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Species-specific responses to landscape features shaped genomic structure within Alaska galliformes

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Abstract

Aim: Connectivity is vital to the resiliency of populations to environmental change and stochastic events, especially for cold-adapted species as Arctic and alpine tundra habitats retract as the climate warms. We examined the influence of past and current landscapes on genomic connectivity in cold-adapted galliformes as a critical first step to assess the vulnerability of Alaska ptarmigan and grouse to environmental change. We hypothesize that the mosaic of physical features and habitat within Alaska promoted the formation of genetic structure across species.

Location: Alaska, United States of America.

Taxa: Ptarmigan and Grouse (Galliformes: Tetraoninae).

Methods: We collected double digest restriction-site-associated DNA sequence data from six ptarmigan and grouse species ($N = 13\text{--}145/\text{species}$) sampled across multiple ecosystems up to ~ 10 degrees of latitude. Spatial genomic structure was analysed using methods that reflect different temporal scales: (1) principal components analysis to identify major trends in the distribution of genomic variation; (2) maximum likelihood clustering analyses to test for the presence of multiple genomic groupings; (3) shared co-ancestry analyses to assess contemporary relationships and (4) effective migration surfaces to identify regions that deviate from a null model of isolation by distance.

Results: Levels of genomic structure varied across species ($\Phi_{ST} = 0.009\text{--}0.042$). Three general patterns of structure emerged: (1) east-west partition located near the Yukon-Tanana uplands; (2) north-south split coinciding with the Alaska Range and (3) northern group near the Brooks Range. Species-specific patterns were observed; not all landscape features were barriers to gene flow for all ptarmigan and grouse and temporal contrasts were detected at the Brooks Range.

Main conclusions: Within Alaska galliformes, patterns of genomic structure coincide with physiographic features and highlight the importance of physical and ecological barriers in shaping how genomic diversity is arrayed across the landscape. Lack of concordance in spatial patterns indicates that species behaviour and habitat affinities play key roles in driving the contrasting patterns of genomic structure.

KEYWORDS

Alaska, effective dispersal, grouse, landscape genomics, population genomic structure, ptarmigan

1 | INTRODUCTION

A population's capacity to respond to changes in the environment depends in part on the ability of individuals to move across the landscape (Wong & Candolin, 2015). The dispersal process is complex, as the decision by individuals to emigrate is influenced by density-dependent processes, behavioural cues and individual propensity (Cayuela et al., 2018). Furthermore, the success of a dispersal event, in terms of arrival at a new locale and successful reproduction, is affected by the individual's ability to navigate across physical barriers, body condition upon arrival, site-specific factors and phenotype interactions with the new environment (Cote et al., 2017). Because the genetic consequences of dispersal can have important implications for population fitness via the maintenance of genetic diversity and the possible introduction of beneficial variants (Frankham, 2015), assessment of gene flow and genetic structuring is vital to understanding the resiliency of populations to stochastic events and environmental change (Cayuela et al., 2018).

Rapid environmental change in the Arctic has wide-ranging ecological consequences (Myers-Smith & Hik, 2016; Post et al., 2009). Alterations in selection regimes influence fitness, with some species responding with northward and altitudinal shifts in their distributions. As species modulate their ranges, community compositions alter, affecting both biotic and abiotic factors (Post et al., 2009). The advance of shrub vegetation into the tundra ecosystem, for example, is expected to influence soil temperature, light reflection, nutrient turnover, carbon cycling and plant–herbivore relationships which may create feedbacks promoting further advancement of shrub and forest vegetation into Arctic and alpine regions (Myers-Smith & Hik, 2016). Species resident to Arctic and alpine ecosystems will likely augment behaviours, and possibly amend movement strategies, in response to changes in vegetation composition (and therefore forage areas) and abiotic conditions, since ecosystem dynamics will be altered throughout the annual cycle (Christie et al., 2014).

Here we present the first comparative assessment of population genomic structure of ptarmigan and grouse (galliformes; subfamily Tetraoninae) species resident to Alaska. The ecosystems and landscapes within Alaska are vast, and comprise the temperate rainforests of the southeast, boreal forests and alpine tundra in the interior, treeless boreal in the west and Arctic tundra along the northern coast. Numerous mountain ranges and rivers bisect the state; the Alaska Range comprises the largest mountain in North America with one of the greatest vertical reliefs in the world. Furthermore, ecosystems within Alaska were shaped by a dynamic glacial history. Glacial sheets fragmented Beringia along the Brooks Range (until 13.5 K BP; Dyke, 2004) as well as proposed smaller refugia in southeastern Alaska (Carrara et al., 2007). Diverse ecoregions and geographical features and the presence of multiple glacial refugia can foster genomic structure within populations (Hewitt, 2004), though how these features affect contemporary patterns of genetic diversity depend on behavioural and biological characteristics of individual species (Zamudio et al., 2016). Differences in levels of philopatric

TABLE 1 Summary of habitat requirements, movement patterns and breeding behaviour exhibited by ptarmigan and grouse of Alaska that may differentially influence genomic structure

Species	Distribution	Habitat	Movement	Territoriality
Rock Ptarmigan	Arctic coastal plain and south	Arctic, sub-Arctic, Alpine Tundra	Nomadic (partial)	Intra-male
White-tailed Ptarmigan	Restricted—South of Alaska Range	Alpine	Elevational	Intra-sexual
Willow Ptarmigan	Arctic coastal plain and south	Arctic, sub-Arctic, Alpine Tundra	Vary—Resident; Short (<160 km; Alaska); Long (<800 km; Manitoba)	Intra-sexual
Ruffed Grouse	Interior Alaska and transplanted in Southcentral Alaska	<i>Populus</i> (spp.)-dominated forests	Resident	Intra-male
Sharp-tailed Grouse	Interior Alaska	Steppe, grassland and mixed-shrub	Short (<35 km)	Intra-male
Sooty Grouse	Southeast Alaska	Coastal rainforest; sub-Alpine forest	Resident; Short	Intra-sexual
Spruce Grouse	Brooks Range and south	Boreal; conifer-dominated forests	Vary—Resident; Short (<15 km)	Intra-sexual

Note: Intra-sexual: territorial agonistic interactions occur between members of the same sex and both sexes defend territories; Intra-male: territorial agonistic interactions occur only among males. Information regarding species characteristics was provided by the Birds of the World species accounts and citations therein (Connelly et al., 2020; Hannon et al., 2020; Martin et al., 2020; Montgomerie & Holder, 2020; Rusch et al., 2020; Schroeder et al., 2020; Zwicker & Bendell, 2020).



behaviour as well as the influence of glacial refugia, for example, have resulted in incongruent patterns of spatial genetic structure between two avian congeners that share similar circumpolar distributions and occupy coastal marine habitats (Pearce et al., 2004; Sonsthagen et al., 2011). The heterogeneous landscape coupled with recent rapid environmental change in the Arctic may exert conflicting pressures on processes influencing genetic structure. For example, topographic features and naturally fragmented landscapes may pose strong barriers to dispersal, whereas conversely, alterations in abiotic conditions will likely promote movement of individuals to track favourable micro-habitats.

Ptarmigan and grouse are common residents in Arctic, sub-Arctic, alpine and boreal ecosystems (Table 1). In Alaska, ptarmigan (rock *Lagopus muta*, white-tailed *L. leucura* and willow *L. lagopus*) and grouse (ruffed *Bonasa umbellus*, sharp-tailed *Tympanuchus phasianellus*, sooty *Dendragapus fuliginosus* and spruce *Falci pennis canadensis*) species are largely sympatric but occupy different micro-habitats during various portions of the annual cycle. Indeed, in winter months, ptarmigan form large mixed-species flocks composed of all three species. Spruce and ruffed grouse can be found in the same stand of deciduous and coniferous trees. Ptarmigan and grouse are not known to form mixed flocks; however, they are found in close geographical proximity (<5 km; see Sonsthagen & Wilson, 2020). Movement patterns vary by species (Table 1). Species occupying alpine habitats display seasonal changes in elevation: those occupying Arctic locales exhibit nomadic movement patterns in response to food availability, and those occupying boreal forests make short migrations between winter and summer areas. Along with differences in movement patterns, species also differ in mating systems (Table 1). Territoriality is common, with males establishing territories close to their kin (MacColl et al., 2000). As ptarmigan and grouse often occupy remote areas, population trends are little known across most of their distributions (Fuglei et al., 2019). In parts of their range, populations are exhibiting declines thought to be caused by climate-associated and forest-successional changes (Henden et al., 2017; Ross et al., 2016) as well as disruptions to population cyclicity (Fuglei et al., 2019). Variation in life-history attributes may differentially affect processes that influence how genomic variation is distributed across the landscape and likely generates contrasting patterns of genomic structure within this subfamily of closely related species.

Previous assessments of genetic structure within ptarmigan and grouse uncovered regional (rock ptarmigan, Caizergues et al., 2003; ruffed grouse, Jensen et al., 2019) and fine-scale (rock ptarmigan, Bech et al., 2009; Costanzi & Steifetten, 2019; willow ptarmigan, Piertney et al., 1998, 2000; Wenzel et al., 2015) differences. Partitions in genetic variation are concordant with subspecific designations in rock ptarmigan (Holder et al., 2004; Pruett et al., 2010), spruce grouse (Barry & Tallmon, 2010), sharp-tailed grouse (Spaulding et al., 2006) and white-tailed ptarmigan (Langin et al., 2018). Furthermore, evidence from markers that differ in their mode of inheritance indicate female-mediated dispersal in willow ptarmigan (Piertney et al., 2000).

Combined, these disparate studies suggest that genetic diversity in galliform species is typically partitioned and influenced by landscape features.

Here we applied a comparative landscape genomics approach to uncover patterns of genomic diversity within a group of six closely related ptarmigan and grouse species that occupy, variously, habitats ranging up to 10 degrees of latitude—from the Pacific coastal forests of southcentral Alaska's Kenai Peninsula to the tundra of the Arctic coastal plain—using reduced representation genomic (double digest restriction-site-associated DNA sequences; ddRAD) data. Comparisons across closely related species can aid in the identification of processes (behavioural and evolutionary) and provide an indication of the strength of forces acting on genetic diversity and how it is arrayed across the landscape. Such comparisons also identify selection regimes that may not be evident when focusing on a single species (McCracken et al., 2009). We applied methods that recover evolutionarily recent and more historical signatures to aid in the identification of potential temporal contrasts in spatial patterns of genomic diversity. As partitions in genetic structure in ptarmigan and grouse studied elsewhere appear to coincide with landscape features, we suggest the mosaic of physical features and habitat within Alaska will likely limit dispersal of individuals and promote the formation of genetic structure. Specifically, we hypothesize that the persistence of glaciation along the Brooks Range has resulted in deep partitions in the genome across species as observed in other herbivores (e.g. Galbreath et al., 2011; Fedorov et al., 2003). Although southcentral (Kenai Peninsula to the Alaska Range) Alaska has been deglaciated since ~13 K BP (Dyke, 2004) and, likely only recently colonized by ptarmigan and grouse, we hypothesize that the Alaska Range continues to serve as a strong contemporary barrier to dispersal across species. We further hypothesize that differences in movement behaviours and habitat affinities (Arctic-alpine tundra vs. boreal forests) influence how genetic variation is distributed across the landscape within species. Species that exhibit irregular movements (e.g. rock ptarmigan and willow ptarmigan) will have lower levels of differentiation across major geographical features than species that are more sedentary (e.g. white-tailed ptarmigan, ruffed grouse). Species that occupy Arctic-alpine tundra (e.g. ptarmigan) will exhibit lower levels of genetic structure relative to those residing in boreal forest (e.g. grouse), as distributions of Arctic species were larger during the Last Glacial Maximum (LGM) and, in contrast to temperate species, have been contracting post-Pleistocene (Kozma et al., 2018). Finally, we lack information that can inform us about how current and predicted changes to the environment will affect ptarmigan and grouse (Henden et al., 2017). Understanding how genetic variation has been shaped by past and current landscapes is a critical first step to assessing the vulnerability of species to environmental change. Specifically, predictions of species-specific responses to past climatic changes in high-latitude ecosystems require accurate phylogeographical inferences to better predict future range shifts and can aid in the identification of populations of high conservation value (Shafer et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Sampling

We sampled six galliform species occurring within Alaska (Figure 1). Sampling for two species, rock ptarmigan ($n = 109$) and willow ptarmigan ($n = 145$), spans ~10 degrees of latitude (~1300 km), from southcentral Alaska (~59.9°N) to the Arctic Ocean (~70.1°N; Figure 1). The remaining species—white-tailed ptarmigan ($n = 49$), spruce grouse ($n = 71$), ruffed grouse ($n = 22$) and sharp-tailed grouse ($n = 13$)—are restricted to south of the Brooks Range. Birds were collected between May and July from 2015 to 2017. Areas with low sample sizes were augmented by hunter-harvested birds (August–April from 2012 to 2017) submitted to the Alaska Department of Fish and Game as part of a wing collection program ($n = 51$) or provided directly by hunters and outfitters ($n = 140$). Only adult hunter-harvested birds were included in the study, see Schroeder and Robb (2005) for age determination methods. As ptarmigan and grouse exhibit limited movement during the non-breeding season (see Table 1 and Merizon et al., 2018) and sample areas were >100 km distant, birds sampled in the same area were pooled regardless of season.

2.2 | Library preparation and read assembly

Laboratory methods and bioinformatic pipelines follow DaCosta and Sorenson (2014; Python scripts available at <http://github.com/BU-RAD-seq/ddRAD-seq-Pipeline>) and Lavretsky et al. (2015). Libraries were indexed with dual 6 base pair (bp) indices and demultiplexed using bcl2fastq 2.20 or MiSeq Reporter software (Illumina). Single-end sequencing (150 bp) was completed on an Illumina HiSeq 2500, HiSeq 4000 or MiSeq. To limit any biases due to sequencing error and/or allelic dropout, a minimum of 10 reads was required per locus, with the second haplotype represented by at least 29% of reads (or 20%–29% of the reads and the haplotype was present in other individuals) to score a locus as heterozygous. Genomic positions of loci were determined by BLAST analysis to the chicken genome (*Gallus gallus*, GenBank assembly 5.0, GCA_000002315.3). The single nucleotide polymorphisms (SNP)-calling pipeline generated between 2744 and 3796 autosomal loci and 109 and 228 Z-linked loci (Table S1 in Appendix S1). All loci had at least 26× coverage per sample with overall median coverage of approximately 100×.

2.3 | Genomic diversity and structure

We calculated nucleotide diversity and composite pairwise estimates of relative divergence (Φ_{ST}) among sampled locations in the R package 'PopGenome' (Pfeifer et al., 2014). We visualized genetic structure using a principal components analysis (PCA) using the R package 'adegenet' (Jombart, 2008) using a haplotypic approach. Only males were included in analyses of Z-linked loci.

Maximum likelihood estimates of population assignments for each individual were obtained with ADMIXTURE 1.3 (Alexander & Lange, 2011; Alexander et al., 2009). Rare SNPs observed in only one individual were excluded from the analysis with no a priori assignment of individuals to populations. Separate analyses were conducted for each species. We ran 100 iterations per analysis and for each population of K ($K = 1$ –10) and tested for optimal values of K using the cross-validation procedure ($cv = 10$). Other values of K were also analysed to explore other possible scenarios of genetic structure that are consistent with species biology (Janes et al., 2017).

We used fineRADstructure (Malinsky et al., 2018) to infer population structure via shared ancestry (first coalescence) based on the autosomal loci. FineRADstructure focuses on the most recent coalescent events providing information on relatedness, which is informative in situations of contemporary gene flow. Samples were assigned to populations using 1,000,000 iterations sampled every 1000 steps with a burn-in of 100,000. We used 10,000 iterations of the tree-building algorithm to assess genetic relationships among clusters. FineRADstructure is a haplotype-based approach; all SNPs were retained.

2.4 | Partitioning of genomic diversity across the landscape

We used the program EEMS (Petkova et al., 2016) to estimate rates of effective migration and levels of genetic diversity relative to geographical distance within just the three ptarmigan species and spruce grouse, since sample sizes and sites were limited within ruffed and sharp-tailed grouse. EEMS uses a stepping-stone model to assess regions where genetic dissimilarity decays more quickly or slowly than expected under a model of isolation by distance (IBD) based on individual migration rates. A migration surface is then interpolated from these effective migration rates across the landscape to identify barriers or corridors to movement. Based on preliminary runs, we adjusted parameters so the accepted proportion was between 10% and 40%. We ran three independent analyses using 1,000,000 burn-in steps followed by 5,000,000 MCMC iterations sampled every 1000 steps for each deme (100, 250, 500). We checked convergence and visualized effective migration and diversity surfaces using the 'rEEMSpots' package in R (Petkova et al., 2016).

3 | RESULTS

3.1 | Genomic diversity and structure

Estimates of nucleotide diversity were similar across sampling locales within species for both autosomal and Z-linked loci (Table S2 in Appendix S1). The extent of genetic structure varied across species

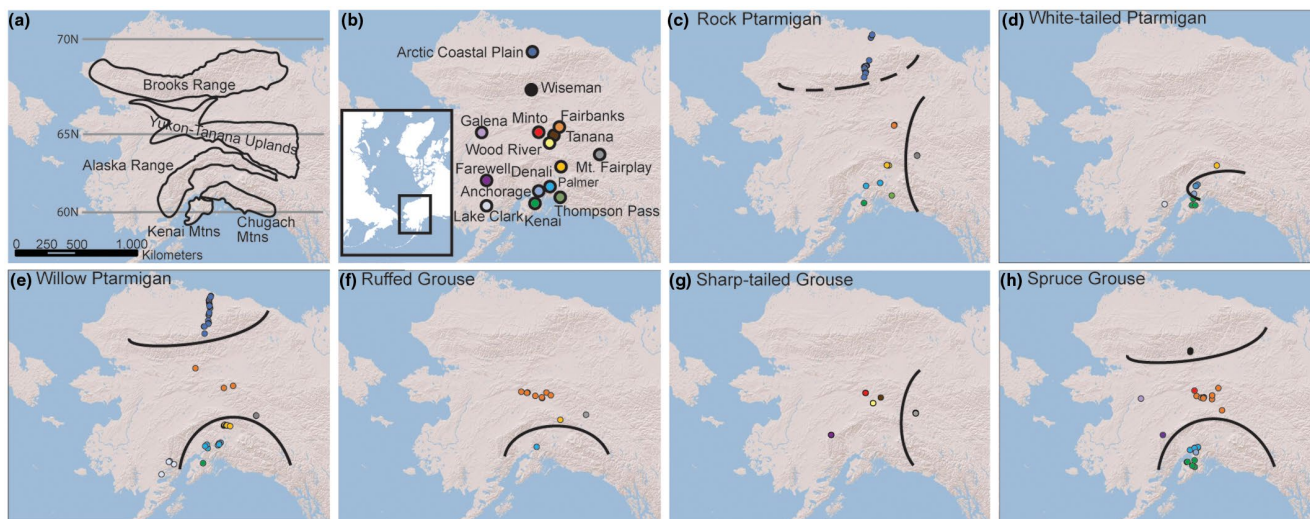


FIGURE 1 Maps of main mountain ranges (a), site names (b) and locations of ptarmigan and grouse samples collected from Alaska (c–h). Sampled sites are represented by a unique colour. Solid lines denote partitions in genomic variation that were detected across multiple analyses. Dash lines denote partitions in genomic variation only observed at co-ancestry plots in fineRADstructure

($\Phi_{ST} = 0.012\text{--}0.042$; Figure 2). Among the ptarmigan, willow (pairwise $\Phi_{ST} = 0.006\text{--}0.063$) and white-tailed (pairwise $\Phi_{ST} = 0.017\text{--}0.025$) ptarmigan exhibited the greatest levels of structure (Figure S1 in Appendix S1). Genetic structure was lowest in rock ptarmigan (pairwise $\Phi_{ST} = 0.005\text{--}0.034$), with the highest inter-population divergence observed between Mt. Fairplay and other sampled sites. Grouse displayed greater genetic structure than ptarmigan, with ruffed grouse ($\Phi_{ST} = 0.042$) exhibiting the highest level of structure, followed by spruce grouse (pairwise $\Phi_{ST} = 0.001\text{--}0.070$) and sharp-tailed grouse ($\Phi_{ST} = 0.012$; Figure S2 in Appendix S1). Levels of genetic structure were similar or slightly higher for Z-linked loci (Figures S3 and S4 in Appendix S1).

Partitions of genomic structure based on Φ_{ST} are reflected in the Admixture and PCA plots and patterns were similar within species for both autosomal and Z-linked loci (Figure 2; Figures S1–S6 in Appendix S1). Rock ptarmigan sampled from Mt. Fairplay were differentiated from samples from all other locales for both clustering analyses. Evidence of long-distance dispersal was also present; three individuals collected at Mt. Fairplay had high membership coefficient values (>0.50) assignments to the other cluster in Admixture and one Mt. Fairplay individual clustered with the multi-location cluster in the PCA. Willow ptarmigan also were partitioned into two clusters—individuals collected in the Arctic and Lake Clark areas clustered together, Denali, Palmer, and Kenai birds in a second cluster with Mt. Fairplay birds showing intermediate membership coefficients. PCA plots of willow ptarmigan also indicate that populations exhibit a pattern of increasing isolation with distance; individuals are arrayed north to south along PC1, apart from Lake Clark, which is the southernmost sampled locale, but centrally located on the plot. There is evidence of long-distance dispersal; two Lake Clark birds had high membership coefficients to the Denali/Palmer/Kenai group and clustered with Kenai and Palmer in the PCA. The two Lake Clark individuals with high PC2 scores likely represent close

familial relationships as indicated by high co-ancestry values estimated in fineRADstructure. Fine spatial scale structure was uncovered for white-tailed ptarmigan, with birds collected from Denali and Kenai loosely clustering together, and birds from the Anchorage and Palmer area clustering together. Both ruffed and spruce grouse appear to have Arctic/interior and southcentral Alaska groupings, though the signature is stronger in spruce grouse. Both Admixture and PCA analyses indicate that spruce grouse exhibit bouts of long-distance dispersal; one bird each from Galena and Minto have high membership coefficients (>0.70) in Admixture and cluster in the PCA with birds sampled from southern sites. Patterns within sharp-tailed grouse are difficult to discern, likely attributable to the limited sample size; however, Mt. Fairplay birds appear to be differentiated from other locales.

Shared co-ancestry matrices generated in fineRADstructure uncovered subtle signatures of genetic structure (Figure 3). Across all species, individuals generally shared greater genetic similarity with other birds sampled from the same locale than with individuals from other sites. There is some evidence of long-distance dispersal for most species as some birds had higher genetic similarity with individuals sampled at different locales. Within rock ptarmigan, four partitions were uncovered—Mt. Fairplay, Arctic, Fairbanks/Denali/Palmer and Thompson Pass—though the Arctic and Thompson Pass groups contained individuals from Fairbanks and Kenai, respectively. White-tailed and willow ptarmigan are highly structured. Multiple groupings were uncovered with Palmer, Denali, Anchorage and Kenai birds mainly grouping by site, in white-tailed ptarmigan. Arctic, Lake Clark, Mt. Fairplay/Fairbanks, Palmer/Kenai and Denali groupings were uncovered for willow ptarmigan. The interior (Fairbanks) and southcentral (Palmer) Alaska birds were largely grouped together within ruffed grouse. Sharp-tailed grouse from Mt. Fairplay had higher co-ancestry values with each other than other interior Alaska locales. Spruce grouse grouped by site.

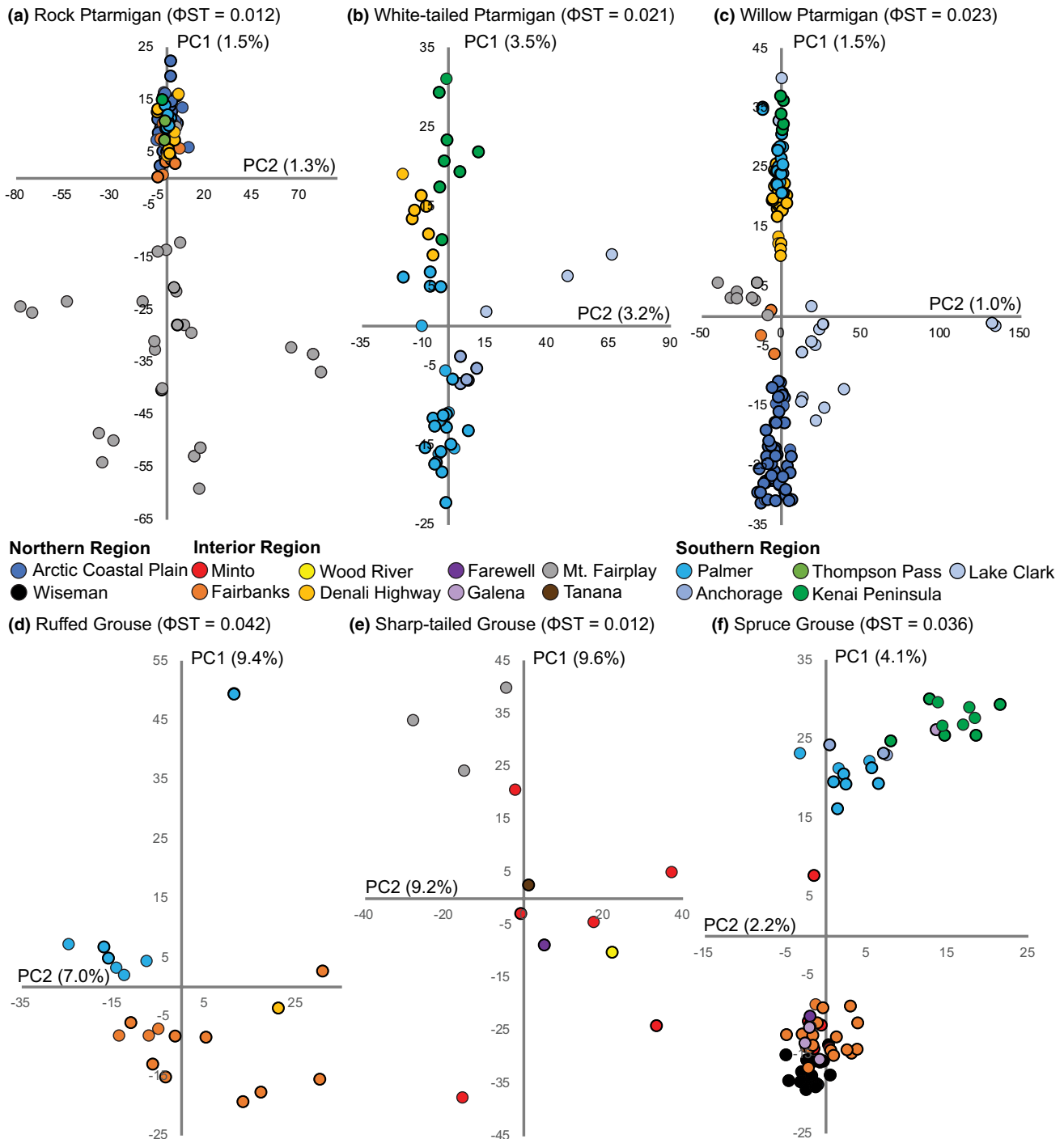


FIGURE 2 Scatter plots of the first two principal components based on restriction-site associated DNA (ddRAD) haplotype sequences (2744 to 3796 autosomal loci) generated from rock ptarmigan (a) white-tailed ptarmigan (b), willow ptarmigan (c), ruffed grouse (d), sharp-tailed grouse (e), and spruce grouse (f) collected in Alaska

3.2 | Genomic diversity across the landscape

Regions where genetic dissimilarity decayed more quickly than expected under a model of IBD were generally congruent across species and these regions largely corresponded with mountain ranges (Figure 4). Willow ptarmigan and spruce grouse demonstrate reduced gene flow rates in locales that coincide with the Brooks Range and Alaska Range.

Willow ptarmigan exhibit more marked restrictions to gene flow than spruce grouse in these regions as evidenced by high posterior probabilities (>0.95). Conversely, the Brooks and Alaska mountain ranges do not appear to hinder movement of rock ptarmigan; rather dispersal is restricted in a region that coincides with the Yukon-Tanana uplands in eastern Alaska. Among white-tailed ptarmigan, the region of reduced gene flow coincides with the Chugach and Kenai mountain ranges.

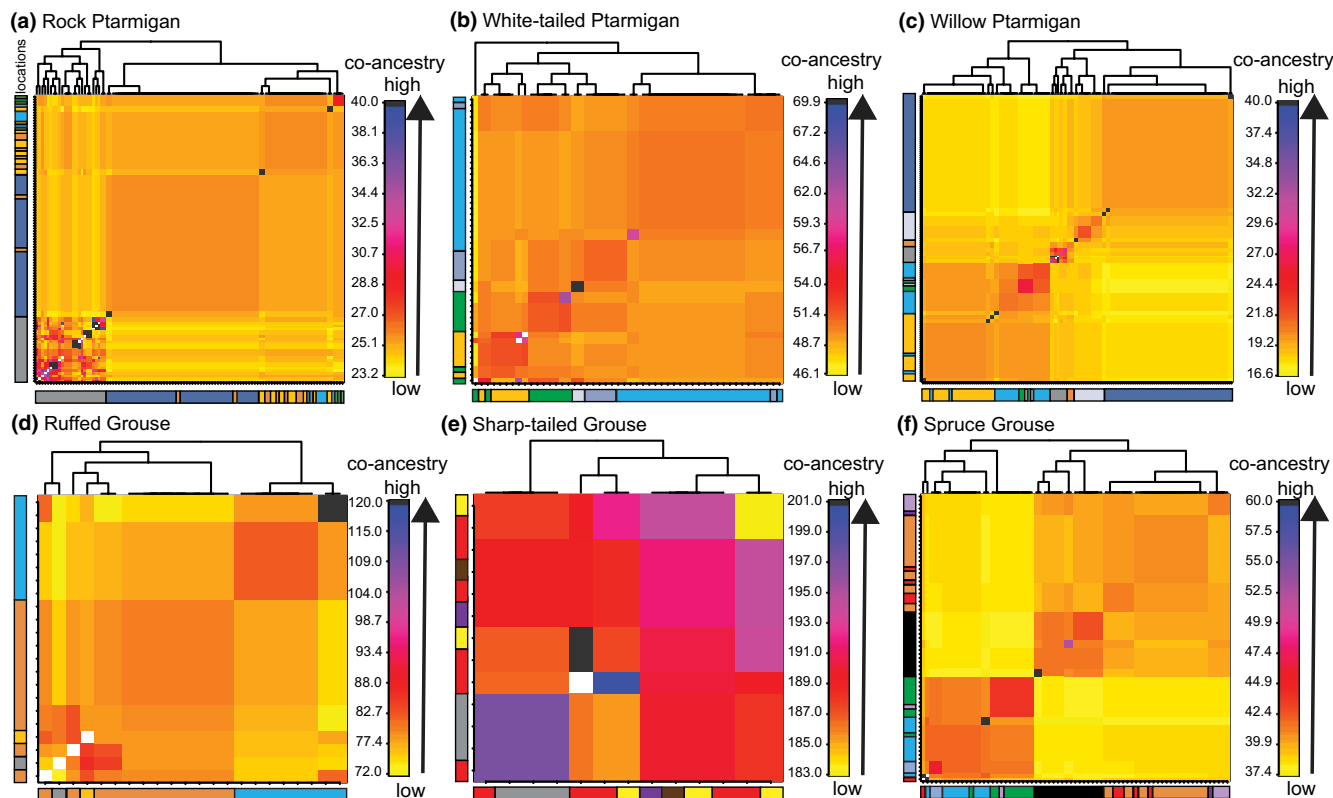


FIGURE 3 Co-ancestry matrix indicating pairwise genetic similarity between Alaska ruffed grouse (a), rock ptarmigan (b), sharp-tailed grouse (c), white-tailed ptarmigan (d), spruce grouse (e) and willow ptarmigan (f) individuals generated in fineRADstructure. The level of inter-individual co-ancestry corresponds to colour scale (located right of the plots): darker colours (e.g. blue and black) represent high levels of genetic similarity and lighter colours (e.g. yellow and orange) indicating lower levels of co-ancestry. Inferred clustering of samples into populations are indicated by the accompanying dendrogram (top of each matrix) and locations of samples are indicated by colour blocks on left and bottom (e.g. black indicates sample from Wiseman, Alaska). Colour blocks correspond to sampling locations indicated in Figure 1. Co-ancestry values were capped at 40–201 for illustrative purposes

4 | DISCUSSION

Current and past landscape features differentially influenced the distribution of genomic variation within and among ptarmigan and grouse species across Alaska. Three general patterns of genomic structure emerged within Alaska ptarmigan and grouse (Figure 1): (1) An east–west partition located near the Yukon–Tanana uplands; (2) A north–south split among interior and southern populations occurring at the Alaska Range and (3) A northern group with variation bisected along the Brooks Range. These shared patterns highlight the importance of environmental and ecological barriers shaping how genomic diversity is arrayed across the landscape in Alaska galliformes.

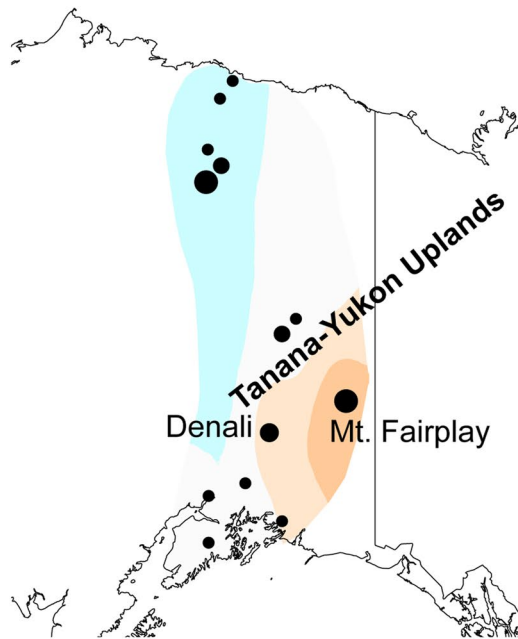
We outlined four hypotheses: (1) glaciation along the Brooks Range resulted in deep partitions in the genome, (2) Alaska Range is a strong contemporary barrier to dispersal across species, (3) species with greater movement affinities will exhibit lower genetic structure and (4) species occupying Arctic–alpine habitats will exhibit lower levels of differentiation than boreal counterparts. Not all patterns conformed to our hypotheses. We uncovered temporal contrasts in signatures of genetic structure between rock ptarmigan and willow ptarmigan sampled across the Brooks Range,

with divergence likely occurring recently within rock ptarmigan as the signature was only detected using first-coalescent analyses, whereas a more historical signature was uncovered in willow ptarmigan as structure was detected across multiple analyses. In addition, there was a lack of structure within rock ptarmigan across the Alaska Range. While the distribution of white-tailed ptarmigan only extends to the Alaska Range, structure was still uncovered along the Chugach and Kenai mountain ranges, highlighting the influence of mountain ranges and corresponding valleys on genomic diversity within this subfamily of birds. Lack of concordance in spatial patterns of genetic variation among certain species, and the presence of species-specific patterns, indicate that species behaviour and habitat affinities still play key roles in driving the contrasting patterns of genomic structure among Alaska galliformes.

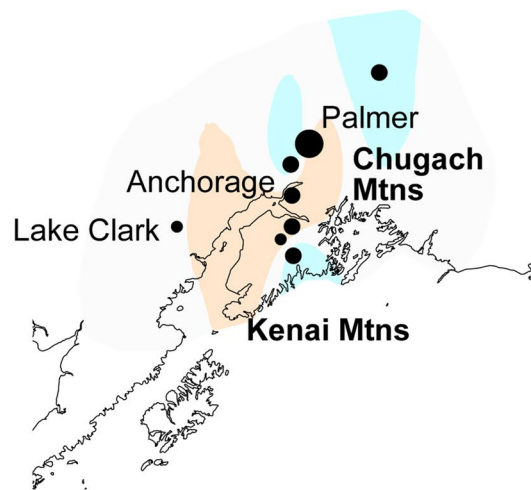
4.1 | Landscape features influencing genomic structure

The presence of a partition in genomic variation coinciding with the Yukon–Tanana uplands in rock ptarmigan and sharp-tailed

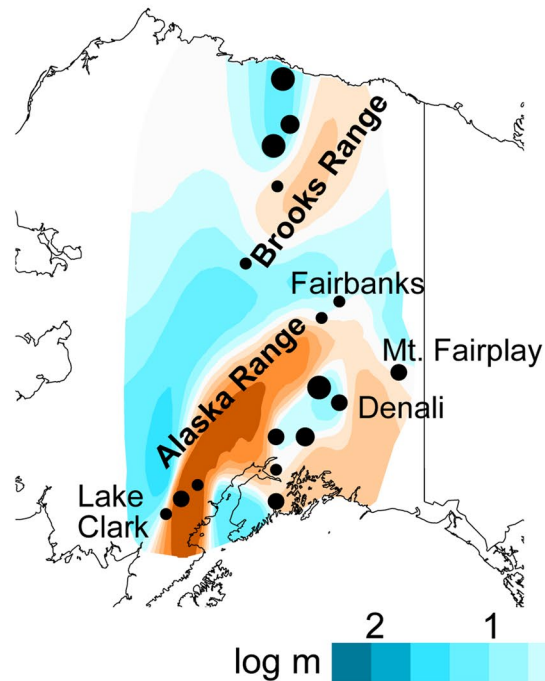
(a) Rock Ptarmigan



(b) White-tailed Ptarmigan



(c) Willow Ptarmigan



(d) Spruce Grouse

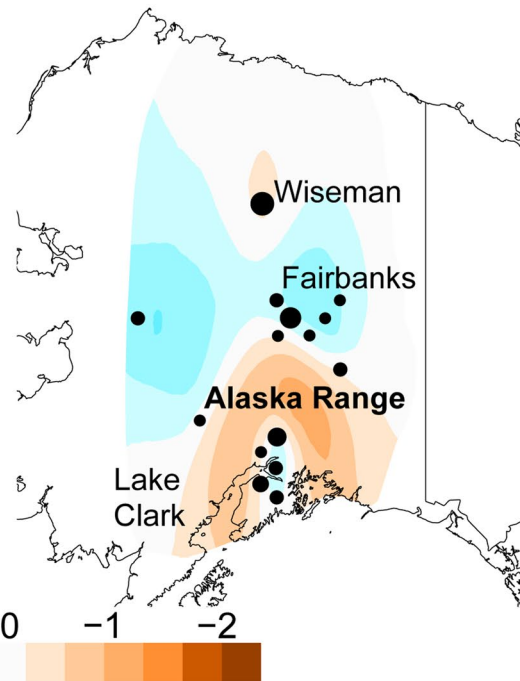


FIGURE 4 Models of effective dispersal rates (log m) inferred by EEMS for ptarmigan and grouse from Alaska. Regions in orange denote areas of low dispersal relative to the average (i.e. barrier) and blue areas denote higher than average dispersal. The size of circle corresponds to the number of individuals represented by the deme

grouse, across multiple analyses, suggests that the heterogeneous landscape within Beringia promoted divergence through isolation in at least two refugia—central Beringia and eastern Beringia—and is concordant with results based on mtDNA (Holder et al., 1999). Eastern Beringia and associated nunataks and peripheral

refugia supported herb–shrub tundra assemblages during the Late Quaternary (Szeicz & MacDonald, 2001) and harboured Arctic and alpine species during the Pleistocene (e.g. Lanier et al., 2015). The Tanana-Yukon uplands are located near the MacKenzie River suture zone (e.g. Fedorov et al., 2003; Fedorov & Stenseth, 2002;



Holder et al., 1999, 2000). Alternatively, genomic structure within eastern Alaska populations may also have been formed via northward expansion of populations south of the ice sheets to their present-day Holocene distribution. However, recent colonization of deglaciated areas via northward expansion leaves predictable genomic signatures, notably reduced genetic variation (Hewitt, 2004), and genomic diversity is not lower in the Mt. Fairplay populations. Furthermore, partitions within mtDNA are consistent with lineages formed in isolation (Holder et al., 1999). Although we cannot explicitly identify the locations of refugial diversification within rock ptarmigan and sharp-tailed grouse, levels of genomic structure and diversity, as well as concordance in patterns with other cold-adapted species, suggest that these species occupied regions within central and eastern Beringia during the LGM.

Genetic discontinuities that coincide with the Alaska Range were detected across multiple analyses and species (willow ptarmigan, ruffed grouse and spruce grouse), indicating that the region contains strong physiographic barriers (river valleys, ptarmigan; mountains/glaciers, grouse) to dispersal. Southcentral Alaska was covered by the Cordilleran Ice Sheet until the Late Wisconsin (~14.5 K BP; Dyke, 2004) and only recently colonized by ptarmigan and grouse; thus, partitions in the genomes appear to have evolved rapidly. Indeed, ruffed grouse ($n = 140$) were transplanted from interior Alaska to southcentral Alaska from 1988 to 1990, where historically no ruffed grouse were present (Steen, 1995), and apparently developed genomic structure ($\Phi_{ST} = 0.042$; Figure 2) within 30 years of translocation at levels comparable to those observed among interior and southcentral populations (willow ptarmigan $\Phi_{ST} = 0.033$ – 0.063 , spruce grouse $\Phi_{ST} = 0.035$ – 0.057 ; Figures S1 and S2 in Appendix S1). This highlights the strength of founder events on genetic diversity in a population with apparent restricted connectivity. Furthermore, multiple long-distance dispersal events by birds sampled in August and September were detected across the Alaska Range, suggesting that birds can readily traverse this large mountain range. If dispersal across mountain ranges are indeed frequent, as suggested by detection herein even with relatively modest sample sizes, presumably gene flow would occur, which contrasts with the observation of genetic structure. The presence of spatial structure suggests that long-distance dispersal events may accrue a fitness cost within willow ptarmigan and grouse. Although individuals are able to cross physiographic barriers and arrive at habitat patches, the likelihood of successful breeding given movement is reduced (e.g. inability to secure territory, reduced energetic reserves, maladapted to microhabitat, etc.) and ultimately fails to result in effective dispersal (Robertson et al., 2018).

Signatures of genetic structure coinciding with the Brooks Range were detected for the three species with an Arctic distribution (Figure 1). Divergence in allelic frequencies was not detected across analyses for all species, however, suggestive of a temporal contrast among species. Evidence for an Arctic grouping is present within willow ptarmigan across analyses, consistent with long-term vicariance and persistence in a refugium north of

the ice shield located along the Brooks Range during the LGM. Demographic breaks coinciding with the Brooks Range have been identified in other Arctic and alpine vertebrates (e.g. Galbreath et al., 2011; Krejsa et al., 2021; Sim et al., 2019; Sonsthagen et al., 2011). Furthermore, population genomic variation is arrayed in an IBD pattern (Figure 2c), which suggests that willow ptarmigan expanded from a single northern Beringia refugium once habitat became available during glacial retreat (e.g. Weksler et al., 2010). Development and subsequent maintenance of genetic structure suggests that once an area was colonized, willow ptarmigan dispersal was restricted. A single population deviates from the latitudinal position of populations along PC1: individuals from Lake Clark, located in southern Alaska but west of the Alaska Range, cluster with Arctic or interior Alaska birds. The association of Lake Clark with the Arctic, potentially along the western coast of Alaska, and interior Alaska suggests that willow ptarmigan are moving among isolated regions through the tundra matrix with the Alaska Range posing as a strong barrier between southern locales. Unfortunately, sampling from the Lake Clark area only included the willow ptarmigan, precluding comparisons across species.

Conversely, genomic structure uncovered among Arctic and interior Alaska rock ptarmigan and spruce grouse populations reflects contemporary rather than historical signatures, as the only analysis that detected partitions between these populations employs a first-coalescence model to evaluate inter-individual relationships. Spruce grouse occupy coniferous forests and the species' range does not extend to the northern slopes of the Brooks Range; we would therefore not expect to detect deep genomic partitions that would signal a long-term retention in a northern Beringian refugium, which did not host extensive coniferous forests. Rather, partitions were likely promoted by restricted dispersal across a physical or ecological barrier post-Pleistocene. Rock ptarmigan, however, are tundra specialists and likely not restricted to south of the Brooks Range during the Pleistocene. Because physiographic barriers do not appear to limit effective dispersal in rock ptarmigan, as suggested by the weak signal of genetic structure across the landscape, other process (behavioural, physiological, etc.) may be influencing patterns in genetic diversity for that species. As the distribution of ptarmigan occupying the Arctic is closely linked to snow and shrub cover (Christie et al., 2014), encroachment of shrub into the Arctic may have altered the ecosystem sufficiently to reduce migration tendencies, thereby reducing opportunities for dispersal, within rock ptarmigan. Furthermore, spatial variance in vital rates have been observed among rock ptarmigan occupying Arctic (low elevation) and alpine (high elevation) tundra ecosystems such that Arctic populations have lower adult survival and larger clutch size than their alpine counterparts (Unander et al., 2016). Across all ptarmigan species, recruitment among habitat patches is a key feature of population dynamics as it enables ptarmigan to persist through stochastic conditions (Martin & Wilson, 2011), that typify high-latitude and high-elevation systems. Rescue by external recruitment infers

no local adaptation (Boyle et al., 2016), however, such that variation in clutch size is the result of phenotypic plasticity and not an evolutionary response of species to variation in selection regimes between Arctic and alpine environs. Although these two environments share a variety of characteristics, unique features of each ecosystem likely require different species adaptations to thrive (Martin, 2001). Biotic and abiotic features of Arctic and alpine tundra ecosystems, therefore, may be sufficiently divergent to limit effective dispersal within rock ptarmigan such that immigrants are less or maladapted to local selection regimes. Additional experiments (common garden, transcriptomic, epigenomic, functional genomic) are needed to test this hypothesis.

4.2 | Species characteristics influencing genomic structure

Although shared patterns of spatial genomic structure suggest that key physiographic, and potentially ecological, barriers to dispersal have played a role in shaping the evolutionary history of Alaska galliformes, species-specific patterns were observed and are likely attributable to variation in movement tendencies. Ptarmigan and grouse exhibit similar dispersal tendencies; adult males display high breeding territory fidelity, adult females show lower fidelity to specific territories but return to the same area, and juveniles disperse (Hannon et al., 2020; Martin et al., 2020). Migration patterns differ among species, and therefore the extent of annual movements may provide an avenue for dispersal. Rock ptarmigan is the only Alaska galliform that does not undertake regular seasonal migration, is weakly structured across the landscape, and for which the Alaska Range does not inhibit dispersal. Nomadism is posited to promote higher gene flow because movements are sporadic (Teitelbaum & Mueller, 2019). Furthermore, rock ptarmigan are capable of long-distance movements (>1000 km; Montgomerie & Holder, 2020). Unique movement tendencies of rock ptarmigan may provide more dispersal opportunities, as natal site fidelity is limited and winter areas likely vary spatially and temporally, enabling homogenization of genomic diversity at the landscape scale and driving the incongruent pattern of spatial variation relative to the other ptarmigan and grouse.

5 | CONCLUSIONS

Cold-adapted species likely experienced range expansions during glacial maxima and contracted to remnant tundra and boreal habitat during interglacial periods. Populations of cold-adapted species, therefore, are currently restricted to interglacial (warm climate) refugia (Stewart et al., 2010). As the climate continues to warm, rapid changes in the Arctic and alpine regions are further stressing cold-adapted species already experiencing range declines. Indeed, models project that rock and willow ptarmigan will lose ~30% of their current range by 2070 (Kozma et al., 2018). Arctic populations may be further isolated if variables other than temperature are

driving local adaptation, as boreal and temperate populations may accrue fitness costs associated with range expansion that reduce their ability to establish at more northern latitudes (e.g. Bjorkman et al., 2017). Furthermore, cold-adapted species have evolved physiological and behavioural mechanisms to thrive in environmental extremes. Research assessing trade-offs in adaptations to Arctic and alpine ecosystems in light of environmental warming is scant, but studies suggest that costs of such adaptations increase at higher temperatures (Scridel et al., 2018). As seen here, Alaska galliformes generally display restricted gene flow across the landscape. We were unable to sample across the entire species' ranges, therefore additional barriers to dispersal or areas of increased connectivity may be present (but see Shirk et al., 2021, regarding the influence of unsampled populations on gene flow). As connectivity is vital to the rescue of ptarmigan populations adversely affected by stochastic events (Martin & Wilson, 2011), continued reduction of Arctic and alpine tundra habitats may further isolate populations and reduce the long-term resiliency of populations (e.g. Bech et al., 2009; Langin et al., 2018). Research on the genomic underpinnings of adaptations to the Arctic ecosystem are needed to identify if there are additional barriers (e.g. physiological) embedded within the warming of subarctic and Arctic landscapes that may further isolate populations, resulting in increased vulnerability to stochastic events.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Raw Illumina read data are accessioned in National Center Biotechnology Information (NCBI) Sequence Read Archive (SRA) database under BioProject PRJNA634168, Biosamples SAMN14995710–SAMN14995715, SAMN14995719–SAMN14995725, SAMN14995729–SAMN14995731, SAMN23227020–SAMN23227413. Detailed sample information is available in Sonsthagen and Wilson, (2020).

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BIOSKETCH

The authors are interested in studying microevolutionary processes involved with species response to environmental, ecological and spatial variables and largely focus on vertebrate systems. Author contributions: All authors conceived of the study; S.A.S. and R.E.W. conducted the field sampling, carried out the molecular work, conducted the analyses and led the writing; S.L.T. contributed significantly to the final manuscript; and all authors approved the manuscript.

SUPPORTING INFORMATION

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