) ± 95% confidence interval (paler lines).

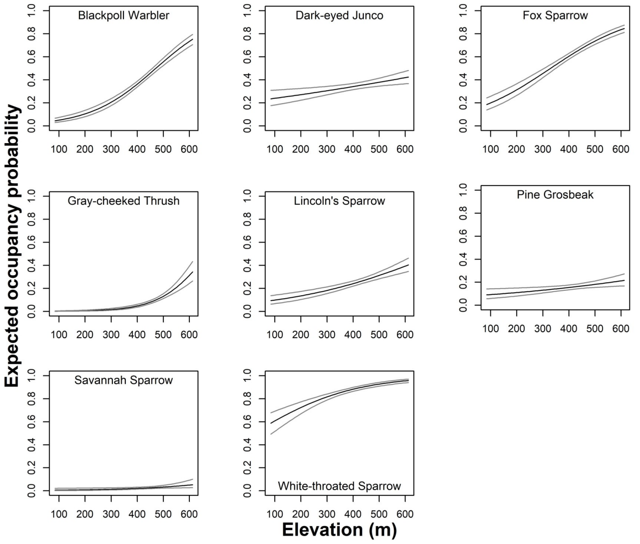
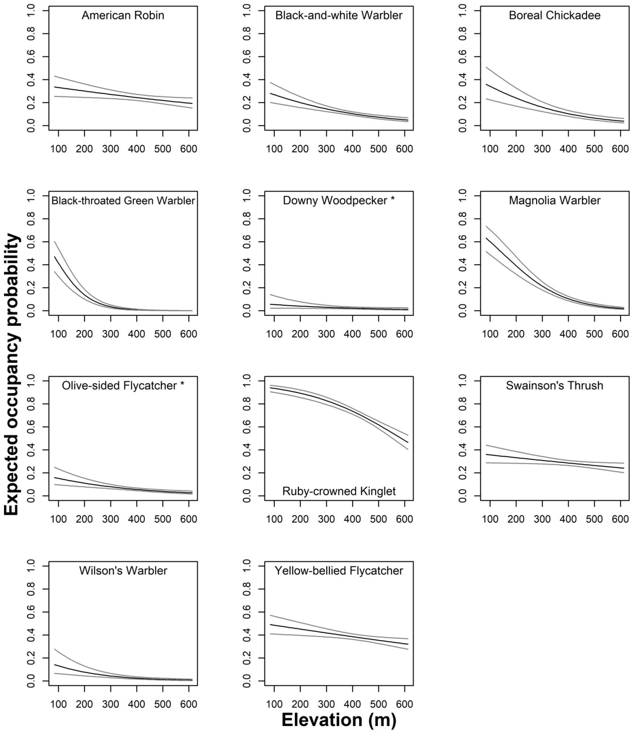


Fig. 3. Bird species that had a negative expected occupancy probability with increasing elevation in 2016 and 2017 in the Long Range Mountains, Newfoundland, Canada. * indicates that the elevation model is either worse than the null model, or of approximately equal predictive power. Plots present expected occupancy probability (dark line) ± 95% confidence interval (paler lines).



communities across mountainous regions. In addressing our first objective regarding the role that elevation plays in the distribution of individual species, we found that, although the range of elevations sampled spanned just 535 m, the distributions of many species were strongly related to elevation. Of the 28 most commonly detected species, occupancy rates increased with increasing elevation for eight species, whereas for 11 species occupancy rates decreased at higher elevations. Based on species accounts (Billerman et al. 2020) and evaluations of habitat associations for boreal songbird species in response to environmental change (Ralston et al. 2019), our findings correspond with general expectations. Some of the most pronounced increases in occupancy at higher elevations were for species typically associated with more northerly boreal ecosystems, including Blackpoll Warbler, Fox Sparrow, Gray-cheeked Thrush, and Lincoln's Sparrow. Conversely, some of the strongest negative relationships between occupancy and elevation were for species that are broadly associated with southern boreal ecosystems, including Black-throated Green Warbler, Magnolia Warbler, and Black-and-white Warbler. Interestingly, the distributions of some species with broad latitudinal ranges were also strongly related to elevation, including Boreal Chickadee and Ruby-crowned Kinglet, which were detected more often at low elevations, and Dark-eyed Junco and White-throated Sparrow, which were more common at higher elevations. Most species that were more common at higher elevations were also negatively associated with our index of red squirrel occupancy, which is not surprising given the strong negative correlation between red squirrel presence and elevation in our study area. Similarly, most species that were more common at lower elevations were positively associated with red squirrels. These latter relationships are not unexpected given the greater abundance of squirrels at lower elevations, and more likely reflect general habitat associations rather than an affinity for co-habiting with red squirrels. This does make it difficult to interpret trends based on red squirrel occupancy independent of elevation, so teasing out the true effect of red squirrels will require other approaches, such as removal or exclusion studies to assess their actual effect on bird occupancy, survivorship, or nesting success.

The elevation distributions for individual species reflect spatial structure of the boreal bird assemblage but also provide insight into which species may be most at risk of extirpation from the island of Newfoundland because of climate change. In other regions of the boreal forest, many high elevation species have experienced upslope shifts in both their upper and lower elevation boundaries, or downslope shifts in their lower boundary (Mizel et al. 2016, DeLuca and King 2017, Kirchman and Van Keuren 2017). Upslope shifts and range contraction of high elevation species, such as Blackpoll Warbler, Fox Sparrow, and Gray-cheeked Thrush, could leave them at higher risk of decline or extirpation than species that are abundant across a broader elevational range. Interestingly, Ralston and Kirchman (2013) projected that Blackpoll Warbler should persist in mountainous regions of western Newfoundland through 2080 based on a contemporary distribution map that showed the species range

Fig. 4. Bird species that had a positive expected occupancy probability with increasing red squirrel occupancy in 2016 and 2017 in the Long Range Mountains, Newfoundland, Canada. * indicates that the red squirrel model is either worse than the null model, or of approximately equal predictive power. Plots present expected occupancy probability (dark line) ± 95% confidence interval (paler lines).

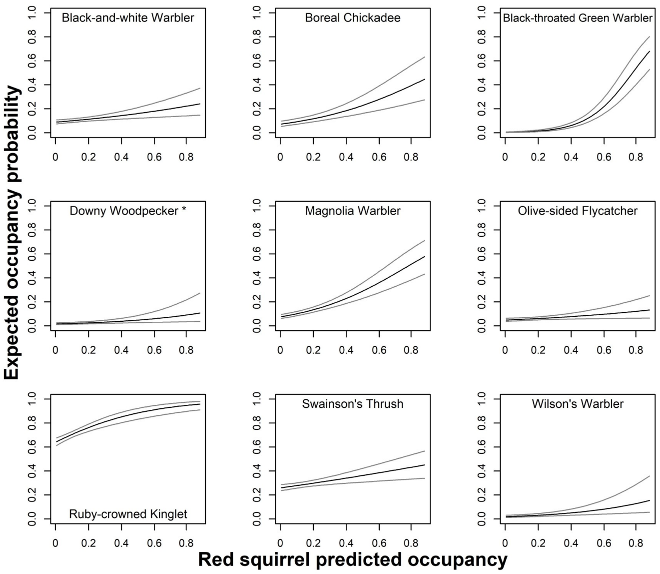
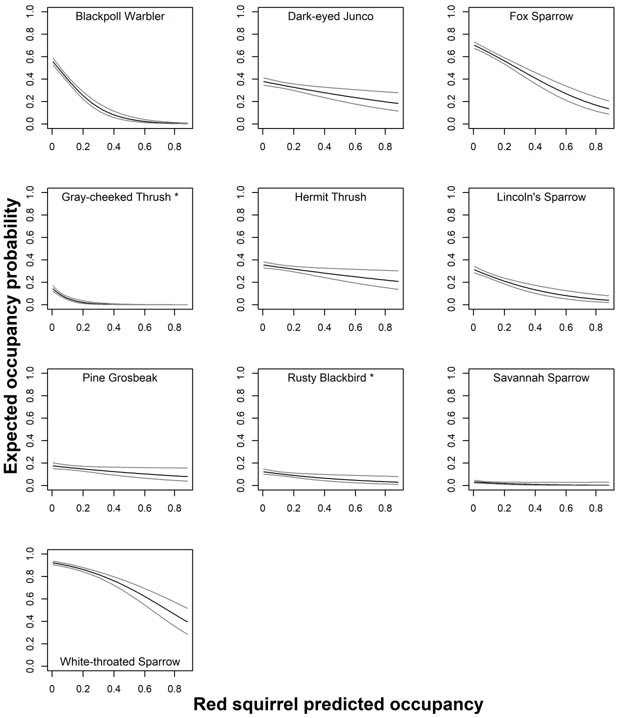


Fig. 5. Bird species that had a negative expected occupancy probability with increasing red squirrel occupancy in 2016 and 2017 in the Long Range Mountains, Newfoundland, Canada. * indicates that the red squirrel model is either worse than the null model, or of approximately equal predictive power. Plots present expected occupancy probability (dark line) ± 95% confidence interval (paler lines).



encompassing the entire island. However, those starting values may have been inflated because of a lack of detailed information on current elevation distribution; our results indicated that Blackpoll Warblers have much higher occupancy rates at higher elevations. Low- or mid-elevation bird species may be in less danger of extirpation because of climate change in the short term, but, provided suitable habitat is available (Stralberg et al. 2015), could experience upslope distribution shifts, encroaching on ranges that were previously occupied by different community members, or by higher elevation species moving downslope (DeLuca and King 2017, Kirchman and Van Keuren 2017, Neate-Clegg et al. 2021). This could cause increased overlap among species having similar ecological niches, leading to increased heterospecific competition (Ralston and DeLuca 2020). In other regions, such elevational overlap by potentially competing species is increasing between Hermit Thrush, Swainson's Thrush, and Bicknell's Thrush, and the presence of a more aggressive species could be constraining others (Aubry et al. 2016, Freeman and Montgomery 2016, DeLuca and King 2017). Clearly, increased baseline data and contemporary distribution information can only serve to increase reliability of modeled future distributions.

Historical data for species distributions on Newfoundland are limited and this constrains our understanding of range expansions and contractions that may have already occurred in response to changing environmental conditions. However, some data on elevational distributions are available for Newfoundland. Lamberton's (1976) surveys in coastal and montane regions of Gros Morne National Park in western Newfoundland are among the few historic records that provide information on high and low elevation boreal bird communities for the island. This work played an integral part in understanding the sudden range contraction of the Gray-cheeked Thrush on Newfoundland to high elevation areas (Whitaker et al. 2015, McDermott et al. 2023), which is also evident in the results presented here. BBS data also have great potential to identify trends in species populations and distributions; however, on Newfoundland, BBS routes are limited to elevations below ~400 m in large part because of a lack of roads in higher elevation areas. This limitation likely also occurs in other mountainous regions of the boreal forest where many of the responses by species to climate change are likely to be most profound. Consequently, high elevation bird species are not properly sampled, and cases such as that of the Newfoundland Gray-cheeked Thrush may be almost entirely overlooked by the BBS network (Robineau-Charette et al. 2023, COSEWIC 2024). This could result in under-estimation of population sizes and range distributions, as well as inaccurate population trend estimates, which could impair species conservation or management.

Our second objective was to identify bird species for which occupancy rate was correlated with squirrel probability of occurrence. Feldman et al. (2023) found that, overall, boreal bird species richness and the occupancy of 20 of 96 species in their northern Québec study area decreased with higher squirrel

Table 2. Model comparisons for species richness relationships with elevation (elev), red squirrels (resq), and year, as assessed for three nesting guilds detected on Newfoundland, Canada (2016 and 2017). For each species group the same a priori set of occupancy models was assessed. Null model appears in bold for ease of reference.

Species group	Model	df	Log likelihood	AICc	ΔAICc	ω
Ground-nesting species	resq + year	4	−3561.82	7133.51	0.00	1.00
	elev + year	3	−3571.83	7151.53	18.02	0.00
	elev	2	−3585.78	7177.41	43.90	0.00
	resq	3	−3587.85	7182.63	49.13	0.00
	year	1	−3591.74	7187.48	53.97	0.00
	null	**0**	**−3605.51**	**7213.02**	**79.52**	**0.00**
Cavity-nesting species	elev + year	7	−1028.65	2073.20	0.00	1.00
	resq + year	3	−1039.21	2084.44	11.23	0.00
	resq	2	−1043.59	2091.19	17.99	0.00
	elev	6	−1039.86	2093.77	20.56	0.00
	year	2	−1047.29	2098.58	25.37	0.00
	null	**0**	**−1058.74**	**2119.48**	**46.28**	**0.00**
Above-ground nesting species	elev + year	4	−3356.86	6723.40	0.00	0.58
	resq + year	3	−3358.13	6724.07	0.67	0.42
	year	2	−3364.79	6733.58	10.18	0.00
	resq	2	−3381.60	6769.12	45.72	0.00
	elev	3	−3397.82	6802.98	79.57	0.00
	null	**0**	**−3405.33**	**6812.67**	**89.27**	**0.00**

Fig. 6. Predicted species richness for ground-nesting species (n = 17), cavity-nesting species (n = 11), and above-ground nesting species (n = 25) in relation to elevation in the Long Range Mountains, Newfoundland, Canada, in 2016 and 2017. Plots present predicted species richness for each grouping (dark lines) ± 95% confidence interval (paler lines) for each category.

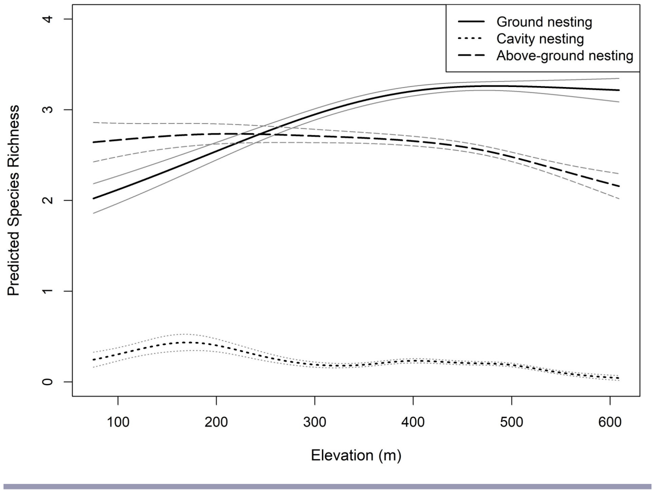
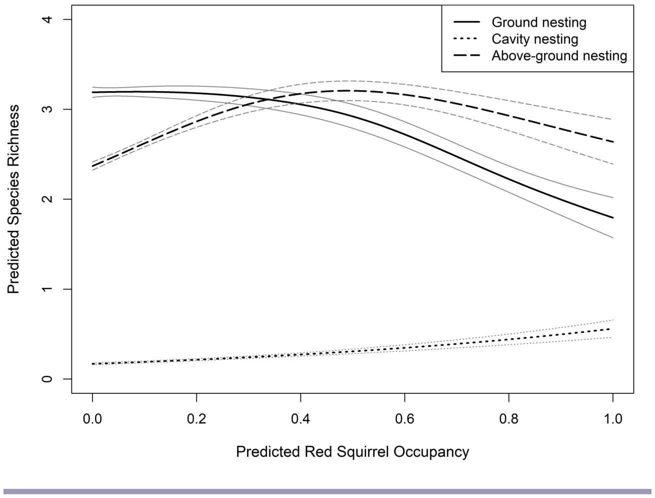


Fig. 7. Predicted species richness for ground-nesting species (n = 17), cavity-nesting species (n = 11), and above-ground nesting species (n = 25) in relation to predicted red squirrel occupancy in the Long Range Mountains, Newfoundland, Canada, in 2016 and 2017. Plots present predicted species richness for each grouping (dark lines) ± 95% confidence interval (paler lines) for each category.



presence. Of the 28 forest bird species we assessed, ten (35.7%) showed an inverse relationship with squirrel probability of occurrence; Savannah Sparrow was the only species in common with the Feldman et al. (2023) study that showed this pattern. Although for some species a negative pattern with respect to squirrels may have resulted from a simple difference in habitat affinity compared to squirrels (e.g., Rusty Blackbird and Savannah Sparrow), such differences are not immediately obvious for others. Further, the breeding ranges of some of these species span broad latitudinal ranges (e.g., Dark-eyed Junco and White-throated Sparrow), suggesting that this pattern may not have resulted from a simple preference for northern boreal vegetation types or bioclimatic conditions that are more prevalent at higher elevations. However, all the species for which squirrel probability of occurrence was a better inverse predictor of occurrence than elevation use open cup ground or shrub nests that may make them more vulnerable to squirrels (Martin and Joron 2003, Willson et al. 2003, Fontaine et al. 2007). Also consistent with this pattern, Dalley et al. (2009) found that nest survival was unusually high for Blackpoll Warbler and White-throated Sparrow at high elevations in our study area, and Thompson et al. (2008) also documented low rates of predation on artificial nests. Future studies should investigate whether the distribution of these species may have been constrained by introduced squirrels, for example through comparison of contemporary and historical patterns of elevation distribution using stop-level BBS data (Robineau-Charette et al. 2023), or comparison between similar squirrel-colonized and squirrel-free off-shore islands adjacent to Newfoundland. Positive relationships between nine species and squirrel probability of occurrence may seem counter-intuitive especially because they are all open cup nesters, but likely reflect habitat associations with the lower elevation forests in which squirrels are most abundant in this landscape (McDermott et al. 2020) rather than causal relationships. Similar to our findings, Feldman et al. (2023) also noted positive associations with squirrel presence for Olive-sided Flycatcher and Ruby-crowned Kinglet, which typically nest high in the forest canopy where squirrel predation is lower (Altman and Salabanks 2020, Swanson et al. 2021), as well as for Canada Jay and Yellow-bellied Flycatcher, for which we did not detect any relationship with squirrels.

Our assessment of relationships between bird species distributions and red squirrel occupancy lacks nuance because of the simplicity of the models we evaluated. We calculated squirrel probability of occurrence for each point based on habitat models developed by using stand age classes for spruce and/or fir cover, elevation, water courses in the area around the point, and the extent of coniferous scrub (McDermott et al. 2020). To avoid complicating model selection and to focus on the main question of the structure of bird assemblages in the context of elevation, we did not include habitat variables in our assessments of models of avian occupancy. Nevertheless, habitat is an important factor affecting bird species distributions (Imbeau et al. 2001, Schieck and Song 2006) and omitting these variables from the analyses could have limited our ability to detect the relationship a bird species has with red squirrels. For example, there are data that implicate red squirrels in strongly limiting the contemporary distribution of Gray-cheeked Thrush on the island of Newfoundland (McDermott et al. 2023, Robineau-Charette et al. 2023, COSEWIC 2024), yet elevation models performed better in our analyses of Gray-cheeked Thrush compared to those including red squirrels. This may have arisen because of underlying habitat associations, which, even before the spread of squirrels, resulted in this species having a bimodal elevation distribution in which it was most abundant at high elevations but also common in coastal habitats (Lamberton 1976, Robineau-Charette et al. 2023). Some of the discrepancies also may have arisen from differences between years in the impact of squirrels on bird species in this community. Squirrels clearly respond to annual variation in cone production as well as to forest structure and composition, with annual squirrel density changing dramatically based on conifer seed availability. The impact of squirrels on songbird populations in the boreal forest is likely the combined result of variable cone crops, changes to forest composition and structure over time, and environmental variability as it affects those features of the forest. Experimentation within this system is needed to clarify the relationships between bird population distributions and elevation, habitat, and red squirrels.

For our third objective we focused on nesting guild species richness to investigate the influence of elevation and red squirrel occurrence on these guilds. Previous assessments of boreal birds instead focused on associations with different successional stages rather than nesting guilds and suggested that late successional species may be successful despite high squirrel abundance, reflecting extensive nesting in the forest canopy, whereas squirrel nest predation pressure may be higher in the understory or at ground level (Sieving and Willson 1998, Feldman et al. 2023). Our findings indicated that there are assemblage-level patterns associated with elevation and suggested that the effects of red squirrels on individual species may be pervasive enough to affect the overall structure and composition of boreal bird assemblages. Ground-nesting species, which are most vulnerable to nest predation (Martin 1995, Fontaine et al. 2007), had the lowest richness at points located at lower elevations, where red squirrels are most abundant. This result is consistent with Sieving and Willson (1998) and Willson et al. (2003) who found that birds nesting on the ground or in low-lying shrubs occur at lower densities as squirrels become more common. In contrast, above-ground nesting species and cavity-nesting species, which are less vulnerable to nest predation by red squirrels (Martin 1995, Siepielski 2006, Fontaine et al. 2007), had higher richness at lower elevations. However, these trends are most likely related, at least in part, to habitat traits rather than just red squirrel occupancy. Comparing population trends for species on Newfoundland to those on the continent using BBS data may help highlight those species that are particularly vulnerable to red squirrel nest predation, as well as comparing avian communities on similar islands with and without squirrels.

Studies noted above have demonstrated the effects of climate change on boreal forest bird populations, and our results suggest that populations of boreal birds in mountainous areas such as western Newfoundland are also likely to show significant change and re-distribution in response to climate change. Consequently, the BBS and other large scale monitoring programs need to actively sample across the elevation gradient or, alternatively, targeted monitoring is needed for montane portions of the boreal forest. Landbird research and monitoring should also incorporate quantification of red squirrel activity. These actions will enable further assessment of responses to climate change by boreal forest songbirds and the broader threats posed as habitats and their inhabitants are modified.

Author Contributions:

Conceptualization: DMW (lead), JPBM and IGW (supporting); data collection and curation: JPBM; analyses: JPBM and IGW (equal), DMW (supporting); writing draft: JPBM and IGW (equal); writing – review and editing: IGW, JPBM, DMW (equal).

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Data Availability:

Data supporting the analyses in this paper are stored in the Memorial University Data Repository (Borealis - https://doi.org/10.5683/SP3/PZCVSO).

LITERATURE CITED

Altman, B., and R. Sallabanks. 2020. Olive-sided Flycatcher (Contopus cooperi), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.olsfly.01

Anderson, M. G., M. Clark, C. E. Ferree, A. Jospe, A. Olivero Sheldon, and K. J. Weaver. 2013. Northeast. Habitat guides: a companion to the terrestrial and aquatic habitat maps. The Nature Conservancy, Eastern Conservation Science, Boston, Massachusetts, USA.

Arsenault, A., R. LeBlanc, E. Earle, D. Brooks, B. Clarke, D. Lavigne, and L. Royer. 2016. Unravelling the past to manage Newfoundland's forests for the future. Forestry Chronicle 92:487-502. https://doi.org/10.5558/tfc2016-085

Aubry, Y., A. Desrochers, and G. Seutin. 2016. Regional patterns of habitat use by a threatened forest bird, the Bicknell's Thrush (Catharus bicknelli), in Quebec. Canadian Journal of Zoology 94:301-309. http://dx.doi.org/10.1139/cjz-2015-0209

Auer, S. K., and D. I. King. 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. Global Ecology and Biogeography 23:867-875. https://doi.org/10.1111/geb.12174

Baldwin, K., L. Allen, S. Basquill, K. Chapman, D. Downing, N. Flynn, W. MacKenzie, M. Major, W. Meades, D. Meidinger, et al. 2019. Vegetation zones of Canada: a biogeoclimatic perspective. [Map] Scale 1:5,000,000. Natural Resources Canada, Canadian Forest Service. Great Lake Forestry Center, Sault Ste. Marie, Ontario, Canada. https://publications.gc.ca/site/eng/9.885047/publication.html

Barry, R. G. 2008. Mountain, weather, and climate. Third edition. Cambridge University Press, Cambridge, UK.

Bateman, B. L., L. Taylor, C. Wilsey, J. Wu, G. S. LeBaron, and G. Langham. 2020. Risk to North American birds from climate change-related threats. Conservation Science and Practice 2:e243. https://doi.org/10.1111/csp2.243

Bayne, E. M., and K. A. Hobson. 2002. Effects of red squirrel (Tamiasciurus hudsonicus) removal on survival of artificial songbird nests in boreal forest fragments. American Midland Naturalist 147:72-79. https://doi.org/10.1674/0003-0031(2002)147[0072:EORSTH]2.0.CO;2

Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, editors. 2020. Birds of the world. Cornell Laboratory of Ornithology, Ithaca, New York, USA. https://birdsoftheworld.org/bow/home

Blake, J. G., and B. A. Loiselle. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. Auk 117(3):663-686. https://doi.org/10.1093/auk/117.3.663

Brandt, J. P. 2009. The extent of the North American boreal zone. Environmental Reviews 17:101-161. https://doi.org/10.1139/A09-004

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer, New York, New York, USA. https://doi.org/10.1007/b97636

COSEWIC. 2024. COSEWIC status report on Gray-cheeked Thrush minimus subspecies Catharus minimus minimus in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ontario, Canada. https://publications.gc.ca/site/eng/9.938289/publication.html

Dalley, K. L., P. D. Taylor, and D. Shutler. 2009. Success of migratory songbirds breeding in harvested boreal forests of northwestern Newfoundland. Condor 111(2):314-325. http://dx.doi.org/10.1525/cond.2009.080104

Damman, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Pages 163-206 in G. R. South, editor. Biogeography and ecology of the island of Newfoundland. W. Junk Publishers, The Hague, The Netherlands.

Darveau, M., L. Bélanger, J. Huot, É. Mélançon, and S. DeBellefeuille. 1997. Forestry practices and the risk of bird nest predation in a boreal coniferous forest. Ecological Applications 7:572-580. https://doi.org/10.1890/1051-0761(1997)007[0572:FPATRO]2.0.CO;2

Davidson, P. J. A., R. J. Cannings, A. R. Couturier, D. Lepage, and C. M. Di Corrado, editors. 2015. The atlas of the breeding birds of British Columbia, 2008–2012. Bird Studies Canada, Delta, British Columbia, Canada. https://www.birdatlas.bc.ca/

DeLuca, W. V., and D. I. King. 2017. Montane birds shift downslope despite recent warming in the northern Appalachian Mountains. Journal of Ornithology 158:493-505. https://doi.org/10.1007/s10336-016-1414-7

DeSante, D. F., D. R. Kaschube, and J. F. Saracco. 2015. Vital rates of North American landbirds. Institute for Bird Populations. https://VitalRatesOfNorthAmericanLandbirds.org

Eyster, H. N., K. M. A. Chan, M. E. Fletcher, and B. Beckage. 2024. Space-for-time substitutions exaggerate urban bird-habitat ecological relationships. Journal of Animal Ecology 93(12):1854-1867. https://doi.org/10.1111/1365-2656.14194

Feldman, M. J., M. J. Mazerolle, L. Imbeau, and N. J. Fenton. 2023. Beaver activity and red squirrel presence predict bird assemblages in boreal Canada. Ornithology 140(2):ukad009. https://doi.org/10.1093/ornithology/ukad009

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43(10):1-23. https://doi.org/10.18637/jss.v043.i10

Fitzgerald A. M., D. M. Whitaker, J. Ralston J. J. Kirchman, and I. G. Warkentin. 2017. Taxonomy and distribution of the imperilled Newfoundland Gray-cheeked Thrush, Catharus minimus minimus. Avian Conservation and Ecology 12(1):10. https://doi.org/10.5751/ACE-00976-120110

Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioral correlates of nest predation. Oikos 116(11):1887-1894. https://doi.org/10.1111/j.0030-1299.2007.16043.x

Freeman, B. G., and G. Montgomery. 2016. Interspecific aggression by the Swainson's Thrush (Catharus ustulatus) may limit the distribution of the threatened Bicknell's Thrush (Catharus bicknelli) in the Adirondack Mountains. Condor 118 (1):169-178. https://doi.org/10.1650/CONDOR-15-145.1

Haché, S., E. M. Bayne, and M.-A. Villard. 2014. Postharvest regeneration, sciurid abundance, and postfledging survival and movements in an Ovenbird population. Condor 116(1):102-112. https://doi.org/10.1650/CONDOR-13-002-R2.1

Hallworth, M. T., A. P. K. Sirén, W. V. DeLuca, T. R. Duclos, K. P. McFarland, J. M. Hill, C. C. Rimmer, and T. L. Morelli. 2024. Boom and bust: the effects of masting on seed predator range dynamics and trophic cascades. Diversity and Distributions 30: e13861. https://doi.org/10.1111/ddi.13861

Imbeau, L., M. Mönkkönen, and A. Desrochers. 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. Conservation Biology 15:1151-1162. https://doi.org/10.1046/j.1523-1739.2001.0150041151.x

Jones, M. T., and L. L. Willey. 2012. Eastern alpine guide: natural history and conservation of mountain tundra east of the Rockies. University Press of New England, Lebanon, New Hampshire, USA. https://doi.org/10.2307/j.ctv1xx9jdz

Kirchman, J. J., and A. E. Van Keuren. 2017. Altitudinal range shifts of birds at the southern periphery of the boreal forest: 40 years of change in the Adirondack Mountains. Wilson Journal of Ornithology 129(4):742-753. https://doi.org/10.1676/16-164.1

Körner, C. 2007. The use of "altitude" in ecological research. Trends in Ecology & Evolution 22(11):569-574. https://doi.org/10.1016/j.tree.2007.09.006

Lait, L. A., and T. M. Burg. 2013. When east meets west: population structure of a high-latitude resident species, the boreal chickadee (Poecile hudsonicus). Heredity 111:321-329. https://doi.org/10.1038/hdy.2013.54

Lamberton, R. D. 1976. Avifaunal survey of Gros Morne National Park. Parks Canada, Rocky Harbour, Newfoundland and Labrador, Canada.

Lees, A. C., L. Haskell, T. Allinson, S. B. Bezeng, I. J. Burfield, L. M. Renjifo, K. V. Rosenberg, A. Viswanathan, and S. H. M. Butchart. 2022. State of the world's birds. Annual Review of Environment and Resources 47:231-260. https://doi.org/10.1146/annurev-environ-112420-014642

Lewis, K. P. 2004. Processes underlying nest predation by introduced red squirrels (Tamiasciurus hudsonicus) in the boreal forest of Newfoundland. Dissertation. Memorial University of Newfoundland. http://research.library.mun.ca/id/eprint/10880

Lewis, K. P., and B. M. Starzomski. 2015. Bird communities and vegetation associations across a treeline ecotone in the Mealy Mountains, Labrador, which is an understudied part of the boreal forest. Canadian Journal of Zoology 93(6):477-486. http://dx.doi.org/10.1139/cjz-2014-0309

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84(3):485-513. https://doi.org/10.1111/j.1469-185X.2009.00085.x

Mainwaring, M. C., I. Barber, D. C. Deeming, D. A. Pike, E. A. Roznik, and I. R. Hartley. 2017. Climate change and nesting behaviour in vertebrates: a review of the ecological threats and potential for adaptive responses. Biological Reviews 92:1991-2002. https://doi.org/10.1111/brv.12317

Manson, K. K. E., J. P. B. McDermott, L. L. Powell, D. M. Whitaker, and I. G. Warkentin. 2020. Assessment of Rusty Blackbird habitat occupancy in the Long Range Mountains of Newfoundland, Canada using forest inventory data. Diversity 12 (9):340. https://doi.org/10.3390/d12090340

Martin, J.-L., and M. Joron. 2003. Nest predation in forest birds: influence of predator type and predator's habitat quality. Oikos 102(3):641-653. https://doi.org/10.1034/j.1600-0706.2003.12040.x

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65 (1):101-127. https://doi.org/10.2307/2937160

Martin, T. E., and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73(2):579-592. https://doi.org/10.2307/1940764

McCain, C. M. 2009. Global analysis of bird elevational diversity. Global Ecology and Biogeography 18(3):346-360. https://doi.org/10.1111/j.1466-8238.2008.00443.x

McCarthy, J. W., and G. Weetman. 2006. Age and size structure of gap-dynamic, old-growth boreal forest stands in Newfoundland. Silva Fennica 40(2):339. https://doi.org/10.14214/sf.339

McDermott, J. P. B., D. M. Whitaker, and I. G. Warkentin. 2020. Constraints on range expansion of introduced red squirrels (Tamiasciurus hudsonicus) in an island ecosystem. Canadian Journal of Forest Research 50(10):1064-1073. https://doi.org/10.1139/cjfr-2019-0369

McDermott, J. P. B., D. M. Whitaker, and I. G. Warkentin. 2023. Spatial segregation between Gray-cheeked Thrush and an introduced nest predator in a managed forest landscape. Avian Conservation and Ecology 18(2):5. https://doi.org/10.5751/ACE-02472-180205

McFarland, K. P., C. C. Rimmer, S. J. K. Frey, S. D. Faccio, and B. B. Collins. 2008. Demography, ecology and conservation of Bicknell's Thrush in Vermont, with a special focus on the Northeastern Highlands. Technical Report 08-03. Vermont Center for Ecostudies, Norwich, Vermont, USA.

Miller, C. V., C. M. Bossu, J. F. Saracco, D. P. L. Toews, C. S. Rushing, A. Roberto-Charron, J. A. Tremblay, R. B. Chandler, M. G. DeSaix, C. J. Fiss, et al. 2024. Genomics-informed conservation units reveal spatial variation in climate vulnerability in a migratory bird. Molecular Ecology 33:e17199. https://doi.org/10.1111/mec.17199

Mizel, J. D., J. H. Schmidt, C. L. McIntyre, and C. A. Roland. 2016. Rapidly shifting elevational distributions of passerine species parallel vegetation change in the subarctic. Ecosphere 7: e01264. https://doi.org/10.1002/ecs2.1264

Mizel, J. D., J. H. Schmidt, C. A. Roland, and C. L. McIntyre. 2023. Tree and shrub expansion at treeline drive contrasting responses in a subarctic passerine community. Journal of Animal Ecology 92(6):1256-1266. https://doi.org/10.1111/1365-2656.13936

Morosinotto, C., R. L. Thomson, and E. Korpimäki. 2010. Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. Journal of Animal Ecology 79(2):327-333. https://doi.org/10.1111/j.1365-2656.2009.01638.x

NABCI. 2000. Bird conservation region descriptions: a supplement to the North American Bird Conservation Initiative Bird Conservation Regions Map. North American Bird Conservation Initiative Committee. https://nabci-us.org/resources/bird-conservation-regions/

Neate-Clegg, M. H. C., S. E. I. Jones, J. A. Tobias, W. D. Newmark, and Ç. H. Şekercioğlu. 2021. Ecological correlates of elevational range shifts in tropical birds. Frontiers in Ecology and Evolution 9:621749. https://doi.org/10.3389/fevo.2021.621749

Pardieck, K. L., D. J. Ziolkowski Jr., M.-A. R. Hudson, and K. Campbell. 2016. North American breeding bird survey dataset 1966 - 2015. Version 2015.1. U.S. Geological Survey (USGS), Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I. Chen, T. D. Clark, R. K, Colwell, F. Danielsen, B. Evengård et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355: eaai9214. https://doi.org/10.1126/science.aai9214

Poulin, J-F., M-A. Villard, and S. Haché. 2010. Short-term demographic response of an old forest specialist to experimental selection harvesting. Écoscience 17(1):20-27. https://doi.org/10.2980/17-1-3297

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18:200-205. https://doi.org/10.1111/j.1600-0587.1995.tb00341.x

Ralston, J., and W. V. DeLuca. 2020. Conservation lessons from the study of North American boreal birds at their southern periphery. Diversity 12(6):257. https://doi.org/10.3390/d12060257

Ralston, J., A. M. FitzGerald, S. E. Scanga, and J. J. Kirchman. 2019. Observations of habitat associations in boreal forest birds and the geographic variation in bird community composition. Wilson Journal of Ornithology 131(1):12-23. https://doi.org/10.1676/18-14

Ralston, J., and J. J. Kirchman. 2012. Continent-scale genetic structure in a boreal forest migrant, the Blackpoll Warbler (Steophaga striata). Auk 129(3):467-478. https://doi.org/10.1525/auk.2012.11260

Ralston, J., and J. J. Kirchman. 2013. Predicted range shifts in North American boreal forest birds and the effect of climate change on genetic diversity in blackpoll warblers (Setophaga striata). Conservation Genetics 14:543-555. https://doi.org/10.1007/s10592-012-0418-y

Raymundo A., T. Micheletti, S. Haché, D. Stralberg, F. E. C. Stewart, J. A. Tremblay, C. Barros, I. M. S. Eddy, A. M. Chubaty, M. Leblond, et al. 2024. Climate-sensitive forecasts of marked short-term and long-term changes in the distributions or abundances of Northwestern boreal landbirds. Climate Change Ecology 7:100079. https://doi.org/10.1016/j.ecochg.2023.100079

Robertson, A. 1993. Forests and climate. Pages 76-88 in A. Robertson, S. Porter, and G. Brodie, editors. Climate and weather of Newfoundland and Labrador. Creative Publishers, St. John's, Newfoundland, Canada.

Robineau-Charette, G., D. M. Whitaker, and I. G. Warkentin. 2023. Change in altitudinal distribution of Newfoundland Gray-cheeked Thrush (Catharus minimus minimus) revealed through historical stop-level breeding bird survey data. Journal of Field Ornithology 94(1):4. https://doi.org/10.5751/JFO-00210-940104

Rowe, J. S. 1972. Forest regions of Canada. Publication No. 1300. Department of the Environment, Canadian Forest Service. Ottawa, Ontario, Canada.

Schieck, J., and S. J. Song. 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: literature review and meta-analyses. Canadian Journal of Forest Research 36(5):1299-1318. https://doi.org/10.1139/x06-017

Sherry, T. W., S. Wilson, S. Hunter, and R. T. Holmes. 2015. Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory songbird. Journal of Avian Biology 46(6):559-569. https://doi.org/10.1111/jav.00536

Siepielski, A. M. 2006. A possible role for red squirrels in structuring breeding bird communities in lodgepole pine forests. Condor 108(1):232-238. https://doi.org/10.1093/condor/108.1.232

Sieving, K. E., and M. F. Willson. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology 79 (7):2391-2402. https://doi.org/10.1890/0012-9658(1998)079[2391:NPAASD]2.0.CO;2

Stralberg, D., E. M. Bayne, S. G. Cumming, P. Sólymos, S. J. Song, F. K. A. Schmiegelow. 2015. Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: a modified refugia approach. Diversity and Distributions 21(9):1112-1128. https://doi.org/10.1111/ddi.12356

Swanson, D. L., J. L. Ingold, and G. E. Wallace. 2021. Ruby-crowned Kinglet (Corthylio calendula), version 1.1. In Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.ruckin.01.1

Thompson, I. D., H. A. Hogan, and W. A. Montevecchi. 1999. Avian communities of mature balsam fir forests in Newfoundland: age dependence and implications for timber harvesting. Condor 101(2):311-323. https://doi.org/10.2307/1369994

Thompson, R. G., I. G. Warkentin, and S. P. Flemming. 2008. Response to logging by a limited but variable nest predator guild in the boreal forest. Canadian Journal of Forest Research 38 (7):1974-1982. https://doi.org/10.1139/X08-049

Whitaker, D. 2015. The colonisation of Newfoundland by red squirrels (Tamiasciurus hudsonicus); chronology, environmental effects and future needs. Osprey 46:23-29. https://www.researchgate.net/publication/306436884

Whitaker, D. M., and S. W. Eaton. 2020. Northern Waterthrush (Parkesia noveboracensis), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.norwat.01

Whitaker, D. M., P. D. Taylor, and I. G. Warkentin. 2015. Gray-cheeked Thrush (Catharus minimus minimus) distribution and habitat use in a montane forest landscape of western Newfoundland, Canada. Avian Conservation and Ecology 10 (2):4. https://doi.org/10.5751/ACE-00778-100204

Willson, M. F., T. L. De Santo, and K. E. Sieving. 2003. Red squirrels and predation risk to bird nests in northern forests. Canadian Journal of Forest Research 81(7):1202-1208. https://doi.org/10.1139/z03-096

Wilson, R. E., S. M. Matsuoka, L. L. Powell, J. A. Johnson, D. W. Demarest, D. Stralberg, and S. A. Sonsthagen. 2021. Implications of historical and contemporary processes on genetic differentiation of a declining boreal songbird: the Rusty Blackbird. Diversity 13(3):103. https://doi.org/10.3390/d13030103

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society B 73 (1):3-36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Appendix Table S1

Bird species detected during point count surveys in 2016 and 2017 in the Main River and upper Humber River watersheds of Newfoundland, Canada, and their associated nesting guild.

Common name	***Scientific name***	**Nesting guild**	**% of sites detected**
Alder Flycatcher *	*Empidonax alnorum*	above-ground	0.7
American Black Duck *†	*Anas rubripes*		0.2
American Goldfinch *	*Spinus tristis*	above-ground	0.1
American Redstart *	*Setophaga ruticilla*	above-ground	0.7
American Robin	*Turdus migratorius*	above-ground	18.1
American Three-toed Woodpecker	*Picoides dorsalis*	cavity	0.2
American Tree Sparrow *	*Spizelloides arborea*	ground	0.1
Black-and-white Warbler	*Mniotilta varia*	ground	9.4
Black-backed Woodpecker *	*Picoides arcticus*	cavity	0.7
Black-capped Chickadee *	*Poecile atricapillus*	cavity	0.9
Blackpoll Warbler	*Setophaga striata*	above-ground	39.3
Black-throated Green Warbler	*Setophaga virens*	above-ground	2.3
Blue-headed Vireo *	*Vireo solitarius*	above-ground	0.3
Boreal Chickadee	*Poecile hudsonicus*	cavity	5.6
Brown Creeper *	*Certhia americana*	cavity	0.2
Canada Goose †	*Branta canadensis*		2.3
Canada Jay	*Perisoreus canadensis*	above-ground	9.4

Common name	***Scientific name***	**Nesting guild**	**% of sites detected**
Cedar Waxwing *	*Bombycilla cedrorum*	above-ground	0.1
Common Goldeneye *†	*Bucephala clangula*		0.1
Common Loon †	*Gavia immer*		1.8
Common Raven *	*Corvus corax*	above-ground	0.8
Common Redpoll *	*Acanthis flammea*	above-ground	0.1
Common Yellowthroat	*Geothlypis trichas*	ground	4.7
Dark-eyed Junco	*Junco hyemalis*	ground	29.4
Downy Woodpecker	*Dryobates pubescens*	cavity	1.6
Fox Sparrow	*Passerella iliaca*	ground	59.1
Golden-crowned Kinglet *	*Regulus satrapa*	above-ground	0.4
Gray-cheeked Thrush	*Catharus minimus*	above-ground	7.7
Greater Yellowlegs †	*Tringa melanoleuca*		8.6
Green-winged Teal *†	*Anas carolinensis*		0.2
Hairy Woodpecker *	*Dryobates villosus*	cavity	1.1
Hermit Thrush	*Catharus guttatus*	ground	32.0
Herring Gull *†	*Larus argentatus*		0.3
Least Flycatcher *	*Empidonax minimus*	above-ground	0.1
Lincoln's Sparrow	*Melospiza lincolnii*	ground	23.2
Magnolia Warbler	*Setophaga magnolia*	above-ground	8.3
Merlin *†	*Falco columbarius*		0.1
Mourning Warbler *	*Geothlypis philadelphia*	ground	0.2

Common name	***Scientific name***	**Nesting guild**	**% of sites detected**
Nashville Warbler *	*Leiothlypis ruficapilla*	ground	0.1
Northern Flicker *	*Colaptes auratus*	cavity	0.7
Northern Hawk Owl *†	*Surnia ulula*		0.1
Northern Waterthrush	*Parkesia noveboracensis*	ground	28.8
Olive-sided Flycatcher	*Contopus cooperi*	above-ground	4.6
Osprey *†	*Pandion haliaetus*		0.1
Palm Warbler *	*Setophaga palmarum*	ground	0.4
Pine Grosbeak	*Pinicola enucleator*	above-ground	12.7
Pine Siskin	*Spinus pinus*	above-ground	3.2
Purple Finch *	*Haemorhous purpureus*	above-ground	0.1
Red-breasted Nuthatch *	*Sitta canadensis*	cavity	0.9
Ring-billed Gull *†	*Larus delawarensis*		0.1
Ring-necked Duck *†	*Aythya collaris*		0.2
Rough-legged Hawk *†	*Buteo lagopus*		0.1
Ruby-crowned Kinglet	*Regulus calendula*	above-ground	65.4
Ruffed Grouse *†	*Bonasa umbellus*		0.2
Rusty Blackbird	*Euphagus carolinus*	above-ground	8.4
Savannah Sparrow	*Passerculus sandwichensis*	ground	2.0
Sharp-shinned Hawk *†	*Accipiter striatus*		0.2
Short-billed Dowitcher *†	*Limnodromus griseus*		0.1
Spotted Sandpiper *†	*Actitis macularius*		0.5

Common name	***Scientific name***	**Nesting guild**	**% of sites detected**
Spruce Grouse *†	*Falcipennis canadensis*		0.3
Swainson's Thrush	*Catharus ustulatus*	above-ground	26.4
Swamp Sparrow *	*Melospiza georgiana*	ground	0.3
Tennessee Warbler *	*Leiothlypis peregrina*	ground	0.5
Tree Swallow	*Tachycineta bicolor*	cavity	4.2
White-throated Sparrow	*Zonotrichia albicollis*	ground	85.8
White-winged Crossbill *	*Loxia leucoptera*	above-ground	0.9
Wilson’s Snipe †	*Gallinago delicata*		8.5
Wilson's Warbler	*Cardellina pusilla*	ground	1.8
Winter Wren	*Troglodytes hiemalis*	cavity	4.1
Yellow Warbler *	*Setophaga petechia*	above-ground	0.3
Yellow-bellied Flycatcher	*Empidonax flaviventris*	ground	35.7
Yellow-rumped Warbler	*Setophaga coronata*	above-ground	47.7

* Species detected at less than 1.5% of survey points. These were eliminated from single-species occupancy analyses.

† Species detected during surveys but not included in single-species occupancy or species richness analyses.

Appendix Table S2

Occupancy model comparisons for individual species (passerines and woodpeckers) with elevation (elev), red squirrels (resq), and year in the Long Range Mountains, Newfoundland, Canada (2016 and 2017). Each model contains a detection term(s) determined to be the best fit (all include site as a random effect), and an a priori set of occupancy terms. Null model appears in bold for ease of reference. Species included were detected at over 1.5% of surveys.

Species	**Detection structure**	**Occupancy structure**	**K**	**AICc**	**ΔAICc**	**ω**	**Log Likelihood**
American Robin (*Turdus migratorius*)	observer + day	elev	12	3201.51	0.00	0.41	-1588.68
	observer + day	elev + year	13	3202.30	0.79	0.27	-1588.06
	observer + day	resq	12	3204.01	2.50	0.12	-1589.93
	observer + day	resq + year	13	3204.50	2.98	0.09	-1589.16
	observer + day	**null**	**11**	**3205.26**	**3.75**	**0.06**	**-1591.56**
	observer + day	year	12	3205.82	4.31	0.05	-1590.83
Black-and-white Warbler (*Mniotilta varia*)	observer + day	year	12	1770.79	0.00	1.00	-873.31
	observer + day	elev + year	13	1813.70	42.92	0.00	-893.76
	observer + day	resq + year	13	1827.90	57.11	0.00	-900.86
	observer + day	elev	12	1881.39	110.60	0.00	-928.61
	observer + day	resq	12	1901.76	130.97	0.00	-938.80
	observer + day	**null**	**11**	**1909.32**	**138.53**	**0.00**	**-943.59**
Blackpoll Warbler (*Setophaga striata*)	observer + day	resq	12	4970.08	0.00	0.65	-2472.96
	observer + day	resq + year	13	4971.38	1.30	0.34	-2472.60
	observer + day	elev	12	4993.58	23.50	0.01	-2484.71
	observer + day	elev + year	13	4995.65	25.57	0	-2484.73
	observer + day	**null**	**11**	**5208.98**	**238.90**	**0**	**-2593.42**
	observer + day	year	12	5210.98	240.90	0	-2593.41
Black-throated Green Warbler (*Setophaga virens*)	observer + day	resq	12	421.11	0.00	0.50	-198.48
	Observer + day	resq + year	13	421.90	0.79	0.34	-197.86
	observer + day	elev	12	423.94	2.83	0.12	-199.89
	observer + day	elev + year	13	425.91	4.79	0.05	-199.86
	observer + day	**null**	**11**	**565.46**	**144.34**	**0.00**	**-271.66**
	observer + day	year	12	567.30	146.19	0.00	-271.57
Boreal Chickadee (*Poecile*	observer + day	elev + year	12	1189.45	0.00	0.83	-582.64
	observer + day	resq + year	12	1192.80	3.35	0.16	-584.32

Species	Detection structure	Occupancy structure	K	AICc	ΔAICc	ω	Log Likelihood
hudsonicus)	observer + day	elev	11	1197.67	8.22	0.01	-587.77
	observer + day	resq	11	1200.38	10.93	0.00	-589.12
	observer + day	year	11	1215.77	26.32	0.00	-596.82
	observer + day	**null**	**10**	**1224.81**	**35.37**	**0.00**	**-602.35**
Canada Jay (*Perisoreus canadensis*)	**Cloud**	**null**	**8**	**1782.52**	**0.00**	**1.00**	**-883.22**
	cloud	resq + year	10	1893.75	111.23	0.00	-936.81
	cloud	year	9	1894.28	111.76	0.00	-938.09
	cloud	elev + year	10	1895.56	113.04	0.00	-937.72
	cloud	resq	9	1939.20	156.68	0.00	-960.55
	cloud	elev	9	1939.84	157.32	0.00	-960.87
Common Yellowthroat (*Geothlypis trichas*)	wind	resq + year	10	718.92	0.00	1.00	-349.40
	wind	**null**	**8**	**934.17**	**215.25**	**0.00**	**-459.05**
	wind	elev + year	10	1003.04	284.12	0.00	-491.46
	wind	resq	8	1082.75	363.83	0.00	-533.34
	wind	year	9	1084.90	365.99	0.00	-533.41
	wind	elev	9	1087.24	368.32	0.00	-534.57
Dark-eyed Junco (*Junco hyemalis*)	day + time + observer	resq + year	14	4473.36	0.00	0.86	-2222.57
	day + time + observer	elev + year	14	4477.06	3.70	0.14	-2224.42
	day + time + observer	year	13	4485.03	11.66	0	-2229.42
	day + time + observer	resq	13	4514.72	41.36	0	-2244.27
	day + time + observer	elev	13	4516.02	42.66	0	-2244.92
	day + time + observer	**null**	**12**	**4523.73**	**50.37**	**0**	**-2249.79**
Downy Woodpecker (*Dryobates pubescens*)	**cloud**	**null**	**8**	**173.81**	**0.00**	**1.00**	**-78.87**
	cloud	resq	9	453.35	279.54	0.00	-217.63
	cloud	elev	9	456.57	282.76	0.00	-219.24
Fox Sparrow (*Passerella iliaca*)	observer + day	elev + year	13	6479.19	0.00	1.00	-3226.50
	observer + day	elev	12	6497.08	17.89	0.00	-3236.46
	observer + day	resq + year	13	6523.46	44.26	0.00	-3248.63
	observer + day	resq	12	6545.43	66.24	0.00	-3260.63
	observer + day	year	12	6628.79	149.60	0.00	-3302.31
	observer + day	**null**	**11**	**6644.53**	**165.33**	**0.00**	**-3311.20**
Gray-cheeked Thrush (*Catharus minimus*)	day + elev	elev	6	1543.60	0.00	0.62	-765.78
	day + elev	elev + year	7	1544.56	0.96	0.38	-765.25
	day + elev	resq + year	7	1561.97	18.37	0	-773.96
	day + elev	**null**	**5**	**1640.85**	**97.25**	**0**	**-815.41**

Species	Detection structure	Occupancy structure	K	AICc	ΔAICc	ω	Log Likelihood
	day + elev	year	6	1641.98	98.38	0	-814.97
	day + elev	resq	6	1740.99	197.39	0	-864.48
Hermit Thrush (*Catharus guttatus*)	observer + day	resq	12	4586.20	0.00	0.52	-2281.02
	observer + day	resq + year	13	4586.78	0.58	0.39	-2280.30
	observer + day	**null**	**11**	**4591.21**	**5.01**	**0.04**	**-2284.54**
	observer + day	year	12	4592.18	5.98	0.03	-2284.01
	observer + day	elev	12	4593.21	7.01	0.02	-2284.52
	observer + day	elev + year	13	4594.18	7.98	0.01	-2284.00
Lincoln's Sparrow (*Melospiza lincolnii*)	observer + day	resq + year	13	3641.95	0.00	0.98	-1807.88
	observer + day	elev + year	13	3650.26	8.31	0.02	-1812.04
	observer + day	resq	12	3663.37	21.42	0	-1819.61
	observer + day	elev	12	3669.09	27.14	0	-1822.47
	observer + day	year	12	3687.61	45.66	0	-1831.73
	observer + day	**null**	**11**	**3705.21**	**63.26**	**0**	**-1841.54**
Magnolia Warbler (*Setophaga magnolia*)	observer + day	elev	12	1531.40	0.00	0.72	-753.62
	observer + day	elev + year	13	1533.28	1.88	0.28	-753.55
	observer + day	resq	12	1598.93	67.53	0	-787.38
	observer + day	resq + year	13	1600.22	68.82	0	-787.02
	observer + day	**null**	**11**	**1654.95**	**123.54**	**0**	**-816.40**
	observer + day	year	12	1656.91	125.50	0	-816.37
Northern Waterthrush (*Parkesia noveboracensis*)	**observer + day**	**null**	**11**	**4331.95**	**0.00**	**0.39**	**-2154.91**
	observer + day	resq	12	4333.33	1.38	0.2	-2154.58
	observer + day	year	12	4333.91	1.96	0.14	-2154.88
	observer + day	elev	12	4333.97	2.02	0.14	-2154.90
	observer + day	resq + year	13	4335.31	3.35	0.07	-2154.56
	observer + day	elev + year	13	4335.93	3.98	0.05	-2154.87
Olive-sided Flycatcher (*Contopus cooperi*)	observer	elev + year	12	766.34	0.00	1.00	-371.09
	observer	resq	11	881.44	115.10	0.00	-429.65
	observer	**null**	**10**	**961.81**	**195.47**	**0.00**	**-470.85**
	observer	elev	11	1056.66	290.32	0.00	-517.26
	observer	resq + year	11	1067.48	301.14	0.00	-522.67
	observer	year	11	1072.28	305.93	0.00	-525.07
Pine Grosbeak (*Pinicola enucleator*)	precipitation	elev + year	8	2428.65	0	0.69	-1206.29
	precipitation	resq + year	8	2430.66	2.01	0.25	-1207.29
	precipitation	year	7	2434.15	5.5	0.04	-1210.04

Species	**Detection structure**	**Occupancy structure**	**K**	**AICc**	**ΔAICc**	**ω**	**Log Likelihood**
	precipitation	elev	7	2438.05	9.4	0.01	-1212
	precipitation	resq	7	2440.73	12.08	0	-1213.34
	precipitation	**null**	**6**	**2443.46**	**14.81**	**0**	**-1215.71**
Pine Siskin (*Spinus pinus*)	time	resq + year	6	445.90	0.00	1.00	-216.93
	time	resq	5	488.92	43.02	0.00	-239.44
	time	**null**	**4**	**489.65**	**43.76**	**0.00**	**-240.82**
	time	elev	5	490.40	44.50	0.00	-240.18
	time	year	5	584.41	138.51	0.00	-287.19
	time	elev + year	6	699.43	253.54	0.00	-343.70
Ruby-crowned Kinglet (*Regulus calendula*)	observer + day	elev + year	13	6503.72	0.00	1	-3238.76
	observer + day	resq + year	13	6547.31	43.59	0	-3260.56
	observer + day	elev	12	6557.22	53.49	0	-3266.52
	observer + day	year	12	6591.96	88.24	0	-3283.90
	observer + day	resq	12	6593.03	89.31	0	-3284.43
	observer + day	**null**	**11**	**6637.71**	**133.99**	**0**	**-3307.78**
Rusty Blackbird (*Euphagus carolinus*)	**wind**	**null**	**8**	**1572.90**	**0.00**	**1.00**	**-778.41**
	wind	resq	9	1770.66	197.75	0.00	-876.28
	wind	resq + year	10	1772.58	199.68	0.00	-876.24
	wind	elev	9	1777.65	204.75	0.00	-879.78
	wind	year	9	1778.59	205.69	0.00	-880.25
	wind	elev + year	10	1779.59	206.69	0.00	-879.74
Savannah Sparrow (*Passerculus sandwichensis*)	cloud	elev	9	521.91	0.00	0.42	-251.91
	cloud	resq	9	523.26	1.35	0.22	-252.58
	cloud	elev + year	10	523.54	1.63	0.19	-251.72
	cloud	resq + year	10	524.72	2.81	0.1	-252.30
	cloud	**null**	**8**	**526.22**	**4.31**	**0.05**	**-255.07**
	cloud	year	9	527.83	5.92	0.02	-254.87
Swainson's Thrush (*Catharus ustulatus*)	wind	resq	9	4094.82	0.00	0.64	-2038.37
	wind	resq + year	10	4096.62	1.79	0.26	-2038.25
	wind	elev	9	4099.76	4.94	0.05	-2040.83
	wind	elev + year	10	4101.31	6.49	0.02	-2040.60
	wind	**null**	**8**	**4102.45**	**7.63**	**0.01**	**-2043.19**
	wind	year	9	4103.99	9.17	0.01	-2042.95
Tree Swallow (*Tachycineta*	day + elev	year	6	699.26	0.00	0.69	-343.61
	day + elev	elev + year	7	701.24	1.99	0.26	-343.59

Species	Detection structure	Occupancy structure	K	AICc	ΔAICc	ω	Log Likelihood
bicolor)	**day + elev**	**null**	**5**	**705.18**	**5.93**	**0.04**	**-347.58**
	day + elev	elev	6	707.10	7.84	0.01	-347.53
	day + elev	resq + year	7	972.02	272.76	0.00	-478.98
	day + elev	resq	6	975.82	276.57	0.00	-481.89
White-throated Sparrow (*Zonotrichia albicollis*)	observer + day	resq + year	13	5877.51	0.00	1	-2925.66
	observer + day	resq	12	5896.46	18.94	0	-2936.15
	observer + day	elev + year	13	5902.09	24.57	0	-2937.95
	observer + day	elev	12	5915.08	37.57	0	-2945.46
	observer + day	year	12	5963.34	85.82	0	-2969.59
	observer + day	**null**	**11**	**5976.75**	**99.23**	**0**	**-2977.31**
Wilson's Warbler (*Cardellina pusilla*)	observer + day + time	elev	13	475.77	0.00	0.71	-224.79
	observer + day + time	elev + year	14	477.74	1.96	0.27	-224.76
	observer + day + time	resq	13	483.51	7.74	0.01	-228.66
	observer + day + time	resq + year	14	485.31	9.54	0.01	-228.55
	observer + day + time	**null**	**12**	**490.95**	**15.18**	**0.00**	**-233.40**
	observer + day + time	year	13	492.88	17.11	0.00	-233.35
Winter Wren (*Troglodytes hiemalis*)	day + time + elev	year	7	981.30	0.00	0.32	-483.62
	day + time + elev	resq + year	8	981.98	0.67	0.23	-482.95
	day + time + elev	**null**	**6**	**982.84**	**1.53**	**0.15**	**-485.40**
	day + time + elev	elev + year	8	983.14	1.84	0.13	-483.53
	day + time + elev	resq	7	983.23	1.93	0.12	-484.59
	day + time + elev	elev	7	984.66	3.36	0.06	-485.30
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	time	elev + year	6	5109.16	0.00	0.93	-2548.56
	time	year	5	5115.19	6.02	0.05	-2552.58
	time	resq + year	6	5116.24	7.08	0.03	-2552.10
	time	elev	5	5127.32	18.15	0	-2558.64
	time	**null**	**4**	**5133.40**	**24.24**	**0**	**-2562.69**
	time	resq	5	5134.88	25.72	0	-2562.43
Yellow-rumped Warbler (*Setophaga coronata*)	observer + day	elev + year	13	6078.59	0.00	0.39	-3026.20
	observer + day	year	12	6078.79	0.20	0.35	-3027.32
	observer + day	resq + year	13	6080.23	1.64	0.17	-3027.02
	observer + day	elev	12	6083.46	4.87	0.03	-3029.65
	observer + day	**null**	**11**	**6083.63**	**5.03**	**0.03**	**-3030.75**
	observer + day	resq	12	6084.87	6.28	0.02	-3030.35