Using a combination of mitochondrial and z-linked sequences, microsatellite data, and spatio-geographic modeling, we examined historical and contemporary factors influencing the population genetic structure of the purple finch (Haemorhous purpureus).

Mitochondrial DNA data show the presence of two distinct groups corresponding to the two subspecies, H. p. purpureus and H. p. californicus. The two subspecies likely survived in separate refugia during the last glacial maximum, one on the Pacific Coast and one east of the Rocky Mountains, and now remain distinct lineages with little evidence of gene flow between them. Southwestern British Columbia is a notable exception, as subspecies mixing between central British Columbia and Vancouver Island populations suggests a possible contact zone in this region. Z-linked data support two mitochondrial groups; however, Coastal Oregon and central British Columbia sites show evidence of mixing. Contemporary population structure based on microsatellite data identified at least six genetic clusters: three H. p. purpureus clusters, two H. p. californicus clusters, and one mixed cluster, which likely resulted from high site fidelity and isolation by distance, combined with sexual selection on morphological characters reinforcing subspecies differences.

**KEYWORDS**
barriers, phylogeography, Pleistocene, population isolation, refugia
Not all barriers are large. Barriers can be small, such as roads (Clark et al., 2010) and agriculture fields (Bush et al., 2011). Behavior, including strong natal site fidelity, migratory routes, foraging sites, or mate choice (Friesen et al., 2007), can lead to reproductive isolation.

The purple finch (*Haemorhous purpureus*) is a North American songbird with two recognized subspecies: *H. p. purpureus* to the east of the Rocky Mountains and *H. p. californicus* on the West Coast (Figure 1). The two subspecies exhibit morphological, plumage, vocal, and behavioral differences, in addition to variation within the subspecies (Wootton, 1996). The only genetic work conducted on the purple finch (Marten & Johnson, 1986) supports the current taxonomy, but is limited in both the number of sample sites (n = 2) and sample sizes (n = 2 and 15). Using a more representative sampling regime covering more of the purple finch’s distribution, and several molecular makers, the aim of this study was to examine the evolutionary history and the effects of dispersal barriers on contemporary genetic patterns.

We examined three hypotheses related to purple finch evolution. First, we hypothesize that given their wide distribution across North America and large number of morphological differences between subspecies, the two subspecies of purple finch have been isolated for a prolonged period of time and likely survived the LGM in separate refugia. The Atlantic Shelf was a refugium for a number of species, including tree species upon which purple finch rely for food and nesting (Brubaker et al., 2005; Walter & Epperson, 2005). We predict the Atlantic Shelf and areas south of ice sheets as candidate refugia for the purple finch given their current distribution.

![FIGURE 1 Assignment of individuals based on BAPS analysis of mtDNA (a) and z-linked (b) loci and STRUCTURE analysis of microsatellite loci (c). Mitochondrial locus (a) shows *H. p. californicus* (purple) and *H. p. purpureus* clusters (orange and green). Z-linked locus (b) shows four clusters corresponding to a predominantly *H. p. californicus* group (blue), a widespread (green), *H. p. purpureus* (yellow), and a cluster with no obvious geographic clustering (gray). Microsatellites (c) show two eastern maritime clusters (orange and yellow), a central continental cluster (green), a western *H. p. purpureus* and VanIs cluster (teal), two *H. p. californicus* clusters (purple and blue). Figure c includes all sampling sites. Map shading depicts the breeding ranges of *H. p. purpureus* (light grey) and *H. p. californicus* (dark grey).](image-url)
Second, with the morphological and behavioral differences and relatively small contact zone between subspecies, we hypothesize no or low levels of gene flow between subspecies. We predict a large number of genetic differences between subspecies, and little haplotype/allele sharing. Third, based on findings from other studies, we hypothesize that contemporary barriers, that is, bodies of water and geographic distance, isolate H. purpureus populations. The straits separating both Newfoundland and Vancouver Island from the mainland correspond to patterns of genetic isolation in other taxa with similar dispersal mechanisms (Holder et al., 2004; Lait & Burg, 2013). We therefore predict populations on either side of these boundaries will be genetically distinct. Given the species large range, we predict isolation by distance. Lastly, we predict higher levels of population differentiation in the nonmigratory H. p. callificoris than the migratory H. p. purpureus, as many sedentary species have been shown to exhibit low dispersal rates (Barrowclough, Groth, Mertz, & Gutierrez, 2004; Burg, Gaston, Winker, & Friesen, 2005; Spellman, Riddle, & Klicka, 2007).

2 | METHODS AND MATERIALS

2.1 | Sample acquisition

Two hundred and sixty-seven purple finches were sampled from 10 populations: Central British Columbia (CBC), Coastal Oregon (CoOR), Labrador (LAB), Michigan (MI), North Dakota (ND), Newfoundland (NL), Nova Scotia (NS), Southern California (SCA), Vancouver Island (VanIs), and Washington (WA) (Figure 1). Individuals were captured across their breeding range in May to July from 2007 to 2013 using 12-m mist nets and playback recordings. Sampling was restricted to summer to reduce the number of migrants caught. A small (<50 μl) blood sample was taken from the brachial vein and the birds were banded and released on site. Blood was stored in 99% ethanol.

2.2 | DNA extraction

Total genomic DNA was extracted from ~10 μl of blood using a modified Chelex extraction (Walsh, Metzger, & Higuchi, 1991). Following extraction, all samples were stored at ~20°C.

2.3 | Mitochondrial and Z chromosome DNA amplification and sequencing

A 707-bp fragment of the AldB region of the Z chromosome was amplified in 178 samples for a total of 306 alleles, using primers AldB6-F and AldB8-R (Hackett et al., 2008). This region on the Z chromosome was amplified using a similar thermal cycling program as the ATP6 reactions with the exception of a 50°C annealing temperature, 2.0 mmol/L MgCl$_2$, and trisodium citrate buffer (New England Biolabs). Successfully amplified samples were sent to NanuQ sequencing service at McGill University, Montreal, Quebec. Sequences were checked and aligned using MEGA v. 5 (Tamura et al., 2011).

2.4 | Microsatellite amplification

Three H. purpureus samples from CBC, NL, and VanIs were used to test 39 microsatellite loci designed from other avian species. Nine loci which worked consistently were screened for polymorphism with another 12 individuals from across the range. A total of seven loci were polymorphic and used to screen 260 samples. Six of the polymorphic loci: CETC 215 (Poláková et al., 2007), Ase18 (Richardson, Jury, Dawson, & Salgueiro, 2000), PAT MP 43 (Otter, Ratcliff, Michaud, & Boag, 1998), Titgata 39, Titgata 02 (Wang, Hsu, Te, & Li, 2005), and CTC 101 (Tarvin, 2006) were amplified using one cycle of 120 s at 94°C, 45 s at 50°C, and 60 s at 72°C; seven cycles of 60 s at 94°C, 30 s at 50°C, and 45 s at 72°C; 25 cycles of 30 s at 94°C, 30 s at 52°C, and 45 s at 72°C; and a final cycle of five minutes at 72°C. A seventh locus, Cuc28 (Gibbs, Tabak, & Hobson, 1999), was amplified with the same program, except annealing $T_{m1}$ and $T_{m2}$ were 45 and 48°C, respectively. The 10 μl PCR containing: 0.2 mmol/L dNTP, 2 mmol/L MgCl$_2$ (2.5 mmol/L for CETC 215 and CETC 215, and 1.5 mmol/L for PAT MP 43), 1 μmol/L each primer, 0.5 μmol/L fluorescently labeled M13 tag.

2.5 | Genetic analyses

2.5.1 | Sequence data

AldB sequences from all known male birds were run through PHASE v. 2.0 (Stephens & Donnelly, 2003) in DnaSP v. 5.1 (Librado & Rozas, 2009) to account for the presence of two Z chromosome sequences in males. Four individuals from NS were removed due to highly dissimilar z-linked sequences, although their mitochondrial sequences matched other purple finches. Haplotype ($h$) and nucleotide diversity ($\pi$) indices were calculated in DnaSP v. 5.1 (Librado & Rozas, 2009) using the modified false discovery rate (FDR) (Benjamini & Hochberg, 1995). Genetic differentiation between sampling sites was examined using $F_{ST}$ values calculated in GENALEX v. 6.5 (Peakall & Smouse, 2006). Due to small sample size ($n \leq 6$), LAB, CoOR, and VanIs sites were removed from all pairwise $F_{ST}$ analysis. $p$-values were corrected using the modified false discovery rate (FDR) (Benjamini & Hochberg, 1995). AMOVA analyses were performed in Arlequin v. 3.5.1.3 to test for the diversity found between the two subspecies, among the populations,
and within the populations (Excoffier & Lischer, 2010). Principal coordinate analysis (PCoA) on $\Phi_{ST}$ and $F_{ST}$ values in gENALEX for mitochondrial DNA and z-linked loci, respectively, allowed us to quantify the variance in our data.

A Bayesian clustering program, BAPS v. 5.2, was used to group individuals as BAPS forms clusters with no a priori defined populations. The analysis was run with the linked loci option (Corander, Waldmann, & Sillanpää, 2003).

The relationships between all haplotypes were examined using statistical parsimony networks created in TCS v. 1.21 (Clement, Posada, & Crandall, 2000) for both mtDNA and z-linked loci. All connections were made with a 95% connection limit.

2.5.2 Microsatellite data

Amplified DNA was run on an acrylamide gel with a ladder and controls on the NEN Model 4300 DNA Analyzer (Licor Biosciences). Individuals missing more than three of the seven loci ($n = 3$) were removed from the analyses. A total of 260 individuals from all 10 populations were successfully genotyped at the seven loci. Populations and loci were checked for deviations from Hardy–Weinberg equilibrium and linkage disequilibrium with GENEPOP (Rousset, 2008), and evidence of large allele dropout, null alleles, and genotyping errors were examined using Microchecker (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004).

Genotype data were run through the Bayesian clustering program STRUCTURE v. 2.3.4 to determine the number of clusters found in the data (Pritchard, Stephens, & Donnelly, 2000). Because this type of analysis uses individuals and is not as sensitive to levels of sampling within populations, LAB, CoOR, and VanIs were included. A burn-in of 50,000 and MCMC length of 150,000 were used with admixture model and loc priors. Ten iterations were performed for each cluster (K) 1-10. Structure Harvester v. 0.6.94 (Earl & vonHoldt, 2012) was used to calculate average likelihoods for each value of K and implement the Evanno method (Evanno, Regnaut, & Goudet, 2005). $\Delta K$ and $\ln P(D)$ were used to determine the optimal number of clusters present. As suggested by Pritchard et al. (2000), a hierarchical analysis was performed by rerunning the analysis for each cluster to test for further structure.

In addition to conducting cluster analysis, genetic differentiation between populations was calculated using Wright’s $F_{ST}$ index (Wright, 1965) and Hedrick’s $G’_{ST}$ (Hedrick & Goodnight, 2005) in gENALEX v. 6.5 (Peakall & Smouse, 2006). Using the $F_{ST}$ values, an AMOVA and a principal coordinate analysis were conducted in Arlequin v. 3.5 (Excoffier & Lischer, 2010).

Discovery of potential barriers was conducted using Barrier v. 2.2 (Manni, Guérard, & Heyer, 2004), which uses geographic information and genetic distance information (pairwise $F_{ST}$ matrices) to map putative barriers according to Monmonier’s algorithm (Monmonier, 1973).

2.6 Isolation by distance

To clarify whether genetic differentiation is a result of geographic distance, Mantel tests were performed comparing genetic and geographic distances to test for isolation by distance. Tests were completed for all three datasets in gENALEX v. 6.5 using shortest geographic distances between sampling sites through suitable forested habitat.

2.7 Spatio-geographic modeling

Spatio-geographic modeling was used to identify potential Pleistocene refugia. Occurrence information for the purple finch (>500,000 occurrences) was obtained from the Global Biodiversity Information Facility. After removing points with no UTMs, potential outliers (outside the expected range), duplicated data, samples from migratory periods, or any data from potentially unreliable sources, 5,710 points remained. Five of the 19 climate layers with ≥0.9 threshold in ENMTools (Warren, Glor, & Turelli, 2008) were used. The climatic layers included maximum temperature of warmest month, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of wettest month, and precipitation of driest month. A file containing the UTMs of the 5,710 purple finch locations was loaded into MaxEnt v. 3.3.3 (Phillips, Anderson, & Schapire, 2006), along with the five Bioclim climatic layers. MaxEnt was run with the recommended hinge only function to reduce model overfit. Ten replicates were run with the cross-validate function. The migratory $H. p. purpureus$ and the resident $H. p. californicus$ were also run separately in case their separate distributions influenced the models, but these did not change the projections and therefore were not included. MaxEnt was then used to model possible distributions during the LGM (21,000 years ago) and LIG (120,000–140,000 years ago).

3 RESULTS

3.1 Sequence data

3.1.1 ATP6 sequence data

Diversity indices for the ATP6 locus varied. Excluding populations with fewer than four individuals, haplotype diversity ranged from 0.270 (SCA) to 0.899 (ND), and nucleotide diversity ranging from 0.0004 (SCA) to 0.0056 (NS) (Table 1). The average nucleotide difference between subspecies was 2.4%. A coalescence time of 1.1 MYA was calculated using the fixed differences in the mitochondrial dataset between the two subspecies.

The ATP6 parsimony haplotype network contained a total of 56 haplotypes. Nineteen of the haplotypes were found in more than one individual and four of these were restricted to a single population. Of the 56 haplotypes, 44 were found in a single individual or population (Table 3a). $H. p. californicus$ and $H. p. purpureus$ formed two distinct clusters with no haplotype sharing (Figure 2a). $H. p. californicus$ had two shared and 13 single haplotypes while $H. p. purpureus$ had 17 shared and 24 single haplotypes.

Pairwise $\Phi_{ST}$ values ranged from 0.000 to 0.960 with the highest $\Phi_{ST}$ value between MI and SCA from different subspecies (Table 2a). Between the two $H. p. californicus$ populations (WA and SCA), $\Phi_{ST}$ was 0.092, while for the five $H. p. purpureus$ populations, $\Phi_{ST}$ values ranged from 0.000 to 0.194. Average $\Phi_{ST}$ between subspecies was 0.9193. All
pairwise comparisons between subspecies were significant and CBC was significantly different from all other H. p. purpureus populations and the two H. p. californicus populations were significantly different from each other.

The significant differentiation between subspecies was supported by AMOVAs. The majority of the variance for the mitochondrial locus was explained by genetic differentiation between subspecies variation (90%), while 9% was explained by differences between individuals, and just 1% of the variation between populations.

Principal coordinate analysis for ATP6 showed coordinate 1 explained most of the variation (87.3%), while coordinates 2 (8.9%) and 3 (3.2%) explained the rest. The first two coordinates explained 96% of the variation and clustered geographically proximal populations together (Figure 3). BAPS identified three clusters for the mitochondrial locus, one H. p. californicus cluster and two predominantly H. p. purpureus clusters (Figure 1a). The two H. p. purpureus clusters showed an east–west gradient with one cluster predominantly occurring in the west and decreasing in frequency to the east, and an eastern cluster that is less common in the west.

### 3.1.2 | AldB sequence data

The final AldB dataset contained 306 sequences. The z-linked chromosome showed lower diversity values than the mitochondrial ATP6, with a range of haplotype diversity values for populations of $n > 4$ from 0.086 in SCA to 0.837 for ND. Nucleotide diversity ranged from 0.0005 in SCA to 0.0069 in ND (Table 1). CBC had one of the highest haplotype diversities ($h = 0.816$) (Table 1).

The z-linked locus shows more haplotype sharing between the two subspecies, but generally separates the subspecies, with the exception of four CoOR, one SCA, and four CBC individuals (Figure 2b). A total of 47 haplotypes were found at this locus. Thirty-six haplotypes were restricted to one sampling site, including 33 that were found in a single individual (Table 3). CBC had the highest overall number of haplotypes (16) and the highest number of shared haplotypes (11) (Table 3).

### 3.1.3 | Genotype data

None of the seven microsatellite loci showed significant effects of large allele dropout or stuttering causing scoring errors for any of the populations. However, CETC 215 showed a homozygote excess, suggesting null alleles in four of the populations (NS, NL, CBC, and SCA), while Microchecker suggested possible null alleles for Titgata 39 with NL and ND samples, for Titgata 02 among NL and CBC samples, and Ase18 among CBC samples. Analyses were run with and without CETC 215; however, the results were not different so CETC 215 was kept in the analysis.

Mean observed heterozygosities ($H_o$), expected heterozygosities ($H_e$), allelic richness ($A_r$), and standard errors (SE) for microsatellite data.

### Table 1: Haplotype ($h$) and nucleotide ($\pi$) diversity values, sample size ($n$), number of haplotypes ($Nh$) in each population at the mitochondrial and z-linked loci

|          | mtDNA ATP | Z chromosome AldB | Microsatellite |
|----------|-----------|-------------------|---------------|
| Pop      | $h$ | $\pi$ | $n$ | $Nh$ | $h$ | $\pi$ | $n$ | $Nh$ | $H_o$ ± SE | $H_e$ ± SE | $A_r$ ± SE | $n$ |
| Vanls    | 0.000 | 0.0000 | 4 | 1 | 0.000 | 0.0000 | 4 | 1 | – | – | – | – |
| CoOR     | 1.000 | 0.0029 | 2 | 2 | 0.786 | 0.0062 | 8 | 4 | – | – | – | – |
| WA       | 0.679 | 0.0015 | 38 | 10 | 0.486 | 0.0017 | 39 | 14 | 0.506 ± 0.092 | 0.592 ± 0.119 | 4.881 ± 1.411 | 39 |
| SCA      | 0.270 | 0.0004 | 28 | 5 | 0.086 | 0.0005 | 46 | 3 | 0.528 ± 0.148 | 0.498 ± 0.13 | 4.494 ± 1.367 | 30 |
| NL       | 0.889 | 0.0026 | 34 | 16 | 0.464 | 0.0024 | 50 | 6 | 0.514 ± 0.128 | 0.572 ± 0.109 | 5.687 ± 1.204 | 33 |
| CBC      | 0.858 | 0.0024 | 53 | 17 | 0.816 | 0.0052 | 56 | 16 | 0.492 ± 0.137 | 0.529 ± 0.142 | 6.517 ± 1.470 | 59 |
| NS       | 0.857 | 0.0056 | 35 | 14 | 0.604 | 0.0038 | 47 | 6 | 0.587 ± 0.116 | 0.659 ± 0.093 | 6.015 ± 1.067 | 42 |
| ND       | 0.899 | 0.0028 | 24 | 14 | 0.837 | 0.0069 | 26 | 12 | 0.431 ± 0.152 | 0.467 ± 0.139 | 4.801 ± 1.298 | 22 |
| MI       | 0.661 | 0.0018 | 19 | 7 | 0.754 | 0.0045 | 26 | 12 | 0.352 ± 0.141 | 0.417 ± 0.129 | 6.583 ± 1.457 | 20 |
| LAB      | 0.733 | 0.0014 | 6 | 3 | 0.500 | 0.0058 | 4 | 2 | – | – | – | – |

$F_{ST}$ values for the z-linked locus ranged from 0.000 to 0.805 (Table 2). The $F_{ST}$ values were lower within species (0.116 in H. p. californicus and 0-0.048 in H. p. purpureus) than between subspecies (0.438–0.805). All pairwise $F_{ST}$ values between subspecies and between the two H. p. californicus populations were significant after corrections for multiple tests. The only H. p. purpureus comparison that was significant was NL–CBC.

The AMOVA from AldB showed 55%, 43%, and 2% of the variation is explained by differences between subspecies, within populations, and among populations, respectively. For AldB, PCoA coordinates 1 and 2 explained 90% and 7% of the variation (Figure 3) and populations clustered according to subspecies. BAPS found a total of four clusters and assigned at least one individual in all but one H. p. purpureus population to the H. p. californicus cluster and several H. p. californicus to a widespread cluster (Figure 1b).
Coordinates 1 and 2 explained a total of 70% of the variation (45% and 25%, respectively), while coordinate 3 explained an additional 16% (Figure 3c). Unlike the mtDNA and z-linked loci, there is no obvious clustering in the PCoA (Figure 3c). Coordinate 1 separates central populations (ND and MI) from the other populations, and coordinate 2 separates eastern (NS and NL) from...
### TABLE 2

Mitochondrial (ATP6) pairwise $\Phi_{ST}$ and z-linked (AldB) pairwise $F_{ST}$ comparisons (below diagonal) and corresponding significance scores (above diagonal). Microsatellite pairwise $F_{ST}$ and $G'_{ST}$ (italicized) comparisons (below diagonal) and corresponding $P$-values (above diagonal). Values in bold remained significant following FDR corrections.

|         | WA   | SCA  | NL   | CBC  | NS   | ND   | MI   |
|---------|------|------|------|------|------|------|------|
| **(a) ATP6** |      |      |      |      |      |      |      |
| *H. p. californicus* | *    | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| SCA | 0.092 | *    | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| *H. p. purpureus* | NL   | 0.898 | 0.932 | *    | <0.0001 | 0.820  | 0.099 | 0.306 |
| CBC | 0.903 | 0.928 | 0.180 | *    | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| NS   | 0.898 | 0.932 | 0.000 | 0.194 | *    | 0.060  | 0.306 |
| ND   | 0.896 | 0.936 | 0.019 | 0.131 | 0.017 | *    | 0.234 |
| MI   | 0.910 | 0.960 | 0.005 | 0.113 | 0.006 | 0.014 | *    |

| **(b) AldB** |      |      |      |      |      |      |      |
| *H. p. californicus* | *    | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| SCA | 0.116 | *    | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| *H. p. purpureus* | NL   | 0.621 | 0.805 | *    | 0.009 | 0.405 | 0.054 | 0.099 |
| CBC | 0.438 | 0.558 | 0.060 | *    | 0.189 | 0.135 | 0.847 |
| NS   | 0.535 | 0.707 | 0.000 | 0.007 | *    | 0.144 | 0.522 |
| ND   | 0.462 | 0.649 | 0.048 | 0.020 | 0.017 | *    | 0.414 |
| MI   | 0.467 | 0.695 | 0.034 | 0.000 | 0.000 | 0.000 | *    |

| **(c) Microsatellites** |      |      |      |      |      |      |      |
| *H. p. californicus* | *    | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 |
| SCA | 0.066/0.105 | *    | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 |
| *H. p. purpureus* | NL   | 0.095/0.131 | 0.080/0.211 | *    | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 |
| CBC | 0.045/0.050 | 0.028/0.081 | 0.053/0.115 | *    | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 |
| NS   | 0.109/0.145 | 0.083/0.203 | 0.076/0.155 | 0.049/0.098 | *    | <0.0001/0.014 | <0.0001/0.014 | <0.0001/0.014 |
| ND   | 0.070/0.070 | 0.047/0.167 | 0.065/0.113 | 0.045/0.055 | 0.09/0.186 | *    | 0.003/0.014 |
| MI   | 0.174/0.213 | 0.13/0.384 | 0.137/0.264 | 0.125/0.223 | 0.14/0.327 | 0.029/0.082 | *    |

Significance values have been corrected for multiple comparisons using the modified FDR and significant comparisons are bolded. Microsatellite pairwise $F_{ST}$ and $G'_{ST}$ (italicized) comparisons (below diagonal) and corresponding $P$-values (above diagonal). Values in bold remained significant following FDR corrections.

western (SCA, CBC, and WA) and central populations. The CBC
*H. p. purpureus* population clusters closer to *H. p. californicus*.

STRUCTURE and Structure Harvester revealed three clusters with the
Evanno method and six clusters using Bayes’ rule (Pritchard et al.,
2000) (Figure 4b). The three clusters separated eastern populations
(NL and NS), central populations (LAB, MI, and ND), and western popu-
lations (WA, CoOR, SCA) with CBC and VanIs showing mixing between
these groups. Hierarchical analysis for each of the three clusters di-
vided the clusters further for a total of six groups: (i) NL, (ii) NS, (iii) LAB,
MI, and ND, (iv) CBC and VanIs, (v) WA, and (vi) CoOr and SCA. CBC in-
dividuals showed mixed ancestry, assigning to the central populations
of ND and MI, and the CBC and VanIs cluster (Figures 3c, 4). BARRIER
2.2 discovered a single barrier between NS and MI separating eastern
populations of LAB, NS, and NL from the other populations.

### 3.2 | Isolation by distance

Isolation by distance was significant using mtDNA ($r^2 = .261, p = .003$)
and z-linked data ($r^2 = .387, p = .001$). However, it was not significant
($r^2 = .018, p = .101$) for microsatellite data.

### 3.3 | Spatio-geographic modeling

The model resulting from running nine climatic layers and over 5,710
occurrence locations performed significantly better than random.
The average omission rate for this model closely resembled the pre-
dicted omission rate, meaning few occurrences were in unsuitable
areas. The area under the curve (AUC) was 0.944 (±0.005), where 0.5
is random and values closer to one denote a greater ability to distin-
guish between suitable and unsuitable habitat (Carstens & Richards,
2007).

The predicted distribution of *H. p. purpureus* closely resembled the
actual distribution (Figure 5a) (Sibley, 2011). Bioclim layer 10
(mean temperature of warmest quarter) and 11 (mean temperature
of coldest quarter) explained 30.2% and 25.3%, respectively, of the
actual distribution (Figure 5a) (Sibley, 2011). Bioclim layer 10
is random and values closer to one denote a greater ability to distin-
guish between suitable and unsuitable habitat (Carstens & Richards,
2007).
| Haplotype | VanIs | CoOR | SCA | WA | CBC | ND | MI | NS | LAB | NL | Total |
|-----------|-------|------|-----|----|-----|----|----|----|-----|----|-------|
| (a) ATP6  |       |      |     |    |     |    |    |    |     |    |       |
| A         | 4     | 1    | 24  | 19 |     |     |    |    |     |    |       |
| B         | 14    | 1    | 1   | 3  | 3   |     |    |    |     |    | 22    |
| C         | 10    | 1    | 2   | 1  | 2   |     |    |    |     |    | 14    |
| D         | 2     | 1    |     |    |     |     |    |    |     |    | 3     |
| E         | 3     |      |     |    |     |     |    |    |     |    |       |
| F         | 1     |      | 3   | 2  |     |     |    |    |     |    | 2     |
| G         | 1     | 1    | 2   |    |     |     |    |    |     |    | 5     |
| H         | 1     | 1    | 1   |    |     |     |    |    |     |    | 2     |
| I         | 1     | 1    |     |    |     |     |    |    |     |    |       |
| J         |       |      |     |    |     |     |    |    |     |    |       |
| K         | 4     | 1    | 4   | 1  | 2   |     |    |    |     |    | 12    |
| L         | 1     |      | 1   |    |     |     |    |    |     |    | 2     |
| M         | 2     | 1    | 1   | 2  | 3   |     |    |    |     |    | 12    |
| N         | 1     | 1    | 1   |    |     |     |    |    |     |    | 5     |
| O         | 1     |      | 1   |    |     |     |    |    |     |    | 3     |
| P         | 2     | 1    | 1   |    |     |     |    |    |     |    | 3     |
| Q         | 1     | 1    | 1   | 2  |     |     |    |    |     |    | 2     |
| R         | 1     |      | 1   |    |     |     |    |    |     |    | 2     |
| S         |       |      |     |    |     |     |    |    |     |    |       |
| #Unique   | 0     | 1    | 4   | 8  | 7   | 5  | 2  | 5  | 0   | 5  | 37    |
| #Private  | 0     | 1    | 4   | 9  | 9   | 5  | 2  | 6  | 0   | 5  | 41    |
| #Haplotypes | 1   | 2    | 5   | 10 | 17  | 14 | 7  | 14 | 3   | 16 | 56    |
| Sample size | 4  | 2    | 28  | 38 | 53  | 24 | 19 | 35 | 6   | 34 | 243   |
| (b) z-Linked locus AldB |       |      |     |    |     |    |    |    |     |    |       |
| A         | 3     | 44   | 24  | 3  |     |     |    |    |     |    | 78    |
| B         | 7     | 2    | 8   | 1  | 7   |     |    |    |     |    | 28    |
| C         | 1     | 7    | 1   | 7  | 3   |     |    |    |     |    | 23    |
| D         | 22    | 10   | 13  | 28 | 36  | 109 |     |    |     |    |       |
| E         | 2     |      | 1   | 1  |     |     |    |    |     |    |       |
| F         | 1     | 4    |     |    |     |     |    |    |     |    | 6     |
| G         | 2     | 1    | 2   |    |     |     |    |    |     |    | 5     |
| H         | 3     | 2    | 1   |    | 1   |     |    |    |     |    | 7     |
| I         | 1     | 2    |     |    |     |     |    |    |     |    | 3     |
| J         | 3     |      | 1   | 1  |     |     |    |    |     |    | 3     |
| K         |       |      |     |    |     |     |    |    |     |    |       |
| L         | 1     | 1    |     |    |     |     |    |    |     |    | 2     |
| M         | 2     | 1    |     |    |     |     |    |    |     |    | 3     |
| N         | 2     |      |     |    |     |     |    |    |     |    | 2     |
| #Unique   | 0     | 1    | 2   | 11 | 5   | 7  | 6  | 0  | 0   | 1  | 33    |
| #Private  | 0     | 1    | 2   | 12 | 6   | 7  | 7  | 0  | 0   | 1  | 36    |
| #Haplotypes | 1  | 4    | 3   | 14 | 16  | 12 | 12 | 6  | 2   | 6  | 47    |
| Sample size | 4  | 8    | 46  | 39 | 56  | 26 | 26 | 47 | 4   | 50 | 306   |
refugia south of the ice sheets, MaxEnt identified suitable habitat off the coast of Newfoundland. LIG projections showed isolation between eastern and western areas of suitable habitat (Figure 5c).

4 | DISCUSSION

4.1 | Multiple refugia

Our results, particularly the AldB and ATP6 loci, provided support for the hypothesis that the two subspecies likely experienced prolonged isolation after a Pleistocene era split approximately 1.1 MYA. *H. purpureus* survived in two different refugia: *H. p. californicus* in one and *H. p. purpureus* in another (Figure 5b). The ENM shows four locations with suitable habitat during the LGM: one within much of the current *H. p. californicus* range on the Pacific Coast, another to the east of the Sierra Nevada Mountains, a third large area south of the ice sheets in the east, and a fourth off the Grand Banks of Newfoundland (Figure 5b).

The current breeding distribution of *H. p. purpureus* lies within previously glaciated areas. This suggests a refugium outside of the current distribution for *H. p. purpureus*, and it possibly persisted in a single refugial area in the southeastern USA (Figure 5). *H. p. purpureus* mtDNA haplotypes, which retain signatures of historical genetic structuring, are distributed across the range and are not divergent (Figures 1a, 2a, 3a), suggestive of expansion from a single refugium. This is supported by the large number of shared haplotypes, pairwise ΦST (except CBC), low among population variation of 1% in mtDNA, and similar haplotype diversity values among populations (Table 1).

ATP and AldB data give a clearer picture of historic distributions of *H. p. californicus*. The lower genetic diversity in SCA and the high nucleotide and haplotype diversity values in WA (Table 1) suggest the *H. p. californicus* refugium was in the northern part of the current range. Diversity values in WA are more congruent with an older population which supports the idea that *H. p. californicus* survived the LGM in a northwestern refugium (Figure 5). Previous studies have purported Pacific Northwest refugia for a number of diverse taxa (Byun, Koop, & Reimchen, 1997; Soltis, Gitzendanner, Strenge, & Soltis, 1997).

The nucleotide and haplotype diversity values of *H. p. californicus* suggest a southward expansion of *H. p. californicus* into SCA. The SCA population has the lowest haplotype and nucleotide diversity values of all the populations with the exception of the undersampled VanIs (Table 1). Low diversity indices can result from bottlenecks or founder effects, and are more common along the periphery of a species range than in the center (Bush et al., 2011; Grus et al., 2009).

4.2 | Contemporary structure

*H. p. purpureus* and *H. p. californicus* populations were able to maintain strong genetic differentiation after postglacial expansion, as evidenced by mtDNA and z-linked loci at many metrics (pairwise ΦST/FST comparisons, AMOVA, PCoA, and BAPS). The mtDNA haplotypes show separation of *H. p. purpureus* populations from *H. p. californicus* (Figure 2). Microsatellite data indicate contemporary structure with significant population genetic differentiation (Table 2) among six isolated groups (Figure 4a). One cluster containing CBC and VanIs grouped both subspecies. While this may be influenced by small population size for VanIs, AldB also suggests mixing in those populations. While mitonuclear discordance is often evidence of incomplete lineage sorting, this phenomenon is not expected to produce the geographic patterns of differentiation seen in our data.

The contemporary mixing between the two subspecies in CBC and VanIs could result from one of three factors. The high genetic diversity (Table 1) in CBC might indicate a separate evolutionary history.
from other H. p. purpureus populations, but secondary contact can also cause high diversity values. Given CBC’s proximity to a potential contact zone with H. p. californicus populations, secondary contact may be a more likely explanation. Admixture in the AldB locus suggests limited secondary contact, for which there is regional evidence in Townsend’s and black-throated green warblers (Dendroica townsendi, D. virens) and Swainson’s thrushes (Catharus ustulatus) (Ruegg, 2007; Toews, Brelsford, & Irwin, 2011). The considerable geographic sampling gap between CBC and the closest sampled H. p. purpureus population in ND may exaggerate the genetic isolation of CBC from other H. p. purpureus populations, especially given the significant IBD. Lastly, differing migratory behaviors could explain the discrepancy between CBC and other H. p. purpureus birds. CBC birds overwinter in the south-western United States, while the other populations of H. p. purpureus that we sampled migrate south to the east of the Rocky Mountains (Wootton, 1996).

STRUCTURE showed mixing among several sampling sites. Interestingly, VanIs (H. p. californicus) individuals clustered with H. p. purpureus birds from CBC (Figures 3c, 4), and the CBC population clustered separately from other H. p. purpureus populations (Figures 3c, 4). CBC and VanIs populations, while from different subspecies, are geographically close in proximity. The sample size for the VanIs population is low (n = 4), three individuals from the well-sampled CBC population shared a haplotype with the VanIs population at the z-linked locus, and another CBC bird grouped with two WA individuals (Figure 2b). The mixing of CBC and VanIs populations is plausible, and further evidence that a H. p. purpureus/H. p. californicus contact zone may exist in south-western BC.

Mixing is also evident in other populations. In SCA and CoOR, we caught three individuals with H. p. purpureus z-haplotypes and H. p. californicus mtDNA haplotypes (Figure 2a,b) amounting to four alleles, one from a SCA female and three from two CoOR males. Despite the fact that H. p. purpureus overwinter in H. p. californicus range, migration routes do not explain the presence of H. p. purpureus z-haplotypes within the H. p. californicus range as H. p. purpureus migrants would not have H. p. californicus mtDNA. We

**FIGURE 4** Hierarchical runs from STRUCTURE (a). After the initial run at K = 3 (top plot), clusters were separated to examine additional structure (bottom plot, K = 6). Statistical output from Structure Harvester (b) suggesting optimal K with ΔK and Ln P(D).
also found CBC *H. p. purpureus* with *H. p. californicus* z-linked alleles and *H. p. purpureus* mtDNA (three individuals, four alleles). The presence of *H. p. purpureus* nuclear DNA within the *H. p. californicus* range and *H. p. californicus* nuclear DNA in the *H. p. purpureus* range, along with the clustering of CBC and VanIs populations, suggests limited gene flow between the two subspecies at some western sites. This could occur through hybridization at a contact zone with male-biased dispersal as the pattern is only seen in nuclear loci. Similar patterns of male gene flow are found in the spectacled eider (*Somateria fischeri*) (Scribner et al., 2001). Secondary contact between groups from separate glacial refugia has been suggested for several species across multiple taxa in western Canada, including mountain goats (*Oreamnos americanus*), boreal chickadees (*Poecile hudsonicus*), and Sitka and white spruce (*Picea sitchensis* and *P. glauca*) (Hamilton & Aitken, 2013; Lait & Burg, 2013; Shafer, Côté, & Coltman, 2011).

**FIGURE 5** Projection of suitable climatic conditions for purple finch in the present day (a), from the LGM (~21,000 years ago) (b), and from LIG (~120,000–140,000 years ago) (c). Areas of suitable conditions in red are based on trained data from 2,710 presence occurrences, five uncorrelated climate layers, and the MIROC-LJP Global Climate Model.
4.3 | Barriers

Both physical and nonphysical barriers correspond to contemporary population genetic patterns in *H. purpureus*. Behavioral differences including migration and site fidelity, and differences in plumage correspond to genetic patterns. Migration behavior can explain the high genetic diversity between subspecies. With the exception of the aforementioned potential mixing in a small number of individuals in the Pacific Northwest, both resident and migratory populations show significant population differences. The nonmigratory *H. p. californicus* have high variation between populations, as evidenced by the disparate genetic diversities of SCA and WA populations (Table 2) and STRUCTURE. The migratory *H. p. purpureus* do exhibit site fidelity, which might explain the observed genetic differentiation. Studies on *H. p. purpureus* in Michigan (Magee, 1924) and New York (Yunick, 1987) show 56.8% and 23.6%, respectively (n = 1,770), of banded birds return to breed in the same area. Similar patterns of low population structure of highly migratory species are found in northern pike (*Esox lucius*) (Miller et al. 2001) and green turtles (*Chelonia mydas*) (Encalada et al., 1996).

Significant correlations were found between geographic and genetic distance in mtDNA and z-linked loci, suggesting that physical distance could also restrict gene flow. Other barriers also play a role as some populations, WA and CoOR, that are geographically close are genetically differentiated. No obvious physical barriers exist between the WA and CoOR sites; however, contemporary gene flow could be restricted between these two populations due in part to plumage differences. Duvall (1945) noted a unique group of Pacific Northwest birds which he termed *Carpodacus purpureus rubidus* (not recognized as a subspecies by the American Ornithologists Union), in which males have darker heads, backs, rumps, and anterior lower parts; females are a darker olive. Both sexes lack motting in the upper back and nape found in other nearby populations (Duvall, 1945). Similar morphological differences are present between the two recognized subspecies. *H. p. californicus* females are more olive green in plumage than *H. p. purpureus*, and *H. p. californicus* males have browner flanks and a duller red rump (Wootton, 1996). Isolation on small spatial scales has also been linked to the influence of suitable habitat on dispersal ability in boreal and black-capped chickadees (*Poecile atricapillus*) (Adams & Burg, 2015; Adams, Lazerte, Otter, & Burg, 2016; Lait & Burg, 2013).

Behavior also plays a role in isolation, as behavioral differences exist with respect to song. The songs of the two subspecies are distinct, and the H. *purpureus* song is more variable (Wootton, 1996). As song is important in mate selection, it may reinforce reproductive isolation similar to assortative mating in *Ficedula* flycatchers (Qvarnström et al., 2010).

**REFERENCES**

Adams, R. V., & Burg, T. M. (2015). Gene flow of a forest-dependent bird across a fragmented landscape. *PLoS ONE*, 10, 1–22.

Adams, R. V., Lazerte, S. E., Otter, K. A., & Burg, T. M. (2016). Influence of landscape features on the microgeographic genetic structure of a resident songbird. *Hereditas* (Edinburgh), 117, 1–10.

Apte, S., Smith, P. J., & Wallis, G. P. (2007). Mitochondrial phylogeography of New Zealand freshwater crayfishes, *Paranephrops* spp. *Molecular Ecology*, 16, 1897–1908.

Barrowclough, G. F., Groth, J. G., Mertz, L. A., & Gutierrez, R. J. (2004). Phylogeographic structure, gene flow and species status in blue grouse (*Dendragapus obscurus*). *Molecular Ecology*, 13, 1911–1922.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B*, 57, 289–300.

Brubaker, L. B., Anderson, P. M., Edwards, M. E., & Lozhkin, A. V. (2005). Beringia as a glacial refugium for boreal trees and shrubs: New perspectives from mapped pollen data. *Journal of Biogeography*, 32, 833–848.

Burg, T. M., Gaston, A. J., Winker, K., & Friesen, V. L. (2005). Rapid divergence and postglacial colonization in western North American Steller’s jays (*Cyanocitta stelleri*). *Molecular Ecology*, 14, 3745–3755.

Bush, K. L., Dyte, C. K., Moynahan, B. J., Aldridge, C. L., Sauls, H. S., Battazzo, A. M., ... Coltman, D. W. (2011). Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. *Conservation Genetics*, 12, 527–542.

Byun, S. A., Koop, B. F., & Reimchen, T. E. (1997). North American black bear mtDNA phylogeography: Implications for morphology and the Haida Gwaii glacial refugium controversy. *Evolution (N Y)*, 51, 1647–1653.

Our study has shown how the evolution of the purple finch has been influenced by a number of evolutionary processes and both historical and contemporary distributions. Prolonged isolation of the two subspecies was maintained during the last glacial maximum and contemporary physical barriers, and behavioral barriers including site fidelity, migration, and assortative mating, have maintained patterns of low gene flow between the two subspecies. Some secondary contact was found in a small portion of their range, although it was limited. The purple finch’s evolutionary history demonstrates how population differences shape behavior and response to barriers to dispersal can influence evolution and, ultimately, speciation.

**CONFLICT OF INTEREST**

We have no conflict of interest to declare.
Carstens, B. C., & Richards, C. L. (2007). Integrating coalescent and ecological niche modeling in comparative phylogeography. Evolution (N Y), 61, 1439–1454.

Clark, R. W., Brown, W. S., Stechert, R., & Zamudio, K. R. (2010). Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conservation Biology, 24, 1059–1069.

Clement, M., Posada, D., & Crandall, K. A. (2000). TCS: A computer program to estimate gene genealogies. Molecular Ecology, 9, 1657–1659.

Corander, J., Waldmann, P., & Sillanpää, M. J. (2003). Bayesian analysis of genetic differentiation between populations. Genetics, 163, 367–374.

Crespi, E. J., Rissler, L. J., & Browne, R. A. (2003). Testing Pleistocene refugia theory: Phylogeographical analysis of Desmognathus wrighti, a high-elevation salamander in the southern Appalachians. Molecular Ecology, 12, 969–984.

Duvall, A. J. (1945). Variation in Dendroica caerulescens. Condor, 47, 202–205.

Earl, D. A., & vonHoldt, B. M. (2012). STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources, 4, 359–361.

Encalada, S. E., Lahanas, P. N., Bjorndal, K. A., Bolten, A. B., Miyamoto, M. M., & Bowen, B. W. (1996). Phylogeography and population structure of the Atlantic and Mediterranean green turtle Chelonia mydas: A mitochondrial DNA control region sequence assessment. Molecular Ecology, 5, 473–483.

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molecular Ecology, 14, 2611–2620.

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources, 10, 564–567.

Fleischer, R. C., McIntosh, C. E., & Tarr, C. L. (1998). Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K – Ar based ages of the Hawaiian Islands to estimate molecular evolutionary rates of individuals using the software STRUCTURE: A simulation study. Molecular Ecology Resources, 10, 564–575.

Friesen, V. L., Burg, T. M., & McCoy, K. D. (2007). Mechanisms of population differentiation in seabirds: Invited review. Molecular Ecology, 16, 1765–1785.

Gibbs, H. L., Tabak, L. M., & Hobson, K. (1999). Characterization of microsatellite DNA loci for a neotropical migrant songbird, the Swainson's thrush (Catharus ustulatus). Molecular Ecology, 8, 1151–1152.

Grus, W. E., Graves, G. R., & Glenn, T. C. (2009). Geographic variation in the mitochondrial control region of black-throated blue warblers (Dendroica caerulescens). Auk, 126, 198.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., ... Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. Science, 320, 1763–1768.

Hamilton, J. A., & Atiken, S. N. (2013). Genetic and morphological structure of a spruce hybrid (Picea sitchensis × P. glauca) zone along a climatic gradient. American Journal of Botany, 100, 1651–1662.

Hedrick, P., & Goodnight, C. (2005). Evolution (N Y), 59, 1633–1638.

Hofreiter, M., Serre, D., Rohland, N., Rabeder, G., Nagel, D., Conard, N., ... Pääbo, S. (2004). Lack of phylogeography in European mammals before the last glaciation. Proceedings of the National Academy of Sciences of the United States of America, 101, 12963–12968.

Holder, K., Montgomerye, R., & Friesen, V. L. (2004). Genetic diversity and management of Nearctic rock ptarmigan (Lagopus mutus). Canadian Journal of Zoology, 82, 564–575.

Jaramillo-Correa, J. P., Beaulieu, J., Khasa, D. P., & Bousquet, J. (2009). Inferring the past from the present phylogeographic structure of North American forest trees: Seeing the forest for the genes. Canadian Journal of Forest Research, 39, 286–307.

Lait, L. A., & Burg, T. M. (2013). When east meets west: Population structure of a high-latitude resident species, the boreal chickadee (Poecile hudsonicus). Heredity (Edinburgh), 111, 321–329.

Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics, 25, 1451–1452.

Mace, M. J. (1924). Notes on the purple finch (Carpodacus purpureus purpureus). Auk, 41, 606–610.

Manni, F., Guérard, E., & Heyer, E. (2004). Geographic patterns of (genetic, morphologic, linguistic) variation: How barriers can be detected by using Monmonier’s algorithm. Human Biology, 76, 173–190.

Marten, J., & Johnson, N. K. (1986). Genetic relationships of North American cardueline finches. Condor, 88, 409–420.

Miller, L. M., Kallemeyn, L., & Senanan, W. (2001). Spawning-site and natal-site fidelity by northern pike in a large lake: mark–recapture and genetic evidence. Transactions of the American Fisheries Society, 130, 307–316.

Monmonier, M. S. (1973). Maximum-difference barriers: An alternative numerical regionalization method. Geographical Analysis, 5, 245–261.

Otter, K., Ratcliffe, L. Michaud, D., & Boag, P. T. (1998). Do female black-capped chickadees prefer high-ranking males as extra-pair partners? Behavioral Ecology and Sociobiology, 43, 25–36.

Peakall, R., & Smouse, P. E. (2006). GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes, 6, 288–295.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. Ecological Modelling, 190, 231–259.

Poláková, R., Vyskočilová, M., Martin, J. F., Mays, H. L., Hill, G. E., Bryja, J., & Albrecht, T. (2007). A multiplex set of microsatellite markers for the scarlet rosemchn (Carpodacus erythrinus). Molecular Ecology Notes, 7, 1375–1378.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. Genetics, 155, 945–959.

Qvarnström, A., Rice, A. M., & Elleghen, H. (2010). Speciation in Ficedula flycatchers. Philosophical Transactions of the Royal Society of London. Series B, Biological sciences, 365, 1841–1852.

Richardson, D., Jury, F., Dawson, D., & Salgueiro, P. (2000). Fifty Seychelles warblers (Acrocephalus sechellensis) microsatellite loci polymorphic in Sylviidae species and their cross-species amplification in other passerine birds. Molecular Ecology, 9, 2226–2231.

Rousset, F. (2008). GENEPOP’007: A complete re-implementation of the GENEPOP software for Windows and Linux. Molecular Ecology Resources, 8, 103–106.

Ruegg, K. C. (2007). Divergence between subspecies groups of Swainson’s thrush (Catharus ustulatus ustulatus and C. u. swainsoni). Ornithological Monographs, 63, 67–77.

Rueness, E. K., Stenseth, N. C., O’Donoghue, M., Boutin, S., Elleghen, H., & Jakobsen, K. S. (2003). Ecological and genetic spatial structuring in the Canadian lynx. Nature, 425, 69–72.

Scribner, K. T., Peterson, M. R., Fields, R. L., Talbot, S. L., Pearce, J. M., & Chesser, R. K. (2001). Sex-biased gene flow in spectacled eiders (Anatidae): Inferences from molecular markers with contrasting modes of inheritance. Evolution, 55, 2105–2115.

Shafer, A. B. A., Côté, S. D., & Coltman, D. W. (2011). Hot spots of genetic diversity descended from multiple Pleistocene refugia in an alpine ungulate. Evolution (N Y), 65, 125–138.

Solit, D. E., Gittendenner, M.A., Streng, D. D., & Solits, P.S. (1997). Chloroplast DNA intraspecific phylogeography of plants from the Pacific Northwest of North America. Plant Systematics and Evolution, 206, 353–373.

Sonsthagen, S. A., Talbot, S. L., Scribner, K. T., & Mccracken, K. G. (2011). Multilocus phylogeography and population structure of common eiders breeding in North America and Scandinavia. Journal of Biogeography, 38, 1368–1380.

Spellman, G. M., Riddle, B., & Klicka, J. (2007). Phylogeography of the mountain chickadee (Poecile gambeli): Diversification, introgression, and expansion in response to Quaternary climate change. Molecular Ecology, 16, 1055–1068.

Stephens, M., & Donnelly, P. (2003). A comparison of Bayesian methods for haplotype reconstruction from population genotype data. American Journal of Human Genetics, 73, 1162–1169.
Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. (2011). MEGAS: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution, 28, 2731–2739.

Tarvin, K. A. (2006). Polymorphic microsatellite loci from the American goldfinch (Carduelis tristis) and their cross-amplification in a variety of passerine species. Molecular Ecology Notes, 6, 470–472.

Toews, D. P. L., Brelsford, A., & Irwin, D. E. (2011). Hybridization between Townsend’s Dendroica townsendi and black-throated green warblers D. virens in an avian suture zone. Journal of Avian Biology, 42, 434–446.

Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., & Shipley, P. (2004). MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes, 4, 535–538.

Walsh, P. S., Metzger, D. A., & Higuchi, R. (1991). Chelex-100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques, 10, 506–513.

Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. Evolution (N Y), 62, 2868–2883.

Wootton, J. (1996). Purple finch (Haemorhous purpureus). The Birds of North America. Online

Wright, S. (1965). The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution (N Y), 19, 395–420.

Wright, S. (1965). The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution (N Y), 19, 395–420.

Wootton, J. (1996). Purple finch (Haemorhous purpureus). The Birds of North America. Online

Wright, S. (1965). The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution (N Y), 19, 395–420.

Wootton, J. (1996). Purple finch (Haemorhous purpureus). The Birds of North America. Online

Wootton, J. (1996). Purple finch (Haemorhous purpureus). The Birds of North America. Online

Wootton, J. (1996). Purple finch (Haemorhous purpureus). The Birds of North America. Online

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Wang, M. T., Hsu, Y. C., Te, Yao C., & Li, S. H. (2005). Isolation and characterization of 12 tetranucleotide repeat microsatellite loci from the green-backed tit (Parus monticolus). Molecular Ecology Notes, 5, 439–442.

Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. Evolution (N Y), 62, 2868–2883.

Yunick, R. P. (1987). Seven multiple-recapture encounters of banded birds. North American Bird Bander, 12, 60–63.