

1 **Comparative phylogeographic analysis suggests a shared history among eastern North American**  
2 **boreal forest birds**

3

4 **Abstract**

5 Phylogeographic structure within high latitude North American birds is likely shaped by a history  
6 of isolation in refugia during Pleistocene glaciations. Previous studies of individual species have come to  
7 diverse conclusions regarding the number and location of likely refugia, but no studies have explicitly  
8 tested for biogeographic concordance in a comparative phylogeographic framework. Here we use a  
9 hierarchical approximate Bayesian computation analysis of mitochondrial DNA sequences from 653  
10 individuals of six bird species that are currently co-distributed in the boreal forest of North America to  
11 test for biogeographic congruence. We find support for congruent phylogeographic patterns across  
12 species, with shallow divergence dating to the Holocene within each species. Combining genetic results  
13 with paleodistribution modeling, we propose that these species shared a single Pleistocene refugium  
14 south of the ice sheets in eastern North America. Additionally, we assess modern geographic genetic  
15 structure within species, focusing on Newfoundland and disjunct high elevation populations at the  
16 southern periphery of ranges. We find evidence for a 'periphery effect' in some species with significant  
17 genetic structure among peripheral populations and between peripheral and central populations. Our  
18 results suggest that reduced gene flow among peripheral populations, rather than discordant  
19 biogeographic histories, can explain the small differences in genetic structure and levels of genetic  
20 diversity among co-distributed boreal forest birds.

21

22 *Keywords:* boreal birds, coalescence, hierarchical approximate Bayesian computation, paleodistribution,  
23 phylogeography, range periphery, spruce-fir

24

## 25 **Lay Summary**

- 26 • Six currently co-distributed eastern boreal birds share a recent phylogeographic history,  
27 expanding from a single common Pleistocene glacial refugia, likely located south of the ice  
28 sheets in eastern North America.
- 29 • This research helps us understand whether species within communities respond in similar ways  
30 to large scale geologic and climatic events.
- 31 • Differences in genetic diversity among boreal species is most likely due to modern processes  
32 such as isolation in peripheral populations, as opposed to discordant histories.
- 33 • We found significant isolating effects of Newfoundland and southern periphery populations in  
34 Northeastern North America, though this appeared to vary across species.

35

36

## 37 **Introduction**

38 Environmental change driven by Pleistocene climate cycles has shaped the geographic patterns  
39 of genetic structure of species globally (Hewitt 2004; Shafer et al., 2010; Pruett et al., 2013; Hirase et al.  
40 2016; Correll et al. 2018). Phylogeographic comparisons among co-distributed species illuminate the  
41 generality of biotic responses to previous climate change (Arbogast and Kenagy 2001), and can improve  
42 predictions of biogeographic responses to contemporary and future environmental challenges (Zink  
43 1996, 2002a; Avise 2000; Hickerson et al. 2010; Avise et al. 2016). Because widespread climatic  
44 processes act on multiple species within biotic communities, we might expect co-distributed species to  
45 show similar phylogeographic patterns, including divergence times, geographic genetic structure, and  
46 locations of Pleistocene refugia. However, comparisons of phylogeographic patterns among broadly co-  
47 distributed species generally reveal varying degrees of genetic divergence among populations, as well as  
48 varying numbers and locations of inferred refugia during the Last Glacial Maximum (LGM, 21 kya). These

49 incongruent patterns at the species level, documented over the past 25 years by increasingly rigorous  
50 phylogeographic studies, seem to support Zink's (1996) early hypothesis that "co-distributed species  
51 reached their current distributions at different times and possibly via different historical routes, and  
52 were subject to different historical events". The recognition that individual members of species  
53 assemblages may have responded idiosyncratically to historical climate change has led community  
54 ecologists to focus more on entire geographic regions and on processes operating on a continuum of  
55 temporal scales (Ricklefs 2008).

56         While a growing number of studies document species-specific patterns of genetic differentiation,  
57 the possibility remains that incongruence among co-distributed species may represent expected  
58 variation due to species-specific population sizes, generation times, and the stochasticity of lineage  
59 sorting rather than unique biogeographic histories (Edwards and Beerli 2000). Due to these effects,  
60 phylogeographic structure can be highly variable, especially when divergence is recent (Neigel and Avise  
61 1986; Omland et al. 2006), and may lead to 'pseudoincongruence', or apparent dissimilarities in modern  
62 day geographic structure despite a shared common history. For example, species that breed at high  
63 latitudes, including the birds of the North American boreal forest, were surely affected by Pleistocene  
64 climate cycles as their distributions were repeatedly shifted southward into refugia during colder glacial  
65 periods, then moved northward again during relatively warmer interglacial periods (Weir and Schluter  
66 2004; Drovetski et al., 2010). Yet, qualitative comparisons of phylogeographic patterns among boreal  
67 forest bird species studied to date (Table 1) reveal that species vary in the degree of genetic divergence  
68 among populations, as well as the number and location of inferred refugia during the Last Glacial  
69 Maximum (LGM, 21 kya). Whether reported differences in the genetic patterns among boreal forest  
70 birds are the result of discordant biogeographic histories, or an example of pseudoincongruence, is  
71 currently not clear because previous studies have generally focused on a single species. Recently  
72 developed, statistically rigorous coalescent-based methods (Hickerson et al. 2006, Dolman and Joseph

73 2012) have been used in comparative phylogeographic studies to test for simultaneous divergence  
74 across species while allowing demographic parameters that can affect the coalescent to vary within  
75 species, such as current and ancestral population sizes (Hickerson et al. 2006a; Chan et al. 2014; Robin  
76 et al. 2015). This approach has been an important advancement in comparative phylogeography  
77 (Hickerson et al. 2010), but to our knowledge has not yet been applied in the study of North American  
78 birds.

79         The locations of Pleistocene refugia can be inferred from fossil records, paleoclimate models,  
80 reconstructed habitats from pollen cores, and the geographic structure of gene pools based on  
81 molecular data (Jackson et al. 1997; Jaramillo-Correa et al. 2004; Provan and Bennet 2008; Nogués-  
82 Bravo 2009; Gérardi et al. 2010). In the current study, we compare the phylogeography of several co-  
83 distributed boreal forest bird species, integrating analyses of new and existing DNA sequence data with  
84 paleo-distribution modeling to address the question of whether, or to what extent, species in this  
85 community have congruent distribution histories. In addition to considering historic environmental  
86 change, we examine the effect of ongoing processes in shaping genetic structure within boreal forest  
87 bird species. In particular, post-glacial isolation of peripheral populations has been suggested as a driver  
88 of divergence within species (Burg et al. 2006; Topp and Winker 2008; Ralston and Kirchman 2012; van  
89 Els et al. 2012 Ralston and Kirchman 2013; Burg et al. 2014). In the northeastern United States and  
90 eastern Canada, isolation on the island of Newfoundland and the ‘archipelago’ of disjunct, high  
91 elevation boreal forest patches may limit gene flow (Ralston and Kirchman 2012; Kirchman and Ralston  
92 2016; FitzGerald et al. 2020). These isolated eastern populations have received less attention than island  
93 populations along the Pacific coast (Brunsfeld et al. 2001; Cook et al. 2001; Topp and Winker 2008) such  
94 that the contribution of eastern peripheral populations to overall genetic structure in the boreal  
95 avifauna is relatively unknown.

96           *History of the North American Boreal Forest and its Bird Community*- In North America, huge  
97 swaths of the boreal forest biome that stretch from Alaska to the Canadian Maritimes have been  
98 covered repeatedly by glacial ice; there were as many as 11 major periods of glaciation across North  
99 America during the Pleistocene (Richmond and Fullerton 1986). Pleistocene glaciations acted as  
100 repeated vicariant events, fragmenting species distributions into isolated refugia which promoted or  
101 maintained genetic divergence leading in some cases to speciation in boreal- and temperate-zone birds  
102 (Mengel 1964; Gill et al. 1993; Hewitt 2000; Drovetski et al. 2004; Weir and Schluter 2004; Lovette  
103 2005; Toews and Irwin 2008). Proposed locations of boreal forest refugia include Beringia, the Pacific  
104 Northwest including coastal islands, the now submerged Atlantic Shelf region in eastern North America,  
105 and regions south of the ice sheets in mid-latitude Rocky Mountains and modern-day southeastern  
106 United States (Pielou 1991; Jaramillo-Correa et al. 2004; Shafer et al. 2010; Ralston and Kirchman 2012;  
107 Lait and Burg 2013; Pruett et al. 2013; Dohms et al. 2017; FitzGerald et al. 2020). Despite this  
108 complexity, some common patterns have emerged from analyses of genetic data from boreal birds that  
109 have become available in the last 16 years.

110           First, many species are comprised of a single clade that extends across northern and eastern  
111 North America from Alaska to Newfoundland (hereafter “boreal”), and one or more clades west of the  
112 Rocky Mountains (hereafter “western montane”). Whereas boreal clades show relatively little genetic  
113 structure or morphological variation, western montane populations tend to be genetically and  
114 phenotypically divergent (Table 1), a pattern also seen in North American mammals (Arbogast and  
115 Kenagy 2001; Hope et al. 2016). Western montane clades comprised of multiple subspecies are thought  
116 to have resided in multiple refugia in the Rockies and coastal Pacific Northwest, with relatively little  
117 secondary contact post-glaciation (Brunsfeld et al. 2001; Topp and Winker 2008; Shafer et al. 2010), a  
118 pattern exemplified in boreal forest birds by the Canada Jay (*Perisoreus canadensis*; van Els et al. 2012;  
119 Dohms et al. 2017; Strickland and Ouellet 2020). Conversely, western montane populations with little

120 genetic structure, such as the Golden-crowned Kinglet (*Regulus satrapa*; Burg et al. 2014), Swainson's  
121 Thrush (*Catharus ustulatus*; Ruegg and Smith 2002; Ruegg et al. 2006), and Pine Grosbeak (*Pinicola*  
122 *enucleator*; Drovetski et al. 2010) may have resided in a single western refugium (Ruegg et al. 2006; Burg  
123 et al. 2014). In some cases, contemporary processes are hypothesized to be more important than  
124 historic isolation in structuring modern populations, as for Dark-eyed Junco (*Junco hyemalis*), where  
125 clades diversified following post-glacial expansion (Mila et al. 2007a, Friis et al. 2016).

126 In contrast to the patterns described above, boreal forest species with distributions that do not  
127 extend west of the Rocky Mountains into the Pacific Northwest, such as Boreal Chickadee (*Poecile*  
128 *hudsonica*) and Blackpoll Warbler (*Setophaga striata*), have fewer subspecies and less genetic structure  
129 (Ficken et al. 1996; Ralston and Kirchman 2012; DeLuca et al. 2013; Lait and Burg 2013). These species'  
130 distributions and genetic structure closely match those of the "boreal" clades in more widespread  
131 species. Yet the inferred number and location of refugia has differed among previous studies that  
132 employed different genetic markers and analytical methods (Table 1). In some cases authors infer a  
133 single eastern refugium for the boreal clade, interpreting weak genetic structure as the result of  
134 isolation by distance or reduced modern gene flow following post-glacial expansion (Mila et al. 2007a;  
135 Ralston and Kirchman 2012; Burg et al. 2014; FitzGerald et al. 2020). In other cases, authors invoke  
136 admixture of weakly diverged populations arising from separate refugia (Colbeck et al. 2008; van Els et  
137 al. 2012; Lait and Burg 2013; Dohms et al. 2017).

138 To disentangle historical versus ongoing processes and test the null hypothesis of congruent  
139 biogeographic histories, we examine the genetic structure and Pleistocene-projected distributions of  
140 five broadly co-distributed boreal forest bird taxa: Yellow-bellied Flycatcher (*Empidonax flaviventris*),  
141 Canada Jay, Boreal Chickadee, Blackpoll Warbler, and the Gray-cheeked/Bicknell's Thrush complex  
142 (*Catharus minimus*, *C. bicknelli*). First, we assess patterns of geographic genetic structure within each of  
143 our study species, analyzing data from a single genetic marker with well-characterized evolutionary

144 dynamics, mitochondrial NADH dehydrogenase subunit 2 (ND2), with special focus on Newfoundland  
145 and high-elevation peripheral populations. Second, we use hierarchical approximate Bayesian  
146 computation (hABC) to test for congruence among species across potential biogeographic breaks. We  
147 then model the paleodistribution of each species to locate potential refugia and assess co-distribution of  
148 taxa during the LGM.

149

## 150 **Methods**

### 151 *Sampling of birds and DNA sequence data*

152 We obtained previously published, complete ND2 sequences (1041 bp) from 70 individuals in  
153 the “boreal” clade of Canada Jay (van Els et al. 2012), 186 Bicknell’s Thrushes, and 77 Gray-cheeked  
154 Thrushes (FitzGerald et al. 2017, 2020) from GenBank. We generated new, complete ND2 sequences  
155 from 83 Yellow-bellied Flycatchers and an additional 15 Canada Jays, and partial sequences from 97  
156 Boreal Chickadees (904 bp) and 125 Blackpoll Warblers (902 bp). Sample sizes ranged from 77-186 per  
157 species (Table 2). Field sites and methods for sample collections are described previously (Ralston and  
158 Kirchman 2012; Lait and Burg 2013; Dohms et al. 2017; FitzGerald et al. 2017, 2020; Ralston et al. 2019).  
159 Briefly, adult individuals were captured throughout their breeding ranges between late-May and July  
160 using mist nets. Most individuals were sampled for blood via brachial venipuncture and released, but a  
161 subset was collected and prepared as voucher specimens with associated frozen tissues. Additional  
162 frozen tissues and toe pad samples from breeding-season specimens were provided by natural history  
163 museum collections: American Museum of Natural History, Cleveland Museum of Natural History, Royal  
164 Ontario Museum, University of Alaska Museum of the North (Appendix 1). Samples cover the “boreal”  
165 distribution of all study taxa (Figure 1; Figure S1), with increased sampling in the southern peripheral  
166 populations of eastern North America (Table 2).

167 We extracted DNA from blood and tissue samples using Qiagen DNeasy Blood and Tissue  
168 Extraction kits (Qiagen, Valencia, California) following manufacturer protocols, or using a modified  
169 chelex procedure (Walsh et al. 1991). We amplified ND2 in polymerase chain reactions (PCR) using  
170 primers L5216 and H6313 from Sorenson et al. (1999) and modified internal primers L5758 and H5776  
171 from FitzGerald et al. (2017). PCR cycle conditions were previously published (Ralston and Kirchman  
172 2012; Dohms et al. 2017; FitzGerald et al. 2017, 2020). The PCR products were visualized on 0.8-2.0%  
173 agarose gels to confirm DNA amplification and no contamination, purified using ExoSAP-IT (Affymetrix,  
174 Santa Clara, California) or an Epoch Life Science GenCatch Advanced PCR Extraction Kit (Epoch Life  
175 Science, Missouri City, Texas), and sequenced in both directions using Sanger sequencing on Applied  
176 Biosystems instruments (Applied Biosystems, Foster City, California). New and downloaded sequences  
177 for each species were aligned using SEQUENCHER (Gene Codes, Ann Arbor, Michigan), and all variable  
178 sites within species alignments were double checked against original chromatograms for accuracy.

179 *Genetic diversity metrics and tests for the “periphery effect”*

180 We measured genetic diversity within each species as the number of haplotypes, nucleotide  
181 diversity ( $\pi$ ), haplotype diversity ( $H_d$ ), and average pairwise number of nucleotide substitutions ( $k$ ) using  
182 DNASP (Rozas et al. 2003). We examined geographic genetic structure within each species by building  
183 median-joining networks using the program Network (Bandelt et al. 1999), and by calculating pairwise  
184  $F_{st}$  between geographic populations in Arlequin (Excoffier and Lischer 2010). We assembled geographic  
185 populations by pooling birds sampled from a single mountain range or geographic region that was  
186 isolated from other such groups by low-elevation areas of unsuitable habitat in the southeastern  
187 periphery of the North American boreal forest, or by distances of greater than 500 km in the relatively  
188 contiguous boreal forest belt in Canada and Alaska. This enabled comparisons of 9 “peripheral isolates”  
189 and 12 “contiguous” populations (Figure 1, Table 2). We did not calculate  $F_{st}$  for populations with fewer  
190 than 7 individuals sampled of a given species.



191 To examine the question of whether peripheral isolates contribute disproportionately to  
192 geographic genetic structure, we plotted pairwise  $F_{st}$  by geographic distance, grouping pairwise  $F_{st}$   
193 values by population categories (i.e. peripheral or contiguous). Pairwise  $F_{st}$  values were therefore  
194 between two peripheral isolates, two contiguous populations, or one peripheral and one contiguous  
195 population. We tested for this periphery effect by using a linear mixed effects model with pairwise  $F_{st}$  as  
196 the dependent variable, population category comparison (i.e. peripheral vs. peripheral, contiguous vs.  
197 contiguous, or peripheral vs. contiguous) as the fixed independent variable, and species as a random  
198 variable. We compared the above model to a model that also included distance as a fixed variable, and  
199 ranked models using AIC. A significant distance term was interpreted as statistical evidence for isolation  
200 by distance across the boreal distribution, and a significant ‘comparison category’ term as evidence of a  
201 periphery effect. We excluded Bicknell’s Thrush (found only in the southeast periphery and southern  
202 Quebec) and Gray-cheeked Thrush (found only on Newfoundland and across the boreal forest to the  
203 north and west of Bicknell’s Thrush) from our  $F_{st}$  analysis, but note that  $F_{st}$  and other measures of gene  
204 flow and geographic structure are reported for these species in two recent papers (FitzGerald et al.  
205 2017, FitzGerald et al. 2020). We similarly test for an isolating effect on Newfoundland using a mixed  
206 effects model with pairwise  $F_{st}$  as the dependent variable, distance and population comparison type (i.e.  
207 comparison including Newfoundland, or not) as fixed independent variables, and species as a random  
208 variable.

### 209 *Tests of historic biogeographic congruence*

210 To test for congruence in the timing of divergences among species, we used an hABC approach  
211 implemented in msBayes (Hickerson et al. 2006a). This approach tests for simultaneous divergence  
212 across species while allowing demographic parameters that can affect coalescence to vary within  
213 species, such as current and ancestral population sizes. We tested for congruence among species across  
214 three models corresponding to potential biogeographic breaks: (1) east versus west, (2) Newfoundland

215 versus east; and (3) periphery versus contiguous range (Figure 1). For the east versus west test, we  
216 defined 'east' as Manitoba and all populations (both 'contiguous' and 'periphery') east of Manitoba,  
217 following results from previous studies (Ralston and Kirchman 2012, Lait and Burg 2013). For the  
218 Newfoundland versus east test, only eastern populations as defined above were included. For the  
219 periphery versus contiguous range test, peripheral populations included those in the Catskill and  
220 Adirondack Mountains of New York, the Green Mountains of Vermont, the White Mountains (New  
221 Hampshire, Maine, southern Quebec), New Brunswick, and Nova Scotia. For this comparison only  
222 Newfoundland was included as a contiguous population as this allowed us to test whether divergence in  
223 *Catharus* is congruent intraspecific divergence within other species as further explained below.

224         While Gray-cheeked Thrush and Bicknell's Thrush represent species-level taxa, they are unique  
225 among boreal forest sister species in that their contact zone is in northeastern North America  
226 (FitzGerald et al. 2020), and their combined distribution closely matches that of other boreal species.  
227 Further, the genetic divergence between these species (2.31%; FitzGerald et al. 2020) is similar to the  
228 levels of divergence present within Canada Jay clades (1.5-5.1%; van Els et al. 2013). We therefore treat  
229 Gray-cheeked/Bicknell's Thrush as a single taxon for some of our comparative analyses to determine  
230 whether divergence within this "boreal" clade is congruent with intraspecific divergences in other taxa.  
231 However, because Bicknell's Thrush only breeds in populations we defined as boreal peripheral and in  
232 southern Quebec, this species was not included in either the east versus west or the Newfoundland  
233 versus east comparisons, so that these tests compared the divergences within Gray-cheeked Thrush to  
234 the other species. Similarly, the Gray-cheeked Thrush rarely breeds in the southern periphery, such that  
235 the southern periphery vs. contiguous range test estimated interspecific divergence between Bicknell's  
236 Thrush and Gray-cheeked Thrush. This specifically allowed us to use the periphery vs. contiguous test to  
237 determine whether any cryptic intraspecific divergence exists within other species congruent with the  
238 interspecific divergence in *Catharus*. For this reason Newfoundland was included in the 'contiguous'

239 instead of the 'periphery' for this analysis. We also ran the periphery versus contiguous test excluding  
240 *Catharus* so as to not bias this test toward incongruent divergence.

241 For each of the biogeographic models, we used msBayes to estimate  $\Psi$ , the number of  
242 divergence events across species, and  $\Omega$ , degree of discordance calculated as the ratio of variance to the  
243 mean in divergence times ( $\tau$ ) across species. Simultaneous divergence across species would be indicated  
244 by  $\Psi=1$  (one divergence event), and  $\Omega=0$  (no variance in  $\tau$  across species). Incongruent divergence across  
245 species would be indicated by  $\Psi>1$  and  $\Omega>0$ . Prior distributions for population parameters for each run  
246 of msBayes followed default and recommended settings (Hickerson et al. 2006a, 2007, Barber and Klicka  
247 2010, Dolmon et al. 2012): upper and lower bounds of  $\theta$  were estimated in msBayes from observed  
248 average pairwise nucleotide differences ( $\pi$ ) within subpopulations, the ancestral upper bound was set at  
249 0.25 times the modern  $\theta$  upper limit, and the upper bound of  $\tau$  was set at 1.0. Because msBayes may be  
250 sensitive to prior distributions (Oaks et al. 2013), we reran a subset of our models with varying upper  
251 bounds of  $\tau$ . We found no qualitative changes in the results from these runs, so we report only on the  
252 default setting. Post divergence migration was set to 0 as we are not interested here in specifically  
253 testing for migration. We simulated 1,000,000 replicate runs under each biogeographic model and  
254 calculate a vector of summary statistics for each that included  $\pi$ , the number of segregating sites within  
255 each population pair normalized by sample size ( $\theta W$ , Watterson 1975), net nucleotide divergence  
256 between each pair of populations ( $\pi_{net}$ , Nei and Li 1979), and the variance in the difference between  $\pi$   
257 and  $\theta W$  (Tajima 1989, Hickerson et al. 2006b). Posterior probabilities of  $\Psi$  and  $\Omega$  were calculated by  
258 comparing these summary statistics from 0.01% of the simulations to those in the observed dataset  
259 (Hickerson et al. 2006a). We concluded congruent divergence across potential biogeographic breaks  
260 among species if posterior estimates of  $\Psi$  were highest for  $\Psi=1$ , and if 95% highest posterior density  
261 (HPD) for  $\Omega$  included 0.0. Because  $\Psi$  values  $>1$  cannot be distinguished very well with a single mtDNA  
262 locus and small number of taxa (*pers. comm.* M. Hickerson), we report any value of  $\Psi$  greater than 1 as a

263 categorical " $\Psi > 1$ ". We calculated Bayes Factors (BF) for  $\Psi = 1$  versus  $\Psi > 1$ , and for  $\Omega \leq 0.025$  versus  $\Omega >$   
264  $0.025$ , and followed the scale suggested by Jeffreys (1961) to determine strength of support from BF  
265 (Dolman and Joseph 2012). We used  $\Omega \leq 0.025$  as a threshold for comparing models with BF as we found  
266 the Local Linear Regression used to calculate posterior estimates in msBayes tended to slightly inflate  
267 values away from zero.

268 We converted divergence estimates ( $\tau$ ) from msBayes into time since divergence ( $t$ ) using the  
269 equation  $t = \tau \theta AVE g / \mu$ , where  $\tau$  is divergence time scaled by mutation rate per generation,  $\theta AVE$  is half  
270 the estimated prior upper bound of  $\theta$ ,  $g$  is generation time in years, and  $\mu$  is the mutation rate per  
271 generation (Barber and Klicka 2010, Dolman and Joseph 2012). We use mutation rate for avian  
272 mitochondrial DNA of  $2.0\% \text{ MY}^{-1}$  (Shields and Wilson 1987; Lovette 2004) and an estimated generation  
273 time of 2.0 years (Ralston and Kirchman 2012). We recognize that our estimates of divergence time are  
274 heavily influenced by our choice of  $\theta$ ,  $g$ , and  $\mu$ , and we therefore interpret divergence times only on a  
275 very broad scale (i.e. Pleistocene versus Holocene).

276 To locate potential refugia and assess co-distribution of taxa during the LGM, we modeled the  
277 paleodistribution of each species in Maxent (Phillips et al. 2006; Elith et al. 2011; Merow et al. 2013)  
278 following previously published methods (Dohms et al. 2017; FitzGerald 2017; FitzGerald et al. 2020). We  
279 used 10 climatic variables that were uncorrelated across the modern-day boreal breeding distribution  
280 (annual mean temperature, mean diurnal range, isothermality, temperature seasonality, mean  
281 temperature of wettest quarter, annual precipitation, precipitation of driest month, precipitation  
282 seasonality, precipitation of warmest quarter, and precipitation of coldest quarter; Hijmans et al. 2005;  
283 Dohms et al. 2017), and the modeled distribution of three boreal tree species (Balsam Fir, *Abies*  
284 *balsamea*; Black Spruce, *Picea mariana*; and Paper Birch, *Betula papyrifera*; FitzGerald 2017) as predictor  
285 variables. Occurrences for each species were taken from previous studies (Ralston and Kirchman 2013;  
286 FitzGerald 2017). The mean number of occurrences per species was 274 (range 158-533). In short, these

287 included georeferenced museum specimens, and for the *Catharus* species, occurrences were  
288 supplemented with audio and visual recordings, standardized avian survey data, and primary literature  
289 reports (FitzGerald 2017). We then projected the ecological niche of each species onto LGM conditions  
290 according to the National Center for Atmospheric Research Community Climate System Model 4  
291 (Vertenstein et al. 2010) and paleodistribution of the three tree species (FitzGerald 2017). We estimated  
292 two different measures of niche overlap, Schoener's D and the I statistic (Warren et al. 2008), currently  
293 and during LGM between all species pairs using ENMTools (Warren et al. 2010). We interpret niche  
294 overlap as the degree of co-distribution currently and during LGM, but use Schoener's D and the I  
295 statistic instead of "range overlap" output from ENMTools because they do not require user-defined and  
296 species-specific thresholds which may influence interpretation (Warren et al. 2010). We test for  
297 differences in niche overlap between the current time period and LGM using paired t tests with a  
298 significance level of 0.05.

299

## 300 **Results**

301 We obtained whole or nearly complete ND2 sequences from a total of 653 individuals across the  
302 six species (Table 3, Appendix 1). Species varied in genetic diversity. Haplotype diversity was lowest in  
303 Boreal Chickadee (Hd= 0.479), Blackpoll Warbler (Hd=0.611), and Bicknell's Thrush (Hd=0.785), with  
304 each of these species showing star-like haplotype networks (Table 3; Figure 1). Haplotype diversity was  
305 higher in Yellow-bellied Flycatcher (Hd= 0.959), Canada Jay (Hd=0.966), and Gray-cheeked Thrush (Hd=  
306 0.866) which each showed much more complex haplotype networks without a single common haplotype  
307 as in the other species (Figure 1). All species showed low intraspecific divergence (average number of  
308 nucleotide differences, k, range 0.653-3.749) and no biogeographic genetic breaks.

309           When distance was included as a fixed term in a mixed effects model of pairwise  $F_{st}$ , the term  
310 was nonsignificant ( $F=0.482$ ,  $p=0.490$ ), and the mixed model excluding distance had a lower AIC.  
311 Together, these results suggest that genetic patterns are not explained by isolation by distance for these  
312 species. In the top mixed model, population comparison category did have a significant effect ( $F= 3.19$ ,  
313  $p=0.047$ ), providing evidence for a periphery effect on genetic differentiation. Pairwise  $F_{st}$  values were  
314 significantly lower among contiguous-contiguous population comparisons than among peripheral-  
315 peripheral population comparisons ( $t= 2.05$ ,  $p=0.044$ ) or between contiguous and peripheral  
316 populations ( $t=2.49$ ,  $p=0.015$ ). This periphery effect varied across species, with larger effect in Blackpoll  
317 Warbler and Canada Jay, and perhaps no effect in Boreal Chickadee and Yellow-bellied Flycatcher  
318 (Figure 2). While there was not a consistent isolating effect of Newfoundland across species ( $F=3.43$ ,  
319  $p=0.069$ ), Newfoundland appeared to be an important population driving the periphery effect in Canada  
320 Jay (Figure 2). Pairwise  $F_{st}$  for this species were significantly higher when one of the populations was  
321 Newfoundland ( $t= 8.18$ ,  $df = 4.77$ ,  $p = 0.001$ ).

322           Despite differences across species in diversity and local genetic structure, comparative hABC  
323 analyses for all potential biogeographic breaks (east versus west, Newfoundland versus east, periphery  
324 versus contiguous range) showed evidence of a single recent divergence in common with all species  
325 (Table 4). For all biogeographic breaks,  $\Psi=1$  had the highest probability with BF ranging from 2.5-3.0  
326 indicating weak support for a single congruent divergence. The dispersion index,  $\Omega$ , was low (0.01-0.02)  
327 for all three breaks with 95%HPD ranges overlapping with zero and BF ranging from 2.53-12.2 indicating  
328 weak to strong support for no variance in divergence times across species (Table 4). For all breaks the  
329 estimated divergence time was in the Holocene, with 95%HPD that overlapped with 0 (Table 4). Only  
330 when Gray-cheeked and Bicknell's Thrushes were included as a single taxon in the periphery versus  
331 contiguous range analysis was there support for incongruent histories among taxa. Here, BF for  $\Psi=1$  and  
332  $\Omega \leq 0.025$  were both less than 1, indicating negative relative support for a congruent divergence and

333 negative relative support for no variation in divergence times, respectively (Table 4). The estimated  
334 divergence time between Gray-cheeked Thrush and Bicknell's Thrush from this analysis was an order of  
335 magnitude larger than for other taxa and fell in the Pleistocene ( $t=55\,257$ , 95%HPD= 0-105 763). Genetic  
336 sequences for these species were separated by 23 substitutions, and had an average sequence  
337 divergence of 2.31%. Together these results indicate that the level of divergence within *Catharus*  
338 thrushes is unique compared to other eastern boreal taxa with a similar distribution.

339 Overlap in distributions were significantly less during LGM compared to present day (paired t  
340 tests, Schoener's D:  $t = 3.894$ ,  $df = 14$ ,  $p = 0.002$ ; I statistic:  $t = 4.271$ ,  $df = 14$ ,  $p = 0.001$ ), though broad  
341 geographic patterns in modeled LGM distributions were similar across species and consistent with  
342 previously published paleodistribution models (Ralston and Kirchman 2012; van Els et al. 2013; Lait and  
343 Burg 2013; FitzGerald et al. 2020). Ecological niche models at the LGM show two potential shared  
344 refugia in eastern North America (Figure 3). One location was a broad band of suitable conditions  
345 extending from mid-latitude Atlantic coast to south-central North America. A second potential refugium  
346 with projected suitable conditions was located in the Grand Banks, a now submerged region of the  
347 Atlantic shelf east of modern-day Newfoundland.

348

## 349 Discussion

350 Our findings support a congruent biogeographic history among the boreal avifauna we  
351 examined, despite differences in patterns of genetic differentiation within species. Boreal Chickadee,  
352 Blackpoll Warbler, and Bicknell's Thrush each showed star-like haplotype networks and lower haplotype  
353 diversity, perhaps suggesting smaller ancestral populations during the LGM and recent or ongoing  
354 diversification. Yellow-bellied Flycatcher, Canada Jay, and Gray-cheeked Thrush each showed much  
355 more complex haplotype networks with greater haplotype diversity, perhaps suggesting larger

356 populations sizes and the maintenance of genetic diversity throughout the Pleistocene. However, our  
357 hABC results suggest that these relatively small differences in genetic differentiation within species that  
358 have previously led to conflicting conclusions about the number of refugia are within the range expected  
359 among species with a shared history, and are likely due to differences in generation time, ancestral  
360 population sizes or the stochasticity of the coalescent process. We conclude from hABC results that our  
361 study species persisted through Pleistocene glacial cycles in a single southern refugium, followed by  
362 Holocene expansion north and westward into the current boreal co-distribution. While our sampling  
363 throughout the contiguous boreal forest in central and western Canada was sparse, we do include  
364 samples from the most geographic disparate parts of each species' breeding range (Figure S1).  
365 Additional sampling from the contiguous boreal forest therefore may reveal unsampled diversity from  
366 western populations, but is unlikely to reveal any deep divergences within the boreal clades that our  
367 current analysis does not. Our analyses focus specifically on boreal clades, defined here as populations  
368 extending across northern and eastern North America from Alaska to Newfoundland, so our results do  
369 not exclude the likelihood that species with extensive distribution and diversification in western North  
370 America (i.e. Canada Jay) also persisted in one or more western or Beringian refugia (van Els et al 2012;  
371 Lait and Burg 2013; Mila et al. 2007a).

372 Genetic congruence tests indicated a single isolating event occurred across species, suggesting a  
373 single LGM refugia for eastern boreal birds. However, our paleodistribution modeling analysis suggested  
374 two possible locations for that refugium. We argue that the most likely location of an eastern refugium  
375 was south of the ice sheets in an area extending from mid-latitude Atlantic coast to south-central North  
376 America. While our paleodistribution models showed this comprising of two disjunct locations for some  
377 species (i.e. Yellow-bellied Flycatcher, Blackpoll Warbler, Figure 3), in reality mid-latitude North America  
378 was likely broadly connected via suitable climates and habitats at the LGM (Davis 1983, Jackson et al.  
379 1997). Pollen and macrofossil evidence support that spruce (*Picea mariana*, *P. glauca*) was present and



380 abundant midcontinent, though Balsam Fir may have been more restricted to unglaciated areas in  
381 current northeastern US (Davis 1983, Jackson et al. 1997). Additionally, abundant fossil evidence exists  
382 for vertebrate life in this area south of the ice sheets (Pielou 1991), including fossil evidence of Canada  
383 Jay, Pine Grosbeak, and several other boreal birds from the Late Pleistocene near the center of our  
384 proposed refugium (Parmalee and Klippel 1982). Another previously proposed location for an eastern  
385 refugium is Grand Banks, on the now submerged Atlantic shelf east of Newfoundland (van Els et al.  
386 2012; Lait and Burg 2013; FitzGerald et al. 2020). This region was climatically suitable according to our  
387 paleodistribution models. However, some have argued the possibility that these coastal refugia were  
388 not in fact ice-free during the LGM, but instead were colonized rapidly following melting, or were  
389 ephemeral throughout the Pleistocene as sea levels changed (Holland 1981; Shaw et al. 2002). This has  
390 led some authors to conclude coastal refugia such as Grand Banks were unlikely to have supported  
391 extensive forested habitat suitable as refugia for vertebrate taxa (Burns et al. 2014). We also note its  
392 northern location and isolation would have made Grand Banks a more difficult destination to reach for  
393 migratory species, and a harsher winter environment for residents to survive. Further its smaller size  
394 would have supported smaller ancestral populations than a more extensive southern refugia. We  
395 therefore argue that forested regions south of the ice sheets are a more plausible location for the  
396 shared refugium of eastern boreal species.

397         Our analysis is unable to discount an alternative possibility that, despite congruent intraspecific  
398 genetic patterns, species existed in different refugia from one another and simultaneously expanded to  
399 inhabit current distribution from different directions. For example, FitzGerald et al. (2020) speculated  
400 that while Bicknell's Thrush inhabited a refugia located in modern day southern United States, Gray-  
401 cheeked Thrush may have persisted in Grand Banks. Similarly, a species may have persisted in a western  
402 refugium and become broadly co-distributed with other boreal species following post-glacial dispersal  
403 that extended eastward, as has been proposed for Dark-eyed Junco (Mila et al. 2007a). Another

404 possibility not further explored in our analysis is that migratory species survived the Pleistocene outside  
405 of our study area, for example in South America at their current wintering range. Migratory behaviors  
406 can evolve quickly within species (Berthold et al. 1992, Able and Belthoff 1998) and may be extensively  
407 or repeatedly modified on the time scale under consideration in this study (Zink 2002b). Zink (2011) has  
408 suggested that this could include several transitions between ‘migratory’ and ‘sedentary’ states within a  
409 lineage since the time of the most recent common ancestor. If true, this could mean currently migratory  
410 species may have been sedentary during the LGM, inhabiting ranges near their current tropical  
411 wintering ranges. In contrast, others have suggested that the circuitous migratory routes in some boreal  
412 species are evidence of a history of expansion from refugia in the northern hemisphere while  
413 maintaining the migratory state (Ruegg and Smith 2002, Ralston and Kirchman 2012). Our current  
414 analysis suggested that genetic divergences were temporally concordant among our study species, but is  
415 less informative regarding geographic concordance. Thus, we cannot exclude the possibilities of our  
416 study species existing in discordant refugia, either in different parts of North America or on separate  
417 continents. However, we argue a LGM boreal avifauna south of the ice sheets in south-eastern North  
418 America with a composition similar to what we see today, including both migratory and sedentary  
419 species, is the most parsimonious explanation given our results.

420           We find that peripheral isolation is more important than geographic distance in genetically  
421 structuring modern populations of boreal birds. The mixed-effects model that excluded distance as an  
422 explanatory variable for pairwise  $F_{st}$  was supported by AIC as the top model. Pairwise  $F_{st}$  was significantly  
423 greater when the comparison included at least one peripheral population. This suggests gene flow may  
424 be limited between peripheral populations isolated in the boreal ‘archipelago’ at the southern extent of  
425 the boreal forest in northeastern United States (Kirchman and Ralston 2016), especially for Blackpoll  
426 Warbler and Canada Jay. Peripheral  $F_{st}$  values were generally higher than pairwise  $F_{st}$  between  
427 contiguous populations for Blackpoll Warbler and Canada Jay, but not for Boreal Chickadee or Yellow-

428 bellied Flycatcher (Figure 2). In Canada Jay, genetic structure among peripheral populations appears to  
429 be driven by the high pairwise  $F_{st}$  between Newfoundland and other populations. Newfoundland has  
430 distinct subspecies or genetically differentiated populations in many bird species (Zink and Dittman  
431 1993; Milot et al. 2000; Colbek et al. 2008; van Els et a. 2012), including a named subspecies of Canada  
432 Jay (*Perisoreus canadensis sanfordi*; Strickland and Ouellet 2020). Limited gene flow following Holocene  
433 colonization, rather than multiple refugia, may be sufficient in explaining genetic structuring in modern  
434 populations. While our mtDNA results are suggestive of limited gene flow among peripheral  
435 populations, future studies using SNPs or multiple faster evolving genetic loci may further resolve  
436 patterns of genetic structure at the periphery, as well as unravel patterns of modern gene flow. Further,  
437 future studies may examine how migratory strategy influences modern gene flow and patterns of  
438 genetic structure. Here, the long distance migrant Blackpoll Warbler shows a greater ‘periphery effect’  
439 than either the nonmigratory Boreal Chickadee or short distance migrant Yellow-bellied Flycatcher.  
440 There does not appear to be current consensus on the impact of migratory strategy on genetic  
441 structure. Some authors have suggested migration promotes dispersal and gene flow among  
442 populations (Boulet and Gibbs 2006), while an explicit test of this hypothesis in a boreal bird, the  
443 Golden-crowned Kinglet, revealed no difference in genetic structure among migratory and nonmigratory  
444 populations (Graham et al. 2020). Because differing biogeographic histories may confound modern  
445 genetic structure, future studies that test this question among species with a shared biogeographic  
446 history, as we have demonstrated for this group of boreal birds, may be informative.

447           Our results suggest a shared history among co-distributed boreal species that vary in natural  
448 history, migratory strategy and levels of intraspecific diversity. Similar to our results, a comparative  
449 analysis of phylogeography in boreal mammals found that the northern and eastern boreal zone held a  
450 single mtDNA clade in all studied species, suggesting a shared biogeographic history likely similar to  
451 what we propose here for boreal birds (Arbogast and Kenagy 2001). This is in contrast to previous

452 studies that have suggested discordant responses to historic climate change or biogeographic events in  
453 birds of North America (Zink 1996, Zink et al. 2001) and elsewhere on the globe (Burney and Brumfield  
454 2009, Qu et al. 2010, Dolman and Joseph 2012), as well as in other taxonomic groups (Taberlet et al.  
455 1998, Soltis et al. 2006). One possible explanation for this unique pattern observed in the eastern  
456 boreal community is that eastern North America is relatively geologically simple, with few natural  
457 dispersal barriers for birds. Mountains and Pleistocene sea ways have been important in structuring  
458 genetic diversity within species in other regions (Taberlet et al. 1998, Brunsfeld et al. 2001, Zink et al.  
459 2001), and complex barriers can lead to discordant genetic structures among species due to differences  
460 in dispersal ability (Burney and Brumfield 2009). This may be especially true in birds which can fly across  
461 landscape features that acts as barriers for other taxa. In a taxonomically comprehensive comparative  
462 phylogeographic study of unglaciated eastern North America, Soltis et al. (2006) found that mobile  
463 species such as birds showed no genetic structure across biogeographic barriers important to most  
464 other taxa. Therefore, the lack of barriers south of the ice sheets in eastern North America might explain  
465 the unique phylogeographic concordance in boreal birds.

466         In summary, our study is the first to account for expected variation in the coalescent process by  
467 using an hABC approach to compare biogeographic histories among North American bird species. We  
468 conclude that birds of the eastern boreal region may have shared a biogeographic history in a single  
469 refugium during the LGM. Phylogeographic differences among species are better explained by variation  
470 in ancestral population sizes or modern isolation and gene flow, rather than by discordant  
471 biogeographic histories. This suggests that the boreal bird community has been relatively stable at least  
472 since the LGM. Future work is needed to determine whether this pattern holds when more members of  
473 the boreal avifauna are analyzed, and the degree to which other avian communities are dynamic or  
474 conserved through geologic time.

475

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