



# Population structure of caribou in an ice-bound archipelago

Deborah A. Jenkins<sup>1,2</sup>  | Glenn Yannic<sup>3</sup> | James A. Schaefer<sup>4\*</sup>  | James Conolly<sup>5</sup> |  
Nicolas Lecomte<sup>2\*</sup>

<sup>1</sup>Environmental and Life Sciences Graduate Program, Trent University, Peterborough, ON, Canada

<sup>2</sup>Canada Research Chair in Polar and Boreal Ecology and Centre d'Études Nordiques, University of Moncton, Moncton, NB, Canada

<sup>3</sup>University of Grenoble Alpes, University of Savoie Mont Blanc, CNRS, LECA (Laboratoire d'Ecologie Alpine), Le Bourget-du-Lac, France

<sup>4</sup>Department of Biology, Trent University, Peterborough, ON, Canada

<sup>5</sup>Department of Anthropology, Trent University, Peterborough, ON, Canada

## Correspondence

Deborah A. Jenkins, Environmental and Life Sciences Graduate Program, Trent University, Peterborough, ON, Canada. Email: debbie.jenkins@sympatico.ca; debbiejenkins@trentu.ca

## Funding information

Queen Elizabeth II Graduate Scholarship in Science & Technology; Symons Trust Fund for Canadian Studies; French American Graduate Scholarship; EWC & IE Curtin Graduate Scholarship; Canada Research Chairs; ArcticNet; Natural Sciences and Engineering Research Council of Canada

Editor: David Green

## Abstract

**Aim:** Archipelagos provide ideal natural systems for testing the effects of isolation and fragmentation of habitats on the genetic makeup of populations—an important consideration, given that many insular species are of conservation concern. Two theories predominate: Island Biogeography Theory (IBT) posits that proximity to the mainland drives the potential for migrants and gene flow. The Central Marginal Hypothesis (CMH) predicts that island populations at the periphery of a species range may experience low gene flow, small population size and high rates of genetic drift. We investigated population genetic structure, genetic diversity and key drivers of diversity for Arctic island-dwelling caribou (*Rangifer tarandus*). Our aim was to inform intraspecific units for conservation and decipher how IBT and CMH could act in an archipelago where isolation is highly variable due to sea ice and open water.

**Location:** Canadian Arctic Archipelago, Canada (Latitude, 55–82°N; Longitude, 61–123°W).

**Methods:** We genotyped 447 caribou at 16 microsatellite loci; these caribou represented two subspecies (*R. t. groenlandicus*, *R. t. pearyi*) and three designatable units. We used hierarchical Bayesian clustering and ordination to determine genetic groups. We evaluated the influence of ecological and geographic variables on genetic diversity using linear mixed-effects models and compared diversity among mainland and island herds.

**Results:** Bayesian clustering revealed nine genetic clusters with differentiation among and within caribou subspecies. Genetic differentiation was explained predominantly by isolation-by-distance across all caribou, even at the scale of subspecies. Island caribou were less genetically diverse than mainland herds; individual heterozygosity was negatively correlated with distance-to-mainland and the extent of autumn ice-free coastline and positively correlated with unglaciated island size.

**Main conclusions:** Our findings underscore the importance of hierarchical analysis when investigating genetic population structure. Genetic diversity and its key drivers lend support to both IBT and CMH and highlight the pending threat of climate change for Arctic island caribou.

## KEYWORDS

Arctic, Bayesian clustering, connectivity, designatable units, genetic diversity, landscape heterogeneity, population structure, *Rangifer tarandus*

\*These authors share senior authorship of this study.

## 1 | INTRODUCTION

Archipelagos provide ideal natural systems for inferring the effects of isolation and fragmentation on the genetic makeup of populations (Harradine et al., 2015; Levin & Parker, 2012). Heterogeneous across broad spatial gradients, archipelagos offer a unique opportunity to assess the consequences of island size and geographic proximity on population differentiation and diversity (Frankham, 1996). Distance to mainland can be important, where proximity affords potential migrants and gene flow (Island Biogeography Theory; MacArthur & Wilson, 1967). Additionally, island populations far from mainland or at the periphery of a range may experience low gene flow, small population size and high rates of genetic drift (Central Marginal Hypothesis [CMH]; Eckert, Samis, & Loughheed, 2008). Remote populations may become genetically distinct and experience inbreeding and low genetic diversity (Frankham, Ballou, & Briscoe, 2002; Harradine et al., 2015; Miller, Eldridge, Morris, Zenger, & Herbert, 2011; Techer et al., 2016), but they may also experience local adaptation and speciation (Petren, Grant, Grant, & Keller, 2005; Slatkin, 1987). Such differentiation sets the stage for identifying hierarchical units of species, subspecies, ecotypes, populations and, when linked to genetics and evolution, evolutionarily significant units (ESU; Moritz, 1994; Ryder, 1986). These “lines” have important consequences for conservation and protection, and the scientific inferences we draw (Pond, Brown, Wilson, & Schaefer, 2016; Schaefer, 2006).

Archipelagos at high latitudes may be particularly informative. Uniquely, sea ice in polar environments can reduce among-island isolation (Geffen et al., 2007; Jenkins et al., 2016) by facilitating the flow of genes, the rescue of small populations and the maintenance of genetic diversity (Carmichael et al., 2007; Noren et al., 2011). For terrestrial animals, sea ice is a platform for dispersal, seasonal interisland and island–mainland migrations and sporadic long-distance movements (Carmichael et al., 2008; Miller, Barry, & Calvert, 2005; Noren et al., 2011; Poole, Gunn, Patterson, & Dumond, 2010). Yet in the Arctic, sea ice is spatially and temporally heterogeneous (Ferguson, Taylor, Born, Rosing-Asvid, & Messier, 2001; Kutschera et al., 2016; Sahanatien & Derocher, 2012); across this immense space, uniformity in connectivity is unlikely.

We might anticipate that the genetic differentiation of terrestrial Arctic populations is not readily predictable based on ice as a simple barrier or facilitator of movement (Jenkins et al., 2016). Indeed, a diversity of factors—both geographic (distance, rugged terrain) and biological (mobility, life-history strategies)—can influence connectivity. Few studies have evaluated the determinants of genetic population structuring in polar environments (but see, e.g., Carmichael et al., 2007; Harris, Moore, Galpern, Tallman, & Taylor, 2014; Jenkins et al., 2016; Noren et al., 2011; Yannic et al., 2017). The Arctic, in particular, is slated to experience profound ecological disruption from climate change and the recession of sea ice (e.g., Post et al., 2013). Understanding the drivers of connectivity will be pivotal for conservation.

Caribou (*Rangifer tarandus*) provide an ideal case study to test for genetic differentiation. Although one species, caribou

are mobile and widely distributed; they are morphologically, behaviourally and genetically variable (McFarlane, Miller, Barry, & Wilson, 2014; Serrouya, Paetkau, McLellan, Boutin, Campbell et al., 2012; Yannic et al., 2014). The taxonomy of *Rangifer* is complex. This species has been variously divided into subspecies (Banfield, 1961), ecotypes (Festa-Bianchet, Ray, Boutin, Côté, & Gunn, 2011; Serrouya, Paetkau, McLellan, Boutin, Campbell et al., 2012; Yannic et al., 2016) and designatable units (DU: a pragmatic alternative to ESU; COSEWIC, 2011; Green, 2005). In the Canadian Arctic Archipelago, two native subspecies, Peary (*R. t. pearyi*; Allen, 1902) and barren-ground caribou (*R. t. groenlandicus*; Borowski, 1780), represent three DUs (COSEWIC, 2011; Figure 1) and encompass multiple herds or geographic populations (COSEWIC, 2011; Jenkins, Campbell, Hope, Goorts, & McLoughlin, 2011; Nagy et al., 2011). Some herds have recently declined (Jenkins, Goorts, & Lecomte, 2012); some are likely extirpated (COSEWIC, 2015a,b; Gunn, Miller, Barry, & Buchan, 2006); and others have recovered through reintroductions or translocations (Ferguson, 1985; Heard & Ouellet, 1994). This diversity is compelling; it challenges conservation efforts and urges us to better understand this taxonomic scheme.

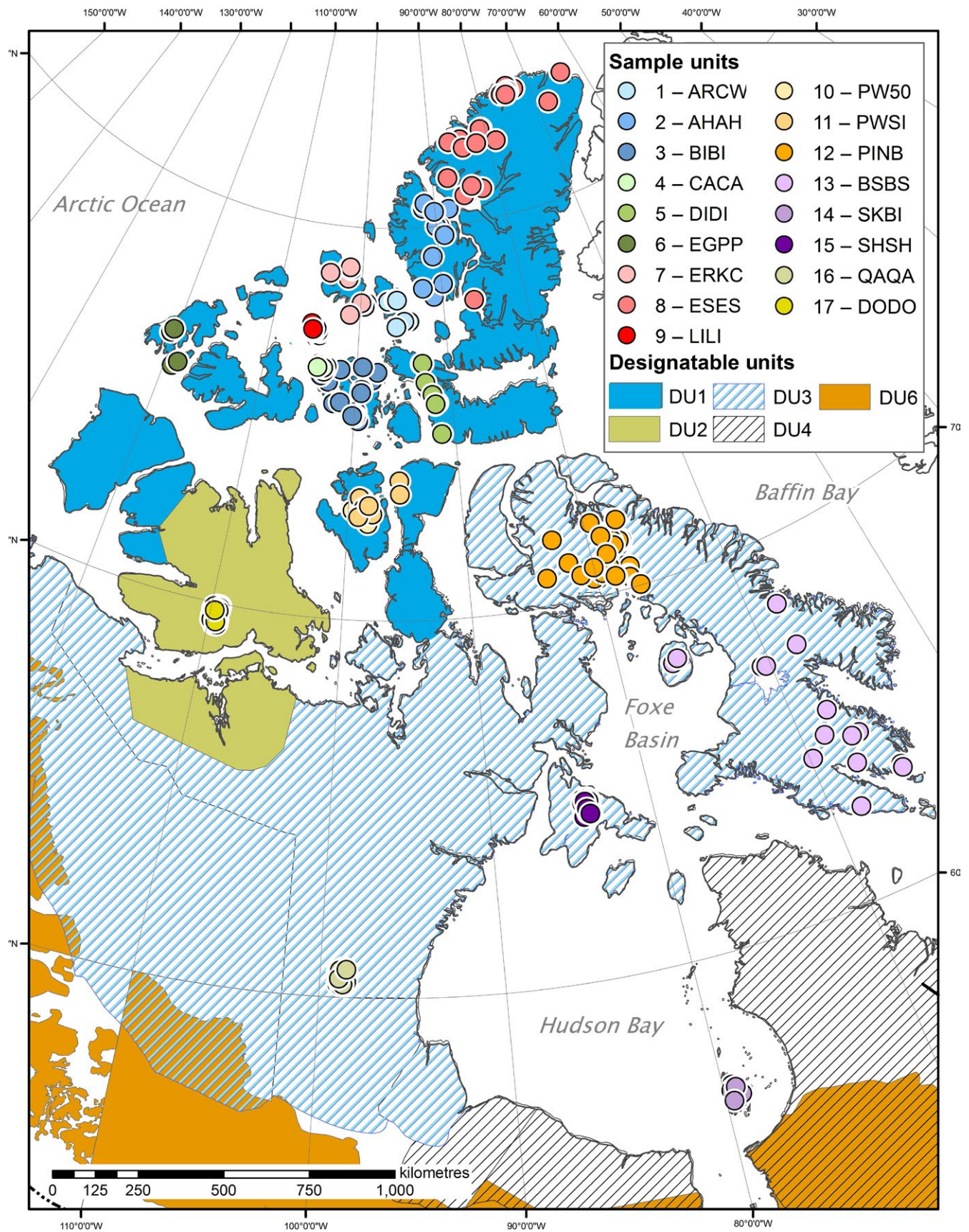
Here, we use genetic markers to determine caribou diversity and population structure in a largely ice-bound archipelago. We used 16 microsatellite loci, ordination and hierarchical Bayesian individual-based clustering to uncover how patterns may change with scale (Schaefer, 2006; Warnock, Rasmussen, & Taylor, 2010). In keeping with caribou, the world's most vagile terrestrial animal (Kelt & Van Vuren, 2001), our study extended across an immense geographic range: 20 Arctic islands and mainland Canada, a latitudinal gradient over 2,000 km. We predicted that one panmictic population was unlikely. Instead, we expected hierarchical genetic structure driven by geographic and ecological complexity and the sheer spatial extent of our sampling. Following CMH (Eckert et al., 2008), we expected genetic diversity to decrease towards the periphery of the range. In turn, we expected island populations to be less diverse than mainland populations and to exhibit diversity in accordance with island and population size (Frankham, 1996). Because mountains and open water can reduce connectivity (Geffen et al., 2007; Qiong et al., 2017), we also expected genetic diversity to be negatively related to rugged terrain and ice-free coastlines. To translate our results for conservation, we mapped our findings and assessed their implications for caribou recovery.

## 2 | METHODS

### 2.1 | Study area

Our study area (>4,000,000 km<sup>2</sup>) extended across the Arctic Archipelago and portions of the Canadian subarctic mainland (Figure 1). The area, characterized by a harsh cold climate and tundra vegetation, lies primarily within the Northern and Southern Arctic ecozones. The Arctic Cordillera, featuring extensive ice fields and





**FIGURE 1** Distribution of 447 caribou samples across the Arctic Archipelago and mainland Canada, representing two native subspecies and three designatable units (DUs; COSEWIC, 2011). Sample unit designations are from Table 1. The map projection is Canada Lambert Conformal Conic [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

glaciers, frames the north-east (Ecological Stratification Working Group, 1995).

Peary and barren-ground caribou are nearly allopatric (Banfield, 1961; Figure 1). Most researchers concur that Peary caribou, with their island distribution, constitute a distinct subspecies, ecotype and DU (Table 1). Barren-ground caribou, which occur on the mainland and southern archipelago, have been regarded as a mix of various types (Table 1): mainland barren-ground or migratory tundra herds (Festa-Bianchet et al., 2011; Mallory & Hillis, 1998), insular or tundra wintering herds (Baffin and Southampton islands; Festa-Bianchet et al., 2011; Jenkins et al., 2012; Mallory & Hillis, 1998) and the Dolphin and Union mainland-migrating herd (Dumond, Sather, &

Harmer, 2013; Nagy et al., 2011). In addition, Southampton caribou were reintroduced from nearby Coats Island (1967; Heard & Ouellet, 1994); feral reindeer (*R. t. tarandus*; Linnaeus, 1758) were introduced to the Belcher Islands (1978; Ferguson, 1985).

## 2.2 | Sample collection

We used 298 samples representing Peary caribou ( $n = 208$ ), barren-ground caribou ( $n = 80$ ) and reindeer ( $n = 10$ ; governments of Nunavut and Northwest Territories; Table 1, Figure 1). Samples included tissue, hair, antler, faecal pellets and faecal surface rubs (using cotton swabs and toothpicks) collected between 1998 and

**TABLE 1** Geographic locations of Arctic island and subarctic mainland caribou included in this study

No.	Sample unit	ID	Subspecies	Ecotype	Long	Lat	N	Sample period
1	Amund Ringnes/Cornwall Is.	ARCW	<i>R. t. pearyi</i>	Island Tundra Wintering	-95.86	78.08	6	2007
2	Axel Heigberg Is.	AHAH	<i>R. t. pearyi</i>	Island Tundra Wintering	-91.20	79.68	20	2007
3	Bathurst Is. Complex	BIBI	<i>R. t. pearyi</i>	Island Tundra Wintering	-100.18	75.92	20	2000–2003
4	Cameron Is.	CACA	<i>R. t. pearyi</i>	Island Tundra Wintering	-103.91	76.48	22	1998 <sup>a</sup> –2003
5	Devon Is.	DIDI	<i>R. t. pearyi</i>	Island Tundra Wintering	-87.63	75.44	10	2002–2003
6	Eglinton/Prince Patrick Is.	EGPP	<i>R. t. pearyi</i>	Island Tundra Wintering	-119.02	76.55	8	1975
7	Ellef Ringnes/King Christian	ERKC	<i>R. t. pearyi</i>	Island Tundra Wintering	-102.29	78.54	16	2007
8	Ellesmere Is.	ESES	<i>R. t. pearyi</i>	Island Tundra Wintering	-78.10	80.30	41	2006
9	Lougheed Is.	LILI	<i>R. t. pearyi</i>	Island Tundra Wintering	-105.21	77.42	42	2007
10	Prince of Wales Is.	PW50	<i>R. t. pearyi</i>	Island Tundra Wintering	-99.10	72.68	10	1950s
11	Prince of Wales/Somerset Is.	PWSI	<i>R. t. pearyi</i>	Island Tundra Wintering	-96.74	73.02	13	1975
12	North Baffin	PINB	<i>R. t. groenlandicus</i>	Island Tundra Wintering	-82.83	71.69	36	2008–2013
13	South Baffin	BSBS	<i>R. t. groenlandicus</i>	Island Tundra Wintering	-70.38	65.88	22	2009–2012
14	Belcher Is.	SKBI	<i>R. t. tarandus</i> <sup>b</sup>	Island Tundra Wintering	-79.66	56.14	10	2009
15	Southampton Is.	SHSH	<i>R. t. groenlandicus</i> <sup>b</sup>	Island Tundra Wintering	-84.25	64.36	76	<sup>c</sup>
16	Qamanirjuaq Herd	QAQA	<i>R. t. groenlandicus</i>	Mainland Migratory Tundra	-99.05	60.29	52	<sup>c</sup>
17	Dolphin & Union Herd	DODO	<i>R. t. groenlandicus</i>	Island-Mainland Migratory	-109.83	69.43	43	<sup>c</sup>

The latitude and longitude represent the centroid of the island, island group or herd and were generated in ArcGIS using the National Topographic Databases layers (1:250,000). Map projection—North Pole Azimuthal Equidistant, Central Meridian -100, Latitude of Origin 72.

<sup>a</sup>Environment and Natural Resources (2014). Peary caribou DNA sample collections, Bathurst Island Complex, July 1998. Unpublished Data. Government of NWT, Yellowknife, NT.

<sup>b</sup>Introduced or reintroduced.

<sup>c</sup>Serrouya, Paetkau, McLellan, Boutin, Jenkins et al. (2012).



2012 during aerial and ground surveys (Gunn & Dragon, 2002; Jenkins et al., 2011, 2012; Miller & Gunn, 2003), collar deployment (Jenkins, 2009a) and harvests by Inuit (Jenkins, 2009b) and also archived DNA and tissues (Table 1). We retrieved genotype data for additional individuals from DRYAD including Southampton Island ( $n = 54$ ), Qamanirjuaq ( $n = 52$ ), and Dolphin and Union herds ( $n = 43$ ; Serrouya, Paetkau, McLellan, Boutin, Campbell et al., 2012; Serrouya, Paetkau, McLellan, Boutin, Jenkins et al., 2012). All genetic data ( $n = 447$ ) were generated at the same laboratory (Wildlife Genetics International, Nelson, BC, Canada) using the same procedure.

Based on geographic herd range, individuals were defined *a priori* into seventeen sample units (i.e., island or multi-island herd, mainland herd; Jenkins et al., 2011; Nagy et al., 2011). We maintained Cameron Island separately due to proximity to both the Loughheed and Bathurst Island herds. Prince of Wales and Prince of Wales–Somerset islands were separated due to sampling period (Table 1); they were included given their conservation value and the possible extirpation of caribou from these islands (Gunn et al., 2006; Jenkins et al., 2011).

### 2.3 | DNA extraction and genotyping

DNA was extracted from tissues using the DNeasy™ Blood and Tissue Kit (Qiagen, Inc., Valencia, CA, USA) following the manufacturer's protocol. For faecal samples, the buffer recovered after a 1-hr surface wash of 1–3 pellets in Qiagen's buffer ATL, was used in the extraction; pellet surface rubs were clipped and processed like tissue. For hair samples with skin, ~2 mm<sup>2</sup> of tissue was used for extraction. Otherwise, the roots from ~10 hairs were clipped for processing (Paetkau, 2003).

Samples were genotyped at 16 microsatellite loci using polymerase chain reaction (PCR) and previously developed markers: BL42, BM4513 and BM6506 (bovine; Bisho et al., 1994); BMS745 and BMS1788 (bovine; Stone et al., 1995); CRH (bovine; Moore, Barendse, Berger, Armitage, & Hetzel, 1992); FCB193 (ovine; Buchanan, Galloway, & Crawford, 1994); OhemD and OhemQ (deer; Jones, Levine, & Banks, 2000); and Rt1, Rt5, Rt6, Rt7, Rt9, Rt24 and Rt27 (caribou; Wilson, Strobeck, Wu, & Coffin, 1997). Individual PCR amplifications were performed on a MJ Research PTC-100 thermocycler (conditions detailed in Table S1). The PCR mixture contained 50 mM of KCL buffer, 0.010% Triton X-100, 160 µg/mL BSA, 160 µM dNTPs, 160 nM of each primer and 1.5–2.0 mg of MgCl<sub>2</sub> in a sample volume of 15 µL. Taq polymerase amount varied with batch strength. Annealing temperature was 54°C, except for OhemQ where it was 60°C. Microsatellite analysis relied on an ABI four-colour sequence detection system on a 310 automated sequencer (Applied Biosystems). Loci were analysed in two sets, which permitted the elimination of poor samples after the first pass. Genotypes were scored using Genotyper software (ABI); error checking followed Paetkau (2003).

### 2.4 | Genetic analysis

To evaluate data completeness and confirm unique individuals, we used MICROSATELLITE TOOL KIT 3.1.1 in Microsoft Excel 2013 (Park,

2008) and “allelematch” (Galpern, Manseau, Hettinga, Smith, & Wilson, 2012) in R 3.2.3 (R Core Team 2015). Deviation from Hardy–Weinberg equilibrium and linkage disequilibrium were tested for each marker and each sampling unit using GENEPOP 4.2.2 (Raymond & Rousset, 1995; Rousset, 2008). For multiple tests, we adjusted error rates using sequential Bonferroni correction (McLaughlin & Sainani, 2014).

Using GENALEX 6.5 (Peakall & Smouse, 2006), we estimated the mean number of alleles ( $N_a$ ), observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ) and unbiased heterozygosity ( $uH_e$ ) for the study area and each sample unit, as well as  $F$ -statistics for each locus across sample units. To account for differences in sample size, we adjusted estimates of allelic richness ( $A_R$ ) and private alleles ( $A_p$ ) for each sample unit using rarefaction based on the smallest diploid sample size (i.e.,  $n = 12$ ) in ADZE 1.0 (Szpiech, Jakobsson, & Rosenberg, 2008). In addition, the inbreeding coefficient ( $F_{IS}$ ) was calculated using R package “diveRsity” (Keenan et al., 2013). We evaluated differences in genetic diversity ( $H_e$ ) between sample units using the Kruskal–Wallis test and Dunn's post hoc test in the “PMCMR” R package (Pohlert, 2016); we repeated analyses for each genetic cluster identified through Bayesian analysis.

### 2.5 | Population differentiation and isolation by distance

To evaluate genetic differentiation among sample units and clusters, we estimated pairwise  $F_{ST}$  (Weir & Cockerham, 1984) and computed bias-corrected, pairwise bootstrapped 95% confidence limits based on 10,000 interactions using “diveRsity” in R. We used the function *heatmap.2* in the package “ggplot” to create a UPGMA dendrogram from sample unit  $F_{ST}$  values. The heatmap illustrated the  $F_{ST}$  matrix and highlighted  $F_{ST}$  groups from pairwise  $F_{ST}$  values.

Isolation by distance (IBD; Wright, 1943, 1946), the tendency for genetic similarity to reflect geographic proximity (Meirmans, 2012), was assessed by comparing matrices of genetic and geographic distance. Here, we used pairwise  $F_{ST}$  for genetic distance. A matrix of geographic distances—based on great-circle distance and representing the shortest distance between points (Nychka, Furrer, Paige, & Sain, 2016)—was calculated using the centroid (Datum WEGS84) of each sample unit in the “fields” package for R (Nychka et al., 2016). To test for IBD, Mantel correlation coefficients (Mantel, 1967) and multivariate Mantel correlograms were calculated based on Spearman correlations and 10,000 permutations using “vegan” in R (Oksanen et al., 2017).

### 2.6 | Multivariate analysis and Bayesian clustering

We performed principal component analyses (PCA) to evaluate genetic variation among caribou using “adeget” 1.4-1 in R (Jombart, 2008). This method has no underlying assumptions regarding population genetics (Vergara et al., 2015). We conducted PCA for all caribou and separately for Peary caribou.

We investigated hierarchical structure using two Bayesian individual-based clustering methods (IBC)—that is non-spatial and spatially explicit models (Ball, Finnegan, Manseau, & Wilson, 2010). We first used STRUCTURE 2.3.3 (Pritchard, Stephens, & Donnelly, 2000) to assign individuals with multilocus genotype data to clusters ( $K$ ) using a Markov chain Monte Carlo algorithm independent of sampling location. An admixture model with correlated allele frequencies was used (Falush et al., 2003; Kopatz et al., 2014). Fifteen independent runs (for  $1 \leq K \leq 10$ ) were performed using 500,000 iterations as a burn-in and an additional 750,000 for data collection. Because replicate runs can provide different solutions, ten runs with the highest likelihood [ $\ln P(D)$ ] were extracted for further analysis. We used STRUCTURE HARVESTER v0.6.94 (Earl & vonHoldt, 2012) to generate mean likelihood scores for each  $K$  and implement the  $\Delta K$  Evanno method (Evanno, Regnaut, & Goudet, 2005). For each  $K$ , individuals were assigned to a cluster based on their highest percentage of membership ( $q$ ), provided this value was  $\geq 0.5$ ; membership coefficients ( $q$ ) were calculated using the greedy algorithm with 10,000 repeats in CLUMMP 1.1.1 (Jakobsson & Rosenberg, 2007). Individuals remained unassigned if the threshold was not met and considered admixed among genetic clusters. To select the most distinct genetic subdivision, we examined the likelihood estimates from STRUCTURE,  $\Delta K$  values (Evanno et al., 2005) and visual plots. We performed a first run in STRUCTURE, assigning individuals to a primary cluster, and repeated the analysis on each of the assigned groups using the above methods ( $1 \leq K \leq 5$ ). We continued until no further substructure was identified (Glass, Walter, Heath, Mandrak, & Corkum, 2015; Hagerty & Tracy, 2010; Rowe & Beebee, 2007).

Next, we evaluated hierarchical structure by incorporating spatial information with multilocus genotype data using TESS 2.3 (Chen, Durand, Forbes, & Francois, 2007; Durand, Chen, & Francois, 2009). When spatial data at the individual level were not available, we generated unique coordinates for each animal based on their prescribed range (Chen et al., 2007; Durand et al., 2009). We used the admixture model which assumes spatial autocorrelation and accounts for clines in allele frequencies and isolation by distance (Francois & Durand, 2010). We performed 15 independent simulations for different maximum numbers of genetic clusters ( $2 \leq K_{\max} \leq 10$ ) with a total of 125,000 sweeps and a burn-in of 50,000. Models were run with a conditional autoregressive (CAR) variance of 1.0, a linear trend surface and a spatial interaction strength of 0.6 to address spatial autocorrelation (Durand et al., 2009; Yannic et al., 2016). As IBD was observed in the area (Jenkins et al., 2016), the linear trend surface option was chosen. For each  $K_{\max}$ , 10 runs with the lowest deviation information criterion (DIC) were selected and exported for analysis. To assess the optimal number of clusters, the average DIC for each  $K$  was plotted against  $K_{\max}$ . Using CLUMMP, the admixture coefficient was averaged across runs for each  $K_{\max}$  (Durand et al., 2009) and the output graphically displayed for each unique value. The number of clusters was inferred by evaluating where the plot stabilized at the lowest DIC and through visual assessment of  $K$  plots (Basto et al., 2016; Durand et al., 2009). After the first run in TESS,

analyses were repeated using the above methods ( $2 \leq K_{\max} \leq 5$ ) until no further substructure was identified.

## 2.7 | Heterozygosity in relation to ecological and geographic factors

To assess the effect of ecological and geographic factors on genetic diversity, we employed linear mixed-effects (LME) models using the “nlme” package in R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017). We built models using individual heterozygosity (HLE) as the response variable. HLE was calculated using the homozygosity index in CERNICALIN V.1 (Aparicio, Ortego, & Cordero, 2006) and logit-transformed to address the bounded nature of the variable (between 0 and 1). To account for small sample sizes, our analysis was limited to sample units with  $>15$  individuals. We treated caribou on Baffin Island as one unit and grouped Cameron Island samples with those from the Bathurst Island Complex (Figure 1).

We investigated the effect of the following independent factors on HLE (Table S2): latitude and longitude (Christiansen & Reyer, 2011), population size (log transformed), island area, glacier-free island area (Frankham, 1996, 1997), distance to mainland (Eckert et al., 2008; Frankham, 1997), subspecies, average annual, spring and fall ice-free coastline (Geffen et al., 2007; Post et al., 2013) and maximum island elevation (Ally, El-Kassaby, & Ritland, 2000). We included sample units or Bayesian clusters as a random effect, accounting for variation within the putative groups and resolving the non-independence of individuals.

To address multicollinearity, we calculated Spearman correlations among predictors in R (Zuur, Ieno, & Elphick, 2010) and removed correlated variables ( $|r| \geq .7$ ). Using the remaining predictor variables, we calculated stepwise variance inflation factor (VIF) using “usdm” package (Naimi, 2015). We sequentially dropped variables with high VIF before recalculating VIF to a final threshold of 2 (Zuur et al., 2010). Finally, to understand the variance explained by our best LME model(s), we calculated the marginal and conditional  $R^2$ , representing the variance explained by fixed versus fixed and random factors (Nakagawa, Schielzeth, & O'Hara, 2013) using the “MuMIn” R package (Barton, 2015).

## 3 | RESULTS

### 3.1 | Genetic diversity and differentiation

In total, 447 unique individuals were confirmed; completeness of the dataset at 16 loci was  $>99\%$ . The mean number of alleles per locus was 6.5 (0.2 standard error [SE]) with a total of 257 alleles across sample units and microsatellite loci. Alleles per loci ranged from 4.7 (0.3 SE) to 8.3 (0.7 SE) on BMS745 and BM4513, respectively (Table S3). The global mean  $F_{IS}$  was 0.02 (0.01 SE) and  $F_{ST}$  was 0.12 (0.01 SE) when averaged across loci and sample regions (Table S4). There were no significant deviations from Hardy–Weinberg equilibrium (HWE) and no evidence of linkage disequilibrium after sequential Bonferroni corrections.

For sample units, adjusted allele richness (alleles/locus) ranged from 3.93 to 4.48 for Peary caribou, 3.71 to 4.87 for island barren-ground caribou and to a maximum of 6.8 for the mainland Qamanirjuaq herd. Similar patterns are apparent for adjusted private allele richness (Table 2). We found a difference in the mean  $H_E$  between sampling units (Kruskal–Wallis  $\chi^2 = 76.22$ ,  $df = 16$ ,  $p < .001$ ). The Qamanirjuaq and Dolphin and Union herds were more diverse than other units.

### 3.2 | Population differentiation and isolation by distance

Based on  $F_{ST}$  values, both the dendrogram and heatmap mainly separated Peary from barren-ground caribou (Figure 2) and showed that the most genetically divergent population was Southampton Island (mean pairwise  $F_{ST}$ :  $0.206 \pm 0.031$ , min: 0.134; max: 0.243). In addition, these patterns were in broad agreement with alternative individual-based methods below, that is PCA (Figure 4) and Bayesian clustering (Figure 5).

We found a significant relationship between genetic and geographic distances among sample units ( $F_{ST}$  – Mantel  $r = .71$ ,  $p < .001$ ; Figure 3a)—a relationship also evident in Peary caribou ( $F_{ST}$  – Mantel  $r = .61$ ,  $p < .001$ ; Figure 3b). Overall, caribou showed positive autocorrelation up to ~600 km (Figure 3c) and Peary caribou (Figure 3d), up to ~250 km.

### 3.3 | Multivariate analysis and Bayesian clustering

The PCA suggested four primary clusters. In two-dimensional space, Peary caribou emerged as distinct from Baffin Island, Southampton

Island and the remaining mainland and island herds (Figure 4a). Notably, at this scale, Peary caribou appeared in one homogenous cluster. In separate analysis of Peary caribou, no major divisions were evident, although there was some east–west separation (Figure 4b).

Hierarchical Bayesian clustering in STRUCTURE revealed nine groups overall (Figure 5a), with three distinct clusters at the first level. These largely corresponded with the native subspecies and reintroduced population. Initially, >90% of the individuals were assigned to one of three clusters with high membership coefficients ( $q > 0.90$ , Table S5): Peary caribou, the reintroduced population on Southampton Island, and a composite of barren-ground caribou (mainland and island) and Belcher Island reindeer. The latter may have been an effect of the small sample size ( $n = 10$ ). Second-level analysis revealed two groups within Peary caribou (north-eastern and west-central), no substructure within Southampton Island and four groups within the barren-ground and Belcher Island group (Qamanirjuaq herd, Baffin Island, Dolphin and Union, and Belcher Island). Third- and fourth-level analyses teased out additional substructure within north-eastern Peary caribou (Figure 5a). All the historical Peary caribou samples clustered with the west-central group where no substructure was found. With the exception of two Qamanirjuaq caribou, at second-level analysis, all individuals assigned to a cluster.

By including individual spatial coordinates, we found broadly similar patterns. Tess suggested nine clusters (Figure 5b). The DIC curve and graphical evaluation of membership coefficients both revealed five initial clusters ( $K_{max} = 5$ ), separating Peary, Southampton Island, Baffin Island and Belcher Island caribou from the Qamanirjuaq and Dolphin and Union group (Figure 5b). Assignments were pronounced: 85% of individuals were assigned to a cluster with  $q > 0.90$  (Table S6); one individual (Qamanirjuaq)

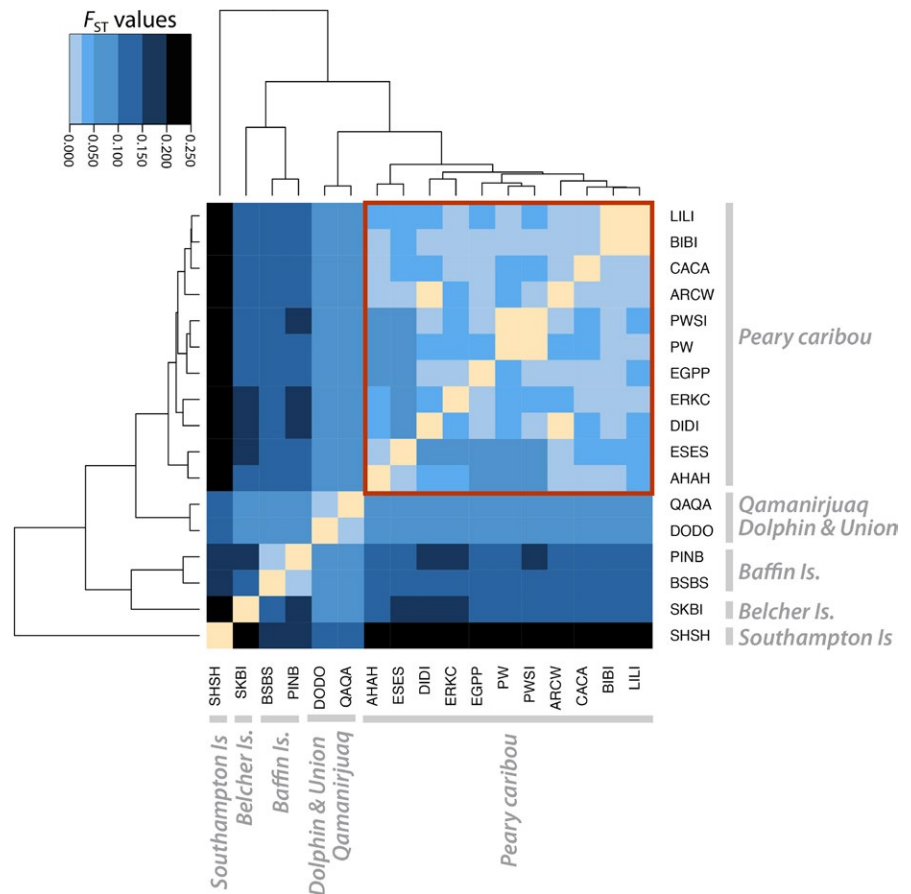
Sample unit	N	Na	$H_o$	$H_E$	$uH_E$	$A_R$	$A_P$	$F_{IS}$
ARCW	6	4.06	0.68	0.65	0.71	4.06	0.04	-0.04 <sup>NS</sup>
AHAH	20	5.63	0.67	0.69	0.71	4.26	0.01	0.03 <sup>NS</sup>
BIBI	20	5.56	0.78	0.72	0.74	4.35	0.00	-0.08*
CACA	22	5.31	0.75	0.71	0.72	4.18	0.00	-0.06*
DIDI	10	4.69	0.65	0.65	0.68	4.07	0.03	0.00 <sup>NS</sup>
EGPP	8	4.75	0.74	0.66	0.70	4.39	0.00	-0.12*
ERKC	16	4.88	0.64	0.65	0.67	3.94	0.01	0.01 <sup>NS</sup>
ESES	41	5.19	0.67	0.69	0.69	4.01	0.03	0.02 <sup>NS</sup>
LILI	42	5.81	0.75	0.71	0.72	4.15	0.02	-0.05*
PW50	10	5.19	0.69	0.67	0.71	4.48	0.06	-0.03 <sup>NS</sup>
PWSI	13	5.44	0.73	0.69	0.72	4.37	0.07	-0.06*
PINB	36	8.75	0.74	0.71	0.72	4.87	0.18	-0.04 <sup>NS</sup>
BSBS	22	7.69	0.69	0.71	0.73	4.82	0.18	0.03 <sup>NS</sup>
SKBI	10	5.25	0.65	0.70	0.74	4.46	0.55	0.08 <sup>NS</sup>
SHSH	76	6.19	0.66	0.67	0.67	3.71	0.36	0.01 <sup>NS</sup>
QAQA	52	14.38	0.85	0.86	0.87	6.84	0.74	0.02 <sup>NS</sup>
DODO	43	10.19	0.84	0.83	0.84	6.07	0.48	-0.02 <sup>NS</sup>

**TABLE 2** Estimates of genetic diversity, number of genotypes (N), mean number of alleles per locus (Na), observed heterozygosity ( $H_o$ ), expected and unbiased expected heterozygosity ( $H_E$ ,  $uH_E$ ), allelic richness averaged over loci ( $A_R$ ), mean number of private alleles per locus ( $A_P$ ) and inbreeding coefficient ( $F_{IS}$ ). Sample unit IDs as in Table 1

$A_R$  and  $A_P$  are based on the minimum sample size of six diploid individuals.

\*Significantly different from 0 based on 10,000 bootstrap 95% confidence intervals.

**FIGURE 2** Pairwise  $F_{ST}$  heatmap and dendrogram based on  $F_{ST}$  values among the 17 caribou sampling locations, Arctic Canada ( $n = 447$ ). The heatmap colour code represents the  $F_{ST}$  matrix considering different discrete  $F_{ST}$  groups from low to high genetic differentiation:  $F_{ST} < 0.001$  (yellow);  $0.001 \leq F_{ST} < 0.025$ ,  $0.025 \leq F_{ST} < 0.05$ ,  $0.05 \leq F_{ST} < 0.10$ ,  $0.10 \leq F_{ST} < 0.15$ ,  $0.15 \leq F_{ST} < 0.20$  and  $0.20 \leq F_{ST} < 0.25$  (shades of blue) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



was unassigned. Progressive partitioning revealed further structure within Peary caribou but also within the Qamanirjuaq–Dolphin and Union group (Figure 5). In the north-east, two small groups, Marvin Peninsula and western Ellesmere Island, were highlighted with third-level analysis.

### 3.4 | Characteristics of clusters

Genetic diversity ( $H_E$ ) was significantly different among clusters derived through Bayesian analysis (STRUCTURE–Kruskal–Wallis  $\chi^2 = 72.807$ ,  $df = 8$ ,  $p < .001$ ; TESS–Kruskal–Wallis  $\chi^2 = 77.869$ ,  $df = 8$ ,  $p < .001$ ). The Qamanirjuaq and Dolphin and Union clusters demonstrated significantly higher diversity than most others. Significant  $F_{IS}$  values (Table S7) provided evidence of non-random mating for small, isolated TESS-derived clusters on Ellesmere Island, and the more spatially dispersed STRUCTURE-derived Ellesmere west-central cluster. Pairwise  $F_{ST}$  ( $p < .05$ ; Table S8) among STRUCTURE and TESS clusters ranged from 0.018 to 0.282 and 0.027 to 0.288, respectively.

### 3.5 | Geographic and ecological drivers of heterozygosity

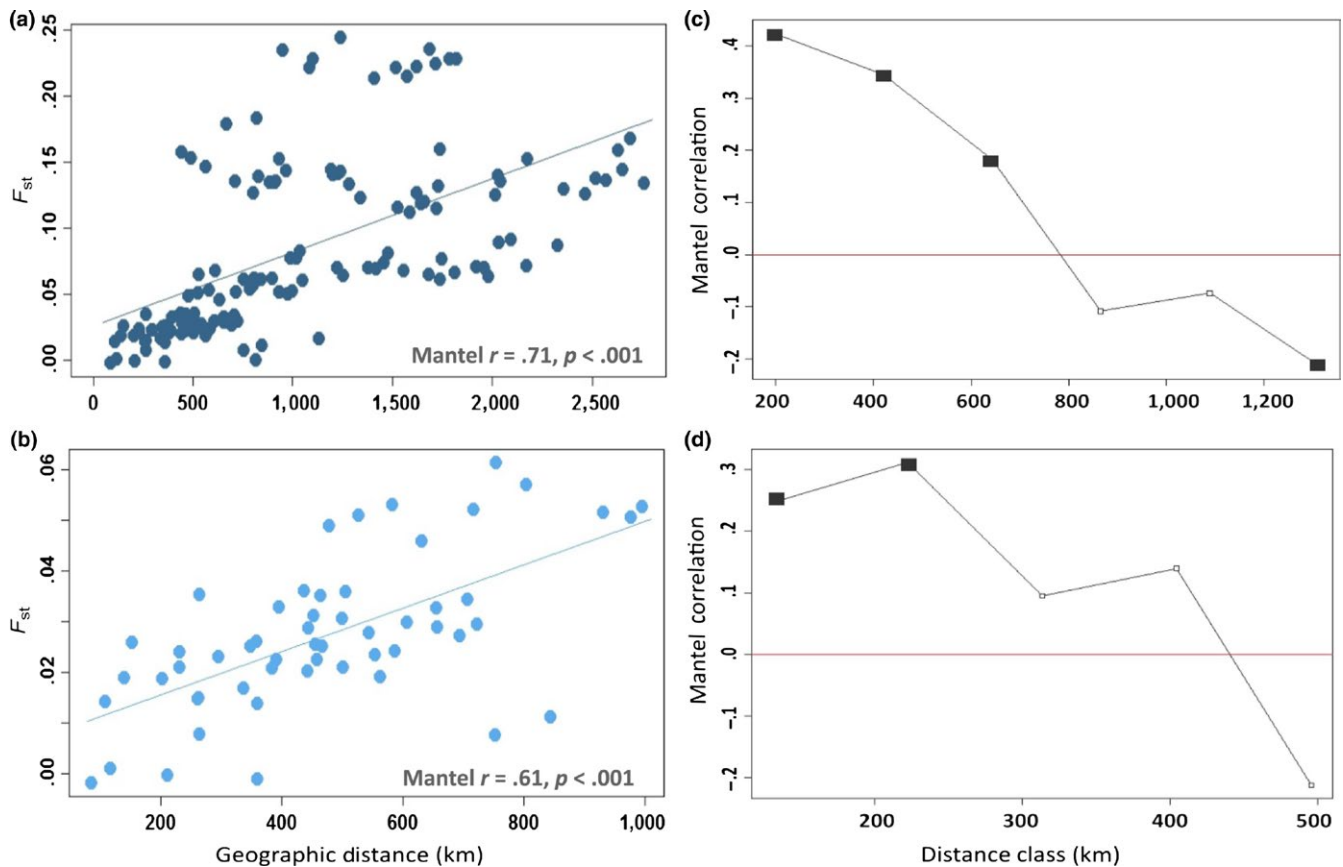
Through correlation analysis and sequential VIF, we selected three explanatory covariates (distance to mainland [NearDis\_km],

effective island size [UnglacArea] and fall ice-free coastline [Fall\_Open\_C]), along with subspecies. At the individual level, including either sample units or Bayesian clusters as a random factor, models consistently showed heterozygosity influenced by distance to mainland, open fall coastline and effective island size (Table 3, Figure 6). Effective island size was the only variable with a consistent positive effect on heterozygosity; distance to mainland and open fall coastline reduced heterozygosity (Table 4). Marginal  $R^2$  for best models indicated fixed effects explained 29% of the variance; random effects did not improve these values.

## 4 | DISCUSSION

Understanding how populations are structured is crucial to conservation (Bowen, Bass, Soares, & Toonen, 2005; Pond et al., 2016). Using multiple approaches, we consistently uncovered strong population differentiation, with similar patterns among caribou across the Canadian Arctic Archipelago. Given the large extent and heterogeneous landscape, we predicted hierarchical organization (Schaefer, 2006). Indeed, we uncovered structure at and below the subspecies level for Peary and barren-ground caribou (Figure 5). Separation between subspecies aligns with Kluttsch, Manseau, Anderson, Sinkins, and Wilson (2017) who established that Peary caribou likely evolved in a separate High Arctic





**FIGURE 3** Correlation between genetic and geographic distances among (a) all 17 caribou units ( $n = 447$ ) and (b) Peary caribou, Arctic Canada ( $n = 208$ ). Corresponding Mantel correlograms (c and d, respectively) identify Mantel  $r$  statistic at each distance class; black squares denote those that are statistically significant ( $p \leq .05$ ) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

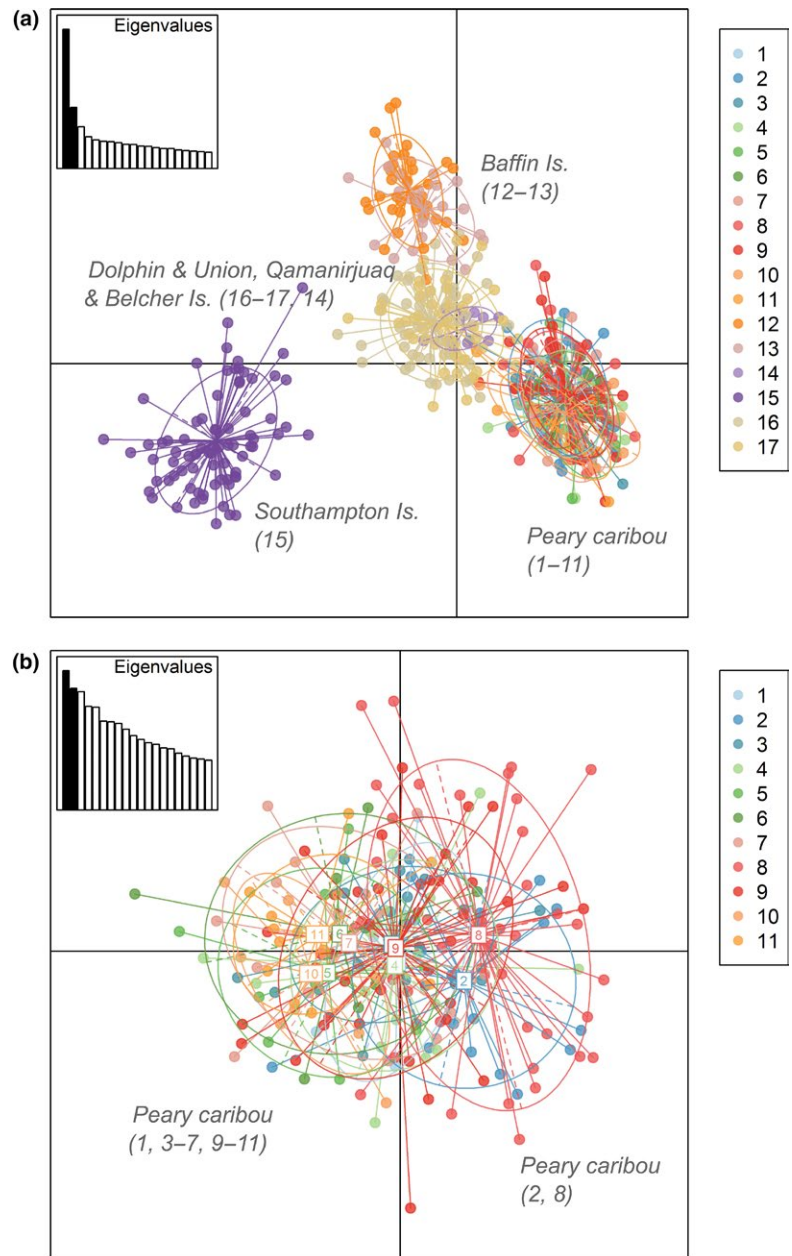
refugium. Within Peary caribou, two clusters comprised multiple islands where sea ice supports movement and gene flow for most of the year (Jenkins et al., 2016). Uniquely, Marvin Peninsula caribou were bounded by deep fiords, rugged mountains and permanent ice sheets that likely represent barriers to movement. This cluster had previously been differentiated based on microsatellites and mtDNA (Peterson, Manseau, & Wilson, 2010).

Including historical samples can be tricky but informative. Time can add an additional layer of consideration when interpreting cluster results (Taylor, Jenkins, & Arcese, 2012; Zigouris, Schaefer, Fortin, & Kyle, 2013). We detected no substructure within the west-central Peary cluster that included historical samples from Prince of Wales, Somerset and Prince Patrick Island. Our results largely agree with McFarlane et al. (2014) and highlight the opportunity for active conservation measures (i.e., reintroductions; Griffith, Scott, Carpenter, & Reed, 1989) to address the near-extirpation of Peary caribou from southern portions of their range (COSEWIC, 2015a,b; Gunn et al., 2006).

The diversity and future of peripheral populations are of increasing interest (Brzosko et al., 2009; Safriel, Volis, & Kark, 1994), as mounting environmental change underscores the evolutionary value of such populations (Lesica & Allendorf, 1995; Sexton,

McIntyre, Angert, & Rice, 2009; Volis, Ormanbekova, Yermekbayev, Song, & Shulgina, 2016). Highlighting the separation from mainland Qamanirjuaq caribou, our study identified three unique clusters of barren-ground caribou at the northern edge of their range (e.g., Baffin, Southampton, and Dolphin and Union). These clusters corresponded largely to island or mainland-migrating herds with significant among-group differentiation (Table S8). High assignment proportions for Baffin and Southampton samples implied range disjunction and discrete populations (Figure 5). Baffin Island, which includes individuals on small proximal islands (e.g., Prince Charles Island), has experienced significant declines over the last three decades (Campbell, Goorts, Lee, Boulanger, & Pretzlaw, 2015; Jenkins et al., 2012) with no direct evidence of island-mainland movements (COSEWIC, 2011; Jenkins et al., 2012; Manning, 1943). Here, insularity and small population size lead to the loss of genetic diversity, susceptibility to genetic drift and differentiation from other barren-ground populations.

Low genetic diversity and genetic differentiation are common in introduced or newly founded populations (Frankham, 1997; Illerai, Spurgin, Rodriguez-Exposito, Nogales, & Randos, 2016) although a number of factors, including founder group size, initial diversity and connectivity are important (Andersen, Simcox, Thomas, &



**FIGURE 4** Caribou cluster analyses, Arctic Canada. (a) Using all caribou ( $n = 447$ ), principal component analysis (PCA) highlights four primary clusters, where axes 1 and 2 separate Southampton Island caribou, Peary caribou and Baffin Island caribou from the remaining herds. Eigenvalues were 0.82 for axis 1 and 0.36 for axis 2, and explained 11.32% and 4.97% of the variance, respectively. (b) For Peary caribou ( $n = 208$ ), PCA illustrates a west-east gradient among these island herds. Herd identification numbers are from Table 1 and Figure 1 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

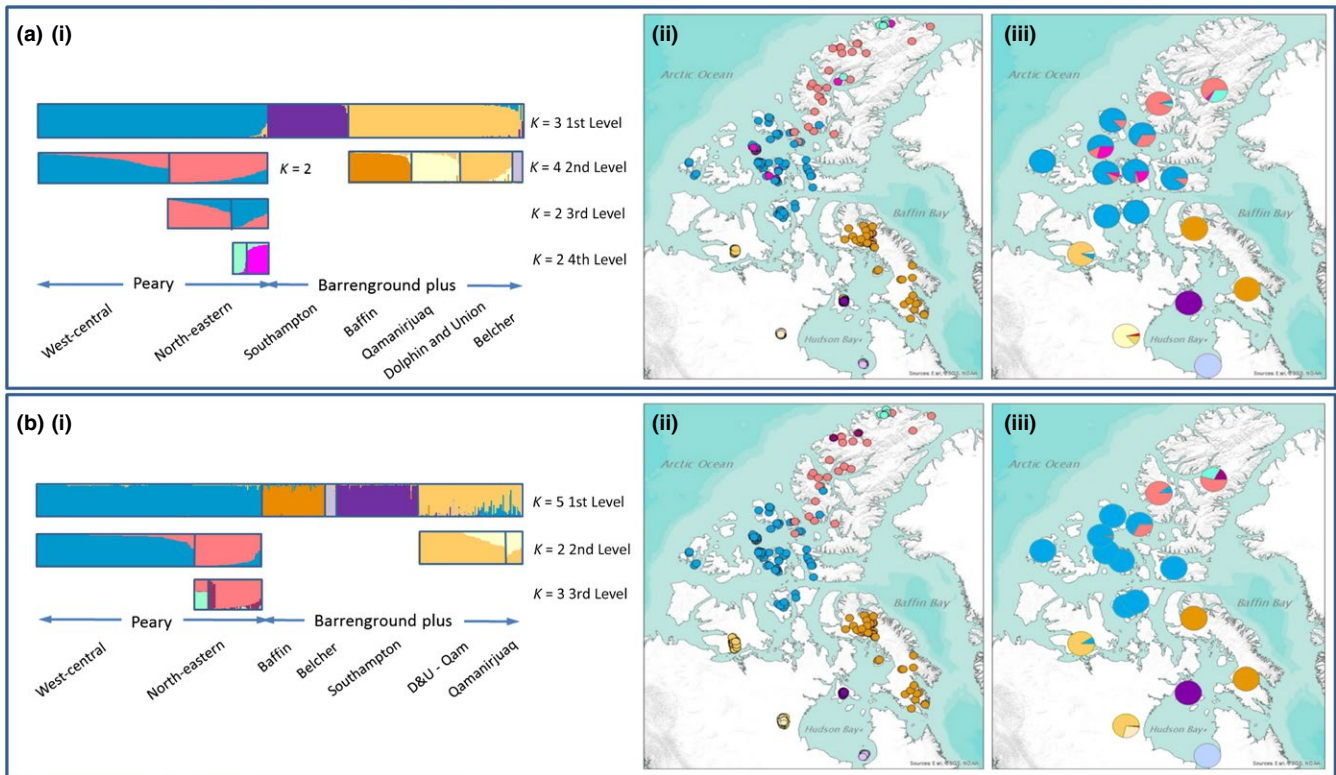
Nash, 2014; IUCN, 2013; Szucs, Melbourne, Tuff, Weiss-Lehman, & Hufbauer, 2017). Our analyses—PCA, Bayesian analysis and pairwise  $F_{ST}$ —converged to establish Southampton Island as the most genetically distinct population (McFarlane et al., 2016; Serrouya, Paetkau, McLellan, Boutin, Campbell et al., 2012). Originating from a small number of individuals, Southampton caribou exemplify the effects of isolation, genetic drift and founder effects on the genetic makeup of populations (Frankham et al., 2002).

Disagreement between multiple Bayesian clustering methods is not uncommon (Ball et al., 2010; Coulon et al., 2008; Yannic et al., 2016). Still, our results demonstrated broad agreement between STRUCTURE and TESS. One exception occurred with Peary caribou (Figure 5). TESS revealed an isolated group on Ellesmere Island; STRUCTURE identified a larger cluster spanning multiple islands. Because we applied a membership threshold of 0.50 and used both

spatial and non-spatial methods, such disagreement may be related to marginal genotypes that could represent admixture or could be resolved with spatial information (e.g., Tess). Additionally, our data revealed IBD, which may create inconsistencies in outcomes (Ball et al., 2010).

#### 4.1 | Genetic diversity and key drivers

Compared to their mainland counterparts, island populations often exhibit reduced genetic diversity (Frankham, 1996, 1997). Such examples include island red fox, *Vulpes vulpes* (Lade, Murrey, Marks, & Robinson, 1996); various Australian macropodids (Eldridge, Kinnear, Zenger, McKenzie, & Spencer, 2004); North American gray wolf, *Canis lupus* (Carmichael et al., 2008); *Ornithorhynchus anatinus* (Furlan et al., 2012); and Svalbard reindeer (Côté et al., 2002).



**FIGURE 5** Assignment of 447 Canadian Arctic caribou, using hierarchical Bayesian cluster analysis with the program STRUCTURE (Pritchard et al., 2000; a) and TESS (Chen et al., 2007; b). Bar plots (i) show the assignment of individuals through multiple hierarchical levels of analysis, revealing nine genetic clusters and substructure among both Peary and barren-ground caribou (plus reindeer). (ii) Maps show cluster membership of each individual in accordance with bar plots, by colour. (iii) Pie charts illustrate the cluster membership of individuals by sample unit [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 3** Best four linear mixed-effects models of logit-transformed individual heterozygosity based on biogeographic predictors with sample unit as random effect<sup>a</sup>. *K* is the number of parameters, AICc is the corrected Akaike information criteria,  $\Delta$ AICc is the difference between the model AICc and the best model AICc, and AICcWt is the Akaike weight

Ranked models	Predictors <sup>b</sup>	<i>K</i>	AICc	$\Delta$ AICc	AICcWt
Model 1	UnglacArea+NearDis_Km+Fall_Open_C	6	752.37	0.00	0.63
Model 2	NearDis_Km+Subspecies+Fall_Open_C	7	754.95	2.59	0.17
Model 3	UnglacArea+NearDis_Km+Subspecies+Fall_Open_C	8	755.20	2.83	0.15
Model 4	UnglacArea+NearDis_Km+Subspecies	7	757.96	5.60	0.04

<sup>a</sup>Similar results were generated when clusters from STRUCTURE and TESS were substituted as the random effect (unpublished; this study).

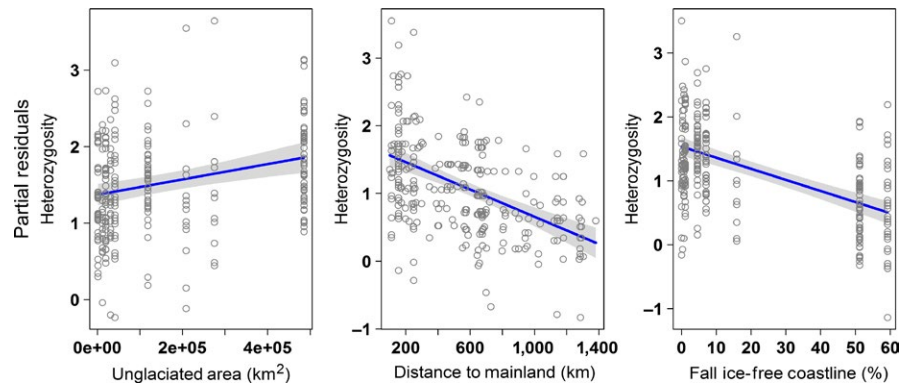
<sup>b</sup>UnglacArea = unglaciated island size (km<sup>2</sup>), NearDis\_Km = distance to mainland (km), Fall\_Open\_C = average fall ice-free coastline (%).

Nevertheless, if immigration is high, island populations may still be genetically diverse (Carmichael et al., 2007; Pemberton et al., 1996; Stronen et al., 2014). As expected, Arctic island caribou populations displayed lower genetic diversity than the mainland populations, likely as a result of small population size and limited gene flow. In accordance with CMH, the most isolated groups exhibited low diversity; diversity was negatively related to distance from mainland (Figure 6). Here, harsh conditions constrain population densities, which are 1–2 orders of magnitude lower than elsewhere in the species range (Jenkins et al., 2011; Schaefer & Mahoney, 2003); immense distances limit the exchange of genes, even for this mobile

animal (Figure 3). Support for CMH is not uncommon (e.g., Eckert et al., 2008; Micheletti & Storfer, 2015); the hypothesis has been upheld even in studies across large spatial extents (McFarlane et al., 2014; Yannic et al., 2014), such as ours.

Island area and distance to mainland are recurrent themes in island biogeography (MacArthur & Wilson, 1967), including studies of the genetics of island-dwelling vertebrates (Harradine et al., 2015; Stronen et al., 2014; Vellend, 2003, 2005). Positive correlations between island area and genetic diversity are commonplace (Cheylan, Granjon, & Britton-Davidian, 1998; White & Searle, 2007), including our study. Additionally, Dolphin and Union and mainland





**FIGURE 6** Plots illustrate our best linear mixed-effects model (LME) explaining genetic diversity (individual level heterozygosity), showing the prediction line (blue), confidence band (grey) and partial residuals for each variable. Variables are described in Table S2 [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**TABLE 4** Estimate of fixed effects produced by the best linear mixed model of individual heterozygosity with sample unit as the random effect ( $SD: 0.06$ ). Estimates were considered as significant (in bold) when the 95% CI did not overlap zero. Marginal and conditional pseudo- $R^2$ -values were 0.289 ( $R^2_m$ ) and 0.296 ( $R^2_c$ ), respectively

Model	Estimate	SE	95% CI	
Intercept	<b>1.74</b>	$1.05 \times 10^{-1}$	1.54	1.95
UnglacArea	<b><math>1.00 \times 10^{-6}</math></b>	$2.5 \times 10^{-7}$	$4.2 \times 10^{-7}$	$1.57 \times 10^{-6}$
NearDis_Km	<b><math>-1.00 \times 10^{-3}</math></b>	$1.3 \times 10^{-4}$	$-1.27 \times 10^{-3}$	$-7.44 \times 10^{-4}$
Fall_Open_C	<b><math>-1.73 \times 10^{-2}</math></b>	$1.9 \times 10^{-3}$	$-2.18 \times 10^{-2}$	$-1.29 \times 10^{-2}$

UnglacArea = unglaciated island size ( $\text{km}^2$ ), NearDis\_Km = distance to mainland (km), Fall\_Open\_C = average fall ice-free coastline (%).

Qamanirjuaq caribou showed expectedly higher genetic diversity (Table 2), re-emphasizing the powerful influence of the mainland and its proximity. At the same time, low genetic differentiation exists among continental barren-ground herds (Jenkins et al., 2016; McFarlane et al., 2014, 2016; Yannic et al., 2017; Zittlau, 2004). Indeed, mixing among mainland populations promotes diversity (McFarlane et al., 2016). In our study area, an ice bridge extends that mixing—that is between the mainland and Victoria Island, where seasonal island-mainland migrations and contact among large heterogeneous populations take place (Dumond et al., 2013; Poole et al., 2010).

For island caribou, sea ice is the corridor that facilitates movement (Jenkins et al., 2016). Indeed, like Arctic foxes (Carmichael et al., 2008; Geffen et al., 2007), ice enhances connectivity for caribou (Figures 5 and 6). Genetic diversity was lower on islands where the extent of the ice-free autumn coastline was greater (Figure 6). This represents a conservation warning. Climate change is anticipated to bring extended seasons of open water to the Arctic (Jenkins et al., 2016). For ice-dependent species, open water can thwart between-island movements (Dalen et al., 2005; Post et al., 2013). Water can be a serious barrier, even to caribou (Dumond et al., 2013), despite their renowned ability to swim (Miller, 1995).

## 5 | CONCLUSIONS

Drawing lines below the species level (e.g., subspecies, populations, DUs) has implications for conservation. In Canada, DUs address such intraspecific diversity, with emphasis on discrete and significant groups for protection under the Species at Risk Act

(COSEWIC, 2015a). Our work points to Baffin Island caribou as an insular and discrete population (Figures 2 and 4-5), geographically and genetically disjunct from both mainland barren-ground (the same subspecies) and island-dwelling Peary caribou. Such biogeographic separation could help focus management and conservation efforts. It may also be indicative of intraspecific diversity (e.g., DUs; Mee, Bernatchez, Reist, Rogers, & Taylor, 2015) and provide evidence of evolutionary significance (COSEWIC, 2015a). Our study points to Baffin Island caribou as a candidate for consideration as a DU.

Populations are often organized hierarchically, as our study shows, even for highly mobile species (Schaefer, 2006). Iterative clustering is the means to reveal substructure at progressively finer spatial scales (Figure 5). For caribou of the Arctic islands, the diversity of mainland versus islands lends support to island theory; the drivers of genetic diversity—distance to mainland and ice-free isolation—lend support to CMH. Our study underscores the enduring relevance of biogeography (Lomolino, Riddle, Whittaker, & Brown, 2010)—particularly for uncovering biological patterns pertinent to conservation, now and for the future.

## ACKNOWLEDGEMENTS

We thank the Government of Nunavut, the Government of Northwest Territories and Dr. R. Serrouya for data, logistics and samples. Thanks to Drs. J. Ray, S. Kutz and W. Burr for valuable input. Funding was provided by NSERC, Queen Elizabeth II Graduate Scholarship in Science & Technology, Symons Trust Fund for Canadian Studies, French American Graduate Scholarship, EWC & IE Curtin Graduate Scholarship, Canada Research Chairs and ArcticNet.

## COMPETING INTERESTS

We have no competing interests.

## DATA ACCESSIBILITY

Genetic data for Southampton Island, Dolphin and Union, and Qamanirjuaq caribou are available from DRYAD; Serrouya, Paetkau, McLellan, Boutin, Jenkins et al. (2012).

For genetic data and samples on Arctic island caribou contact the Department of Environment, Government of Nunavut; Environment and Natural Resources, Government of Northwest Territories.

All sea ice GIS layers are available as raster files, from the National Snow and Ice Data Center, Sea Ice Index.

## ORCID

Deborah A. Jenkins  <http://orcid.org/0000-0001-7543-3028>

James A. Schaefer  <http://orcid.org/0000-0002-3416-1748>

## REFERENCES

- Ally, D., El-Kassaby, Y. A., & Ritland, K. (2000). Genetic diversity, differentiation and mating system in mountain hemlock (*Tsuga mertensiana*) across British Columbia. *Forest Genetics*, 7, 97–108.
- Andersen, A., Simcox, D. J., Thomas, J. A., & Nash, D. R. (2014). Assessing reintroduction schemes by comparing genetic diversity of reintroduced and source populations: A case study of the globally threatened large blue butterfly (*Maculinea anion*). *Biological Conservation*, 175, 34–41. <https://doi.org/10.1016/j.biocon.2014.04.009>
- Aparicio, J. M., Ortego, J., & Cordero, P. J. (2006). What should we weigh to estimate heterozygosity, alleles or loci? *Molecular Ecology*, 15, 4659–4665. <https://doi.org/10.1111/j.1365-294X.2006.03111.x>
- Ball, M. C., Finnegan, L., Manseau, M., & Wilson, P. (2010). Integrating multiple analytical approaches to spatially delineate and characterize genetic population structure: An application to boreal caribou (*Rangifer tarandus caribou*) in central Canada. *Conservation Genetics*, 11, 2131–2143. <https://doi.org/10.1007/s10592-010-0099-3>
- Banfield, A. W. F. (1961). A revision of the reindeer and caribou, genus *Rangifer*. *National Museum of Canada, Bulletin 177, Biological Series*, 66, 1–137.
- Barton, K. (2015). *MuMIn Version 1.15.6. Multi-model inference*. R package.
- Basto, M. P., Santos-Reis, M., Simões, L., Grilo, C., Cardoso, L., Cortes, H., ... Fernandes, C. (2016). Assessing genetic structure in common but ecologically distinct carnivores: The stone marten and red fox. *PLoS ONE*, 11(1), e0145165. <https://doi.org/10.1371/journal.pone.0145165>
- Bisho, M. D., Kappes, S. M., Keele, J. W., Stone, R. T., Sunden, S. L. F., Hawkins, G. A., ... Beattlie, C. W. (1994). A genetic linkage map for cattle. *Genetics*, 196, 619–639.
- Bowen, B. W., Bass, A. L., Soares, L., & Toonen, R. J. (2005). Conservation implications of complex population structure: Lessons from the loggerhead turtle (*Caretta caretta*). *Molecular Ecology*, 14, 2389–2402. <https://doi.org/10.1111/j.1365-294X.2005.02598.x>
- Brzosko, E., Wroblewska, A., Ratkiewicz, M., Till-Bottraud, I., Nicole, F., & Baranowska, U. (2009). Genetic diversity of *Cypripedium calceolus* at the edge and in the centre of its range in Europe. *Annales Botanici Fennici*, 46, 201–214. <https://doi.org/10.5735/085.046.0303>
- Buchanan, F. C., Galloway, S. M., & Crawford, A. M. (1994). Ovine microsatellites at the OarFCB5, OarFCB19, OarFCB20, OarFCB48, OarFCB129 and OarFCB226 loci. *Animal Genetics*, 25, 60.
- Campbell, M., Goorts, J., Lee, D., Boulanger, J., & Pretzlaw, T. 2015. *Aerial Abundance Estimates, Seasonal Range Use, and Spatial Affiliations of the Barren-Ground Caribou* (*Rangifer tarandus groenlandicus*) on Baffin Island – March 2014 Government of Nunavut, Department of Environment, Nunavut.
- Carmichael, L. E., Kritzan, J., Nagy, J. A., Dumond, M., Johnson, D., Veitch, A., & Strobeck, C. (2008). Northwest passages: Conservation genetics of Arctic Island wolves. *Conservation Genetics*, 9, 879–892. <https://doi.org/10.1007/s10592-007-9413-0>
- Carmichael, L. E., Krizan, J., Nagy, J. A., Fuglei, E., Dumond, M., Johnson, D., ... Strobeck, C. (2007). Historical and ecological determinants of genetic structure in arctic canids. *Molecular Ecology*, 16, 3466–3483. <https://doi.org/10.1111/j.1365-294X.2007.03381.x>
- Chen, C., Durand, E., Forbes, F., & Francois, O. (2007). Bayesian clustering algorithms ascertaining spatial population structure: A new computer program and a comparison study. *Molecular Ecology Notes*, 7, 747–756. <https://doi.org/10.1111/j.1471-8286.2007.01769.x>
- Cheylan, G., Granjon, L., & Britton-Davidian, J. (1998). Distribution of genetic diversity within and between Western Mediterranean island populations of the black rat *Rattus rattus* (L. 1758). *Biological Journal of the Linnean Society*, 63, 393–408.
- Christiansen, D. G., & Reyer, H. U. (2011). Effects of geographic distance, sea barriers and habitat on the genetic structure and diversity of all-hybrid water frog populations. *Heredity*, 106, 25–36. <https://doi.org/10.1038/hdy.2010.37>
- COSEWIC (2011). *Designatable Units for Caribou (Rangifer tarandus) in Canada*. Ottawa, ON: Committee on the Status of Endangered Wildlife in Canada.
- COSEWIC (2015a). *COSEWIC assessment and status report on the Peary Caribou Rangifer tarandus pearyi in Canada*. Ottawa, ON: Committee on the Status of Endangered Wildlife in Canada.
- COSEWIC (2015b). *Guidelines for recognizing Designatable Units*. Committee on the Status of Endangered Wildlife in Canada. Retrieved from <http://www.cosewic.gc.ca/default.asp?lang=En&n=DD31EAE-1>
- Côté, S. D., Dallas, J. F., Marshall, F., Irvine, R. J., Langvatn, R., & Albon, S. D. (2002). Microsatellite DNA evidence for genetic drift and philopatry in Svalbard reindeer. *Molecular Ecology*, 11, 1923–1930. <https://doi.org/10.1046/j.1365-294X.2002.01582.x>
- Coulon, A., Fitzpatrick, J. W., Bowman, R., Stith, B. M., Makarewicz, C. A., Stenzler, L. M., & Lovette, I. J. (2008). Congruent population structure inferred from dispersal behaviour and intensive genetic surveys of the threatened Florida scrub-jay (*Aphelocoma coerulescens*). *Molecular Ecology*, 17, 1685–1701. <https://doi.org/10.1111/j.1365-294X.2008.03705.x>
- Dalen, L., Fuglei, E., Hersteinsson, P., Kapel, C. M. O., Roths, J. D., Samelius, G., ... Angerbjörn, A. (2005). Population history and genetic structure of a circumpolar species: The arctic fox. *Biological Journal of the Linnean Society*, 84, 79–89.
- Dumond, M., Sather, S., & Harmer, R. (2013). Observation of Arctic Island barren-ground caribou (*Rangifer tarandus groenlandicus*) migratory movement delay due to human induced sea-ice breaking. *Rangifer*, 33, 115–122. <https://doi.org/10.7557/2.33.2.2533>
- Durand, E., Chen, C., & Francois, O. (2009). *TESS Version 2.3 Reference Manual*. Retrieved from <http://membres-timc.imag.fr/Olivier.Francois/manual.pdf>.
- 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. <https://doi.org/10.1007/s12686-011-9548-7>
- Eckert, C. G., Samis, K. E., & Loughheed, S. C. (2008). Genetic variation across species' geographical ranges: The central-marginal

- hypothesis and beyond. *Molecular Ecology*, 17, 1170–1188. <https://doi.org/10.1111/j.1365-294X.2007.03659.x>
- Ecological Stratification Working Group (1995). *A national ecological framework for Canada*. Ottawa/Hull, ON: Agriculture and Agri-food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch.
- Eldridge, M. D. B., Kinnear, J. E., Zenger, K. R., McKenzie, L. M., & Spencer, P. B. S. (2004). Genetic diversity in remnant mainland and 'pristine' island populations of three endemic Australian macropodids (Marsupialia): *Macropus eugenii*, *Lagorchestes hirsutus* and *Petrogale lateralis*. *Conservation Genetics*, 5, 325–338. <https://doi.org/10.1023/B:COGE.0000031148.59923.a>
- 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. <https://doi.org/10.1111/j.1365-294X.2005.02553.x>
- Falush, D., Wirth, T., Linz, B., Pritchard, J. K., Stephens, M., Kidd, M., ... Suerbaum, S. (2003). Traces of human migrations in *Helicobacter pylori* populations. *Science*, 299, 1582–1585. <https://doi.org/10.1126/science.1080857>
- Ferguson, M. A. D. (1985). *Population status of introduced reindeer on the Belcher Islands, Northwest Territories, in March 1982*. Frobisher Bay, NWT: NWT Wildlife Service.
- Ferguson, S., Taylor, M. K., Born, E. W., Rosing-Asvid, A., & Messier, F. (2001). Activity and movement patterns of polar bears inhabiting consolidated versus active pack ice. *Arctic*, 54, 49–54.
- Festa-Bianchet, M., Ray, J. C., Boutin, S., Côté, S. D., & Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: An uncertain future. *Canadian Journal of Zoology*, 89, 419–434. <https://doi.org/10.1139/z11-025>
- Francois, O., & Durand, E. (2010). Spatially explicit Bayesian clustering models in population genetics. *Molecular Ecological Resources*, 10, 773–784. <https://doi.org/10.1111/j.1755-0998.2010.02868.x>
- Frankham, R. (1996). Relationship of genetic variation to population size in wildlife. *Conservation Biology*, 10, 1500–1508. <https://doi.org/10.1046/j.1523-1739.1996.10061500.x>
- Frankham, R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity*, 78, 311–327. <https://doi.org/10.1038/hdy.1997.46>
- Frankham, R., Ballou, J. D., & Briscoe, D. A. (2002). *Introduction to conservation genetics*. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9780511808999>
- Furlan, E., Stoklosa, J., Griffiths, J., Gust, N., Ellis, R., Huggins, R. M., & Weeks, A. R. (2012). Small population size and extremely low levels of genetic diversity in island populations of the platypus, *Ornithorhynchus anatinus*. *Ecology and Evolution*, 2, 844–857. <https://doi.org/10.1002/ece3.195>
- Galpern, P., Manseau, M., Hettinga, P., Smith, K., & Wilson, P. (2012). Allelmatch: An R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. *Molecular Ecology Resources*, 12, 771–778. <https://doi.org/10.1111/j.1755-0998.2012.03137.x>
- Geffen, E., Waidyaratne, S., Dalen, L., Angerbjorn, A., Vila, C., Hersteinsson, P., ... Wayne, R. K. (2007). Sea ice occurrence predicts genetic isolation in the Arctic fox. *Molecular Ecology*, 16, 4241–4255. <https://doi.org/10.1111/j.1365-294X.2007.03507.x>
- Glass, W. R., Walter, R. P., Heath, D. D., Mandrak, N. E., & Corkum, L. D. (2015). Genetic structure and diversity of spotted gar (*Lepisosteus oculatus*) at its northern range edge: Implications for conservation. *Conservation Genetics*, 16, 889–899. <https://doi.org/10.1007/s10592-015-0708-2>
- Green, D. M. (2005). Designatable units for status assessment of endangered species. *Conservation Biology*, 19, 1813–1820. <https://doi.org/10.1111/j.1523-1739.2005.00284.x>
- Griffith, B., Scott, J. M., Carpenter, J. W., & Reed, C. (1989). Translocation as a species conservation tool: Status and strategy. *Science*, 245, 477–480. <https://doi.org/10.1126/science.245.4917.477>
- Gunn, A., & Dragon, J. (2002). *Peary caribou and muskox abundance and distribution on the western Queen Elizabeth Islands, Northwest Territories and Nunavut*. June–July 1997. Northwest Territories Department of Resources, Wildlife and Economic Development. Northwest Territories.
- Gunn, A., Miller, F., Barry, S., & Buchan, A. (2006). A near-total decline in caribou on Prince of Wales, Somerset, and Russell islands, Canadian Arctic. *Arctic*, 59, 1–13.
- Hagerty, B. E., & Tracy, C. R. (2010). Defining population structure for the Mojave desert tortoise. *Conservation Genetics*, 11, 1795–1807. <https://doi.org/10.1007/s10592-010-0073-0>
- Harradine, E. L., Andrew, M. E., Thomas, J. W., How, R. A., Schmitt, L. H., & Spencer, P. B. (2015). Importance of dispersal routes that minimize open-ocean movement to the genetic structure of island populations. *Conservation Biology*, 29, 1704–1714. <https://doi.org/10.1111/cobi.12555>
- Harris, L. N., Moore, J.-S., Galpern, P., Tallman, R. F., & Taylor, E. B. (2014). Geographic influences on fine-scale, hierarchical population structure in northern Canadian populations of anadromous Arctic Char (*Salvelinus alpinus*). *Environmental Biology of Fishes*, 97, 1233–1252. <https://doi.org/10.1007/s10641-013-0210-y>
- Heard, D. C., & Ouellet, J.-P. (1994). Dynamics of an introduced caribou population. *Arctic*, 47, 88–95.
- Illerai, J. C., Spurgin, L. G., Rodriguez-Exposito, E., Nogales, M., & Randos, J. C. (2016). What are we learning about speciation and extinction from the Canary Islands? *Ardeola*, 63, 15–33. <https://doi.org/10.13157/arla.63.1.2016.rp1>
- IUCN (2013). *Guidelines for reintroductions and other conservation translocations*. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission.
- Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, 23, 1801–1806. <https://doi.org/10.1093/bioinformatics/btm233>
- Jenkins, D. (2009a). *Space Use and Movement Patterns of North Baffin Caribou*. Department of Environment, Government of Nunavut, Nunavut.
- Jenkins, D. (2009b). *Caribou health monitoring: caribou sample collection for disease monitoring and genetic analysis*. Department of Environment, Government of Nunavut, Nunavut.
- Jenkins, D. A., Campbell, M., Hope, G., Goorts, J., & McLoughlin, P. (2011). *Recent trends in abundance of Peary caribou (Rangifer tarandus pearyi) and Muskoxen (Ovibos moschatus) in the Canadian Arctic Archipelago, Nunavut*. Department of Environment, Government of Nunavut, Nunavut.
- Jenkins, D. A., Goorts, J., & Lecomte, N. (2012). *Estimating the abundance of South Baffin caribou*. Department of Environment, Government of Nunavut, Nunavut.
- Jenkins, D. A., Lecomte, N., Schaefer, J. A., Olsen, S. M., Swingedouw, D., Côté, S. D., ... Yannic, G. (2016). Loss of connectivity among island-dwelling Peary caribou following sea ice decline. *Biology Letters*, 12, 20160235. <https://doi.org/10.1098/rsbl.2016.0235>
- Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24, 1403–1405. <https://doi.org/10.1093/bioinformatics/btn129>
- Jones, K. C., Levine, K. F., & Banks, J. D. (2000). DNA-based genetic markers in black-tailed and mule deer for forensic applications. *California Fish and Game*, 86, 115–126.
- Keenan, K., McGinnity, P., Cross, T. F., Crozier, W. W., Prodöhl, P. A., & O'Hara, R. B. (2013). diveR: An R package for the estimation and exploration of population genetics parameters and their associated



- errors. *Methods in Ecology and Evolution*, 4, 782–788. <https://doi.org/10.1111/2041-210X.12067>
- Kelt, D., & Van Vuren, D. (2001). The ecology and macroecology of mammalian home range area. *The American Naturalist*, 157, 637–645. <https://doi.org/10.1086/320621>
- Klutsch, C. F. C., Manseau, M., Anderson, M., Sinkins, P., & Wilson, P. J. (2017). Evolutionary reconstruction supports the presence of a Pleistocene Arctic refugium for a large mammal species. *Journal of Biogeography*, 44, 2729–2739. <https://doi.org/10.1111/jbi.13090>
- Kopatz, A., Eiken, H. G., Aspi, J., Kojola, I., Tobiassen, C., Tirronen, K. F., ... Hagen, S. B. (2014). Admixture and gene flow from Russia in the recovering northern European brown bear. *PLoS ONE*, 9, 1–10.
- Kutschera, V. E., Frosch, C., Janke, A., Skirnisson, K., Bidon, T., Lecomte, N., ... Hailer, F. (2016). High genetic variability of vagrant polar bears illustrates importance of population connectivity in fragmented sea ice habitats. *Animal Conservation*, 19, 337–349. <https://doi.org/10.1111/acv.12250>
- Lade, J., Murrey, N., Marks, C., & Robinson, N. (1996). Microsatellite differentiation between Phillips Island and mainland Australia populations of red fox *Vulpes vulpes*. *Molecular Ecology*, 5, 81–87. <https://doi.org/10.1111/j.1365-294X.1996.tb00293.x>
- Lesica, P., & Allendorf, F. W. (1995). When are peripheral populations valuable for conservation? *Conservation Biology*, 9, 753–760. <https://doi.org/10.1046/j.1523-1739.1995.09040753.x>
- Levin, I. I., & Parker, P. J. (2012). Philopatry drives genetic differentiation in an island archipelago: Comparative population genetics of Galapagos Nazca boobies (*Sula granti*) and great frigatebirds (*Fregata minor*). *Ecology and Evolution*, 2, 2775–2787. <https://doi.org/10.1002/ece3.386>
- Lomolino, M. V., Riddle, B. R., Whittaker, R. J., & Brown, J. H. (2010). *Biogeography* (4th ed.). Sunderland, MA: Sinauer Associates Inc.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton Monographs in Population Biology, no. 1. Princeton, NJ: Princeton University Press.
- Mallory, F. F., & Hillis, T. (1998). Demographic characteristics of circumpolar caribou populations: Ecotypes, ecological constraints, releases, and population dynamics. *Rangifer Special Issue*, 10, 49–60.
- Manning, T. H. (1943). Notes on the mammals of south and central west Baffin Island. *Journal of Mammalogy*, 24, 47–59. <https://doi.org/10.2307/1374780>
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27, 209–220.
- McFarlane, K., Gunn, A., Campbell, M., Dumond, M., Adamczewski, J., & Wilson, G. (2016). Genetic diversity, structure and gene flow of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) in Canada. *Rangifer*, 36, 1–24. <https://doi.org/10.7557/2.36.1.3577>
- McFarlane, K., Miller, F. L., Barry, S. J., & Wilson, G. A. (2014). An enigmatic group of arctic island caribou and the potential implications for conservation of biodiversity. *Rangifer*, 34, 73–94. <https://doi.org/10.7557/2.34.1.2953>
- McLaughlin, M. J., & Sainani, K. L. (2014). Bonferroni, Holm, and Hochberg corrections: Fun names, serious changes to p values. *PM&R*, 6, 544–546.
- Mee, J. A., Bernatchez, L., Reist, J. D., Rogers, S. M., & Taylor, E. B. (2015). Identifying designatable units for intraspecific conservation prioritization: A hierarchical approach applied to the lake whitefish species complex (*Coregonus* spp.). *Evolutionary Applications*, 8, 423–441. <https://doi.org/10.1111/eva.12247>
- Meirmans, P. G. (2012). The trouble with isolation by distance. *Molecular Ecology*, 21, 2839–2846. <https://doi.org/10.1111/j.1365-294X.2012.05578.x>
- Micheletti, S. J., & Storfer, A. (2015). A test of the central-marginal hypothesis using population genetics and ecological niche modelling in an endemic salamander (*Ambystoma barbouri*). *Molecular Ecology*, 24, 967–979. <https://doi.org/10.1111/mec.13083>
- Miller, F. L. (1995). Inter-island water crossings by Peary caribou, south-central Queen Elizabeth Islands. *Arctic*, 48, 8–12.
- Miller, F., Barry, S., & Calvert, W. (2005). Sea-ice crossings by caribou in the south-central Canadian Arctic Archipelago and their ecological importance. *Rangifer, Special Issue*, 16, 77–88.
- Miller, E. J., Eldridge, M. D. B., Morris, K. D., Zenger, K. R., & Herbert, C. A. (2011). Genetic consequences of isolation: Island tamar wallaby (*Macropus eugenii*) populations and the conservation of threatened species. *Conservation Genetics*, 12, 1619–1631. <https://doi.org/10.1007/s10592-011-0265-2>
- Miller, F., & Gunn, A. (2003). Catastrophic die-off of Peary caribou on the western Queen Elizabeth Islands, Canadian High Arctic. *Arctic*, 56, 381–390.
- Moore, S. S., Barendse, W., Berger, K. T., Armitage, S. M., & Hetzel, D. J. S. (1992). Bovine and Ovine DNA microsatellites from the EMBL and Genbank databases. *Animal Genetics*, 23, 463–467.
- Moritz, C. (1994). Defining 'Evolutionarily Significant Units' for conservation. *Trends in Ecology and Evolution*, 9, 373–375. [https://doi.org/10.1016/0169-5347\(94\)90057-4](https://doi.org/10.1016/0169-5347(94)90057-4)
- Nagy, J. A., Johnson, D., Larter, N. C., Campbell, M., Derocher, A. E., Kelly, A., ... Croft, B. (2011). Subpopulation structure of caribou (*Rangifer tarandus* L.) in arctic and subarctic Canada. *Ecological Applications*, 21, 2334–2348. <https://doi.org/10.1890/10-1410.1>
- Naimi, B. (2015). *usdm Version 1.1-15. Uncertainty Analysis for Species Distribution Models*. R package. Retrieved from <http://CRAN.R-project.org/package=usdm>.
- Nakagawa, S., Schielzeth, H., & O'Hara, R. B. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Noren, K., Carmichael, L., Fuglei, E., Eide, N. E., Hersteinsson, P., & Angerbjorn, A. (2011). Pulses of movement across the sea ice: Population connectivity and temporal genetic structure in the arctic fox. *Oecologia*, 166, 973–984. <https://doi.org/10.1007/s00442-011-1939-7>
- Nychka, D., Furrer, R., Paige, J., & Sain, S. (2016). *Fields Version 8.4.1: Tools for Spatial Data*. R package. Retrieved from <http://CRAN.R-project.org/package=fields>.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., ... Wagner, H. (2017). *Vegan: Community Ecology Package*. R Package Version 2.4-3
- Paetkau, D. (2003). An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology*, 12, 1375–1387. <https://doi.org/10.1046/j.1365-294X.2003.01820.x>
- Park, S. (2008). *Excel microsatellite toolkit, Version 3.1.1*. Dublin, Ireland: Animal Genomics Lab website, University College.
- Peakall, R. O. D., & Smouse, P. E. (2006). GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, 6, 288–295. <https://doi.org/10.1111/j.1471-8286.2005.01155.x>
- Pemberton, J. M., Smith, J. A., Coulson, T. N., Marshall, T. C., Slate, J., Paterson, S., ... Clutton-Brock, T. H. (1996). The maintenance of genetic polymorphism in small island populations: Large mammals in the Hebrides. *Philosophical Transactions of the Royal Society B - Biological Sciences*, 351, 745–752. <https://doi.org/10.1098/rstb.1996.0069>
- Peterson, S., Manseau, M., & Wilson, P. (2010). Bottlenecks, isolation, and life at the northern range limit: Peary caribou on Ellesmere Island, Canada. *Journal of Mammalogy*, 91, 698–711. <https://doi.org/10.1644/09-MAMM-A-231.1>

- Petren, K., Grant, P. R., Grant, B. R., & Keller, L. F. (2005). Comparative landscape genetics and the adaptive radiation of Darwin's finches: The role of peripheral isolation. *Molecular Ecology*, *14*, 2943–2957. <https://doi.org/10.1111/j.1365-294X.2005.02632.x>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2017). *nlme: Linear and nonlinear mixed effects models*. R package nlme Version 3.1-131. Retrieved from <http://CRAN.R-project.org/package=nlme>.
- Pohlert, T. (2016). *The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR)*. R package. Retrieved from <http://CRAN.R-project.org/package=PMCMR>.
- Pond, B. A., Brown, G. S., Wilson, K. S., & Schaefer, J. A. (2016). Drawing lines: Spatial behaviours reveal two ecotypes of woodland caribou. *Biological Conservation*, *194*, 139–148. <https://doi.org/10.1016/j.biocon.2015.12.005>
- Poole, K. G., Gunn, A., Patterson, B. R., & Dumond, M. (2010). Sea ice and migration of the Dolphin and Union caribou herd in the Canadian Arctic: An uncertain future. *Arctic*, *63*, 414–428.
- Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., ... Walker, D. A. (2013). Ecological consequences of sea-ice decline. *Science*, *341*, 519–524. <https://doi.org/10.1126/science.1235225>
- Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*, 945–959.
- Qiong, L., Zhang, W., Wang, H., Zeng, L., Birks, H. J. B., & Zhong, Y. (2017). Testing the effect of the Himalayan mountains as a physical barrier to gene flow in *Hippophae tibetana* Schlect. (Elaeagnaceae). *PLoS ONE*, *12*, e0172948. <https://doi.org/10.1371/journal.pone.0172948>
- R Development Core Team (2015). *R version 3.2.3: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raymond, M., & Rousset, F. (1995). GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. *Journal of Heredity*, *86*, 248–249. <https://doi.org/10.1093/oxfordjournals.jhered.a111573>
- Rousset, F. (2008). genepop'007: A complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources*, *8*, 103–106. <https://doi.org/10.1111/j.1471-8286.2007.01931.x>
- Rowe, G., & Beebee, T. J. (2007). Defining population boundaries: Use of three Bayesian approaches with microsatellite data from British natterjack toads (*Bufo calamita*). *Molecular Ecology*, *16*, 785–796. <https://doi.org/10.1111/j.1365-294X.2006.03188.x>
- Ryder, O. A. (1986). Species conservation and systematics: The dilemma of subspecies. *Trends in Ecology and Evolution*, *1*, 9–10. [https://doi.org/10.1016/0169-5347\(86\)90059-5](https://doi.org/10.1016/0169-5347(86)90059-5)
- Safriel, U. N., Volis, S., & Kark, S. (1994). Core and peripheral populations and global climate change. *Israel Journal of Plant Sciences*, *42*, 331–345. <https://doi.org/10.1080/07929978.1994.10676584>
- Sahanatien, V., & Derocher, A. E. (2012). Monitoring sea ice habitat fragmentation for polar bear conservation. *Animal Conservation*, *15*, 397–406. <https://doi.org/10.1111/j.1469-1795.2012.00529.x>
- Schaefer, J. A. (2006). Towards maturation of the population concept. *Oikos*, *112*, 236–240. <https://doi.org/10.1111/j.0030-1299.2006.13763.x>
- Schaefer, J. A., & Mahoney, S. P. (2003). Spatial and temporal scaling of population density and animal movement: A power law approach. *Ecoscience*, *10*, 496–501. <https://doi.org/10.1080/11956860.2003.11682797>
- Serrouya, R., Paetkau, D., McLellan, B. N., Boutin, S., Campbell, M., & Jenkins, D. A. (2012). Population size and major valleys explain microsatellite variation better than taxonomic units for caribou in western Canada. *Molecular Ecology*, *21*, 2588–2601. <https://doi.org/10.1111/j.1365-294X.2012.05570.x>
- Serrouya, R., Paetkau, D., McLellan, B. N., Boutin, S., Jenkins, D. A., & Campbell, M. (2012). *Data from: Population size and major valleys explain microsatellite variation better than taxonomic units for caribou in western Canada*. Dryad Digital Repository. <https://doi.org/10.5061/dryad.250c3s47>
- Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 415–436. <https://doi.org/10.1146/annurev.ecolsys.110308.120317>
- Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, *236*, 787–792. <https://doi.org/10.1126/science.3576198>
- Stone, R. T., Pulido, J. C., Duyk, G. M., Kappes, S. M., Keele, J. W., & Beattie, C. W. (1995). A small-insert bovine genomic library highly enriched for microsatellite repeat sequences. *Mammalian Genome*, *6*, 714–724. <https://doi.org/10.1007/BF00354294>
- Stroten, A., Navid, E., Quinn, M., Paquet, P. C., Bryan, H., & Darimont, C. (2014). Population genetic structure of gray wolves (*Canis lupus*) in a marine archipelago suggests island-mainland differentiation consistent with dietary niche. *BMC Ecology*, *14*, 1–9.
- Szpiech, Z. A., Jakobsson, M., & Rosenberg, N. A. (2008). ADZE: A rarefaction approach for counting alleles private to combinations of populations. *Bioinformatics*, *24*, 2498–2504. <https://doi.org/10.1093/bioinformatics/btn478>
- Szucs, M., Melbourne, B. A., Tuff, T., Weiss-Lehman, C., & Hufbauer, R. A. (2017). Genetic and demographic founder effects have long-term fitness consequences for colonizing populations. *Ecology Letters*, *20*, 436–444. <https://doi.org/10.1111/ele.12743>
- Taylor, S. S., Jenkins, D. A., & Arcese, P. (2012). Loss of MHC and neutral variation in Peary caribou: Genetic drift is not mitigated by balancing selection or exacerbated by MHC allele distributions. *PLoS ONE*, *7*, e36748. <https://doi.org/10.1371/journal.pone.0036748>
- Techer, M. A., Clémencet, J., Simiand, C., Portlouis, G., Reynaud, B., Delatte, H., ... Roubik, D. (2016). Genetic diversity of the honeybee (*Apis mellifera* L.) populations in the Seychelles archipelago. *Insect Conservation and Diversity*, *9*, 13–26. <https://doi.org/10.1111/icad.12138>
- Vellend, M. (2003). Island biogeography of genes and species. *American Naturalist*, *162*, 358–365. <https://doi.org/10.1086/377189>
- Vellend, M. (2005). Species diversity and genetic diversity: Parallel processes and correlated patterns. *American Naturalist*, *166*, 199–215. <https://doi.org/10.1086/431318>
- Vergara, M., Basto, M. P., Madeira, M. J., Gomez-Moliner, B. J., Santos-Reis, M., Fernandes, C., & Ruiz-Gonzalez, A. (2015). Inferring population genetic structure in widely and continuously distributed carnivores: The stone marten (*Martes foina*) as a case study. *PLoS ONE*, *10*, e0134257. <https://doi.org/10.1371/journal.pone.0134257>
- Volis, S., Ormanbekova, D., Yermekbayev, K., Song, M., & Shulgina, I. (2016). The conservation value of peripheral populations and a relationship between quantitative trait and molecular variation. *Evolutionary Biology*, *43*, 26–36. <https://doi.org/10.1007/s11692-015-9346-3>
- Warnock, W. G., Rasmussen, J. B., & Taylor, E. B. (2010). Genetic clustering methods reveal bull trout (*Salvelinus confluentus*) fine-scale population structure as a spatially nested hierarchy. *Conservation Genetics*, *11*, 1421–1433. <https://doi.org/10.1007/s10592-009-9969-y>
- Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, *38*, 1358.

- White, T. A., & Searle, J. B. (2007). Genetic diversity and population size: Island populations of the common shrew, *Sorex araneus*. *Molecular Ecology*, 16, 2005–2016. <https://doi.org/10.1111/j.1365-294X.2007.03296.x>
- Wilson, G. A., Strobeck, C., Wu, L., & Coffin, J. W. (1997). Characterization of microsatellite loci in caribou *Rangifer tarandus*, and their use in other artiodactyls. *Molecular Ecology*, 6, 697–699. <https://doi.org/10.1046/j.1365-294X.1997.00237.x>
- Wright, S. (1943). Isolation by distance. *Genetics*, 28, 114–138.
- Wright, S. (1946). Isolation by distance under diverse systems of mating. *Genetics*, 31, 39–50.
- Yannic, G., Ortego, J., Pellissier, L., Lecomte, N., Bernatchez, L., & Côté, S. D. (2017). Linking genetic and ecological differentiation in an ungulate with a circumpolar distribution. *Ecography*, 40, 1–15.
- Yannic, G., Pellissier, L., Ortego, J., Lecomte, N., Couturier, S., Cuyler, C., ... Côté, S. D. (2014). Genetic diversity in caribou linked to past and future climate change. *Nature Climate Change*, 4, 132–137. <https://doi.org/10.1038/nclimate2074>
- Yannic, G., St-Laurent, M.-H., Ortego, J., Taillon, J., Beauchemin, A., Bernatchez, L., ... Côté, S. D. (2016). Integrating ecological and genetic structure to define management units for caribou in Eastern Canada. *Conservation Genetics*, 17, 437–453. <https://doi.org/10.1007/s10592-015-0795-0>
- Zigouris, J., Schaefer, J. A., Fortin, C., & Kyle, C. J. (2013). Mitochondrial DNA sequence variation and post-glacial recolonization in wolverines (*Gulo gulo*) from across their circumpolar distribution. *PLoS ONE*, 8(12), e83837. <https://doi.org/10.1371/journal.pone.0083837>
- Zittlau, K. (2004). *Population genetic analyses of North American caribou* (*Rangifer tarandus*). PhD Dissertation. University of Alberta, Edmonton, Alberta.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

## BIOSKETCH

Deborah A. Jenkins is a PhD Candidate at Trent University, co-supervised at Université de Moncton. Her principal focus is the ecology and conservation of Arctic ungulates. With a broad interest in biogeographical gradients and scaling effects, her research elucidates ecological patterns of multiple species to better understand how they respond to environmental heterogeneity and climate change. All authors have interest in caribou ecology and conservation in Arctic regions.

Author contributions: D.A.J. conceived the study with helpful input from G.Y., J.A.S and N.L. D.A.J. collected and analysed the data with input from G.Y., J.A.S, J.C. and N.L. D.A.J. wrote the manuscript with the help of all co-authors.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Jenkins DA, Yannic G, Schaefer JA, Conolly J, Lecomte N. Population structure of caribou in an ice-bound archipelago. *Divers Distrib*. 2018;24:1092–1108. <https://doi.org/10.1111/ddi.12748>