ISLANDS, UNGULATES, AND ICE: THE RESPONSE OF CARIBOU TO A CHANGING ENVIRONMENT

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ABSTRACT

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Central to wildlife conservation and management is the need for refined, spatially explicit knowledge on the diversity and distribution of species and the factors that drive those patterns. This is especially vital as anthropogenic disturbance threatens rapid large-scale change, even in the most remote areas of the planet. My dissertation examines the influence of land- and sea-scape heterogeneity on patterns of genetic differentiation, diversity, and broad-scale distributions of island-dwelling ungulates in the Arctic Archipelago. First, I investigated genetic differentiation among island populations of Peary caribou (*Rangifer tarandus pearyi*) in contrast to continental migratory caribou (*Rangifer tarandus*) and evaluated whether genetic exchange among Peary caribou island populations was limited by the availability of sea ice – both now and in the future. Differentiation among both groups was best explained by geodesic distance, revealing sea ice as an effective platform for Peary caribou movement and gene flow. With future climate warming, substantial reductions in sea ice extent were forecast which significantly increased resistance to caribou movement, particularly in summer and fall. Second, I assessed genetic population structure and diversity of northern caribou and deciphered how Island Biogeography Theory (IBT) and Central Marginal Hypothesis (CMH) could act in an archipelago where isolation is highly variable due to the dynamics of sea ice. Genetic differentiation among continental and island populations was low to moderate. In keeping with IBT and CMH, island-dwelling caribou displayed lower genetic diversity compared to mainland and mainland migratory herds; the size of islands (or population range) positively influenced genetic diversity, while distance-to-mainland and fall ice-free coastlines negatively influenced genetic diversity. Hierarchical structure analysis revealed multiple units of caribou diversity below the species level. Third, I shifted my focus to the terrestrial landscape and explored the elements governing species-environment relationships. Using species distribution models, I tested the response of caribou and muskoxen to *abiotic* versus *abiotic* + *biotic* predictors, and included distance to heterospecifics as a proxy for competitive interactions. Models that included biotic predictors outperformed models with abiotic predictors alone, and biotic predictors were most important when identifying habitat suitability for both ungulates. Further, areas of high habitat suitability for caribou and muskoxen were largely disjunct, limited in extent, and mainly outside protected areas. Finally, I modelled functional connectivity for two genetically and spatially disjunct groups of island-dwelling caribou. For High Arctic caribou, natural and anthropogenic features impeded gene flow (isolation-by-resistance); for Baffin Island caribou we found panmixia with absence of isolation-by-distance. Overall, my dissertation demonstrates the varying influences of contemporary land- and sea-scape heterogeneity on the distribution, diversity and differentiation of Arctic ungulates and it highlights the vulnerability of island-dwelling caribou to a rapidly changing Arctic environment.

KEY WORDS: genetic diversity, population structure, landscape genetics, isolation-by-distance, Circuitscape, Least-Cost-Path, Island Biogeography Theory, Central Marginal

Hypothesis, MaxEnt, Eltonian Noise Hypothesis, Bayesian cluster analysis, connectivity, *Rangifer tarandus*, Canadian Arctic Archipelago, *Ovibos moschatus*

PREFACE

My dissertation has been written in manuscript form, and each data chapter has been published or is being prepared for submission to a peer-reviewed journal. Chapter 2 was published in Biology Letters, Chapter 3 in Diversity and Distributions, and Chapter 4 in Global Ecology and Conservation. Chapter 5 is nearing submission. Thus, the style of each manuscript varies slightly as formatting is specific to journal requirements. Importantly, all of my research was completed in collaboration with others. I have identified my coauthors on the title page of each chapter and use the plural 'we' throughout my dissertation.

Photo: Debbie Jenkins

Peary caribou on Axel Heiberg Island in April 2007

DEDICATION

This work is dedicated to my remarkable parents, Joe and Helen (Howard) Jenkins.

How lucky am I — that my world has been framed by such fun and loving parents. I owe them so much. My passion for the outdoors and all things wild is a testament to them. As long as I can remember, they have had me out camping, filling bird feeders, and playing in the woods. My mom and dad nurtured my curiosity in nature and we explored wild places together. Through them, I have learnt the inimitable value of family and the enduring promise of education and hard work. My mom and dad are a bright light — a constant inspiration. I love and miss them deeply.

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Ode to my extended community

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CHAPTER 1

GENERAL INTRODUCTION

Understanding the response of wildlife to environmental heterogeneity is an enduring pursuit, heightened now by the rapid intensification of human-driven transformation of the biosphere (Barber et al. 2008, Lewis and Maslin 2015, McGill et al. 2015). Indeed, global-scale environmental change, including the unprecedented loss and fragmentation of habitat (Watson et al. 2018), the declines and losses in biological diversity (IPBES 2019), and a changing and unpredictable climate (Barber et al. 2008, Lewis and Maslin 2015), have upset the ecological stage (Maxwell et al. 2016).

Human-driven disturbance has extensively and directly modified appreciable proportions of the terrestrial (77% - excluding Antarctica; Watson et al. 2018) and marine environments (87%; Watson et al. 2018), driving declines in wildlife populations (IPBES 2019, WWF 2020, Penjor et al. 2021) and accelerating species extinction rates (Ceballos et al. 2015, IPBES 2019). Remaining areas of wilderness provide a focus for conservation efforts — by providing baselines, protecting intact populations, securing functioning ecosystems, buffering against species extinction (Watson et al. 2018, Di Marco et al. 2019) — while climate warming threatens to modify even intact land- and sea-scape habitats.

The retreat and thinning of Arctic sea ice represents one such change. A critical biome, Arctic sea ice supports a diversity of species (e.g., polar bear *Ursus maritimus*, ringed seal *Pusa hispida*, walrus *Odobenus rosmarus*, Arctic fox *Vulpes lagopus*; Moore and Huntington 2008, Laidre et al. 2008, Norén et al. 2011) and unique populations, including terrestrial ungulates (i.e., Dolphin and Union caribou *Rangifer tarandus groenlandicus*, Poole et al. 2010; Svalbard reindeer *Rangifer tarandus platyrhynchus*; Peeters et al. 2020). Importantly, these animals meet their life-history requirements through use or interactions with sea ice (i.e., mating, denning, resting, dispersal, migration; Post et al. 2013, Macias-Fauria and Post 2018).

For insular terrestrial ungulates, these threats are particularly poignant in the Arctic Archipelago where sea ice acts as a bridge between islands for most of the year. Here, the loss of Arctic sea ice could acutely modify the opportunity for crossing fjords (Joly 2012) and for inter-island or island-mainland movements (Miller et al. 2005, Pool et al. 2010, Peeters et al. 2020), reducing access to seasonal habitats and restricting gene flow, among other changes (Post et al. 2013, Macias-Fauria and Post 2018). The cumulative consequences of such modifications include range loss, population declines, increased isolation and genetic drift, and the breakdown of metapopulation structure (Miller et al. 2005, Poole et al. 2010, Post et. al. 2013, Mallory and Boyce, 2018); such change could compromise population viability and intensify extinctions (Frankham 2002, Peeters et al. 2020). Indeed, the loss of sea ice habitat and connectivity is an emerging crisis (Macias-Fauria and Post 2018) and island populations are particularly vulnerable (Ricketts et al. 2005, Cardillo et al. 2006, Veron et al. 2019).

ISLANDS – A FOCUS FOR BIOLOGICAL THEORY AND CONSERVATION

Islands are a longstanding feature of biological understanding, providing vast insight into ecological patterns and processes such as niche partitioning and species-area relationships, as well as the unique evolutionary force of isolation (Diamond 1975, Triantis et al. 2005, Cabral et al. 2014, Matthews et al. 2019). For biologists, a particularly important milestone was MacArthur and Wilson's (1967) Equilibrium Theory of Island Biogeography. These authors posited that the richness of species on islands represents a dynamic balance between colonization and extinction, where the rate of colonization is a function of isolation and the rate of extinction a function of island area (MacArthur and Wilson 1967). Indeed, many studies have since demonstrated how species richness (often referred to as species diversity) relates positively to island area and inversely to isolation (Gentile and Argano 2005, Kalmar and Currie 2006, Ackerman et al. 2007, Spengler et al. 2011). More recently, the theory has been expanded to explore genetic diversity as a correlate of species diversity, leading to the prediction that species on large islands with high immigration rates will have greater genetic diversity than the same species on smaller, more isolated islands (Vellend 2003, Vellend and Geber 2005, McGlaughlin 2014). At the population level, a corresponding biogeographical theory — the Central Marginal Hypothesis, further predicts that populations at the edge of a species range will be small, isolated, and subject to low gene flow and high rates of genetic drift (Eckert et al 2008). It follows that these geographically marginal populations could exhibit low genetic diversity and heightened genetic differentiation (Frankham 2002). Such populations may be genetically and phenotypically divergent from central populations and as such, have high conservation value in the face of rapid environmental change (Lesica and Allendorf 1995).

Indeed, spatial heterogeneity and environmental gradients have a significant influence on ecosystem processes, from habitat selection to functional connectivity and gene flow (Taylor et al. 1993, Kie et al. 2002, Soule et al. 2004, Kindlmann and Burel 2008). Species-level responses to environmental heterogeneity may be expressed as differences in habitat use, range size, movement patterns, and species interactions (Levin 1992). These responses, in turn, can drive ecotype distinction owing to differences in behaviors and phenotypes, usually in relation to the environment (Noren et al. 2011, Morrison 2012, Pond et al. 2016), population differentiation and structure (Serrouya et al. 2012), evolutionary divergence (Klütsch et al. 2017), and speciation (Harter et al. 2015). Thus, how island species respond to environmental heterogeneity can serve to test and expand our biogeographical understanding and inform the conservation of insular populations and species.

Such knowledge is critical. Islands have been the epicenter of plant and animal extinctions. Insular environments host 75 % of documented vertebrate extinctions and almost half of extant endangered species (Russell and Kueffer 2019). With limited refuge from human disturbance, island species are vulnerable to a host of anthropogenic impacts including habitat loss, exploitation, and invasive species (Russel and Kueffer 2019). Even species on relatively pristine islands are vulnerable to extinction. Largely unspoilt, the Canadian Arctic Archipelago is among the world’s largest archipelagos, and a hotspot for latent extinction risk among mammals – namely, an area where mammal species have a high likelihood to decline towards extinction (Cardillo et al. 2006). Yet, wildlife conservation measures on these islands tend to be limited, including area-based habitat protection for Arctic ungulates.

ARCTIC UNGULATES – SPECIES OF CULTURAL AND ECOLOGICAL IMPORTANCE

Caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) are the only hoofed mammals adapted to the harsh environment of the Arctic Archipelago (Festa-Bianchet et al. 2011, Dobson et al. 2015). Still, their large body size and 'slow' life-history traits (i.e., long gestation, low reproductive output) leave them vulnerable to environmental perturbations (Festa-Bianchet et al. 2011, Berger et al. 2018, Kutz et al. 2015). Remnants of the ice age, caribou and muskoxen are ecologically and socially significant – crucial to Arctic people and Arctic ecosystems (Festa-Bianchet et al. 2011, Cuyler et al. 2020). For millennia, these ungulates have played a central role in the culture of indigenous people (Lent 1999, Gordon 2005), providing food, skins for clothing, and a strong sense of identity and well-being (Taylor 2005, Kutz et al. 2014, Willox et al. 2015). Across the landscape, they are fundamental to both ecosystem structure and function (Gaston and Fuller 2008, Gunn et al. 2011, Cuyler et al. 2020). Their foraging and their dispersal of nutrients and seeds in fecal pellets influence the composition and biomass of plant communities. Their presence also supports a range of predators, scavengers, and parasites; thus, they play a key role in the complex movement of energy and material (Gray 1987, Heard and Ouellet 1994, Eskelinen and Oksanen 2006, Post and Pedersen 2008, Gunn et al 2011).

In the Canadian Arctic, the range of muskoxen overlaps almost entirely with Peary caribou (*R. t. pearyi*; Jenkins et al. 2011) and portions of the range of continental barren-ground caribou (*R. t. groenlandicus*); introduced herds of muskoxen also occur in northern Quebec and the Yukon (Hénaff and Crête 1989, Ferguson and Gauthier 1992, Reynolds 1998). Research suggests that differences in morphology, physiology, and behaviour likely limit species interactions (Klein 1992, 1999) and enable caribou and muskoxen to use habitat and forage differently (Larter and Nagy 2004). Nonetheless, the potential for competitive interactions is a perennial issue, largely driven by declining caribou populations where muskoxen numbers have persisted or increased (Vincent and Gunn 1981, Gunn et al. 1991, Gunn and Dragon 1998).

Interspecific competition is an important ecological process with well-documented influences on habitat selection, speciation, extinction, and the structuring of ecological communities (Diamond 1975, Schluter and McPhail 1992). Understanding how species respond to competition has led to the enduring principle of Competitive Exclusion (Hardin 1960) – *'complete competitors cannot coexist'* - and related concepts of niche (Hutchinson 1959). Classically, questions of competition have been explored through removal experiments (Connell 1961, Redfield et al 1977) and empirical studies of community assemblage (e.g., Diamond 1975), but also measures of niche overlap and niche breadth (e.g., Schaefer et al. 1996, Bertolino et al. 2013). More recently, predictive models have shown promise in revealing biotic interactions, including competition (Mpakari et al. 2017, Neves et al. 2019).

In this regard, species distribution models (SDMs) have emerged as an important ecological tool (Elith and Leathwick 2009). Following the Eltonian Noise Hypothesis —

that physical features set the limits of species distributions at large spatial extents (Soberon and Nakamura 2009) — SDMs are typically dominated by abiotic predictors, estimating species-environment relationships and habitat suitability (Elith et al. 2011). Recent SDM studies, however, challenge this notion and underscore the important role of biotic interactions in determining distributions (Atauchi et al. 2018, Palacio and Girini 2018). Thus, for sympatric caribou and muskoxen, SDMs may provide insights into their interactions and spatial ecology – addressing critical information gaps for these iconic Arctic species.

Despite their importance, caribou and muskoxen, like many large terrestrial herbivores around the world, are facing population declines; several populations are threatened with extirpation (Ripple et al. 2015). Although muskoxen are classified globally as Least Concern according to IUCN criteria (Gunn and Forchhammer 2008) and considered stable or increasing in Canada, they were nearly extirpated in Canada at the turn of the 20th century (Cuyler et al. 2020) and have recently experienced multiple mortality events in the Canadian Arctic Islands (Kutz et al. 2015). In contrast, caribou face serious conservation concerns across their Holarctic range, where they are assessed as Vulnerable under the IUCN Red List criteria due to a 40% decline in abundance over three generations (Gunn 2016). In Canada, the future of caribou is uncertain (Festa-Bianchet et al. 2011, WWF-Canada. 2020); populations are declining and disappearing (Schaefer 2003, Gunn et al. 2006, Hebblewhite et al. 2009), even in the most remote reaches of their Arctic island range (Mallory et al. 2020).

A SPECIES OF CONSERVATION CONCERN

A circumpolar species, caribou are widely distributed across a variety of arctic and subarctic habitats, including 12 of 15 recognized ecozones in Canada (Gunn et al. 2011). Below the species level, their diversity in Canada has been recognized in five subspecies (Peary, barren-ground, Grant's, woodland, and Dawson's; Banfield 1961), twelve Designatable Units (COSEWIC 2011), and various ecotypes (sedentary or migratory, Bergerud 1994; insular, barren-ground, montane, or woodland, Mallory and Hillis 1998; migratory, boreal, or mountain, Hummel and Ray 2008). Only Peary and barren-ground subspecies occur at extreme latitudes in Canada, where they are nearly allopatric (Banfield 1961). Peary caribou are nationally endemic (Enns et al. 2020) and occur almost exclusively on islands, while barren-ground caribou occupy the mainland tundra and a small number of islands (e.g., Baffin Island, Coats Island, Southampton Island; Gunn et al. 2011, Festa-Bianchet et al. 2011). Peary caribou are listed as Endangered in Canada (Canada Gazette Part II, Vol 145, No4, 2011-02-16) under the *Species At-Risk Act* (SARA, 2002), recently assessed as Threatened (COSEWIC 2015), and some populations may have been extirpated (e.g., Prince of Wales and Somerset islands, Gunn et al. 2006; Axel Heiberg Island, Mallory et al. 2020). Barren-ground caribou were assessed as Threatened in Canada (COSEWIC 2016), and populations on islands, such as Baffin Island, have declined by over 95% since the early 1990s (Jenkins et al. 2012; Campbell et al. 2015). The extent to which island-dwelling caribou represent separate genetic populations or subpopulations below the subspecies level is an active area of research (COSEWIC 2011, Jenkins et al. 2011, Klütch et al. 2017, this study), particularly for herds in the eastern Archipelago.

Scale is key to understanding interspecific and landscape-species interactions (Levin 1992, Schaefer and Messier 1995, Schaefer et al. 1996, Mayor et al. 2009) and biogeographical gradients − *studies across a broad spatial scope* − can serve as natural experiments (Diamond 1975, Serrouya et al. 2012, Legagneux et al. 2014, Poley et al. 2014). Because ecological processes can occur at different spatial and temporal scales (Levin 1992, Boyce et al. 2006) and are contingent on variation in habitat conditions (Jenkins 2005), the patchwork of arctic islands provides a natural laboratory to elucidate the ecological patterns of multiple species, the processes that sustain them, and their responses to environmental heterogeneity.

GOALS AND OBJECTIVES

The overarching aim of my thesis is to determine the influence of environmental heterogeneity on the distribution and connectivity of caribou and their genes. I capitalized on a rare assemblage of field observations and samples, as well as spatially explicit environmental data, to develop large-scale genetic and species distribution models to support conservation. To this end, I identified key aspects of population structure, important habitat, limiting factors, and functional connectivity across a broad expanse of the Canadian Arctic.

My specific objectives were to (a) predict how climate change is likely to influence the extent of sea ice and modulate population connectivity for island-dwelling caribou, comparing extant connectivity to future projections under multiple climate change scenarios; (b) determine caribou diversity and population structure across the

Canadian Arctic, and identify patterns of genetic diversity in relation to the geographic and ecological complexity of the land- and sea-scape through the lens of Island Biogeography Theory and the Central Marginal Hypothesis; (c) model the winter distribution and niche characteristics of High Arctic Peary caribou and muskoxen, and test the Eltonian Noise Hypothesis to identify the key drivers of these winter distributions; and (d) model the influence of land and sea-scape features on the movement and gene flow of island-dwelling caribou, and estimate functional connectivity across this remote archipelago.

HOMAGE TO FIELD WORK

Collecting data and samples from species that are rare, threatened, or elusive is difficult (Barbosa 2017). In the vast, remote, and harsh environment of the Arctic Archipelago, this strain is paired with challenging logistics and extreme costs. My research benefitted from years of sample and survey efforts – ground and aerial surveys that rendered observations of winter occupancy as well as samples of feces and tissue (Jenkins et al. 2011, Jenkins and Goorts 2011, Jenkins et al. 2012), community-based monitoring that provided additional direct observations and samples of caribou (Jenkins 2009), and the generosity of other research scientists and community and government partners who augmented these observations by sharing data and samples (i.e., Serrouya et al. 2012, Environment and Natural Resource 2014). Together, these immense efforts provided the fine resolution geolocation data essential for species distribution modeling (Chapter 4) and the georeferenced samples for the study of population genetics and landscape genetics (Chapters 2, 3, 5) while spanning the broad spatial extent conducive for such biogeographic study.

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CHAPTER 2

LOSS OF CONNECTIVITY AMONG PEARY CARIBOU FOLLOWING SEA ICE DECLINE

A version of this chapter has been published

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ABSTRACT

Global warming threatens to reduce population connectivity for terrestrial wildlife through significant and rapid changes to sea ice. Using genetic fingerprinting, we contrast extant connectivity in island-dwelling Peary caribou in northern Canada with continental-migratory caribou. We next examined how sea-ice contractions in the last decades modulated population connectivity and explored the possible impact of future climate change on the long-term connectivity among island caribou. We found a strong correlation between genetic and geodesic distances for both continental and Peary caribou, even after accounting for the possible effect of sea surface. Sea ice has thus been an effective corridor for Peary caribou, promoting inter-island connectivity and population mixing. Using a time series of remote sensing sea ice data, we show that landscape resistance in the Canadian Arctic Archipelago has increased by approximately 15% since 1979 and it may further increase by 20 to 77% by 2086 under a high-emission scenario (RCP 8.5). Under the persistent increase in greenhouse gas concentrations, reduced connectivity may isolate island-dwelling caribou with potentially significant consequences for population viability.

Keywords:

Caribou, connectivity, gene flow, Canadian Arctic Archipelago, landscape genetics, isolation by distance.

1. INTRODUCTION

Connectivity is critical for the persistence of natural living populations in dynamic landscapes (Hanski and Gaggiotti, 2014). By facilitating dispersal, connectivity allows the demographic and genetic rescue of declining populations, alleviating the potential for inbreeding depression and increasing persistence time (Frankham, 2005). Connectivity can indeed facilitate the colonization of suitable habitats that, in a harsh and variable environment, may be crucial to the long-term persistence of populations (Frankham, 2005; Fischer and Lindenmayer, 2007). Doing so, connectivity supports gene flow between populations and enhances local genetic diversity, which reduces inbreeding and eases the effects of genetic drift in small populations (Broquet et al. 2010). Global warming is expected to have a significant effect on these ecological processes – modifying landscape suitability for species (Yannic et al. 2014a) and ushering in rapid changes in connectivity (Gilg et al. 2012; Post et al. 2013).

Sea ice represents an important bridge for wildlife that use ice as a platform for dispersal and migration (Gilg et al. 2012; Post et al. 2013). Its loss and thinning could impede movement and induce a cascade of unprecedented effects (Gilg et al. 2012). For Arctic fox (*Vulpes lagopus*), ice allows for long-distance movements, giving rise to a genetically homogeneous population that spans the North American and Svalbard archipelagos (Noren et al. 2011). For wolves (*Canis lupus*), it mediates movement among islands and the mainland, allowing for recolonization of extirpated populations (Carmichael et al. 2008). For caribou (*Rangifer tarandus*), sea ice acts as a bridge for seasonal inter-island or island-mainland migrations (Miller et al. 2005; Poole et al. 2010).

The long-term viability of island caribou may thus depend on sea-ice connectivity (Dumond et al. 2013).

Compared with herds on the mainland (figure 1), endangered Peary caribou (*R. tarandus pearyi*) occur almost exclusively in the Canadian Arctic Archipelago, which is connected by sea ice most of the year (COSEWIC, 2004). This subspecies has declined dramatically, driven by extreme, unpredictable weather events, and is part of a non-equilibrium grazing system characterized by periodic die-offs and extensive long-distance movements to access forage (Miller and Barry, 2009). Some caribou make extensive and seasonal inter-island movements (Miller et al. 2005; Jenkins and Lecomte, 2012). We surmise that, while island caribou display high levels of connectivity and low genetic distinctiveness among populations, their frequent use of sea ice and low abundance makes them particularly vulnerable to sea-ice loss.

Here we use population genetic, remote sensing and climatic projections to examine how climate change and sea-ice extent modulate population connectivity for island caribou in the most complex archipelago of the Arctic. We asked the following questions: (i) Does genetic structure among Peary caribou differ from migratory tundra caribou on the mainland? (ii) Are genetic exchanges among Peary caribou limited by availability of sea ice for travel between islands? (iii) How will climate change and the retreat of sea ice affect the connectivity among caribou in this archipelago? To quantify these relationships, we analysed environmental and genetic patterns across an immense region, spanning most of the North American Arctic.

2. MATERIALS AND METHODS

(a) Study area and genetic data

The study area extends across the Canadian Arctic Archipelago and into subarctic Canada and Alaska, USA (figure 1a). Genetic samples were obtained from herds of migratory-tundra caribou and Peary caribou, and genotyped at 16 microsatellite locus (figure 1a and table 1). Pairwise F_{ST} were computed according to Weir and Cockerham (1984) (electronic supplementary material).

(b) Analysis of genetic data

We first tested the log-transformed geodesic distances as predictors of genetic differentiation ($F_{ST}/(1-F_{ST})$) separately among herds of migratory tundra (continental) and Peary caribou (island), referred to as the isolation-by-distance model (IBD). Next, we examined whether the current seawater is currently limiting connectivity among Peary caribou, assuming that genetic distances between population pairs increase with cost-weighted distances measured along the optimal least-cost path (LCP) connecting populations. Sea ice should allow caribou movements, while ice-free seawater impedes dispersal among islands (Poole et al. 2010, Leblond et al. 2016). We calculated LCP weighted for the presence of seawater using the R package '*gdistance*' (R Development Core Team, 2016) following a procedure described in (Yannic et al. 2014b). We then contrasted an IBD model (equivalent to a fully permeable landscape), with a model, where land surfaces were assigned a value of 1, while water (with or without ice) was given a lower connectivity value from weak (0.001) to partially permeable (0.9). The connectivity value of water was first evaluated according to an optimization approach (see the electronic supplementary material). To determine which model (IBD or LCP) had the greatest support as a predictor of genetic differentiation, we used three complementary approaches: Mantel tests (Mantel, 1967), multiple regressions on distance matrices (MRDM, Legendre et al. 1994), and maximum-likelihood population-effects models (MLPE, Clarke et al. 2002). We ranked candidate models according to the proportion of explained genetic variance and by calculating Akaike's information criterions (electronic supplementary material).

(c) Connectivity changes overtime

To assess changes in connectivity over time, we retrieved monthly Arctic sea ice extent, 1979 to 2015, available at the National Snow and Ice Data Center (University of Colorado, Boulder, USA). Future sea-ice predictions were extracted from the climate EC-Earth model assuming two different emission scenarios, RCP 4.5 (moderate) and 8.5 (high), every 10 years, from 2016-2086 (Wisz et al. 2015). We predicted a decrease in connectivity among locations adversely affected by sea-ice decline, owing to longer ice-free seasons. Connectivity was estimated in the past (for each month from 1979 to 2015) and to the future with LCPs calculating: (i) among the eight Peary caribou populations, (ii) on 1000 occurrence points randomly sampled across the Peary caribou range, and (iii) only considering the shortest straight lines between islands. To estimate connectivity change over the years, we next averaged monthly LCP estimates. Based on observations that caribou are reluctant long-distance swimmers (Leblond et al. 2016; Miller, 1995), we followed the protocol above giving sea ice and land mass a value of 1, while ice-free waters were considered not permeable to movement. Because LCPs were all highly correlated (all Pearson's $r > 0.86$), we only presented results based on random occurrences that we considered most representative of connectivity changes in the entire region.

3. RESULTS AND DISCUSSION

The strong linear correlation between genetic and geodesic distances for both Peary caribou (Mantel's $r = 0.61$, $p < 0.001$; MRDM $R^2 = 0.38$, $p < 0.001$) and continental caribou herds (Mantel's $r = 0.78$, $p < 0.001$; MRDM $R^2 = 0.61$, $p < 0.001$) suggests that populations are isolated by distance irrespective of landscape features (figure 1*b*; table S2). All three statistical methods used to rank models indicated that adding a weight to the water did not explain more genetic variance in comparison with a simple IBD model (ΔAICc < 2; electronic supplementary material, table S2). Caribou are able to swim and cross up to 3-10km (Miller, 1995), rarely more (Leblond et al. 2016), but swimming is much less efficient and more energetically costly than walking on ice or land mass (see Leblond et al. (2016) and references therein). Observations of caribou trips of several hundred kilometres on sea ice are regularly recorded, up to a 380 km walk (Miller et al. 2005). We observed linear IBD, suggesting that sea ice was an effective corridor allowing connectivity among Peary caribou populations. Additionally, the differences in slope for Peary caribou and migratory tundra caribou can partially be explained by differences of population densities (CARMA, 2016, see electronic supplementary material).

Based on the time series of remote sensing detection of Arctic sea ice, our LCP analysis estimates that landscape resistance in the Canadian Arctic Archipelago increased by roughly 15% between 1979 and 2015, owing to a broader seasonal window without sea ice (figure 2). Our results indicate that the loss of sea ice will translate into an increase in landscape resistance of 20% by 2086 according to the moderate RCP4.5 emission scenario and by up to 77% according to the RCP8.5 scenario (figure 2a). This more resistant landscape may adversely affect population connectivity by hampering dispersal, annual migrations and escape from unpredictable but reoccurring episodes of severe weather (Miller et al. 2005).

In the past, the annual landscape resistance was maximal during the sea ice-free season (mostly September) and minimal the rest of the year (figure 2*b,c*). Following RCP projections, the ice-free season will increase in the future, especially according to the RCP8.5 model that predicts an increase of approximately 150% in landscape resistance from July to November (figure 2*b,c*).

For Peary caribou, a temporal and spatial shift in sea-ice extent may be adversely critical. Some caribou show fidelity to wintering and calving grounds with access based on inter-island migrations associated with land-fast sea ice (Miller et al. 2005; Jenkins and Lecomte, 2012). Although movement data are limited, spring migration has been recorded in April-June, while autumn movements occurred in September-November (Miller et al. 2005; Jenkins and Lecomte, 2012). Predicted delays in sea-ice formation or early break-up could alter or prevent such migration, with detrimental effects on calving success, body condition, or survival. In areas where anthropogenic activities have compromised sea-ice structure (*e.g.*, ice breaking transits), caribou halt migration and aggregate (along the shoreline) until freeze up occurs (Dumond et al. 2013). Hence, our connectivity estimates are conservative and probably underestimate the impact of sea-ice change on wildlife. Based solely on sea-ice occurrence, they did not include sea-ice quality or structure, which may further influence movement patterns and energetics (Jenkins and Lecomte, 2012; Sahanatien and Derocher, 2012). Compared to species (*e.g.*, Arctic fox), which can use floating sea ice, caribou may only be able to cross when sea ice is stable and continuous. Mortalities, due to drowning or exposure after breaking through ice, have been documented (COSEWIC, 2004; Poole, et al. 2010; Dumond et al. 2013). Thus over the long-term, the collapse of sea-ice connectivity could increase demographic and genetic isolation, undercutting population viability and persistence.

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FIGURES

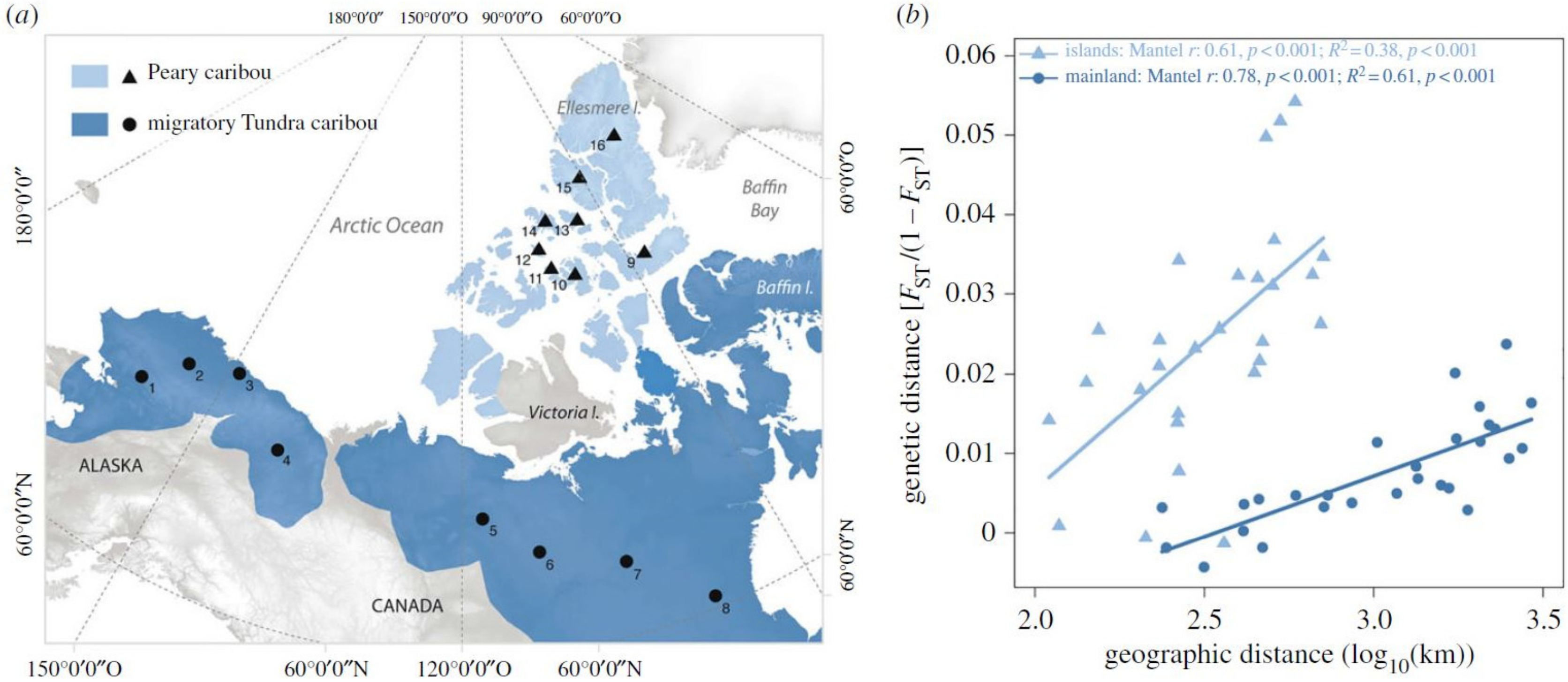

Figure 1. (a) Map of the study area. Shaded areas correspond to the range of continental –migratory tundra caribou and island-dwelling Peary caribou. (b) Correlation between genetic and geographical distances among caribou populations. Colours correspond to continental (circles; dark blue) and island herds (triangles; light blue); herds (1-16) are from Table 1.

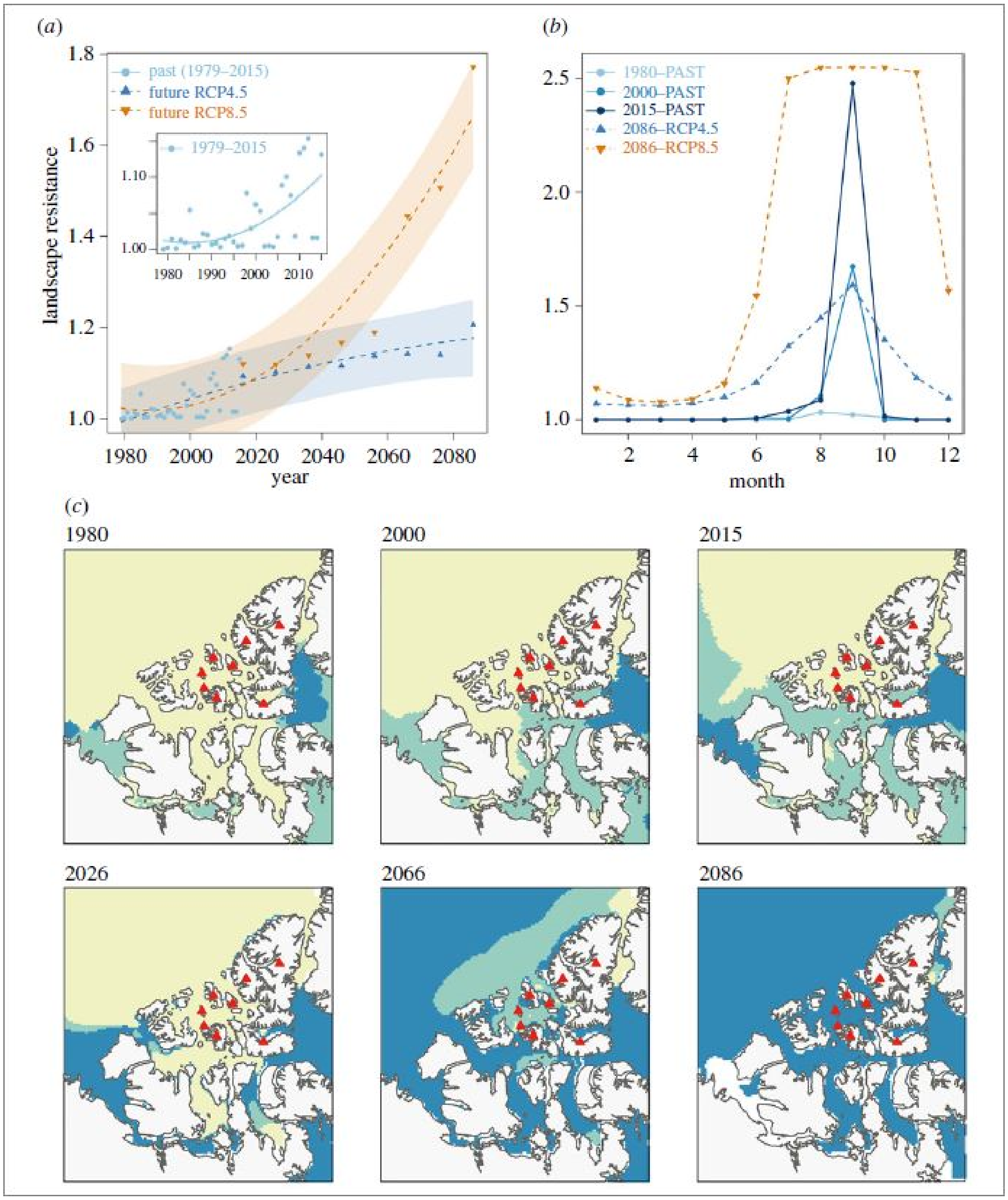

Figure 2. (a) Connectivity changes overtime in the Canadian Arctic region for the past (1979-2015) and the next 70 years following the RCP4.5 and RCP8.5 models. The inset details the connectivity trend over 1979-2015. Trend lines and 95% CI of the predicted connectivity changes are represented with solid and shaded areas, respectively; (b) monthly connectivity changes over time for selected years between 1980 and 2015 and in 2086 following the RCP8.5 and RCP4.5 models; (c) observed (past) and forecasted (future) maximum sea-ice extent in the Canadian Arctic region for selected years between

1979-2015 and 2026-2086 following the RCP8.5 models. December (blue), July (green), and September (yellow). Note that colours overlap and sea-ice extent is always at its maximum in December. Red triangles correspond to sampling locations for Peary caribou.

TABLES

Table 1. Geographical locations of continental migratory tundra and island-dwelling Peary caribou (Canada, Alaska). Herd locations identified (1-16) on Figure 1(a). Animal manipulations followed guidelines of the Canadian Council on Animal Care.

Ecotype	Herd	Province/State	Country	Lat	Long	N
Migratory tundra	Western Arctic (1)	Alaska	USA	67,52	-158,3	25[1]
	Teshekpuk (2)	Alaska	USA	69,21	-154,79	20[1]
	Central Arctic (3)	Alaska	USA	70,02	-148,95	22[1]
	Porcupine (4)	Yukon	Canada	67,67	-141,04	29[1]
	Bluenose East (5)	NW Territories	Canada	66,13	-117,85	31[1]
	Bathurst North (6)	NW Territories	Canada	64,44	-112,42	28[1]
	Ahiak/Beverly (7)	Nunavut	Canada	63,255	-104,44	50[1]
	Qamanirjuaq (8)	Nunavut	Canada	60,52	-97,94	22[1]
Peary caribou	Amund Ringnes/Cornwall Is. (13)	Nunavut	Canada	78,08	-95,86	6[2]
	Axel Heiberg Is. (15)	Nunavut	Canada	79,68	-91,20	20[2]
	Bathurst Is. Complex (10)	Nunavut	Canada	75,92	-100,17	20[2,3]
	Cameron Is. (11)	Nunavut	Canada	76,48	-103,91	22[2]
	Devon Is. (9)	Nunavut	Canada	75,44	-87,63	10[2]
	Ellef Ringnes/King Christian (14)	Nunavut	Canada	78,54	-102,29	16[2]
	Ellesmere Is. (16)	Nunavut	Canada	80,30	-78,10	41[2]
	Lougheed Is. (12)	Nunavut	Canada	77,42	-105,21	42[2]
TOTAL						404

[1](Yannic et al. 2014a); [2] this study; [3] Environment and Natural Resource. 2014. Peary caribou DNA sample collections, Bathurst Island Complex, July 1998. Unpublished Data. Government of NWT, Yellowknife, NT.

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Authors' Contributions

L.P. and G.Y. conceived the study. D.A.J., J.A.S., N.L., S.D.C. and G.Y. acquired the genetic data. S.M.O. and D.S. (polar oceanographers) provided oceanographic data. D.A.J., G.Y., and L.P analysed the data, contributed to the interpretation of the results and writing of the paper. All co-authors contributed to the text and interpretation of the results. All authors gave final approval for publication and agreed to be accountable for all aspects of the content therein.

Competing Interests

We have no competing interests.

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Supplementary Materials

LOSS OF CONNECTIVITY AMONG ISLAND-DWELLING PEARY CARIBOU FOLLOWING SEA ICE DECLINE

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This file contains additional Information on Methods and Results

Additional information on funding statement:

Partners of Caribou Ungava are ArcticNet, Natural Sciences and Engineering Research Council of Canada (NSERC), Hydro-Québec, Glencore-Mine Raglan, Fédération des Pourvoiries du Québec, CircumArctic Rangifer Monitoring & Assessment network (CARMA), Ministère du Développement durable, de l'Environnement et des Parcs du Québec (MDDEFP), Labrador and Newfoundland Wildlife Division, First Air, Makivik Corporation, Fédération québécoise des chasseurs et pêcheurs, Fondation de la Faune du Québec, Tata Steel Canada, Air Inuit, Azimut Exploration, Institute for Environmental Monitoring and Research and Canada Foundation for Innovation. High Arctic projects that provided data and samples for this research were largely funded by the Department of Environment, Government of Nunavut, Nunavut Wildlife Management Board, Polar Continental Shelf Project, Environment and Natural Resource, Government of NWT and the Canadian Wildlife Service. Thanks are also due to Parks Canada.

METHODS

Sample collection

Between 1998 and 2008 Peary caribou samples were collected across the Canadian Arctic Archipelago, primarily during aerial and ground surveys (Gunn and Dragon, 2002; Jenkins et al. 2011). These samples included caribou tissue, antler, and fecal pellets. For continental migratory tundra caribou, sampling procedures are detailed in (Yannic et al. 2014).

Genetic Data

We obtained genetic data from 404 caribou genotyped at 16 microsatellites for continental migratory caribou (Yannic et al. 2014) and for island-dwelling Peary caribou (Wildlife Genetics International, Nelson, BC. Canada). For island-dwelling Peary caribou, genotyping was performed by Wildlife Genetics International Inc. (D. Paetkau; Nelson, BC, Canada). Genomic DNA was extracted from all tissues using a QIAGEN DNeasy Blood and Tissue kit (QIAGEN Germantown, MD, USA), following manufacturer protocol. For faecal samples, a 1-hour surface wash of 1–3 pellets in QIAGEN's buffer ATL was used before extraction. Individuals were genotyped for 16 microsatellite markers: BL42, BM4513, BMS745 (Bishop et al. 1994); Rt1, Rt5, Rt6, Rt7, Rt9, Rt24, Rt27 (Wilson et al. 1997); BM6506, BMS1788 (Stone et al. 1995); CRH (Roche et al. 1998), FCB193 (Buchanan and Crawford, 1993); and OhD, OheQ (Jobin et al. 2008). PCR amplifications were carried out in a final volume of 15-µl in simplex reactions, with 50 µM of KCl Buffer, 0.1% Triton X-100, 160 µg/ml BSA, 160 µM dNTPs, 1.5-2.0 mM $MgCl_2$ and Taq polymerase. Annealing temperature ranging from 54°C to 60°C. Amplification products were run on an ABI PRISM 3100 (Applied Biosystems) automated DNA sequencer and alleles were scored using Genotyper Applied Biosystems (ABI) and error checking followed Paetkau (2003).

Pairwise F_{ST} were estimated according to Weir and Cockerham (1984) using either FSTAT v2.9.3 (Goudet, 1995, 2005) or the package '*diveRsity'* 1.9.89 (Keenan et al. 2013) implemented in R (R Development Core Team, 2016). FSTAT was also used to test for linkage disequilibrium and departure from Hardy–Weinberg equilibrium (HWE) in each sample. All tests involved in the genetic analyses mentioned here were based on 10 000 permutations. There was no significant deviation from HWE in any sample (no significant F_{IS} value) and no evidence of linkage disequilibrium after adjustments for multiple tests (Bonferroni corrections were applied).

Landscape genetics

We calculated the geodesic geographic distance between pairs of populations, based on the great circle distance using the package 'geosphere' 1.2-27 (Hijmans, 2014) of R (R Development Core Team, 2016), and according to the 'Vincenty (ellipsoid)' method. We examined the influence of seawater on connectivity based on a conductance surface using a digital elevation model available from Worldclim (www.worldcom.org) with a 1-km resolution (Hijmans et al. 2005). We used a modeling optimization approach to determine the conductance (1/resistance) of seawater (with or without ice), following a procedure described in (Shirk et al. 2010; Graves et al. 2013). Varying model parameters (here the conductance value given to seawater), this approach identifies a peak of support for the model that most highly related to genetic differentiation, *i.e.*, the model with the highest Mantel's correlation between geographic distance and genetic distance. We assigned a value of 1 to pixels on land and we gave a lower connectivity value for seawater ranging from weak (0.001) to partially permeable (0.9) values. Least-cost paths were calculated among all pairs of populations using the *costDistance* function implemented in the '*gdistance'* 1.1-4 (van Etten, 2014)] R package. Connections were allowed between all eight surrounding cells of each pixel. We also used the *CostDistance* function to calculate distances among populations on a completely 'flat landscape' based on a raster layer in which all cells had an equal value (conductance: land=1 and seawater=1). Parameter optimization indicated that a conductance value of 0.3 for seawater best fit the observed genetic data (figure S1).

Finally, following Geffen et al. (2007), we used landscape genetic models weighted for the occurrence of sea ice among sampling locations for Peary caribou to evaluate the net effect of sea ice on gene flow. We calculated sea ice occurrence probabilities among islands over the last ~35 years (1979-2015), i.e., for each pixel we estimated the number of years with sea ice/the number of years of sea ice survey. We focused on three time periods biologically relevant for caribou (March; annual peak of maximum sea ice extent; Spring [April-June] and Fall [September –November] that correspond to seasonal migration periods; see main text). We then assigned a conductance value of 1 for landmass, of 0.3 for open water (ice free water) and a probability of occurrence for sea ice, normalized between 0.3 and 1. At such latitudes, our results showed that over the past ca. 35 years, the probability of sea ice occurrence among islands was on average equal or very close to 1; so that LCP models based on sea ice occurrence were all very highly correlated to the LCP model obtained for a "flat landscape" (see Table S2). These results confirmed that sea ice has, so far, been a very effective corridor for Peary caribou.

Statistical analyses

We examined the relationships between genetic and geographic distances, using different approaches, *i.e.*, Mantel tests (Mantel, 1967), multiple regressions on distance matrices (MRDM, Legendre et al. 1994) and maximum-likelihood population-effects models (MLPE, Clarke et al. 2002). The MLPE model uses a residual covariance structure to account for the non-independence of pairwise distances (*i.e.*, each pairwise distance is associated with two populations; Legendre et al. 1994; Clarke et al. 2002), and is becoming a standard approach in landscape genetic studies (Van Strien et al. 2012; Jha, 2015; Jaffé et al. 2016; Quéméré et al. 2016). Mantel' tests and MRDMs were implemented in the R library 'ecodist' (Goslee and Urban, 2007) using 1,000 randomization to assess significance. MLPEs were fitted with REML estimation as implemented in the R package '*gls'* (Pinheiro et al. 2016), utilizing the corMLPE R package (https://github.com/nspope/corMLPE). We selected the best fixed effect models (*i.e.,* IBD vs LCP) fitted by maximum log-likelihood (ML) using the Akaike's Information Criterion for finite sample size (AICc) as implemented in the *R* package 'AICcmodavg' (Mazerolle, 2016), and calculated ΔAICc and AICc weights. Models with ΔAICc≤2 were considered equivalent (Burnham and Anderson, 2002). In addition, we calculated pseudo-R^2 values for the MLPE models with the *sem.model.fits* function of the package 'piecewiseSEM' (Lefcheck, 2015). Marginal R^2 (R^2_{M}) corresponds to the variance explained by fixed factors. We standardized all variables using a z-transformation to facilitate comparison of model parameter estimates.

Oceanographic models and climate projections

We used a dynamic numerical model to describe future oceanographic conditions. We considered the EC-Earth projection based on the EC-Earth Atmosphere Ocean General Circulation Models (AOGCMs) system, and participating in the Coupled Model Intercomparison Project Phase 5 (CMIP5). EC-Earth includes the ocean module NEMO (Nucleus for European Modeling of the Ocean) a sea ice model (LIM2), and a land surface (HTESSEL) component, coupled to the IFS atmospheric forecast system via OASIS3. The NEMO ocean configuration had a resolution of 1°×1° with a meridional refinement to 1/3° at the equator, referred to as the ORCA1 grid. We used a tri-polar grid with poles over land (Siberia, Canada, Antarctica) to avoid singularity at the North Pole. The ocean model had 42 vertical z-layers, with the finest vertical spacing in the surface layer (10m). Two emission scenarios were considered within the EC-Earth projection: the RCP4.5 and RCP8.5 scenarios (RCP stands for Representative Concentration Pathway) where the numbers 4.5 and 8.5 represent the net radiative forcing (in W/m^2) at the top of the atmosphere due to anthropogenic emissions and land-use over the period 2016-2100.

The RCP4.5 and RCP8.5 scenarios used here correspond to intermediate to high greenhouse gas emissions, respectively. They reflect a broad range of potential environmental changes and uncertainties related to the combination of scenarios and climate models under consideration. For the RCP4.5 scenario, the global average temperature warming is 2-3°C by the end of the 21st century as compared to over 4ºC for the RCP8.5 scenario.

RESULTS

Population Genetic Structure

Pairwise genetic differentiation among island-dwelling Peary caribou herds are low to moderate and range from 0.000 to 0.051 (mean±SD=0.024±0.013) and from 0.000 to 0.023 (mean±SD=0.007±0.006) for continental migratory tundra herds (Table S1 and Jenkins et al. (2016). We observed a highly supported relationship between genetic and geographic distances (*i.e.*, IBD) for the Canadian Arctic Peary caribou herds (Mantel's r: 0.61, P<0.001) and for the continental migratory tundra caribou herds (Mantel's r: 0.78, P<0.001). The slope of the relationships however differs between the two regions and is larger for the Canadian Arctic Peary caribou herds (β=0.039±0.007, t=5.87, P<0.001) in comparison to the continental migratory tundra caribou herds (β= 0.015±0.002, t=6.26, P<0.001). Assuming IBD in a two-dimensional space, the inverse of the slope of these regressions are estimates of the product $4D\pi\sigma^2$, where D is the effective population density and σ^2 is the mean squared parent–offspring distance (Rousset, 1997). If D can be independently estimated, then σ^2 gives a synthetic descriptor of dispersal that can be compared across regions (Luximon et al. 2014). The ratio of slopes between continental migratory-tundra caribou (subscript c) and island-dwelling Peary caribou (subscript i) gives $D_c\sigma_c^2 = 2.6 \times D_i\sigma_i^2$. For Peary caribou, group sizes are typically small (Festa-Bianchet et al. 2011) and the whole population size was estimated at 13,200 individuals in 2011 across the Canadian Arctic archipelago (update from COSEWIC (2004)). Given differences of population size among Peary caribou and migratory-tundra caribou, up to orders of magnitude (CARMA, 2016), we predict that the difference of slopes between data sets is partially driven by differences of effective population density D.

Table S1. Pairwise F_{ST} values among caribou herds (below diagonal) and geodesic distances (above diagonal) among caribou herds. The significance of F_{ST} was tested by permuting individuals 10,000 times among samples (non-significant pairwise F_{ST} in bold)

a) Among migratory tundra caribou (mainland)

	WesA	Tesh	CenA	Porc	BluE	Bath	AhBv	Qama
Western Arctic	--	237	469	732	1752	2063	2465	2922
Teshekpuk	**0.003**	--	244	588	1578	1893	2286	2744
Central Arctic	**-0.002**	**-0.002**	--	412	1350	1665	2053	2510
Porcupine	0.005	0.005	**0.000**	--	1024	1332	1738	2193
Bluenose East	0.012	0.006	0.007	0.011	--	316	714	1170
Bathurst North	0.011	0.003	**0.006**	0.008	**-0.004**	--	414	862
Ahiak/Beverly	0.023	0.013	0.016	0.020	**0.003**	0.004	--	458
Qamanirjuaq	0.016	0.011	0.009	0.013	**0.005**	**0.004**	**0.004**	--

b) Among Peary caribou (islands)

	ARCW	AHAH	BIBI	CACA	DIDI	ERKC	ESES	LILI
Amund Ringnes/Cornwall Is.	--	205	264	266	361	154	444	233
Axel Heiberg Is.	**0.018**	--	469	460	481	266	263	398
Bathurst Is. Complex	**0.015**	0.024	--	118	350	297	697	212
Cameron Is.	**0.008**	0.021	**0.001**	--	454	233	710	110
Devon Is.	**-0.001**	0.047	**0.025**	0.031	--	503	585	508
Ellef Ringnes/King Christian Is.	**0.025**	0.033	0.023	**0.021**	0.030	--	529	142
Ellesmere Is.	**0.020**	**0.014**	0.026	0.034	0.051	0.049	--	659
Lougheed Is.	**0.024**	0.031	**-0.001**	0.014	0.036	0.019	0.031	--

Table S2. Landscape predictors of genetic differentiation among Peary Caribou and among migratory tundra caribou. Mantel's, multiple regressions on distance matrices (MRDM), and results of linear mixed effects (MLPE) models showing the relationship between pairwise genetic distance and geographic distances. Models with ΔAICc < 2 are considered equivalent. AICc weight (ωi) are given.

		Mantel		MRDM			MLPE			AIC		
		r	p-value	β	p-value	R^2	β	p-value	R^2_M	AICc	ΔAICc	ωi
Among Peary caribou (islands)												
	Geodesic	0.61	0.003	0.61	0.003	0.38	0.58	0.002	0.39			
IBD	Flat (land=1; seawater=1)	0.63	0.002	0.63	0.001	0.39	0.60	0.001	0.39	71.54	1.1	0.37
	Sea cost (land=1; seawater=0.3)	0.64	0.001	0.64	0.001	0.41	0.58	0.001	0.41	70.44	0.0	0.63
LCP	March	0.63	0.002	0.63	0.002	0.40	0.60	0.001	0.39			
	Spring	0.63	0.002	0.63	0.002	0.40	0.60	0.001	0.39			
	Autumn	0.63	0.002	0.63	0.002	0.40	0.60	0.001	0.40			
	(land=1; seawater=0.3; sea ice=P_{occ})											
Among migratory tundra caribou (mainland)												
	Geodesic	0.78	0.005	0.78	0.003	0.61	0.79	0.001	0.54			
IBD	Flat (land=1; seawater=1)	0.77	0.004	0.77	0.004	0.59	0.78	0.001	0.54			

P_{occ} = Seasonal probability of sea ice occurrence estimated over the 1979-2015 period.

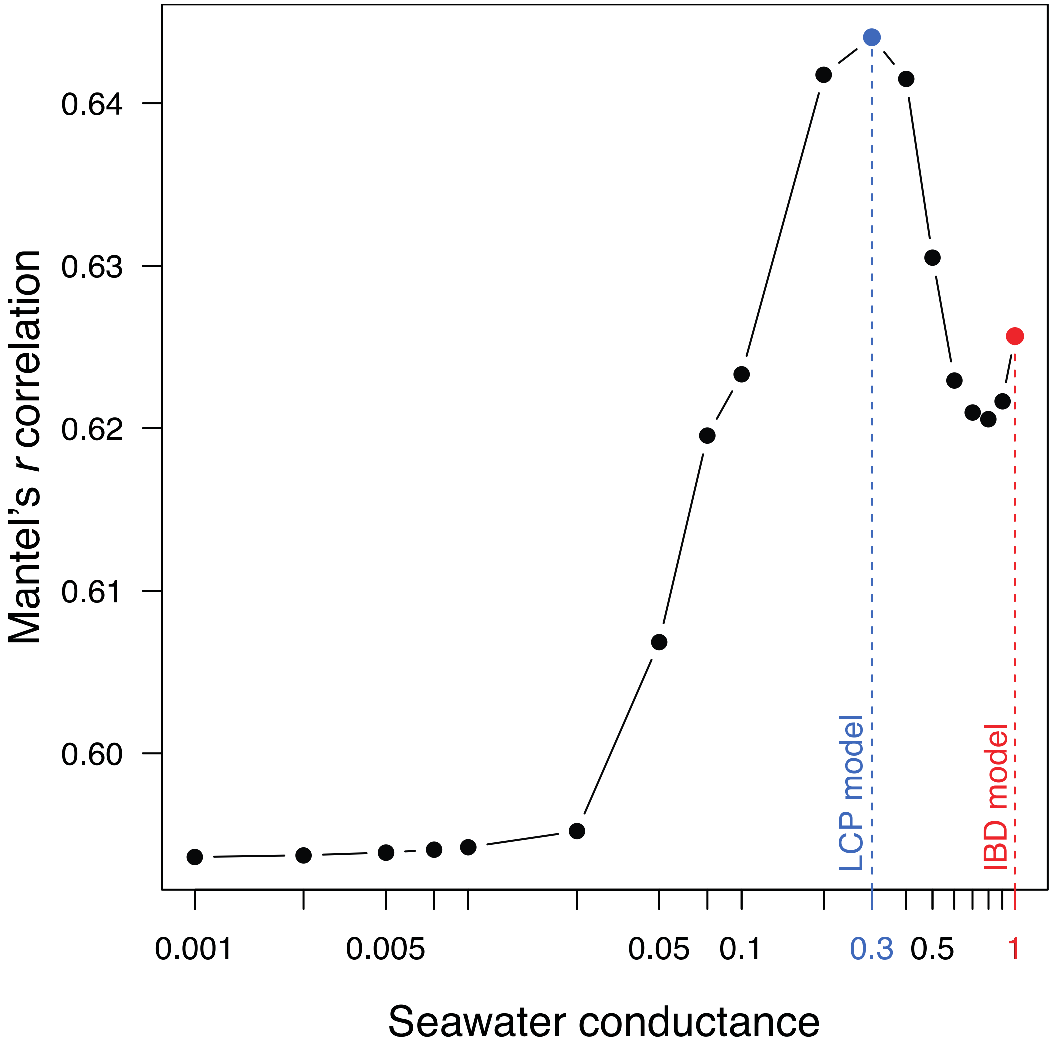

Figure S1. Hypotheses for seawater conductance indicated an optimal value of 0.3 with tested connectivity values ranging from weak (0.001) to partially permeable (0.9) raster surface.

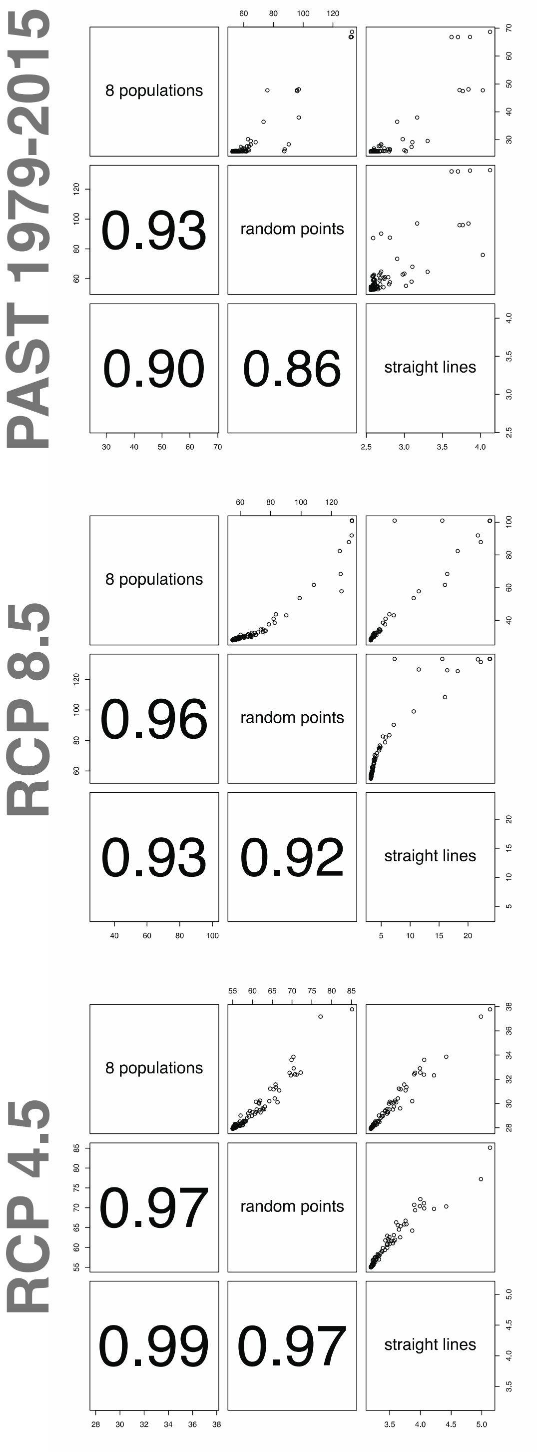

Figure S2 Correlation among LCP distances based on i) the 8 Peary caribou populations, ii) 1,000 occurrence points randomly sampled across the Peary caribou range, and iii) only considering the shortest straight lines between islands.

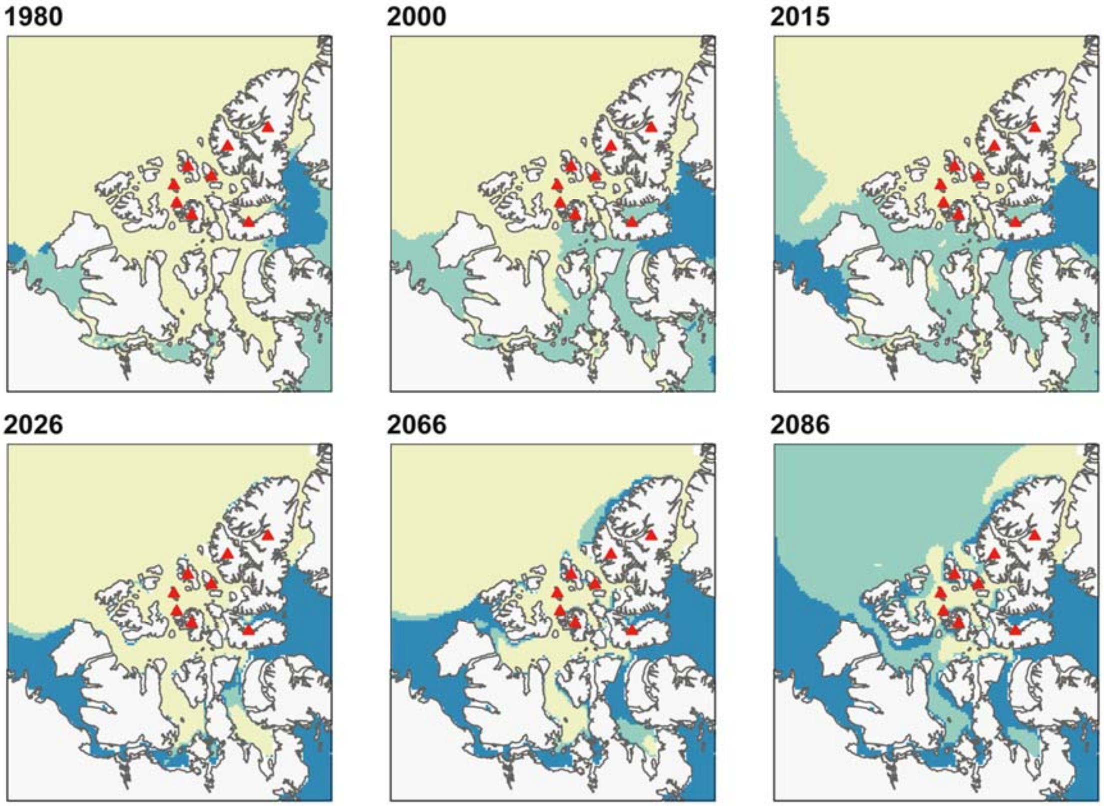

Figure S3. Observed (past) and forecasted (future) maximum sea ice extent in the Canadian Arctic region for selected years between 1979-2015 and 2026-2086 following the RCP 4.5 model. Colours correspond to December (blue), July (green), and September (yellow). Note that colours from December to September overlap and sea ice extent is always at its maximum in December.

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CHAPTER 3

POPULATION STRUCTURE OF CARIBOU IN AN ICE-BOUND ARCHIPELAGO

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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*

1. INTRODUCTION

Archipelagos provide ideal natural systems for inferring the effects of isolation and fragmentation on the genetic makeup of populations (Levin and Parker, 2012; Harradine et al., 2015). 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 and 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 et al., 2008). Remote populations may become genetically distinct and experience inbreeding and low genetic diversity (Frankham et al., 2002; Miller et al., 2011; Harradine et al., 2015; Techer et al., 2016), but they may also experience local adaptation and speciation (Slatkin, 1987; Petren et al., 2005). 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; Ryder, 1986; Moritz, 1994). These “lines” have important consequences for conservation and protection, and the scientific inferences we draw (Schaefer, 2006; Pond et al., 2016).

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 inter-island and island-mainland migrations and sporadic long-distance movements (Miller et al., 2005; Carmichael et al., 2008; Poole et al., 2010; Noren et al., 2011). Yet in the Arctic, sea ice is spatially and temporally heterogeneous (Ferguson et al., 2001; Sahanatien and Derocher, 2012; Kutschera et al., 2016); 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; Noren et al., 2011; Harris et al., 2014; Jenkins et al., 2016; 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, behaviorally and genetically variable (Serrouya et al., 2012; McFarlane et al., 2014; Yannic et al., 2014). The taxonomy of *Rangifer* is complex. This species has been variously divided into subspecies (Banfield, 1961), ecotypes (Festa-Bianchet et al., 2011; Serrouya et al., 2012; Yannic et al., 2016) and designatable units (DU: a pragmatic alternative to ESU; Green, 2005; COSEWIC, 2011). In the Canadian Arctic Archipelago, two native subspecies, Peary (*R. t. pearyi*; Allen, 1902) and barren-ground caribou (*R. t. groendlandicus*; Borowski, 1780), represent three DUs (COSEWIC, 2011; Figure 1) and encompass multiple herds or geographic populations (COSEWIC, 2011; Jenkins et al., 2011; Nagy et al., 2011). Some herds have recently declined (Jenkins et al., 2012); some are likely extirpated (Gunn et al., 2006; COSEWIC, 2015a,b); and others have recovered through reintroductions or translocations (Ferguson, 1985; Heard and 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 et al., 2010). In keeping with caribou, the world's most vagile terrestrial animal (Kelt and Van Vuren, 2001), our study extended across an immense geographic range: twenty 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^2) 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 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 and Hillis, 1998), insular or tundra wintering herds (Baffin and Southampton islands; Mallory and Hill, 1998; Festa-Bianchet et al., 2011; Jenkins et al., 2012), and the Dolphin and Union mainland-migrating herd (Nagy et al., 2011; Dumond et al., 2013). In addition, Southampton caribou were reintroduced from nearby Coats Island (1967; Heard and 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 1998-2012 during aerial and ground surveys (Gunn and Dragon, 2002; Miller and Gunn, 2003; Jenkins et al., 2011; Jenkins et al., 2012), 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 et al., 2012a; Serrouya et al., 2012b). 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 Lougheed 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^{TM} Blood and Tissue Kit (Qiagen, Inc., Valencia, CA, USA) following the manufacturer's protocol. For faecal samples, the buffer recovered after a 1-hour 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^2 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, BM6506 (bovine; Bisho et al., 1994), BMS745, BMS1788 (bovine; Stone et al., 1995), CRH (bovine; Moore et al., 1992), FCB193 (Ovine; Buchanan et al., 1994), OhemD, OhemQ (deer; Jones et al., 2000), and Rt1, Rt5, Rt6, Rt7, Rt9, Rt24, Rt27 (caribou; Wilson et al., 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 ug/ml BSA, 160uM dNTPs, 160 nM of each primer, and 1.5 - 2.0 mg of $MgCl_2$ in a sample volume of 15ul. 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-color sequence detection system on a 310 automated sequencer (Applied Biosystems). Loci were analyzed 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 et al., 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 and Rousset, 1995; Rousset, 2008). For multiple tests, we adjusted error rates using sequential Bonferroni correction (McLaughlin and Sainani, 2014).

Using GENALEX 6.5 (Peakall and Smouse, 2006), we estimated the mean number of alleles (Na), 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 et al., 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 Fst (Weir and 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 et al., 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 'adegenet' 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 et al., 2010). We first used STRUCTURE 2.3.3 (Pritchard et al., 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 [LnP(D)] were extracted for further analysis. We used STRUCTURE HARVESTER v0.6.94 (Earl and vonHoldt, 2012) to generate mean likelihood scores for each K and implement the ΔK Evanno method (Evanno et al., 2005). For each K, individuals were assigned to a cluster based on their highest percentage of membership (q), provided this value was ≥ 0.5; membership coefficients (q) were calculated using the greedy algorithm with 10,000 repeats in CLUMMP 1.1.1 (Jakobsson and 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, ΔK 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 (Rowe and Beebee, 2007; Hagerty and Tracy, 2010; Glass et al., 2015).

Next, we evaluated hierarchical structure by incorporating spatial information with multilocus genotype data using TESS 2.3 (Chen et al., 2007; Durand et al., 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 and Durand, 2010). We performed 15 independent simulations for different maximum numbers of genetic clusters ($2 \leq \text{Kmax} \leq 10$) 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 Kmax, 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 Kmax. Using CLUMMP, the admixture coefficient was averaged across runs for each Kmax (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 (Durand et al., 2009; Basto et al., 2016). After the first run in TESS, analyses were repeated using the above methods ($2 \leq \text{Kmax} \leq 5$) 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 et al., 2017). We built models using individual heterozygosity (HLE) as the response variable. HLE was calculated using the homozygosity index in CERNICALIN V.1 (Aparicio et al., 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 and Reyer, 2011), population size (log transformed), island area, glacier-free island area (Frankham, 1996, 1997), distance-to-mainland (Frankham, 1997; Eckert et al., 2008), subspecies, average annual, spring and fall ice-free coastline (Geffen et al., 2007; Post et al., 2013), and maximum island elevation (Ally et al., 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 et al., 2010) and removed correlated variables ($|r| \geq 0.7$). 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 et al., 2013) using the ‘MuMln’ 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 Fis 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 3.93-4.48 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 χ^2= 76.22, df = 16, p <0.001). 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 ± 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 = 0.71, $p<0.001$; Figure 3a) – a relationship also evident in Peary caribou (F_{ST} - Mantel r = 0.61, $p<0.001$; 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 Qamanijuaq 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 (Kmax = 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) 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, $p < 0.001$; TESS - Kruskal-Wallis $\chi^2 = 77.869$, df = 8, $p < 0.001$). The Qamanirjuaq and Dolphin and Union clusters demonstrated significantly higher diversity than most others. Significant Fis 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} ($p < 0.05$; 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 et al., 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 Klutsch et al. (2017) who established that Peary caribou likely evolved in a separate High Arctic 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 et al., 2010).

Including historical samples can be tricky but informative. Time can add an additional layer of consideration when interpreting cluster results (Taylor et al., 2012; Zigouris et al., 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 et al., 1989) to address the near-extirpation of Peary caribou from southern portions of their range (Gunn et al., 2006; COSEWIC 2015).

The diversity and future of peripheral populations are of increasing interest (Safriel et al., 1994; Brzosko et al., 2009), as mounting environmental change underscores the evolutionary value of such populations (Lesica and Allendorf, 1995; Sexton et al., 2009; Volis et al., 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 (Jenkins et al., 2012; Campbell et al., 2015) with no direct evidence of island-mainland movements (Manning 1943; COSEWIC, 2011; Jenkins et al., 2012). 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 et al., 2016) although a number of factors, including founder group size, initial diversity and connectivity are important (IUCN, 2013; Andersen et al., 2014; Szucs et al., 2017). Our analyses – PCA, Bayesian analysis and pairwise F_{ST} – converged to establish Southampton Island as the most genetically distinct population (Serrouya et al., 2012a; McFarlane et al., 2016). 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 (Coulon et al., 2008; Ball et al., 2010; 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 et al., 1996); various Australian macropodids (Eldridge et al., 2004); North American gray wolf, *Canis lupus*, (Carmichael et al., 2008); *Ornithorhynchus anatinus* (Furlan et al., 2012); and Svalbard reindeer (Côté et al., 2002). Nevertheless, if immigration is high, island populations may still be genetically diverse (Pemberton et al., 1996; Carmichael et al., 2007; 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 constraint population densities, which are 1-2 orders of magnitude lower than elsewhere in the species range (Schaefer and Mahoney, 2003; Jenkins et al., 2011); 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 and 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 and Wilson, 1967), including studies of the genetics of island-dwelling vertebrates (Vellend, 2003, 2005; Stronen et al., 2014; Harradine et al., 2015). Positive correlations between island area and genetic diversity are commonplace (Cheylan et al., 1998; White and Searle, 2007), including our study. Additionally, Dolphin and Union and mainland Qamanijuaq 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 (Zittlau, 2004; McFarlane et al., 2014, 2016; Jenkins et al. 2016; Yannic et al., 2017). 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 (Poole et al. 2010; Dumond et al., 2013).

For island caribou, sea ice is the corridor that facilitates movement (Jenkins et al., 2016). Indeed, like Arctic foxes (Geffen et al., 2007; Carmichael et al., 2008), 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).

4.2 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 (Figure 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 et al., 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 et al., 2010) – particularly for uncovering biological patterns pertinent to conservation, now and for the future.

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FIGURES

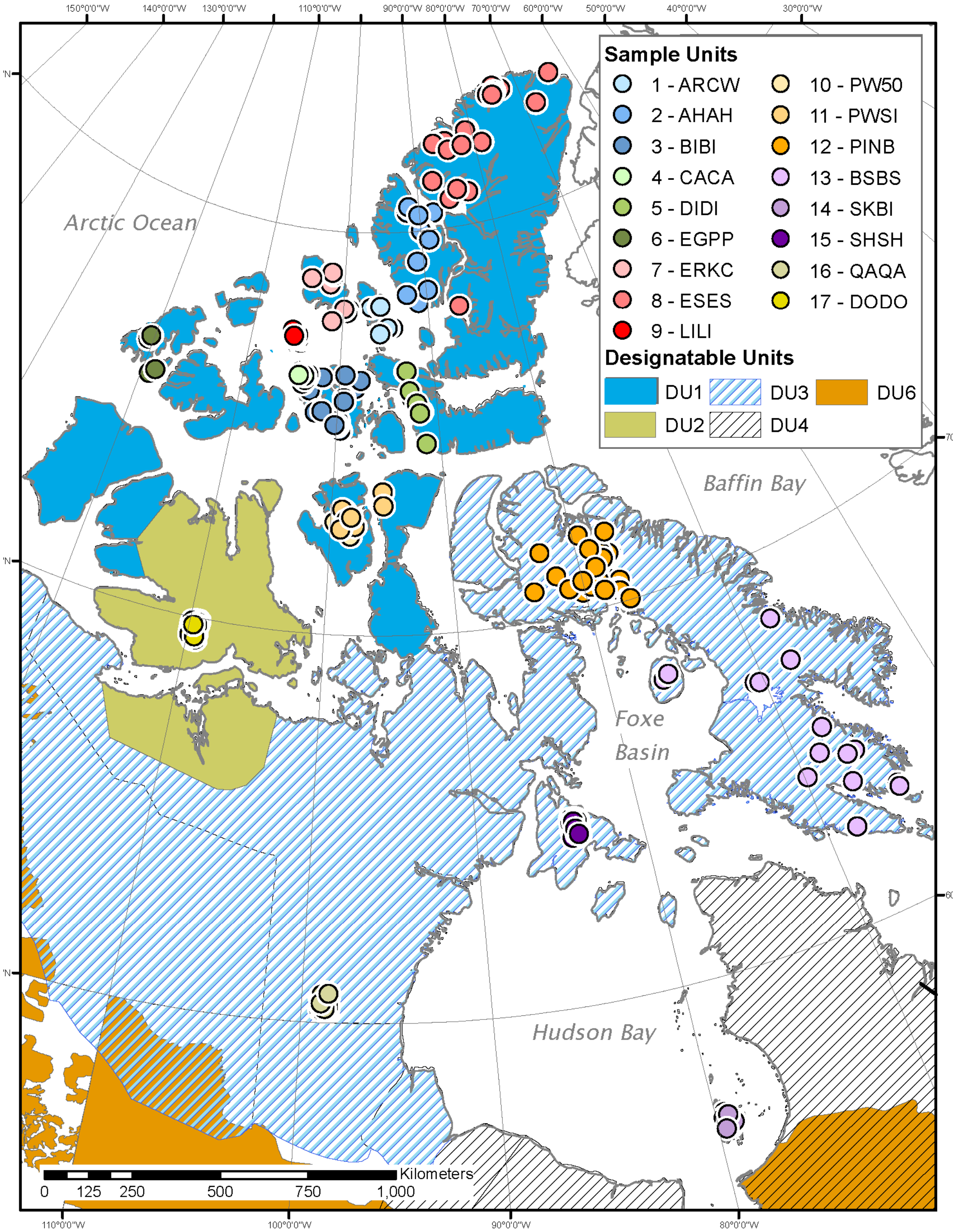

Figure 1. Distribution of 447 caribou samples across the Arctic Archipelago and mainland Canada, representing two native subspecies and three designatable units (DUs; COSEWIC, 2011). Sample unit designations are from Table 1. The map projection is Canada Lambert Conformal Conic

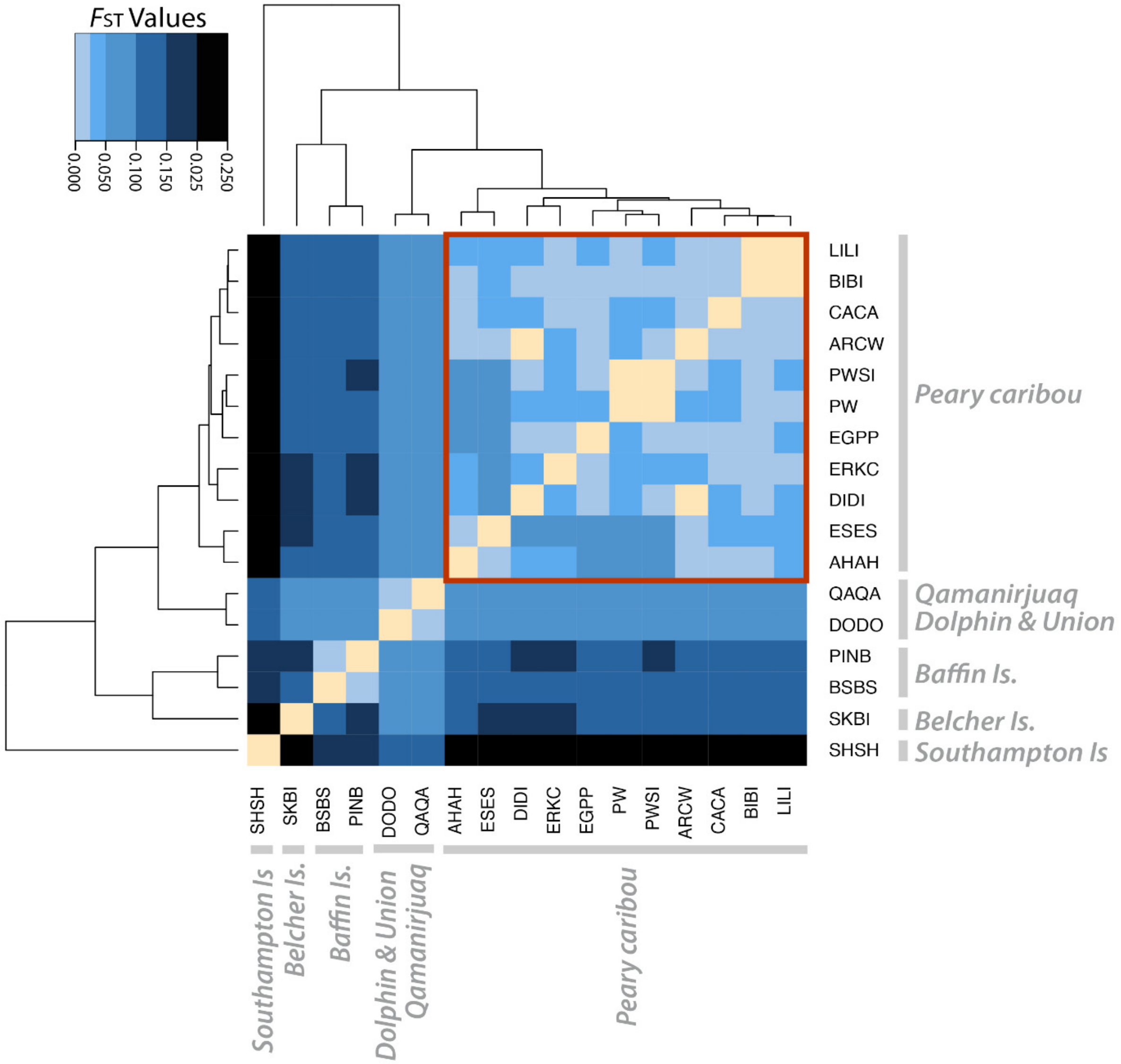

Figure 2. Pairwise F_{ST} heatmap and dendrogram based on F_{ST} values among the 17 caribou sampling locations, Arctic Canada (n = 447). The heatmap colour code represent the F_{ST} matrix considering different discrete F_{ST} groups from low to high genetic differentiation: $F_{ST} < 0.001$ (yellow); $0.001 \leq F_{ST} < 0.025$, $0.025 \leq F_{ST} < 0.05$, $0.05 \leq F_{ST} < 0.10$, $0.10 \leq F_{ST} < 0.15$, $0.15 \leq F_{ST} < 0.20$ and $0.20 \leq F_{ST} < 0.25$ (shades of blue).

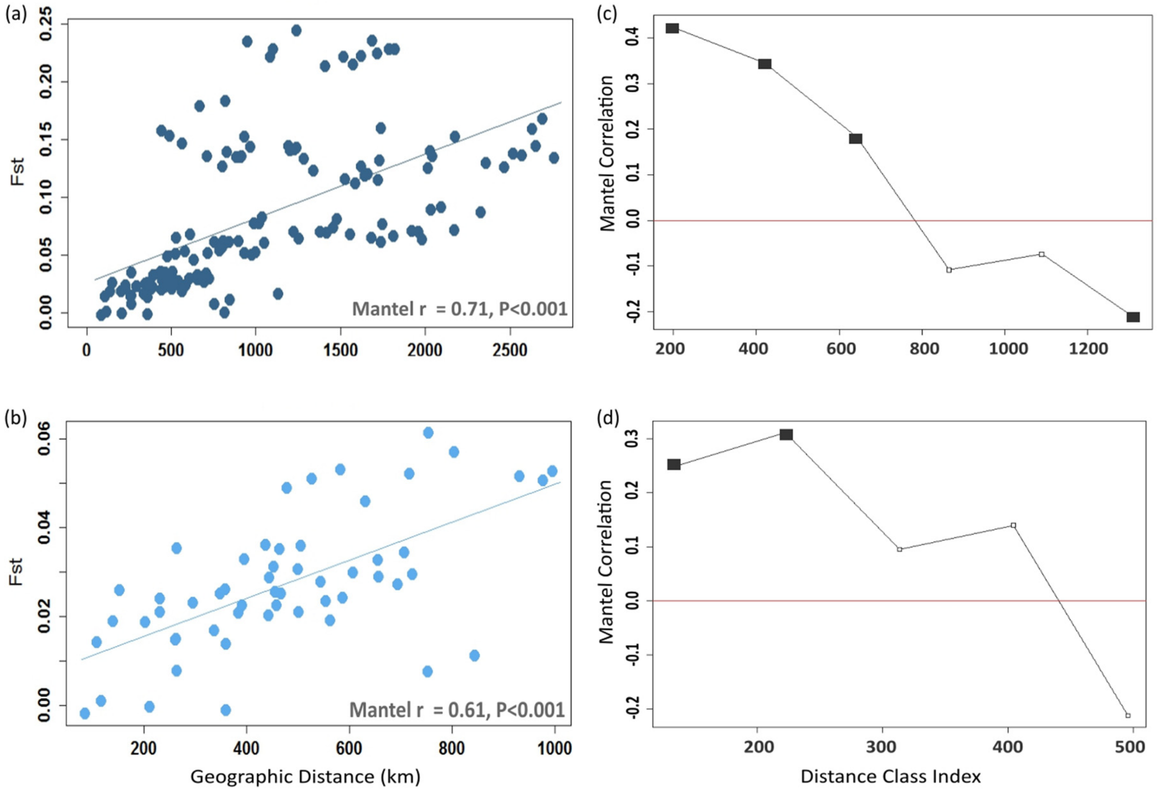

Figure 3. Correlation between genetic and geographic distances among (a) all 17 caribou units (n = 447) and (b) Peary caribou, Arctic Canada, (n = 208). Corresponding Mantel correlograms (c and d, respectively) identify Mantel *r* statistic at each distance class; black squares denote those that are statistically significant ($p \leq 0.05$).

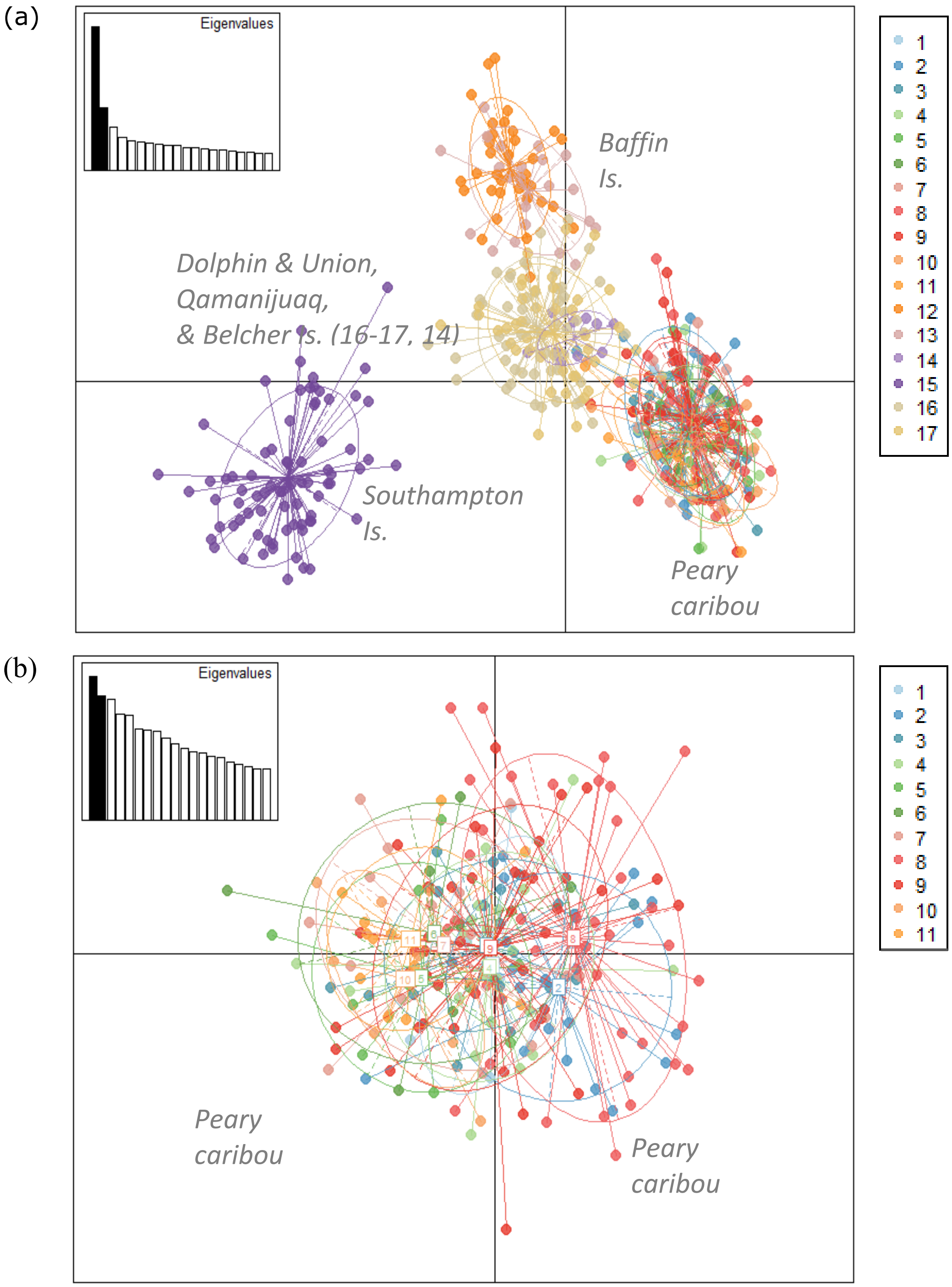

Figure 4. Caribou cluster analyses, Arctic Canada. a) Using all caribou (n = 447), principal component analysis (PCA) highlights four primary clusters, where axes 1 & 2 separate Southampton Island caribou, Peary caribou, and Baffin Island caribou from the remaining herds. Eigenvalues were 0.82 for axis 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.

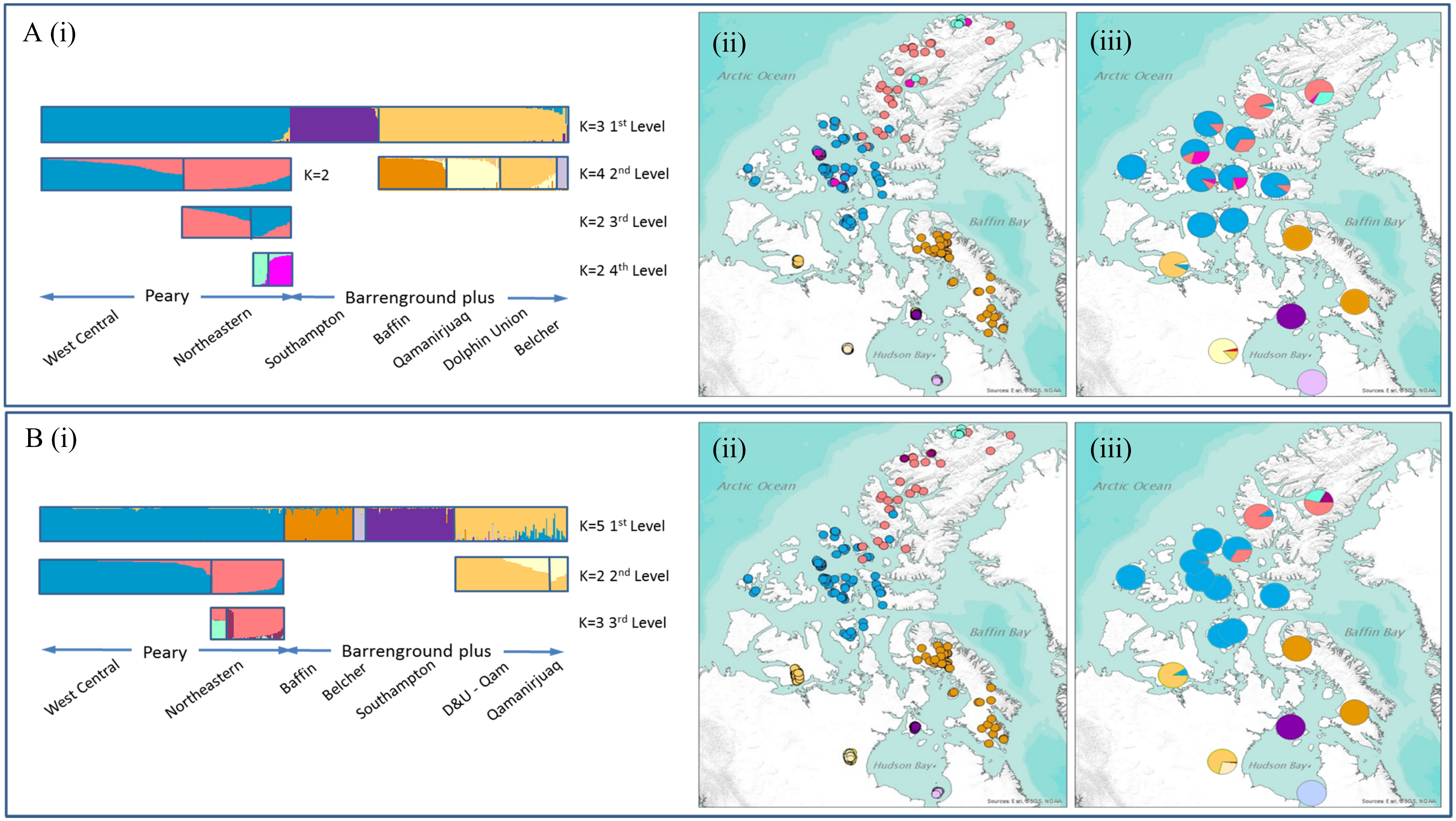

Figure 5. Assignment of 447 Canadian Arctic caribou, using hierarchical Bayesian cluster analysis with the program STRUCTURE (Pritchard et al. 2000; A) and TESS (Chen et al., 2007; B). Bar plots (i) show the assignment of individuals through multiple hierarchical levels of analysis, revealing nine genetic 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.

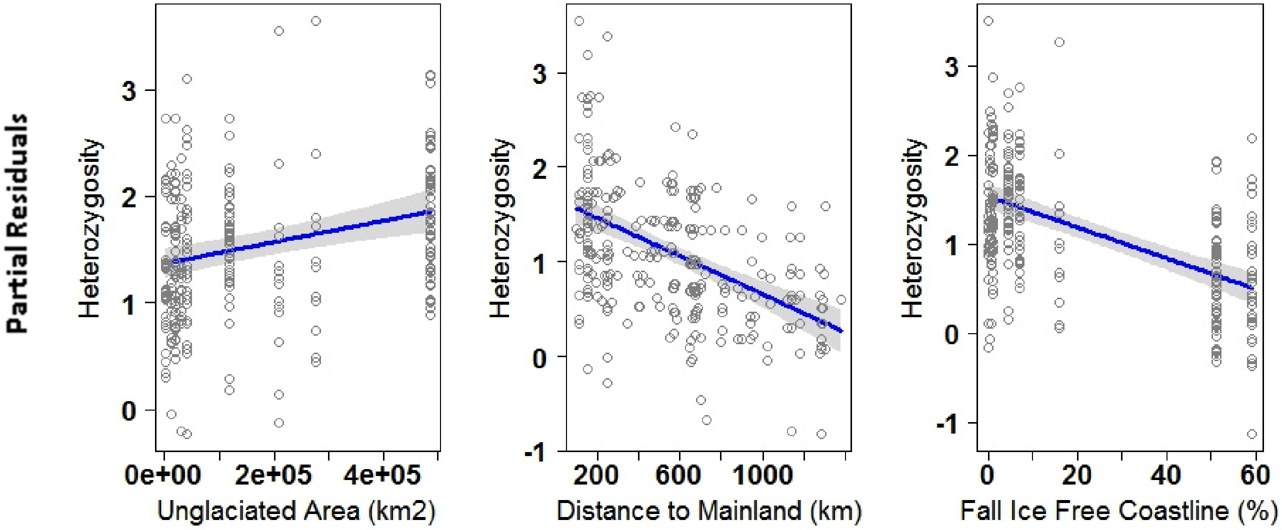

Figure 6. Plots illustrate our best linear mixed effects model (LME) explaining genetic diversity (individual level heterozygosity), showing the prediction line (blue), confidence band (grey), and partial residuals for each variable. Variables are described in Table S2.

TABLES

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	*R. t. pearyi*	Island Tundra Wintering	-95.86	78.08	6	2007
2	Axel Heigberg Is.	AHAH	*R. t. pearyi*	Island Tundra Wintering	-91.20	79.68	20	2007
3	Bathurst Is. Complex	BIBI	*R. t. pearyi*	Island Tundra Wintering	-100.18	75.92	20	2000-03**
4	Cameron Is.	CACA	*R. t. pearyi*	Island Tundra Wintering	-103.91	76.48	22	1998-2003
5	Devon Is.	DIDI	*R. t. pearyi*	Island Tundra Wintering	-87.63	75.44	10	2002-03
6	Eglinton/Prince Patrick Is.	EGPP	*R. t. pearyi*	Island Tundra Wintering	-119.02	76.55	8	1975
7	Ellef Ringnes/King Christian	ERKC	*R. t. pearyi*	Island Tundra Wintering	-102.29	78.54	16	2007
8	Ellesmere Is.	ESES	*R. t. pearyi*	Island Tundra Wintering	-78.10	80.30	41	2006
9	Lougheed Is.	LILI	*R. t. pearyi*	Island Tundra Wintering	-105.21	77.42	42	2007
10	Prince of Wales Is.	PW50	*R. t. pearyi*	Island Tundra Wintering	-99.10	72.68	10	1950s
11	Prince of Wales/Somerset Is.	PWSI	*R. t. pearyi*	Island Tundra Wintering	-96.74	73.02	13	1975
12	North Baffin	PINB	*R. t. groenlandicus*	Island Tundra Wintering	-82.83	71.69	36	2008-13
13	South Baffin	BSBS	*R. t. groenlandicus*	Island Tundra Wintering	-70.38	65.88	22	2009-12
14	Belcher Is.	SKBI	*R. t. tarandus**	Island Tundra Wintering	-79.66	56.14	10	2009
15	Southampton Is.	SHSH	*R. t. groenlandicus**	Island Tundra Wintering	-84.25	64.36	76	***
16	Qamanirjuaq Herd	QAQA	*R. t. groenlandicus*	Mainland Migratory Tundra	-99.05	60.29	52	***
17	Dolphin & Union Herd	DODO	*R. t. groenlandicus*	Island-Mainland Migratory	-109.83	69.43	43	***

* Introduced or reintroduced. ** Environment and Natural Resources. 2014. Peary caribou DNA sample collections, Bathurst Island Complex, July 1998. Unpublished Data. Government of NWT, Yellowknife, NT. *** Serrouya, R., Paetkau, D., McLellan, B.N., Boutin, S., Jenkins, D.A., and 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, http://dx.doi.org/10.5061/dryad.250c3s47

Note: 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

Table 2: Estimates of genetic diversity, number of genotypes (N), mean number of alleles per locus (Na), observed heterozygosity (Ho), 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 (Fis). Sample unit IDs as in Table 1.

Sample Unit	**N**	**Na**	**Ho**	**H_E**	**uH_E**	**A_R**	**A_P**	**Fis**	
ARCW	6	4.06	0.68	0.65	0.71	4.06	0.04	-0.04	NS
AHAH	20	5.63	0.67	0.69	0.71	4.26	0.01	0.03	NS
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	NS
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	NS
ESES	41	5.19	0.67	0.69	0.69	4.01	0.03	0.02	NS
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	NS
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	NS
BSBS	22	7.69	0.69	0.71	0.73	4.82	0.18	0.03	NS
SKBI	10	5.25	0.65	0.70	0.74	4.46	0.55	0.08	NS
SHSH	76	6.19	0.66	0.67	0.67	3.71	0.36	0.01	NS
QAQA	52	14.38	0.85	0.86	0.87	6.84	0.74	0.02	NS
DODO	43	10.19	0.84	0.83	0.84	6.07	0.48	-0.02	NS

Note: A_R and A_P are based on the minimum sample size of 6 diploid individuals. * Significantly different from 0 based on 10000 bootstrap 95% confidence intervals

Table 3. Best four linear mixed effects models of logit transformed individual heterozygosity based on biogeographic predictors with sample unit as random effect[a]. K is the number of parameters, AICc is the corrected Akaike Information Criteria, ΔAICc is the difference between the model AICc and the best model AICc, and AICcWt is the Akaike weight.

Ranked Models	**Predictors**[b]	**K**	**AICc**	**ΔAICc**	**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

[a] Similar results were generated when clusters from STRUCTURE and TESS were substituted as the random effect (unpublished; this study).

[b] UnglacArea = unglaciated island size (km^2), NearDis_Km = distance-to-mainland (km), Fall_Open_C = average fall ice-free coastline (%)

Table 4. Estimate of fixed effects produced by the best linear mixed model of individual heterozygosity with sample unit as the random effect (standard deviation: 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^2m) and 0.296 (R^2c), respectively.

Model	**Estimate**	**SE**	**95% CI**	
Intercept	**1.74**	1.05×10^{-1}	1.54	1.95
UnglacArea	**1.00×10^{-6}**	2.5×10^{-7}	4.2×10^{-7}	1.57×10^{-6}
NearDis_Km	**-1.00×10^{-3}**	1.3×10^{-4}	-1.27×10^{-3}	-7.44×10^{-4}
Fall_Open_C	**-1.73×10^{-2}**	1.9×10^{-3}	-2.18×10^{-2}	-1.29×10^{-2}

UnglacArea = unglaciated island size (km^2), NearDis_Km = distance to mainland (km), Fall_Open_C = average fall ice-free coastline (%)

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Data Accessibility

Genetic data for Southampton Island, Dolphin & Union, and Qamanijuaq caribou are available from DRYAD; Serrouya 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.

Author contributions

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

Competing interests

We have no competing interests.

Supplementary Materials

Population structure of caribou in an ice bound archipelago

Jenkins et al. 2018

This file contains additional information on Methods and Results

Table 1s. Conditions for PCR

Locus	**Dye**	**Primer 1**	**Primer 2**	**Genbank Accession #**	**Reference**
Rt1	HEX	TGC CTT CTT TCA TCC AAC AA	AGA CCC ATC TTC CCA TCC TCT T	U90737.1	Wilson et al. 1997
RT5	FAM	CAG CAT AAT TCT GAC AAG TG	GTT GAG GGG ACT CGA CTG	U90738	Wilson et al. 1997
RT6	FAM	TTC CTC TTA CTC ATT CTT GG	GTC GGA TTT TGA GAC TGT TAC	U90739.1	Wilson et al. 1997
Rt7	TET	CCT GTT CTA CTC TTC TTC TC	ACT TTT CAC GGG CAC TGG TT	U90740.1	Wilson et al. 1997
Rt9	TET	TGA AGT TTA ATT TCC ACT CT	CAG TCA CTT TCA TCC CAC AT	U90741.1	Wilson et al. 1997
Rt24	FAM	CAG TTT AAC CAG TCC TCT GTG	GTG TAT CCA TCT GGA AGA TTT CAG	U90746	Wilson et al. 1997
Rt27	HEX	TTG TAA CAC AGC AAA AGC ATT	CCA AAG ACC CAA CAG ATG	U90748.1	Wilson et al. 1997
BL42	TET	GCA TTT TTG TGT TAA TTT CAT GC	ACA AGT CAA GGT CAA GTC CAA ATG CC	EU009439.1	Bishop et al. 1994
BM4513	TET	TCA GCA ATT CAG TAC ATC ACC C	GCG CAA GTT TCC TCA TGC	G18507.1	Bishop et al. 1994
BM6506	HEX	GTG GTA AAG AGA TGG CAT AGC A	AAC TTA GCA ACT TGA GCA TGG	G18455.1	Bishop et al. 1994
BMS1788	HEX	ATT CAT ATC TAC GTC CAG ATT CAG ATT TCT TG	GGA GAG GAA TCT TGC AAA GG	G18700.1	Stone et al. 1995 [1]
BMS745	HEX	AG GGA CTT GTT ACC CGT GG	TGC AAG CTG TGA GGA GGA G	G18744.1	Stone et al. 1995[2]
CRH	FAM	CTC GCT CAC CTG CAG AAG CAC C	GCT GAG CAG CCG TCT AAG TTT GC	M22853	Moore et al. 1992; (Roche et al. 1998)
FCB193	HEX	TTC ATC TCA GAC TGG GAT TCA GAA AGG C	GCT TGG AAA TAA CCC TCC TGC ATC CC	L01533.1	Buchannan and Crawford, 1993
OhemD	TET	TTG CTG CTT GCT TGT CTA AT	AGA GCC TCG TCT TTT CAT TC	F102247.1	Jones et al. 2000; (Levine et al. 2000)
OhemQ	HEX	AGA CCT GAT TAC AAT GTG TCA GTG AAG GTC TTC	GAT GGA CCC ATC CAG GCA ACC ATC TAG	AF102241.1	Jones et al. 2000; (Levine et al. 2000[3])

[1] added 10 bases to the 5' end of primer 1 (w536) for sequencer lane efficiency, [2]modified primer 1 from Stone et al. 1995 & [3]both primers from Levine et al. 2000

Table 2s. Description of the ecological and geographic variables used in our study

Independent Variable	**Description**	**Supporting Reference/Info**
Latitude_U (WGS84)	Measured in the field using GPS units; for samples with no location, we used the center point of the island/range, which was extracted in ArcMap.	Miraldo et al. 2016
Longitude_U (WGS84)	See Above	
PopSize	The estimated population size as identified in the literature for the time period closest to the sample collection date.	Frankham 1996
LogPop	Log transformed population size	Frankham 1996
IslandArea (km^2)	The estimated area of the island (or population range) determined from the literature. For Qamanirjuaq caribou, the population range was used.	Frankham 1996
Unglac Area (km^2)	The estimated unglaciated area of the study islands, calculated by subtracting the glaciated areas (determined in GIS) from estimated island size.	Jenkins et al. 2011
NearDis (km)	Straight line geographic distance from each sample location to the mainland coast; calculated in ArcMap	Frankham 1996
Annual_Open_C (%)	Using monthly sea ice extent raster data (1995- 2010), we measured the ice free coastline for each month across 15 years in ArcMap, calculated the 15 year average ice free coast, divided it by the length of the island coast, and multiplied by 100.	Sea Ice Index, National Snow and Ice Data Center
Spri_Open_C (%)	Using sea ice extent raster data for April-June (1995-2010), we measured the ice free coastline for each month across 15 years in ArcMap, calculated the 15 year average spring ice free coast, divided it by the length of the island coast, and multiplied by 100.	Sea Ice Index, National Snow and Ice Data Center
Fall_Open_C (%)	Using sea ice extent raster data for Sept – Nov (1995-2010), we measured the ice free coastline for each month across 15 years in ArcMap, calculated the 15 year average fall ice free coast, divided it by the length of the island coast, and multiplied by 100.	Sea Ice Index, National Snow and Ice Data Center
Max_Elevation (m)	As an index of ruggedness, the maximum elevation for each sample unit was calculated in ArcMap using DEM and geoprocessing tools.	
Subspecies	Peary, Barrenground (BG), BG Introduced	

Table 3s. For each locus, the sample size (N), number of different alleles (Na), observed heterozygosity (Ho), and expected heterozygosity (He), calculated globally and across sample units.

Loci	**Global**				**Across Sample Units (mean)**			
	N	**Na**	**Ho**	**He**	**N**	**Na**	**Ho**	**He**
BM4513	476	21	0.809	0.910	26.4	8.3	0.809	0.796
BMS745	477	11	0.683	0.781	26.5	4.7	0.681	0.677
Rt5	477	17	0.683	0.832	26.5	6.1	0.665	0.670
Rt7	476	13	0.670	0.758	26.4	5.1	0.607	0.596
Rt1	477	14	0.803	0.886	26.5	7.7	0.818	0.776
Rt24	477	16	0.625	0.824	26.5	6.1	0.636	0.658
Rt27	477	16	0.763	0.804	26.5	6.1	0.708	0.685
BL42	477	24	0.686	0.741	26.5	6.3	0.666	0.675
BM6506	473	14	0.738	0.860	26.3	6.2	0.744	0.704
BMS1788	477	22	0.811	0.875	26.5	7.6	0.829	0.787
CRH	473	22	0.778	0.837	26.3	6.9	0.779	0.749
FCB193	476	10	0.679	0.777	26.4	5.6	0.636	0.633
OhD	477	14	0.748	0.833	26.5	6.6	0.738	0.717
Rt6	476	14	0.731	0.824	26.4	6.8	0.704	0.720
Rt9	477	14	0.757	0.840	26.5	6.1	0.728	0.739
OheQ	464	20	0.739	0.879	25.8	7.3	0.751	0.735
Grand Mean	475.4	16.4	0.731	0.829	26.4	6.5	0.719	0.707

Table 4s. F-statistics and estimates of gene flow (Nm) over all sampling regions for each locus.

	Fis	**Fit**	**Fst**	**Nm**
BM4513	-0.016	0.101	0.116	1.912
BMS745	-0.005	0.102	0.106	2.105
Rt5	0.008	0.167	0.160	1.308
Rt7	-0.019	0.114	0.130	1.672
Rt1	-0.055	0.067	0.116	1.910
Rt24	0.033	0.198	0.170	1.216
Rt27	-0.034	0.077	0.107	2.080
BL42	0.013	0.108	0.096	2.355
BM6506	-0.057	0.097	0.146	1.466
BMS1788	-0.054	0.034	0.083	2.767
CRH	-0.039	0.049	0.084	2.709
FCB193	-0.004	0.121	0.125	1.751
OhD	-0.030	0.082	0.109	2.054
Rt6	0.023	0.127	0.107	2.087
Rt9	0.016	0.108	0.094	2.402
OheQ	-0.021	0.126	0.145	1.476
Mean	-0.015	0.105	0.118	1.954
SE	0.007	0.010	0.006	0.116

Table 5s. Mean and standard deviation of individual admixture, by cluster and level of analysis in STRUCTURE.

Level 1, All, K=3

Cluster	S_1	s.d.	S_2	s.d.	S_3	s.d.
Southampton - SH	**0.98**	0.05	0.01	0.05	0.00	0.01
Barrenground - BG	0.01	0.05	**0.96**	0.07	0.03	0.05
Peary caribou - PC	0.00	0.01	0.01	0.04	**0.98**	0.05

Level 2, BG, K=4

Cluster	S_1	s.d.	S_2	s.d.	S_3	s.d.	S_4	s.d.
Baffin Island	**0.94**	0.07	0.03	0.04	0.02	0.03	0.01	0.02
Qamanirjuaq	0.02	0.04	**0.90**	0.09	0.06	0.07	0.02	0.03
Dolphin & Union	0.03	0.05	0.10	0.12	**0.85**	0.14	0.01	0.02
Belcher Island	0.00	0.00	0.03	0.05	0.02	0.03	**0.94**	0.08

Level 2, PC, K=2

Cluster	S_1	s.d.	S_2	s.d.
West-central	**0.80**	0.15	0.20	0.15
Northeastern	0.16	0.13	**0.84**	0.13

Level 3, PC-Northeastern, K=2

Cluster	S_1	s.d.	S_2	s.d.
PC Northeastern	**0.77**	0.12	0.23	0.12
Ellesmere plus	0.24	0.15	**0.76**	0.15

Level 4, Ellesmere plus, K=2

Cluster	S_1	s.d.	S_2	s.d.
Ellesmere & WC	**0.92**	0.06	0.08	0.06
Ellesmere - Marvin Pen.	0.12	0.05	**0.88**	0.04

Table 6s. Mean and standard deviation of individual admixture, by cluster and level of analysis in TESS.

Level 1, All, K=5

Cluster	S_1	s.d.	S_2	s.d.	S_3	s.d.	S_4	s.d.	S_5	s.d.
Peary	0.00	0.01	0.00	0.00	0.00	0.01	**0.98**	0.05	0.01	0.05
Baffin Island	0.01	0.02	0.00	0.00	**0.95**	0.06	0.03	0.05	0.00	0.00
Southampton	**0.98**	0.06	0.00	0.00	0.01	0.03	0.00	0.01	0.01	0.03
Qam - D&U	0.03	0.04	0.02	0.04	0.01	0.03	0.09	0.12	**0.85**	0.11
Belcher Island	0.00	0.00	**0.97**	0.05	0.00	0.00	0.00	0.00	0.02	0.05

Level 2, PC, K=2

Cluster	S_1	s.d.	S_2	s.d.
West-central	**0.93**	0.10	0.07	0.10
Northeastern	0.08	0.12	**0.92**	0.12

Level 2, Qam-D&U, K=2

Cluster	S_1	s.d.	S_2	s.d.
D&U - Qam	**0.86**	0.17	0.14	0.17
Qam	0.38	0.09	**0.62**	0.09

Level 3, PC-Northeastern, K=2

Cluster	S_1	s.d.	S_2	s.d.	S_3	s.d.
Ellesmere - NW	0.02	0.03	**0.89**	0.09	0.09	0.07
Ellesmere - Marvin P	**0.59**	0.00	0.00	0.00	0.40	0.00
PC Northeastern	0.08	0.07	0.07	0.07	**0.85**	0.09

Table 7s. Estimates of genetic diversity; number of multi-locus genotypes (N), mean number of alleles (Na), observed heterozygosity (Ho), 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 (Fis) where * identifies values significantly different from 0 based on 10000 bootstrap 95% confidence intervals.

STRUCTURE	N	Na	Ho	H_E	uH_E	A_R	A_P	Fis		Description
S_1.1	75	5.94	0.66	0.66	0.67	4.20	0.44	0.01		Southampton
S_2.1	58	9.56	0.72	0.72	0.72	6.02	0.38	0.00		Baffin
S_2.2	45	13.88	0.84	0.86	0.87	8.76	1.38	0.02		Qamanirjuaq
S_2.3	46	10.75	0.84	0.83	0.84	7.62	0.75	-0.02		D&U
S_2.4	10	5.25	0.65	0.70	0.74	5.25	0.74	0.08		Belcher
S_3.1	120	7.81	0.73	0.72	0.72	5.14	0.11	-0.01		PC West-central
S_3.21	58	6.13	0.70	0.71	0.72	4.88	0.12	0.01		PC Northeastern
S_3.221	19	4.81	0.76	0.67	0.68	4.42	0.01	-0.14	*	Ellesmere & PC WC
S_3.222	14	3.50	0.59	0.55	0.57	3.47	0.03	-0.06		Ellesmere - Marvin P

TESS	N	Na	Ho	H_E	uH_E	A_R	A_P	Fis		Description
T_4	76	6.19	0.66	0.67	0.67	3.86	0.42	0.01		Southampton
T_2	58	9.56	0.72	0.72	0.72	5.19	0.39	0.00		Baffin
T_5.2	14	9.94	0.83	0.83	0.86	7.40	1.08	0.00		Qamanirjuaq
T_5.1	76	14.06	0.84	0.85	0.85	7.03	0.84	0.00		D&U, Qam
T_3	10	5.25	0.65	0.70	0.74	4.70	0.59	0.08		Belcher
T_1.1	150	7.88	0.73	0.72	0.73	4.62	0.09	-0.01		PC West Central
T_1.23	43	5.94	0.69	0.70	0.71	4.32	0.05	0.01		PC Northeastern
T_1.21	7	3.56	0.71	0.59	0.63	3.56	0.14	-0.22	*	Ellesmere - NW
T_1.22	12	3.13	0.58	0.53	0.55	2.98	0.00	-0.11	*	Ellesmere - Marvin P

Table 8s. Pairwise Fst values (according to Weir & Cockerham (1984)) among genetic clusters generated by STRUCTURE and TESS. Significant Fst values are highlighted in blue. Boldface font indicates the largest values. Cluster names are from Table 5s & 6s.

STRUCTURE

	S_1.1	S_2.1	S_2.2	S_2.3	S_2.4	S_3.1	S_3.21	S_3.221	S_3.222	
S_1.1										Southampton
S_2.1	**0.18**									Baffin
S_2.2	**0.14**	0.08								Qamanirjuaq
S_2.3	**0.14**	0.07	0.02							D&U
S_2.4	**0.24**	0.15	0.07	0.09						Belcher
S_3.1	**0.21**	0.13	0.08	0.07	0.13					PC West Central
S_3.21	**0.22**	0.13	0.08	0.07	0.15	0.03				PC Northeastern
S_3.221	**0.24**	0.14	0.09	0.08	0.16	0.04	0.05			Elles. & PC WC
S_3.222	**0.28**	0.18	0.14	0.14	0.23	0.08	0.08	0.08		Elles. – Marvin P

TESS

	T_1.1	T_1.21	T_1.22	T_1.23	T_2.0	T_3.0	T_4.0	T_5.1	T_5.2	
T_1.1										PC West Central
T_1.21	0.11									Elles. - NW
T_1.22	0.08	0.21								Elles. – Marvin P
T_1.23	0.03	0.08	0.08							PC Northeastern
T_2.0	0.13	0.17	0.18	0.13						Baffin
T_3.0	0.13	0.21	0.24	0.15	0.16					Belcher
T_4.0	**0.21**	**0.27**	**0.29**	**0.22**	**0.18**	**0.23**				Southampton
T_5.1	0.06	0.10	0.15	0.07	0.07	0.08	0.13			D&U, Qam.
T_5.2	0.10	0.14	0.18	0.10	0.10	0.08	0.16	0.03		Qamanirjuaq

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CHAPTER 4

BIOTIC INTERACTIONS GOVERN THE DISTRIBUTION OF COEXISTING UNGULATES IN THE ARCTIC ARCHIPELAGO — A CASE FOR CONSERVATION PLANNING

A version of this chapter has been published

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ABSTRACT

Climate change and biodiversity loss underscore the need for conservation planning, even in remote areas. Species distribution models (SDMs) can help identify critical habitat for reserve design and selection, and have quickly advanced to the fore of ecological inquiry. Such models are typically dominated by abiotic factors, following the Eltonian Noise Hypothesis (ENH) that physical features set the limits of species distributions. Nevertheless, recent studies challenge this notion and highlight the importance of biotic interactions. Resolving this discrepancy could have significant implications for conservation and ecological understanding.

To test these ideas, we build distribution models for two large herbivores, muskoxen (*Ovibos muschatus*) and Peary caribou (*Rangifer tarandus pearyi*), systematically observed across a vast spatial extent – 65 islands spanning 800,000 km^2 in the Canadian High Arctic. To test the ENH we fit SDMs with two sets of predictors: (1) abiotic only (i.e. topographic, climatic) and (2) abiotic + biotic (i.e. vegetation communities, distance-to-heterospecifics). We evaluated these models and spatially estimated habitat suitability for each species. We found both sets of models had good predictive ability, although biotic variables (i.e. proportion of grass-lichen-moss) improved model performance and substantially narrowed areas of high habitat suitability. Niche overlap between caribou and muskoxen was moderate and highly suitable areas were spatially disjunct between species and largely outside protected areas.

These results fail to support the ENH. Our study implies that biotic features, although often overlooked, may be important to the performance of SDMs and vital in identifying priority areas for conservation. For these large herbivores, reflecting trophic interactions in SDMs was essential when estimating areas of conservation value. Our approach helps prepare the way for improved projections regarding the prospects for wildlife while laying the foundation for biologically relevant protected areas.

KEYWORDS caribou, Eltonian Noise Hypothesis, MaxEnt, muskoxen, protected areas, species distribution models

1. INTRODUCTION

Understanding the geographic and ecological distributions of species is a longstanding quest (Grinnell 1914, Hutchinson and MacArthur 1959). With global disruptions in climate, declines in wildlife, and growing anthropogenic disturbance, the need has become urgent (Young et al. 2016). In response, broad-scale species distribution models (SDMs) have emerged as a fundamental tool in conservation assessment, planning, and decision-making (Kremen et al. 2008, Schmolke et al. 2010) with emphasis on protecting biodiversity, habitat, biocultural landscapes, and climate refugia (Keppel et al. 2012, Guisan et al. 2013, Li et al. 2016). SDMs, often based on abiotic features alone, have proliferated due to the availability of abiotic variables on a global scale (Araújo et al. 2019). SDMs typically assume species are distributed independent of other species (Guisan and Thuiller 2005). This focus on abiotic features conforms to the Eltonian Noise Hypothesis — i.e., that species distributions are unaffected by biotic interactions (e.g. competition, herbivory) at large spatial extents and coarse resolutions (Soberon and Nakamura 2009). Yet, recent broad-scale studies illustrate biotic predictors can constrain a species range, and that including these features can consequently improve species distribution models (Heikkinen et al. 2007, Broennimann et al. 2012, Araújo et al. 2014, Atauchi et al. 2018). By reflecting biotic interactions, such models can provide more robust predictions and a strong foundation for planning (Thuiller et al. 2018, Palacio and Girini 2018).

Despite their utility, accounting for biotic interactions can be difficult owing to their complexity (Aragon et al. 2018) and the challenge of representing dynamic and potentially fine-grained interactions at a macro scale (Soberon and Nakamura 2009, Wisz et al. 2013). On the other hand, the distributions of species can be valuable proxies for biotic interactions (e.g., commensalism, Atauchi et al. 2018; herbivory, Thuiller et al. 2018) when supported by knowledge of interspecific interactions (Wisz et al. 2013). Accounting for competition is less straightforward, however, owing to the dynamic nature of predictors (Anderson 2017) and the scarcity of methods to represent competition in grid cells (Mpakairi et al. 2017).

Multi-herbivore ecosystems provide valuable test cases. Among ungulates, for example, interactions with heterospecifics may include direct and indirect competition for resources and space, but also apparent competition mediated by shared predators or parasites (Rettie and Messier 2000, Rostro-Garcia et al. 2015). Species responses to competition have led to the enduring concepts of competitive exclusion (Hardin 1960) and niche (Hutchinson and MacArthur 1959). Notably, these processes are difficult to uncover using correlative distribution models (Wisz et al. 2013, Anderson 2017), but adding biotic variables in SDMs could improve our understanding of biogeographical patterns and interspecific relationships.

Relatively uncomplicated in structure, the Arctic lends itself to testing ecological relationships (Schaefer et al. 1996). In Canada, endangered Peary caribou *Rangifer tarandus pearyi* and muskoxen *Ovibos moschatus* (Fig. 1) occur on remote islands — the only ungulates adapted to this environment (Festa-Bianchet et al. 2011, Dobson et al. 2015). Interactions between these species is a longstanding and widespread issue that remains unresolved (Smits 1989, Larter and Nagy 1997, Rozenfeld et al. 2012), and a concern voiced by many Arctic Indigenous communities (Taylor 2005, Jenkins et al. 2010a,b, COSEWIC 2015). On some islands, numbers have risen and fallen in tandem; others show caribou population growth coincident with muskox extirpation or, conversely, the near-extirpation of caribou with rising muskox numbers (Klein 1999, Gunn et al. 2006, Jenkins et al. 2011). Indeed, morphological, physiological and behavioral differences may limit interspecific competition and promote exploitation of different habitats (Klein 1992, 1999, Larter and Nagy 2004). Further, the patchiness of food resources, particularly during periods of snow cover, may be limiting for these large herbivores (Schaefer et al. 1996), and result in patchiness in species distributions. By uncovering environmental relationships and patterns (Araújo et al. 2014), the addition of biotic interactions in SDMs may enhance knowledge of both species and highlight areas of conservation value (Guisan et al. 2013).

Here, we use SDMs to quantify the distribution and niche characteristics of Peary caribou and muskoxen across the Canadian Arctic Archipelago ─ an immense swath of these species' ranges. We focus on late winter, a season of heightened environmental stress and depleted body condition, coincident with the fitness and physiological demands of calving (Miller and Gunn 2003a,b). We tested the Eltonian Noise Hypothesis by using abiotic predictors alone, and then incorporating vegetation types and proximity to heterospecifics, as proxies for biotic interactions. Following Araújo et al. (2014), we predicted that (P1) models using *abiotic-only* variables would perform at least as well as models that included biotic predictors; and (P2) abiotic variables would remain the most important features of both *abiotic-only* and *abiotic+biotic* models. Finally, using our best models, we compared spatial estimates of high habitat suitability, and identified areas of conservation value in relation to protected areas in this vast and largely intact wilderness.

2. MATERIALS AND METHODS

2.1 Study area and study species

Our study extends across the eastern Canadian range of Peary caribou and muskoxen: 65 islands and roughly 800,000 km^2 (Fig. 2A; Jenkins et al. 2011, Cuyler et al. 2019). Both species are ecologically and culturally significant (Taylor 2005, Yannic et al. 2014, 2017). At a broad scale, their primary predator, the Arctic grey wolf (*Canis lupus arctos*), occurs at low numbers and can be scarce or absent from many islands (Miller and Reintjes 1995). Wolves are generally associated with areas of high muskox density, although non-ungulate prey are also important (Mech 2007, Larter 2013, Dalerum et al. 2018). Muskoxen predator-prey relationships, including associated impacts on Peary caribou, have been identified as a knowledge gap (COSEWIC 2015, Cuyler et al. 2019). Observations of wolves during our study were infrequent.

This landscape varies (west-east) from low, rolling tundra in the Northern Arctic ecozone to mountains, exposed bedrock, and ice fields in the Arctic Cordillera ecozone (Ecological Stratification Working Group 1995). The climate is cold and dry, with extensive periods of snow cover (~ 10 months a year; Canadian Climate Normals 1981-2010) and darkness (6 -18 weeks without daylight; https://www.timeanddate.com/sun/canada; Coops et al. 2008). The short growing season and shallow soils support sparse, patchy vegetation dominated by dwarf herbs, lichens, and moss (Walker et al. 2005). Six protected areas include national parks, national wildlife areas, and migratory bird sanctuaries (Fig. 2). According to national and international targets, the Northern Arctic Ecozone is underrepresented by protected areas (7.1% protected; Environmental and Climate Change Canada 2019).

2.2 Species Distribution Models

To predict late-winter distributions and to assess the contribution of biotic interactions, we built SDMs from abiotic predictors and a combination of abiotic and biotic variables. We used maximum entropy modelling (MaxEnt Version 3.4.1; Phillips and Dudik 2008), given its predictive performance, extensive use, suitability for presence-only data, and continuous prediction of habitat suitability (Elith et al. 2006, 2011, Broennimann et al. 2012). MaxEnt contrasts background environmental conditions with conditions at known species locations. As an index of habitat suitability, this approach estimates species distributions across the landscape (Phillips et al. 2006, Phillips and Dudik 2008) We used the presence-only approach, recognizing true absences are difficult to record, particularly for mobile species (Lobo et al. 2010). Instead, we generated random points (n= 20,000) to sample the terrestrial environment (Phillips and Dudik 2008, Elith et al. 2011, Barbet-Massin et al. 2012, Merow et al. 2013); the marine environment was excluded, despite possible sea-ice crossings (Jenkins et al. 2016, Schmidt et al. 2016). To improve model performance and predictions of habitat suitability, we followed recommendations for species-specific tuning of model settings and minimizing spatial autocorrelation (described below; Anderson and Gonzalez 2011, Muscarella et al. 2014, Radosavljevic and Anderson 2014).

2.3 Occurrence records and environmental variables

2.3.1 *Occurrence data*

Caribou and muskoxen are gregarious, so we used georeferenced observations to represent individuals in separate social groups. These observations were of animals, trails, and feeding sites in snow cover (Fig. 2) derived from systematic late-winter (April-May) aerial surveys (2001-2008) and unsystematic ground surveys (2000-2006; ~10% of the data; Jenkins et al. 2011; Environment 2013). The number of locations varied by year, species and survey type (see Jenkins et al. 2011).

We considered systematic aerial observations representative of geographic and environmental space (Wisz et al. 2008). In contrast, ground surveys were non-systematic and occasionally overlapped with aerial surveys (Jenkins et al. 2011). We buffered ground observations by 2 km (average daily winter movement of muskoxen; Jingfors 1982). Overlapping observations were thinned to one location, unless separated by at least one day; aerial locations were preserved over ground locations (Radosavljevic and Anderson 2014). We further reduced observations to one per grid cell (Phillips and Dudık 2008) — in all, retaining 535 caribou and 1519 muskox locations. All geoprocessing occurred in ArcMap 10.6.1 (ESRI, 2018a) unless stated otherwise.

2.3.2 *Environmental variables*

To characterize habitat variation, we considered a suite of 18 abiotic and biotic predictors (see Appendix A, Table A.1) of putative ecological relevance to our species (Elith et al. 2011). We used geophysical variables that were derived from a digital elevation model (DEM) at 1-km resolution – a resolution to match the grain of our other environmental data – downloaded from the National Centers for Environmental Information (Globe Version 1.0; Hastings et al. 1999), from which aspect and slope were calculated using Spatial Analyst Tools (Surface) in ArcMap 10.6.1 (ESRI 2018a). Average monthly climate data (1970—2000; April and May) were downloaded at a 30-s (~ 1 km at equator) spatial resolution (including minimum temperature [°C], maximum temperature [°C], average temperature [°C], precipitation [mm], solar radiation [kJ m^{-2} day^{-1}], and wind speed [m s^{-1}]; WorldClim2, Fick and Hijmans 2017) which we then averaged across the winter study period. Snow depth was derived from the Canadian Meteorological Centre (CMC) Daily Snow Depth Analysis Data using monthly means of snow depth (24-km resolution, April and May, 2000—2008), which we then averaged across months and years.

Land cover types (Table A.1) were derived from the 2010 North American Land Cover categorical dataset from the Canada Centre for Remote Sensing/Canada Centre for Mapping and Earth Observation, Natural Resources Canada (30-m resolution; Latifovic et al. 2017). To develop continuous layers for each land cover type, from entirely unproductive land cover (i.e. snow and ice) to a series of vegetation types, we resampled the data and determined the proportion of each land cover type in each grid cell (577 m) using ArcGIS Pro (ESRI 2018b). To incorporate heterospecifics as a biotic predictor, we generated separate continuous Euclidean distance rasters, distance-to-muskoxen and distance-to-caribou, based on our field observations of animals.

In ArcMap 10.6.1, we standardized all layers in extent and projection (North Pole Lambert Azimuthal Equal Area; Elith et al. 2006). For our base layers, i.e., elevation and climate, this resulted in a cell size of approximately 577 m x 577 m, which we standardized across layers. To address collinearity between predictor layers, we ran pair-wise Pearson correlations (r) using SDMtoolbox v2.2c (Brown 2014, Brown et al. 2017), and excluded one variable from any pair where $|r| \geq 0.6$ (Dormann et al. 2007, Phipps et al. 2017). Our results revealed strong positive correlations among late-winter average, maximum, and minimum temperatures ($r > 0.90$). Additionally, snow and ice was positively correlated with elevation ($r = 0.74$) and negatively correlated with barren land ($r = –0.65$). We removed maximum and minimum temperature, as well as snow and ice, maintaining elevation and barren land (areas of low primary productivity) within the final set of 15 abiotic and biotic factors (Table 1).

2.4 Model tuning and performance

To derive input parameters, we ran models for each species. We used *abiotic-only* and *abiotic+biotic* predictors and tested 7 combinations (L, Q, H, LQ, LQH, LQHP, LQHPT; where L=linear, Q=quadratic, H=hinge, P=product, and T=threshold) and 8 regularization multiplier values (RM: 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4) — a total of 224 models. Due to the large study area, and the potential for environmental gradients, heterogeneity, and spatial autocorrelation, we employed spatially independent cross-validation (Radosavljevic and Anderson 2014). Specifically, we used checkerboard2 partitioning in ENMeval R package, an approach that masks geographical structure (Radosavljevic and Anderson 2014). The data were subdivided into 4 bins based on a hierarchical checkerboard distribution (i.e. 4 x 4) to equally partition geographic space and represent environmental heterogeneity in each bin (Radosavlejevic and Anderson 2014, Muscarella et al. 2014). Cross-validation for final models followed Beumer et al. (2019).

For each model, we assessed predictive performance, overfitting, goodness-of-fit, and model complexity (Radosavljevic and Anderson 2014). These analyses were completed using the ENMEval package in R (Muscarella et al. 2104), unless stated otherwise.

A common measure of predictive performance is the area under the curve (AUC) of the receiver operating characteristic plot (ROC), where AUC =1 represents perfect discriminatory ability, AUC > 0.75 useful models, and AUC = 0.5 no better than random (Elith et al. 2006, Phillips and Dudik 2008). We generated AUC for training and testing (AUCTRAIN, AUCTEST; Muscarella et al. 2014) and evaluated performance using AUCTEST.

We also calculated the partial receiver operating characteristic (PROC) area under the curve (AUCPROC; ENMGadgets package in R; Barve and Barve 2013) which gives priority to omission over commission errors, as recommended for presence-only data (Peterson et al. 2008, Lobo et al. 2010). We estimated ratios (AUCRATIO) by comparing AUCPROC to null expectations with bootstrapping (1000 replicates, 50% of evaluation data; 2% error among occurrence data). When AUCRATIOS are significant and greater than one, model performance is better than random (Peterson et al. 2008).

To detect overfitting, we calculated the difference between AUC_{TRAIN} and AUC_{TEST} (AUC_{DIFF}), the minimum training presence omission rate (OR_{MIN}), and the 10% training omission rate (OR_{10}). Overfitting is typically indicated by higher AUC_{DIFF} and by $OR_{MIN} > 0$ and $OR_{10} > 10\%$ (Warren and Seifert 2011). To balance goodness-of-fit and model complexity (Palacio and Girini 2018), we calculated Akaike's Information Criterion for small sample size (AIC_c: Burnham and Anderson 2002). We favoured models with low ΔAIC_c (i.e. $AICc_{OPT}$).

Finally, we evaluated candidate models and selected optimal settings to balance low omission rates (i.e. OM_{MIN}), high predictive performance (i.e. AUC_{TEST}, AUC_{PROC}), and low model complexity (i.e. ΔAIC_c; Atauchi et al. 2018). To allow replication, our final model set was run in MaxEnt Version 3.4.1, using optimization settings, 20 replicates, 20,000 background points, and cross-validation on a subsample of presence data (75% training, 25% testing) with a random seed.

2.5 Variable importance and response curves

As measures of variable importance, we generated percent contribution and permutation importance in MaxEnt Version 3.4.1. The first identifies the contribution of each environmental variable to model fitting; the second identifies the change in training AUC when the variable is randomized across presence and background data (Phillips 2017). The influence of a variable on the model is demonstrated by the change in AUC, where a large decrease in AUC corresponds to strong dependence (Searcy and Shaffer 2016). Response curves show the relationship between each predictor variable and the prediction of habitat suitability while holding other variables constant (Merow et al. 2013, Phillips 2017).

2.6 Spatial predictions of habitat suitability, niche characteristics, and protected areas

Using the logistic output, we mapped potential habitat suitability for caribou and muskoxen based on the best *abiotic-only* and *abiotic+biotic* models. We estimated spatial niche overlap, contrasting *abiotic-only* models vs *abiotic+biotic* models, using Schoener's D (Schoener 1968; ENMTools Version 1.4.4; Warren et al. 2010, Warren and Seifert 2011). Using two thresholds of habitat suitability (HS ≥ 0.5; HS ≥ 0.75), we measured extent and overlap of habitat (sum of pixels) and calculated the proportion of habitat in protected areas.

3. RESULTS

3.1 Model performance

Species-specific tuning resulted in 224 *abiotic-only* and *abiotic+biotic* models, with moderate to good explanatory power ($0.73 \leq \mathrm{AUC}_{\mathrm{TEST}} \leq 0.88$; $0.74 \leq \mathrm{AUC}_{\mathrm{PROC}} \leq 0.90$) and predictive accuracy ($0.00 \leq \mathrm{OM}_{\mathrm{MIN}} \leq 0.01$) for both species in all but one model. According to $\mathrm{AUC}_{\mathrm{DIFF}}$ and $\mathrm{OR}_{\mathrm{MIN}}$, overfitting was low for *abiotic-only* and *abiotic+biotic* models, further supported by OR_{10} (0.074 – 0.136) across models and species. Best models based on $\mathrm{AIC}_{\mathrm{cOPT}}$ and $\mathrm{AUC}_{\mathrm{PROC}}$ revealed $\mathrm{AIC}_{\mathrm{cOPT}}$ with only slightly lower predictive power (e.g. $\mathrm{AUC}_{\mathrm{TEST}}$) but reduced complexity (i.e. fewer parameters; Table A.2). For both species, there was high spatial overlap between all model predictions (0.64 ≤ Schoener's D ≤ 0.99).

For caribou and muskoxen, biotic variables improved model performance (AUCPROC and AUCTEST); AIC_c declined when biotic variables were included. Notably, caribou models had slightly higher performance (AUCPROC and AUCTEST) than muskox models (Table A.2). Below, we report AIC_cOPT models, given their reduced complexity but strong similarity to AUCPROC.

3.2 Environmental predictors of habitat suitability

In *abiotic-only* models, elevation and precipitation were the main influences on habitat suitability for caribou; elevation and wind were most important for muskoxen (Table 1). For both species, the relative contribution of these variables was > 50%. Aspect and slope were consistently minor influences. High habitat suitability (HS > 0.75) differed slightly between species — i.e., for caribou, low-moderate elevation (<626 m asl) and low precipitation (2.2 – 9.1 mm), whereas for muskoxen, low elevation (<219 m asl) and light winds (<2.87 m s^{-1}; Fig. 3).

When we added biotic variables, the proportion of grass-lichen-moss and barren-lichen-moss had the greatest influence on habitat suitability, with a combined contribution >60% for both species (Table 1). For muskoxen, wind was third in importance, while precipitation and wind were the next most influential features for caribou. For both species, distance to heterospecifics contributed little (<2%) to habitat suitability. Even small proportions of grass-lichen-moss (>0.0 for muskoxen; >0.28 for caribou) and barren-lichen-moss (> 0.0 for muskoxen; >0.09 for caribou) had high habitat suitability (HS > 0.75). For muskoxen, such areas had near-zero to low winds (0.22 – 5.12 m s^{-1}) whereas for caribou, areas of high habitat suitability exhibited moderate winds (2.1 – 5.67 m s^{-1}) and low precipitation (2.6 – 9.35 mm; Fig. 3).

3.3 Spatial predictions of habitat suitability, niche characteristics, and protected areas

Regardless of species, we found modest differences between *abiotic-only* and *abiotic+biotic* model predictions of habitat suitability (Schoener's $D_{\text{PC A-AB}}$ = 0.73; Schoener's $D_{\text{MX A-AB}}$ =0.74). Suitable habitat for caribou occurred in the northwest, particularly Axel Heiberg, Amund Ringnes, Lougheed, and Bathurst Island Complex (Fig. 4). In contrast, the most suitable habitat for muskoxen occurred primarily in the northeast, particularly the low-lying areas of eastern Axel Heiberg Island, west-central Ellesmere Island, and the far-eastern peninsula on Devon Island (Fig. 4). Spatial niche overlap between caribou and muskoxen was moderate (Schoener's $D_{\text{PC-MX A}}$ = 0.64; Schoener's $D_{\text{PC-MX AB}}$ = 0.66). For both species, areas of high habitat suitability were limited (Table 2, Fig. 5); they declined by as much as 42% when we included biotic variables.

From our best *abiotic+biotic* models, the estimated area of habitat suitability (HS > 0.5) for caribou and muskoxen overlapped by 42%, but by 17% at the higher threshold (HS > 0.75). These areas represent a small portion of the study area (i.e. 6.9% and 1.3%, respectively; Table 2). The majority of important habitat (>85%) occurred outside protected areas (Table 2, Fig. 5) — i.e., only 13% of prime late-winter caribou habitat and 9% of prime late-winter muskoxen habitat (HS > 0.75) is protected. Of this, the majority was in two parks: Qausuittuq National Park for caribou (~70%) and Quttinirpaaq National Park for muskoxen (~90%).

4. DISCUSSION

Increasingly, researchers are emphasizing biotic interactions in species distributions, even at broad spatial scales (Atauchi et al. 2018, Palacio and Girini 2018). Such findings challenge the Eltonian Noise Hypothesis that abiotic factors govern species distributions over large extents (Soberon and Nakamura 2009). Contrary to our predictions, we found (P1) SDMs of late-winter distribution of Peary caribou and muskoxen improved by including vegetation communities (Table A.2), and (P2) abiotic variables failed to remain the most important predictors in *abiotic+biotic* models (Table 1). In our study, biotic features, representing vegetation and heterospecifics, were not correlated with abiotic variables (| r | < 0.6), implying that they captured new aspects of habitat (Soberon and Nakamura 2009, Araújo et al. 2014). As well, the strong positive relationship between habitat suitability and grass-lichen-moss and barren-lichen-moss suggest forage resources are critical for both species (Schaefer and Messier 1995a, Rettie and Messier 2000), and signal herbivory as the likely driver of species distributions. During winter, muskoxen consistently select for higher forage abundance across spatial scales (Schaefer and Messier 1995a) while regional studies, like ours, identified vegetated areas as important muskox habitat across seasons and years (Table 1, Fig. 3; Beumer et al. 2019). That caribou favored grass-lichen-moss while muskoxen were most strongly associated with barren-lichen-moss communities (Table 1) emphasizes the metabolic requirements and high-quality diet of caribou (Parker and Ross 1976, Klein 1992, 1999) — a largely mobile species in contrast to predominantly sedentary muskox (Klein 1999, Beumer et al. 2019). Nevertheless, whether these differences in niche reflect biotic interactions, such as competitive exclusion and apparent competition (Holt and Bonsall 2017), is not reconcilable with our data.

Demonstrating competition is difficult (Araújo and Guisan 2006); including competitive interactions in SDMs is rare (Mpakairi et al. 2017). This rarity is likely due to the complexity of rasterizing this mechanism and difficulties in establishing competitive interactions from simple, static observations (Connell 1980, Yackulic 2017). We expected caribou habitat suitability might improve with increasing distances-to-muskoxen, potentially indicative of apparent competition and the avoidance of shared enemies. However, proximity to heterospecifics contributed little to our models (Table 1). Indeed, including potential competitors may not improve model performance while vegetation can be an important predictor of animal-plant interactions (Bateman et al. 2012; cf. Mpakairi et al. 2017).

Our study focused on late winter, a period of energetic and demographic stress for arctic caribou and muskoxen (Thomas and Edmonds 1993, Miller and Gunn 2003a,b, Joly 2011). While our analysis was restricted to this season, arctic snow cover can impose appreciable fitness costs (Miller and Barry 2009, Callaghan et al. 2011). For caribou and muskoxen, severe snow and icing can result in reproductive failure and mass die-offs (Miller and Gunn 2003b, Miller and Barry 2009, Schmidt et al. 2019). Our finding that muskox habitat suitability was related to low winds, rather than precipitation or snow cover (Spencer and Lensink 1970), was unexpected. While snow depth is not static, and the resolution of our analysis was rather coarse, arctic snow cover is renowned for its strong spatial variation and relative consistency across years (Pruitt 1978, Schaefer and Messier 1995b). Our study likely captured this coarse-scale variation, but muskoxen may react to snow at a finer grain (Schaefer and Messier 1995a), using micro-habitats to overcome unfavorable conditions (Klein et al. 1993). Additionally, the absence of wind may provide energetic benefits, particularly to parturient cows and neonates. Our study overlapped with the calving season of muskoxen (April - June; Lent 1991) and we observed ~1500 newborns throughout the study area (Jenkins et al. 2011). In contrast, low precipitation was important to caribou, underscoring winter precipitation as energetically and demographically taxing to ungulates (Thomas and Edmonds 1983, Joly 2011). Snow and rain-on-snow can limit access to forage, already sparse and low in nutrients (Albon et al. 2017, Schmidt et al. 2018), and snow can amplify movement costs (Parker et. al. 1984). Thus, areas of low precipitation likely favor access to forage (i.e. potentially higher-quality foods), a determinant of caribou survival during the energetically stressful pre-calving period (Thomas and Edmonds 1983, Biddlecomb 1992, Larter and Nagy 2004, Joly 2011).

Mapping species-environment relationships provides a geographic depiction of potential habitat (Araújo and Guisan 2006). In our study, biotic interactions drove the distributions and appeared to constrain muskox and caribou habitat (Fig. 4). Our *abiotic-only* models performed well, but they underperformed in comparison to *abiotic+biotic* models (Table A.2) and estimated broader areas of habitat suitability (Atauchi et al. 2018), potentially devoid of critical forage resources. In contrast, Johnson et al. (2016) modeled range-wide Peary caribou distribution by season with the selected abiotic top model for late-winter distribution including precipitation, snow depth and wind speed as predictors. These models combined spatially and temporally disjointed observations (i.e. from surveys, radio-telemetry, Inuit Knowledge) and used predictors from coarse climate data (25 km) to fine categorical land cover (30 m). Our models differed in output and approach. By accounting for data resolution and independence, sample period, and spatial autocorrelation, and by incorporating continuous, fine-resolution predictors, our models had stronger predictive performance (average test AUC = 0.87 vs 0.78) and revealed a strong association with vegetation cover. Indeed, robust models of current and future distributions are often strongly influenced by plant species (Atauchi et al. 2018, Palacio and Girini 2018, Thuiller et al. 2018).

Mapping habitat suitability can serve conservation, especially in determining areas of high conservation value as candidate protected areas for rare and endangered species (Guisan and Thuiller 2005, Guisan et al. 2013). Our results reveal that protection of late-winter habitat is limited for caribou and muskoxen (Fig. 5, Table 2). These areas of conservation value lie largely outside protected habitat ($\geq$85%), a circumstance not uncommon for mobile caribou (Taillon et al. 2012). The National Parks system in Canada has focused on geographic and bioregional representation; less on protecting biodiversity, viable populations, and ecosystem integrity (Manseau et al. 2001, Deguise and Kerr 2004). We were not, therefore, surprised by our findings. Bias in siting new parks is a national and global issue; the potential for agriculture and resource extraction has typically been favored over ecological considerations (Joppa and Pfaff 2009, Lopoukhine et al. 2012). Indeed, critical winter habitat, calving grounds, and climate refugia have long been emphasized in the ecology of muskoxen and Peary caribou (Thomas et al.

1981, Ferguson 1995, Jenkins et al. 2011, Poole et al. 2015); species that are central to the culture and security of Arctic Indigenous communities. As our study underscores, such areas are strikingly absent from protected areas.

5. CONCLUSIONS

Species distribution modeling can be a powerful conservation tool. When based on robust location data and meaningful predictors, SDMs can inform conservation, with potentially better prospects for wildlife. To date, however, biotic features have largely been ignored. Contrary to Eltonian Noise Hypothesis, biotic predictors were essential to identifying late-winter habitat of these large herbivores. Habitat that is likely important to their physiological and metabolic requirements and a reflection of trophic interactions.

Suitable conditions for wildlife often occur outside protected areas (Deguise and Kerr 2004), as our study shows. We focused on a biologically crucial period in a remote, but increasingly threatened area. Still largely intact, the Arctic represents important but vanishing opportunities to protect large areas of wildlife habitat. Such areas help meet national and international conservation obligations while supporting the persistence of key Arctic species, crucial for tundra ecosystems and for Inuit communities, in a changing environment. More generally, our approach helps prepare the way for improved large-scale projections regarding the prospects for wildlife, while laying the foundation for biologically relevant protected areas.

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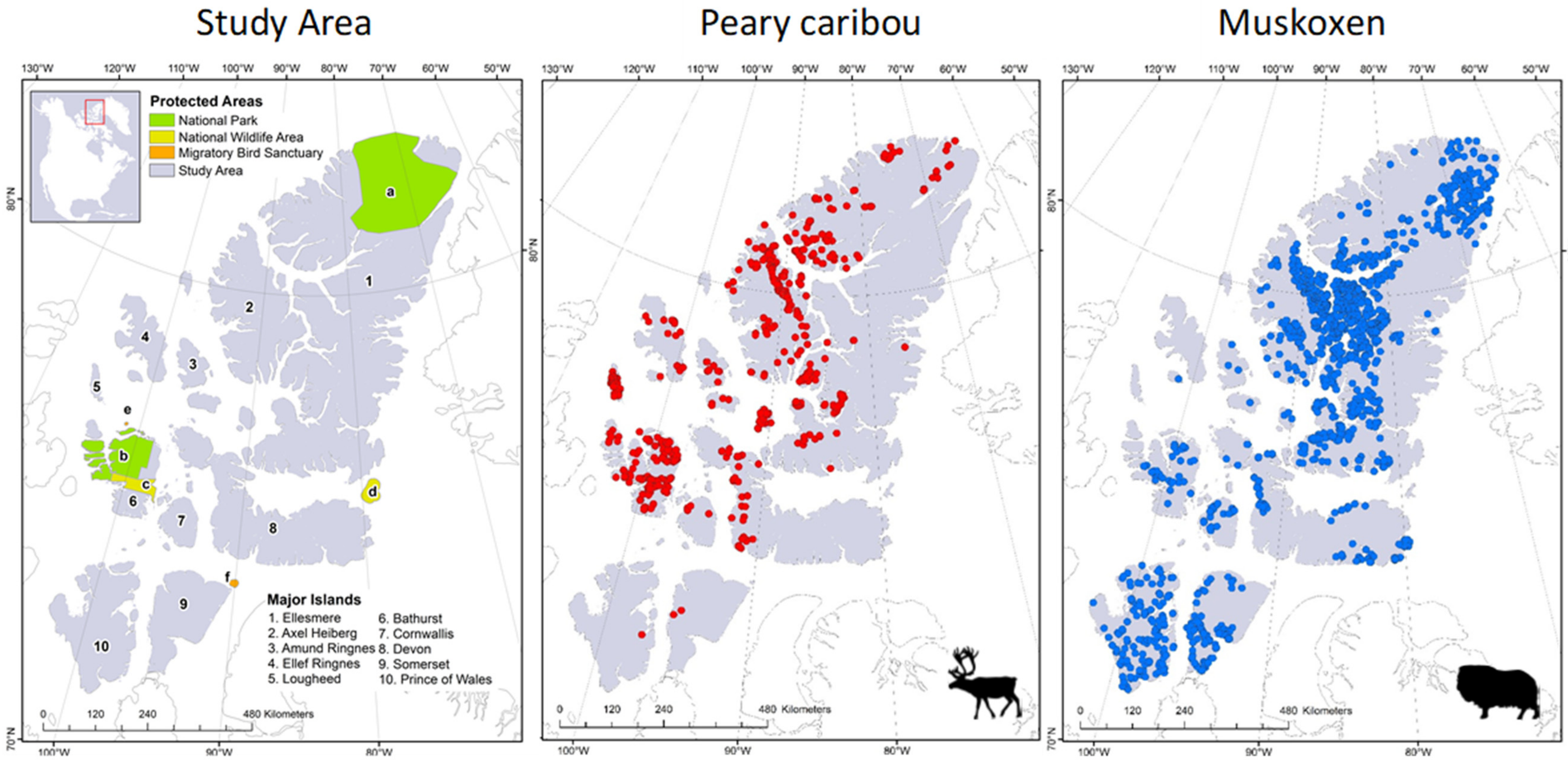
FIGURES

Figure 1. Peary caribou (A, B) and muskoxen (C, D) in the rugged treeless habitat of the Canadian High Arctic Islands. Photos by Kevin Rawlings (A, C), and D.A.J. (B, D).


Study Area

Peary caribou

Muskoxen

Figure 2. Study area in the Arctic Archipelago (71° - 83°N, 61° - 106°W), Canada, including six protected areas: (a) Quttinirpaaq National Park (37,775 km^2), (b) Qausuittuq National Park (11,000 km^2), (c) Polar Bear Pass National Wildlife Area (2636 km^2), (d) Nirjutiqavvik National Wildlife Area (1783 km^2), (e) Seymour Island Migratory Bird Sanctuary (53 km^2), and (f) Prince Leopold Island Migratory Bird Sanctuary (304 km^2). Occurrence records for Peary caribou (red) and muskoxen (blue), 2000-2008, derived from aerial and ground surveys. We geoprocessed the data to one geographic datum (i.e. WGS84) and projection (North Pole Lambert Azimuthal Equal Area, centered on 84°W, 78°N.

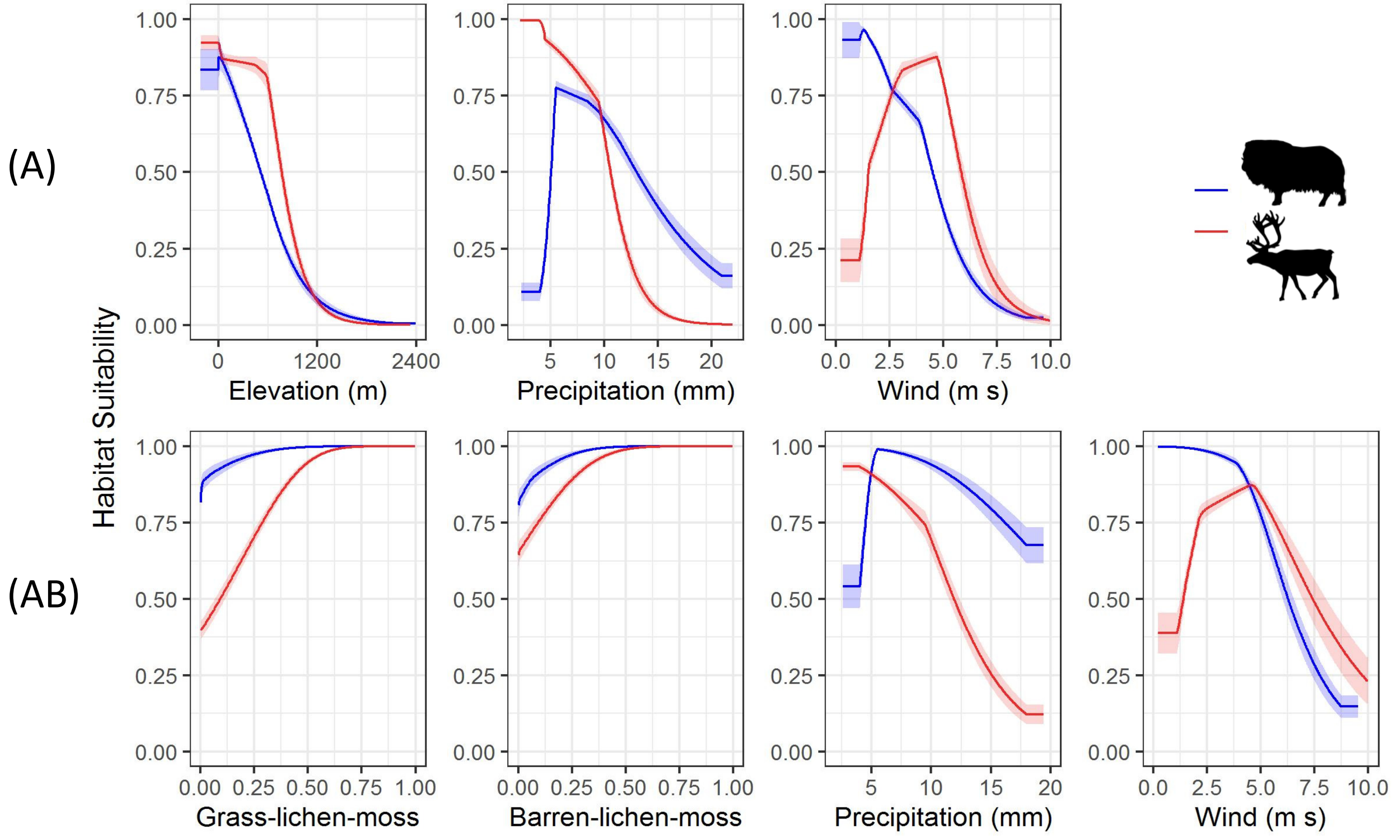


Figure 3. Response curves (+/- std) showing the relationship between habitat suitability and most important predictor variables in *abiotic* models (A) and *abiotic+biotic* models (AB).

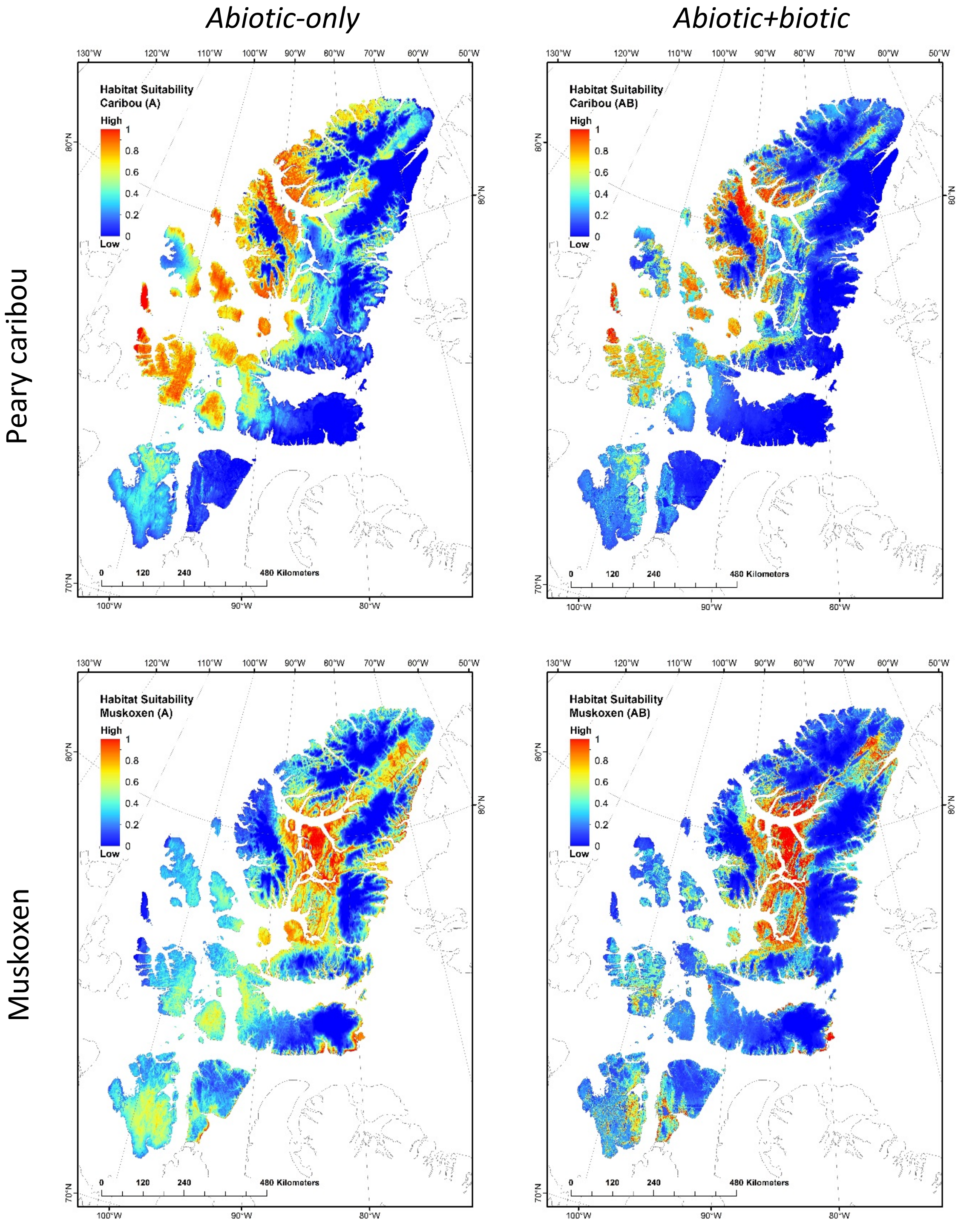


Figure 4. Predictions of habitat suitability for Peary caribou and muskoxen across the north-eastern Arctic Archipelago, representing species-specific *abiotic-only* and *abiotic+biotic* models.

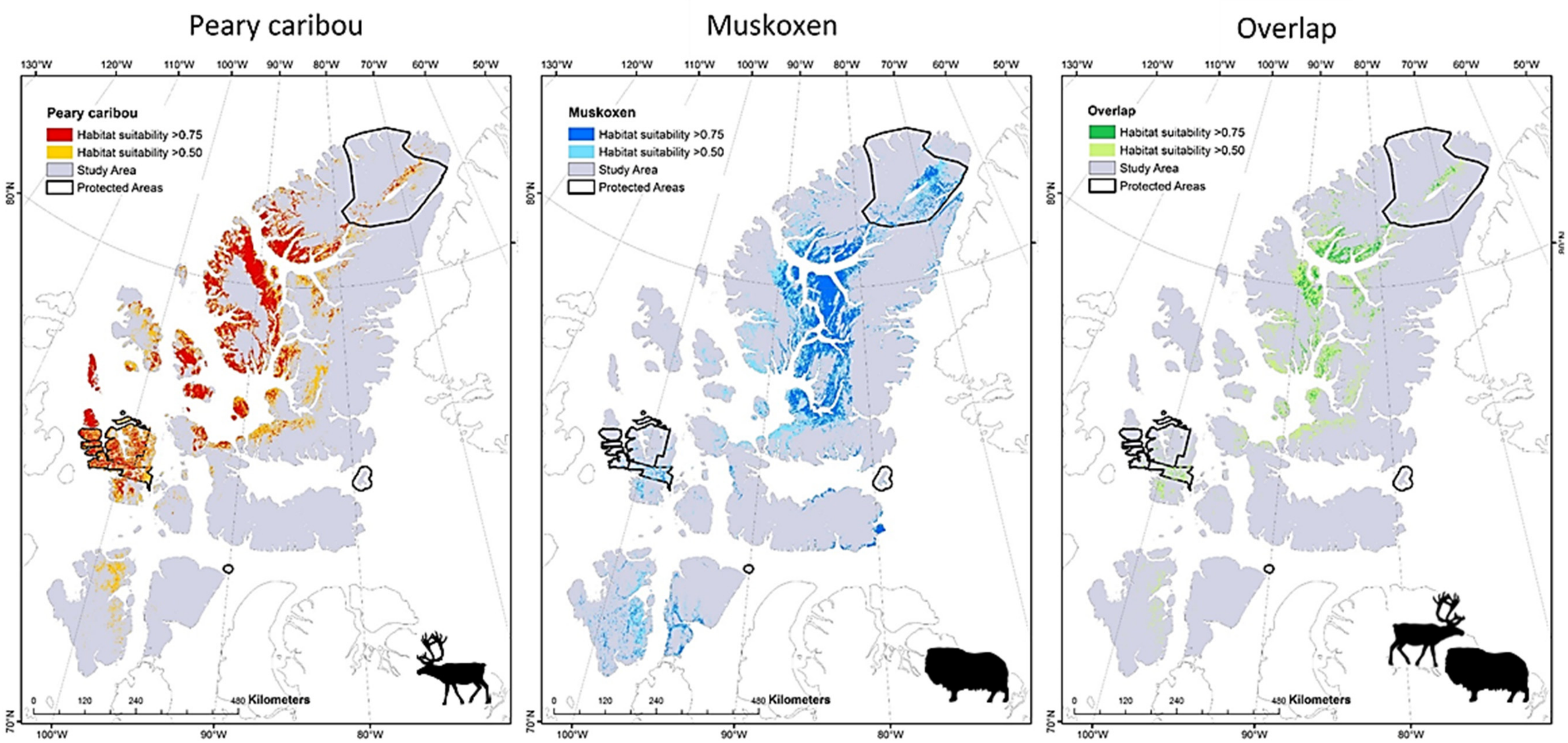


Figure 5. Areas with high habitat suitability from two habitat suitability thresholds (HS > 0.5, HS > 0.75) for Peary caribou and muskoxen, in relation to protected areas. Overlap between species is highlighted separately.

TABLES

Table 1. The estimated relative contribution of each environmental variable, percent contribution and permutation importance (in parentheses), to habitat suitability models for Peary caribou (PC) and muskoxen (MX) for best *abiotic-only* and *abiotic+biotic* models based on $AICc_{OPT}$ (see Table A.2 and Results). An em dash (—) marks variables not included in the models.

Variables	*Abiotic-only*		*Abiotic+biotic*	
	PC	MX	PC	MX
Aspect	1.7 (1.2)	2.4 (2.4)	0.3 (0.1)	0.8 (1.0)
Elevation	30.7 (26.8)	33.1 (32.4)	3.7 (6.2)	3.0 (5.3)
Precipitation	26.7(22.6)	7.2 (7.1)	6.1 (7.6)	2.3 (3.3)
Solar Radiation	0.9 (0.4)	16.4 (12.1)	1.7 (0.2)	2.9 (1.9)
Avg. Snow Depth	8.5(13.3)	10.2 (6.9)	4.3 (8.3)	2.0 (2.7)
Slope	1.2 (1.3)	1.7 (2.8)	0.1 (0.1)	0.4 (0.7)
Avg. Temperature	20.8(25)	2.7 (5.3)	5.4 (5.7)	1.6 (3.1)
Wind Speed	9.5(9.2)	26.3 (31.1)	5.7 (3.4)	10.2 (13.1)
Shrubland-Lichen-Moss	—	—	0 (0)	4.0 (3.5)
Grassland-Lichen-Moss	—	—	46.5 (40.9)	23.2 (19.6)
Barren-Lichen-Moss	—	—	21.7 (16.3)	45.5 (34.2)
Wetlands	—	—	0 (0)	0.0 (0.4)
Barren Land	—	—	2.9 (8.8)	2.2 (8.9)
Distance-to-caribou	—	—	—	2.1 (2.3)
Distance-to-muskoxen	—	—	1.6 (2.4)	—

Table 2. Total area, protected area, and overlapping area with habitat suitability (HS) scores above 0.5 and 0.75 for Peary caribou (PC) and muskoxen (MX), based on *abiotic+biotic* models (AICc$_{\text{OPT}}$). *Abiotic-only* values provided for contrast.

	Area with HS > 0.5		Area with HS > 0.75		Protected Area of HS > 0.5		Protected Area of HS > 0.75	
Model	km^2	% *	km^2	% *	km^2	%**	km^2	%**
Abiotic+biotic models								
Peary caribou	67,068	16.2	33,021	8.0	10,311	15.4	4,294	13.0
Muskoxen	68,333	16.5	31,938	7.7	7,773	11.4	2,888	9.0
Overlap	28,582	6.9	5,384	1.3	2,611	9.1	378	7.0
Abiotic-only models								
Peary caribou	114,977	27.7	41,425	10.0				
Muskoxen	102,688	24.8	34,706	8.4				

* in relation to the terrestrial study area (414,639 km^2)

** in relation to the Area of HS (> 0.5 or > 0.75).

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Data Availability Statement – Observation data are sensitive and archived with the Nunavut Department of Environment. Environment. 2013. Peary caribou and muskoxen observations, High Arctic Islands, 2000-2008. Unpublished Data. Government of Nunavut, Iqaluit, Nunavut. Raster file sources are identified in Table A.1 and freely available.

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APPENDIX A

Table A.1. Original (grey) and derived environmental layers for *abiotic-only* and *abiotic+biotic* distribution models of Peary caribou and muskoxen, Canadian Arctic Archipelago.

Environmental Predictor	Spatial Resolution	Description	Source
Elevation	~ 1 km	DEM; Elevation above mean sea level; continuous 1 - 2394 m	National Centers for Environmental Information
Elevation	577 m	Elevation above mean sea level	Hastings, D.A., Dunbar, P. K., Elphingston, G.M., Bootz, M., Murakami, H., … et al., 1999.
Aspect	577 m	9 categories; Flat, North, Northeast, East, Southeast, South, Southwest, West, Northwest	
Slope	577 m	Continuous; 0-50 degrees	
Bioclimatic Variables	~ 1 km	Monthly Long-term Average 1970-2000	WorldClim Version 2
Min Temp (°C)	577 m	Avg April -May	Fick, S.E. and Hijmans, R.J. 2017.
Max Temp (°C)	577 m	Avg April -May	
Avg Temp (°C)	577 m	Avg April -May	
Prec (mm)	577 m	Avg April -May	
Solar Rad. (kJ m-2 day1)	577 m	Avg April -May	
Wind Speed (m s)	577 m	Avg April -May	
Snow depth	~24 km	Monthly average snow depth by year (2000 to 2008); averaged across months (April-May), and years.	National Snow and Ice Data Center, Canadian Meteorological Centre, Daily Snow Depth Analysis Data
Avg. Snow Depth (cm)	577 m		
Land cover	30 m	2010 Land Cover Map of North America; categorical	Natural Resources Canada
Shrubland-Lichen-Moss	577 m	proportion of subpolar or polar shrubland-lichen-moss (Code 11)	Latifovic, R., Pouliot, D., and Olthof, I. 2017.
Grassland-Lichen-Moss	577 m	proportion of subpolar or polar grassland-lichen-moss (Code 12)	
Barren-Lichen-Moss	577 m	proportion of subpolar or polar barren-lichen-moss (Code 13)	
Wetland	577 m	proportion of wetland (Code 14)	
Barren Land	577 m	proportion of barrenland; <10% vegetation cover (Code 16)	
Snow and Ice	577 m	proportion of snow and ice (Code 19)	
Euclidean distance		Derived in ArcMap using animal observations for each species	Animal observations collected during surveys.
Distance-to-muskox (m)	577 m		
Distance-to-caribou (m)	577 m		

Table A.2. Evaluation of selected models based on $\mathrm{AICc}_{\mathrm{OPT}}$ and $\mathrm{AUC}_{\mathrm{PROC}}$ for Peary caribou (PC) and muskoxen (MX) using *abiotic-only* (A) and *abiotic+biotic* (AB) predictors.

Model	Feature Class	RM	$\mathrm{AUC}_{\mathrm{TRAIN}}$	$\mathrm{AUC}_{\mathrm{TEST}}$	$\mathrm{AUC}_{\mathrm{DIFF}}$	$\mathrm{AUC}_{\mathrm{PROC}}$	$\mathrm{AUC}_{\mathrm{RATIO}}$	$\mathrm{OR}_{\mathrm{MIN}}$	OR_{10}	AICc	# of Para.
$\mathrm{AICc}_{\mathrm{OPT}}$											
PC – A	LQHP	1.5	0.83	0.81	0.02	0.83	1.66	0.002	0.128	14540	91
PC – AB	LQHP	3	0.88	0.87	0.01	0.88	1.75	0.002	0.109	14076	62
MX – A	LQHP	1	0.81	0.80	0.01	0.81	1.62	0.001	0.102	41223	153
MX – AB	LQHP	2	0.87	0.86	0.01	0.87	1.73	0.003	0.113	40007	96
$\mathrm{AUC}_{\mathrm{PROC}}$											
PC – A	LQHP	0.5	0.85	0.83	0.03	0.85	1.70	0.005	0.124	14578	145
PC – AB	LQHP	0.5	0.91	0.88	0.03	0.90	1.80	0.009	0.134	14342	206
MX – A	H	0.5	0.81	0.80	0.01	0.81	1.63	0.001	0.106	41307	185
MX – AB	LQHP	1.5	0.87	0.85	0.01	0.87	1.74	0.002	0.109	40055	134

CHAPTER 5

LANDSCAPE CONNECTIVITY AMONG ISLAND-DWELLING CARIBOU – WHERE ICE AND HUMAN ACTIVITY AMPLIFY HABITAT DISCONTINUITY

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ABSTRACT

Functional connectivity is important to the persistence of wildlife. It facilitates movement and gene flow, and is vital to genetic diversity, metapopulation dynamics, and range shifts in a changing world. Connectivity may be particularly important for large mobile animals. For endangered island-dwelling caribou, known to disperse over large areas including across the Arctic sea ice, the threat of future environmental change is real. Protecting caribou habitat and its linkages is vital and depends on identifying these areas at commensurate, broad spatial scales. Using simultaneous multi-surface optimization, we modelled and mapped the drivers of caribou connectivity across ca. 2 million km^2 of the Canadian Arctic Archipelago. We assessed hierarchical genetic structure, identified two genetically discrete groups, and evaluated individual-based landscape genetics within these groups. We tested whether land- and sea-scape heterogeneity (isolation-by-resistance) or geographic distance (isolation-by-distance) better accounted for gene flow and genetic variation. We found evidence of both isolation-by-resistance and panmixia with absence of isolation-by-distance, depending on the genetic group. For the High Arctic Group, we found that glaciers, low sea ice concentrations and human trails impeded functional connectivity, while intact sea ice was an important platform for inter-island movements. For the Baffin Island Group, our models suggested that gene flow has been unrestricted, emphasizing that organism-landscape relationships can vary across space. Our study identifies critical movement pathways for an iconic Arctic species and supports broad scale conservation and planning across a vast expanse of islands and ice.

1.0 INTRODUCTION

Landscape connectivity among populations is increasingly threatened by rapid environmental change, including habitat loss and fragmentation, with detrimental ecological and evolutionary consequences on biodiversity (Taylor et al. 2006, Heller and Zavaleta 2009, Haddad et al. 2015, Bennett 2017, Thatte et al. 2020). To meet this challenge, the study of functional connectivity — how species respond to patterns of landscape structure (Taylor et al. 1993, Kindlmann and Burel 2008) — has advanced to the forefront of conservation planning (Belote et al. 2020, Hilty et al. 2020, Lemieux et al. 2021). Indeed, functional connectivity is a key conservation metric (Tucker et al. 2018), vital to restore biological diversity, rescue small populations, uphold meta-population structure, support range shifts, and maintain population viability in a changing world (Carmichael et al. 2008, Howell et al. 2018, Marrotte et al. 2020, Peeters et al. 2020).

Functional connectivity is particularly important for large, mobile animals (Benitez-Lopez et al. 2010, Hein et al. 2012, Tucker et al. 2018). Mobile species are prone to decline and extinction (Woodroffe and Ginsberg 1998, Rabinowitz and Zeller 2010), especially where landscapes are altered or permeability is diminished (Soule et al. 2004, Wilcove and Wikelski 2008). Across the globe, human infrastructure and activity have disrupted wildlife movement (Doherty et al. 2021), with significant reductions in movement among many species of nonvolant mammals (Tucker et al. 2018). For some migrating ungulates, long-distance movements have been critically impaired (Kauffman et al. 2021), and in some cases, even eliminated (Harris et al. 2009, Mueller et al. 2011, Williams et al. 2021). Because movement at different spatial and temporal scales supports a myriad of activities (from feeding and predator avoidance to dispersal) and functions (from seed dispersal to metapopulation dynamics; Soule et al. 2004, Kool et al. 2013, Roffler et al. 2016; Tucker et al. 2018), the loss of landscape permeability may have far-reaching consequences for wildlife and ecosystems (Imong et al. 2014, Soule et al. 2004, Tucker et al. 2018, Doherty et al. 2021).

The means to analyze and understand functional connectivity are rapidly expanding (McRae et al. 2008, Luque et al. 2012, Spear et al. 2016, Marrotte and Bowman, 2017, Barbosa et al. 2018, Osipova et al. 2019, Phillips et al. 2021) with increasing emphasis on connectivity conservation (Barnett and Belote 2021, Lemieux et al. 2021, WWF and CanPAC 2021). After decades of poor on-the-ground implementation, this need is urgent (Balbar et al. 2019, Hilty et al. 2020, Brennan et al. 2021). Analytically, relating genetic data to environmental layers is a powerful approach that marries genetic variation with landscape heterogeneity (Balkenhol et al. 2016, Wittische et al. 2019, Thatte et al. 2020). Electrical circuit theory (based on random-walk theory; McRae 2006, McRae et al. 2008) permits the modeling of such functional connectivity: multiple movement pathways can be predicted by accounting for resistance to landscape features (Dickson et al. 2018). Quantifying landscape resistance — the cost of moving across space — is key to these analyses but rarely is the true cost of movement known for any given species (Zeller et al. 2012, Spear et al. 2016). To address this challenge, researchers have developed simultaneous multi-surface optimization that combines genetic differentiation, machine learning, and non-linear transformations to parameterize landscape variables and build composite resistance surfaces (Peterman 2018). By integrating these methods in R (R Core Team 2020), and using Julia language to speed processing (Dickson et al. 2018, Anantharaman et al. 2019), multiple models of landscape resistance can be developed to identify, test and map the drivers of functional connectivity, even over large spatial extents (Dickson et al. 2018, Peterman 2018).

In regions subject to environmental change, such as the Arctic, the need to understand connectivity is urgent. Facing a cocktail of threats, the Arctic has warmed by double the global average (~ 2 C° above the 1981-2010 mean; Ballinger et al. 2020), driving losses in the extent, thickness, and duration of sea ice (Meredith et al. 2019). In turn, this has increased interest and scope in resource development (i.e., resource extraction, transportation infrastructure; National Research Council 2015, EJA 2019) and shipping (Dawson et al. 2018, Meredith et al. 2019, PAME 2020). In the Canadian Arctic, during 1990-2015, the distance travelled by ships grew by over 150% (Dawson et al. 2018). To make matters worse, climate change threatens the complete loss of summer and fall sea ice within 65 years (Jenkins et al. 2016). Such pressures underscore the need to identify and protect connectivity, particularly for species that cross between islands on sea ice, as conservation opportunities are quickly vanishing (Hodgson et al. 2009, Jenkins et al. 2020, WWF and CanPac 2021).

For species that use a vast matrix of habitats and ecosystems, the challenge of understanding and conserving connectivity is especially acute (Geffen et al. 2007, Marrotte et al. 2020, LaCava et al. 2021). Caribou (*Rangifer tarandus*) are a textbook example — a vagile, wide-ranging species known to disperse over large areas that include Arctic sea ice (Poole et al. 2010, Jenkins et al. 2016, Peeters et al. 2020). In the Canadian Arctic Archipelago, caribou distributions are driven by vegetation cover and are associated with areas of low elevation (Jenkins et al. 2020, Jenkins et al. 2021 [in prep]). Rugged, mountainous terrain and extensive glaciers are largely unsuitable and likely act as barriers to movement (Jenkins et al. 2018, Jenkins et al. 2020, Jenkins et al. 2021 [in prep]). Some caribou use sea ice as a platform for seasonal inter-island or island-mainland migration (Miller et al. 2005, Poole et al. 2010, Jenkins and Lecomte 2012), for dispersal, and for escape during severe weather (Miller and Barry 2009). Nevertheless, these island-dwelling caribou are genetically structured at multiple scales (i.e., subspecies, populations, and subpopulations; Jenkins et al. 2016, Klütsch et al. 2017, Jenkins et al. 2018), signifying that their movements and dispersal are restricted. Some island populations have declined substantially (i.e., Baffin Island; Jenkins et al. 2012, Campbell et al. 2015), while others face possible extirpation (i.e., Prince of Wales, Somerset and Russel island; Gunn et al. 2006; Axel Heiberg Island; Mallory et al. 2020). The potential for their recovery and persistence is linked in part to the flow of individuals and genes — a function of both land- and sea-scape connectivity (Jenkins et al. 2016, Jenkins et al. 2018). Although connectivity varies across this patchy, resource-poor network of islands and ice (Jenkins et al. 2016, 2018, Mallory and Boyce 2019), how the combination of land- and sea-scape features influences gene flow is largely unknown.

Here, using simultaneous multi-surface optimization, we modelled and mapped the drivers of caribou connectivity across ca. 2 million km^2 of the Canadian Arctic Archipelago. To define the spatial extent of our analyses, we first assessed hierarchical genetic structure based on 18 microsatellite loci, then identified spatially and genetically discrete groups and evaluated individual-based genetic variation within these groups. We tested whether land- and sea-scape heterogeneity (the hypothesis of isolation by resistance [IBR]; McRae 2006) or geographic distance (the hypothesis of isolation by distance [IBD]; Wright 1943, 1946) influenced gene flow and patterns of genetic variation. Although caribou are highly mobile, we expected that caribou connectivity would be influenced by discontinuity in terrestrial habitat — particularly, fragmentation by sea ice and glacial ice. We predicted that glaciers would impede movement (Hansen et al. 2010, Rosvold 2016, Peeters et al. 2020) while intact sea ice would enhance connectivity (Jenkins et al. 2018, Peeters et al. 2020). Furthermore, because caribou are sensitive to anthropogenic disturbance (Mahoney and Schaefer 2002, Schaefer 2003, Vistnes and Nellemann 2008, Festa-Bianchet et al. 2011, Plante et al. 2018), we predicted that functional connectivity would be obstructed by human infrastructure and activity. Finally, we used our best models to identify and map functional connectivity for caribou across the vast Arctic biome.

2.0 METHODS

2.1 Study Area

Our study area is remote; it lies between 62° to 82° north and 60° to 107° west. Approximately 2,024,000 km^2, it extends across the central and eastern High Arctic islands, Canada. Islands vary in size (i.e., <1 km^2 to >500,000 km^2), shape and isolation; they are all situated within the Arctic Cordillera and Northern Arctic ecozones. The area is topographically heterogeneous, extending from low-lying plains to steep mountainous terrain (up to ~2600 m asl) where glaciers and icefields are extensive (Figure 1A). The treeless landscape is characterized by barren grounds and patchy tundra vegetation (i.e., grasses and sedges, mosses, lichens, and dwarf shrubs; Latifovic et al. 2017). Although largely uninhabited by humans, 13 communities and three weather stations (Eureka, Nanisivik [a former mining community], and Canadian Forces Station Alert) are connected by air (Tretheway et al. 2021), extensive snowmobile/ATV trails (Freeman 1976a, 1976b, 1976c, Aporta 2004, 2009), and seasonal (mainly open-water) shipping routes (Johnston et al. 2017, Dawson et al. 2018; Figure 1B, C). Roads occur at a small scale (all unpaved), within communities and at weather stations such as Eureka. With the exception of Arctic Bay and Nanisivik (21 km apart), no communities or weather stations are linked by road (Tretheway et al. 2021).

To advance our results for conservation and management, we set our study area to match Nunavut's jurisdictional boundary in the High Arctic (Keller et al. 2015). Our study area encompasses the eastern range of endangered Peary caribou (*Rangifer tarandus pearyi*; Species at Risk Act 2011 [www.sararegistry.gc.ca]) and the most northern distribution of threatened Barren-ground caribou (R. t. groenlandicus; COSEWIC 2016) in Canada.

2.2 Genetic Data

We reanalysed a subset of genotypes previously used to investigate population structure and genetic diversity of caribou across northern Canada (Jenkins et al. 2018) but increased the number of microsatellite markers by two (i.e., n=18, Koskinen et al. 2004; details in Supplemental Information). Here, we focused on island-dwelling caribou in the eastern Arctic Archipelago (Figure 1A). The sampling included 252 individuals (135 females, 108 males, 9 unknown) from 12 island or multi-island herds (Jenkins et al. 2011, Nagy et al. 2011, Jenkins et al. 2018; Table 1S). We expanded genetic diversity and structure analyses from Jenkins et al. (2018) and used the results to establish the spatial extent of our landscape genetic analysis (see Supplemental Information; Figure 1S, 2S).

2.3 Landscape genetics

To understand how land- and sea-scape heterogeneity influence gene flow, we measured isolation by distance (IBD) and isolation by resistance (IBR) among individuals, within each genetic group, using a suite of rasterized data on natural and anthropogenic features. Given that caribou are highly mobile (Bergman et al. 2000) and, in the Arctic Archipelago, are unevenly distributed and exhibit spatial overlap between fine-scale genetic clusters (Jenkins et al. 2018; this study), we analysed landscape genetics using an individual approach (Miller et al. 2018, Marrotte et al. 2020) at a level where genetic groups were spatially discrete (High Arctic Island and Baffin Island groups). Here we focused on samples collected across the study area during 1998-2013 (see Supplemental Information). We thinned observations to one per raster cell (at 1-km resolution) to help minimize spatial autocorrelation (see below; Marrotte et al. 2020).

2.3.1. Genetic Distance - We estimated pairwise genetic differentiation between individuals within each genetic group, specifically, the proportion of shared alleles (Dps; Bowcock et al. 1994; Shirk et al. 2017) using adegenet (Jombart 2008) in R, and Rousset's a (AR; Rousset, 2000; Shirk et al. 2017, Peeters et al. 2020) using the program SPAGeDI (Hardy and Vekemans 2002). Because these measures of genetic distance were highly correlated (Mantel correlation coefficient; $|r| > 0.85$), we used 1 minus the proportion of shared alleles as a measure of genetic distance in our models (Shirk et al. 2017, Kjeldsen et al. 2019, Thatte et al. 2020; Marrotte et al. 2020).

2.3.2 Environmental Data - Based on documented relationships of caribou and the environment, we identified a suite of environmental variables that putatively influence caribou connectivity in the Canadian Arctic Archipelago (Table 2S). We represented these variables as continuous raster layers and resampled them to 1-km resolution to balance resolution and the computation time of landscape connectivity analyses. We used ArcMap 10.6.1 (ESRI 2018a) or ArcGIS Pro (ESRI 2018b) for geoprocessing. Landscape variables included: (1) Elevation (Jenkins et al. 2020), (2) Ruggedness (Fullman et al. 2017), (3) Proportion of Vegetation (i.e. grass and barren lichen-moss; Jenkins et al. 2020), (4) Proportion of Glacier (Hansen et al. 2010, Rosvold 2016, Peeters et al. 2020), (5) Inverse Fall, Spring, and March Sea Ice Concentration (Jenkins et al. 2016, 2018, Dumond et al. 2013, Peeters et al. 2020), (6) Distance to Nearest Community and (7) Distance to Nearest Trail (Vistnes and Nellemann 2008, Polfus et al 2011, Newton et al. 2015, Boulanger et al. 2021; details in Table 2S). To recognize the natural discontinuity in terrestrial habitat, we included a sea ice layer (above) in all models; this layer differentiated between land and average sea ice concentrations (derived from monthly Arctic sea ice data for 1979-2015 [Table 2S]; National Snow and Ice Data Center, University of Colorado, Boulder, CO, USA). We used the inverse of sea ice concentrations as it seemed intuitive when relating sea ice values to resistance.

All layers were standardized in resolution (cell size = 1 km), extent and projection (i.e., North Pole Lambert Azimuthal Equal Area, Central Meridian 84°W, Latitude of Origin 78°N). We anticipated that human activities would be spatially aggregated. To evaluate this possibility, we separately mapped the Low Impact Shipping Corridor which represented ~ 80% of ship travel during 2012-2014 (Chénier et al. 2017) and we correlated Distance to Shipping Corridor to other rasterized anthropogenic features, including Distance to Trail. Mining camps, roads and airstrips associated with Baffinland Iron Mines on Baffin Island are extensive but were not included here as they were relatively recent features on the landscape. That is, much of the development overlapped with or occurred after the period of sample collection (i.e., Regulatory Approval for project 2012; lupit.nunavut.ca/portal.search.php).

To address collinearity among our predictor variables, we evaluated raster correlations using Raster Tools in ArcMap 10.6.1 (ESRI 2018) and variance inflation factor (VIF) using the R package usdm (Naimi et al. 2014). We retained one variable in each pair or group of highly correlated features ($r >|0.7|$) and reduced the total variable set to a target VIF of <3 (Zuur et al. 2010).

We used our genetic cluster analysis to help identify the spatial extent of raster layers. Specifically, islands encompassing discrete genetic clusters were considered separately; each was buffered by 70 km (approximately 10% of the island group width) to reduce edge effects during analysis (Koen et al. 2010, Koen et al. 2014). Our buffer intercepted Greenland, which was beyond the extent of our land cover data (i.e., the Canadian border). Thus, to complete our analysis, we simply partitioned each land cover type equally among these cells and removed the buffer from our final map(s) (Koen et al. 2010, Marrotte et al. 2020).

2.3.3 Resistance Surfaces - To address the complexity of assigning costs to multiple landscape features, we used a genetic algorithm optimization framework, which aims to improve the relationship between pairwise genetic distance and pairwise landscape resistance (Peterman 2018). Specifically, we created and optimized resistance surfaces at the level of individuals within discrete genetic groups (Anantharaman et al. 2019; Marrotte et al. 2020; LaCava et al. 2021) using functions in the R package ResistanceGA (v 4.1-0.45; Peterman et al. 2014, Peterman 2018). Following Marrotte et al. (2020), we used the genetic algorithm default parameters, but modified transformations to include inverse-reverse monomolecular and inverse monomolecular data transformations for continuous surfaces (Zeller et al. 2017, Peterman 2018) in line with the predicted positive or negative effect of variables on gene flow. Once all raster values were rescaled between 0 and 10 (i.e., to allow direct comparison; Peterman 2018), we calculated pairwise ecological distance using genetic sample locations and multiple environmental rasters in Circuitscape Julia (v0.1.0; Anantharaman et al. 2019). During optimization, ResistanceGA used linear mixed-effects models with a maximum likelihood population effects parameter (here based on individuals) to evaluate genetic distance as a function of ecological distance (drawing on R package "lme4'; Bates et al. 2015). We used log-likelihood (LL) as the objective function, such that each optimization attempts to improve model fit by maximizing the LL (Peterman 2017, Peterman 2018). To test for IBD, we estimated pairwise geographic distance using a raster surface where all cells were given a value of 1 (representing a homogeneous surface). To validate models, we ran a subset of our models twice, as recommended by Peterman (2018). Notably, all multi-surface models included a land and sea-ice layer to recognize the stark dichotomy in our study area, and the terrestrial nature of our study species (Marrotte et al. 2020). For our best MLPE models, we present the log-likelihood as a measure of model performance, and the marginal (m) and conditional (c) R2 values, which represent the variance explained by fixed versus fixed and random factors.

2.3.4 Model Selection - Using ResistanceGA (Peterman 2018), we carried out simultaneous multi-surface optimization and used a model selection framework to compare their ability to model genetic distance. We compiled each set of candidate models (including the IBD [or Distance] and intercept-only models [Null]) and selected our best model based on the Akaike Information Criterion corrected for sample sizes (AICc; Burnham and Anderson 2002). Because IBD is inherent in all models, we compared our suite of models to IBD and included the statistical Null to clearly identify if IBD was supported in the absence of IBR (Marrotte et al. 2020, Peterman and Pope 2021). Notably, we used the default to estimate k, where k equals the number of parameters optimized plus the intercept (k-category 2; Peterman 2017). Thus, for each continuous surface, k equals 3 plus 1 for the intercept (i.e., the scale parameter, shape parameter, transformation, and intercept). For each categorical surface, k equals the number of categories plus one for the intercept. To assess the 'robustness' of our results to different approaches to penalizing models, we also calculated AICc based on k-category 4, where k was specified as the number of surfaces plus the intercept (Peterman et al. 2014; Peterman 2018).

2.3.5 Model Validation - To validate our model selection results and reveal sensitivity owing to specific individuals, we completed a pseudo bootstrap analysis using a subsample of individuals in ResistanceGA (Peterman 2018). Specifically, we subsampled the optimized resistance distance and genetic distance matrices at 75% and with 5000 iterations re-evaluated the resistance-genetic distance relationship for our models (Peterman 2018, Wittische et al. 2019). We refit the linear mixed-effects models and ranked our models based on average AICc scores, derived from k-category 2 values.

2.3.6 Variable Contributions and Response Curves - For each model we estimated the percent contribution of each variable surface to the final composite resistance surface using ResistanceGA (Peterman 2018). Additionally, we generated response curves to show the relationship between the original data and the transformed values for each predictor variable (Peterman 2018).

2.4 Mapping Functional Connectivity

Using electrical circuit theory and our best species-specific resistance surface, we modelled and mapped functional connectivity (McRae et al. 2008, Dickson et al. 2016, 2018, Marrotte et al. 2020) using a point-based method (Koen et al. 2014, Phillips et al. 2021). Specifically, we randomly placed nodes around the perimeter of the study area (i.e., 95 peripheral nodes) and estimated the current density across our best composite resistance surfaces using Circuitscape in Julia (Anantharaman et al. 2019). Next, we cropped the current density maps to remove the nodes and buffer (Koen et al. 2014). The resulting cell values (i.e., current density) can be interpreted as "the probability of use by a moving animal" (McRae et al. 2008, Koen et al. 2014, Wittische et al. 2019) — here, a prediction of functional connectivity for island-dwelling caribou. Low current densities are indicative of multiple movement pathways while higher values identify pinch points where movement options are constrained (McRae et al. 2008).

3.0 RESULTS

3.1 Landscape genetics

After addressing spatial autocorrelation by thinning the multi-locus genotypes, we analysed landscape-genetic relationships with a total of 160 unique individuals representing two spatially disjunct genetic clusters (High Arctic Island group, 112 Peary caribou; Baffin Island group, 48 barren-ground caribou; Figure 2 and 2S).

3.1.1 Genetic Distance - For Peary caribou, genetic distance (1 minus the proportion of shared alleles) ranged between 0.25 - 0.89, and 0.36 - 0.83 for Barren-ground caribou. In the High Arctic group (study area 785,605 km^2), individual Peary caribou were separated by geographic distances up to 1,000 km, while Barren-ground caribou in the Baffin Island group (study area 1,089,055 km^2) were separated by as much as 1,200 km (Figure 2).

3.1.2 Environmental Data - Through correlation and VIF analysis, we reduced our candidate environmental layers (see Supplemental Information). For the High Arctic group, we found strong positive correlations among Fall, Spring and March Sea Ice Concentrations ($r > 0.95$), and between Elevation and Glaciers ($r = 0.80$; Table 3S); these relationships held true for the Baffin Island group, although the correlation between Elevation and Glaciers was lower ($r = 0.65$; Table 4S). We retained Glaciers over Elevation to reduce correlations with other variables (i.e., Ruggedness, Sea Ice Concentration). Regarding sea ice, we retained Fall Sea Ice as it captured the greatest across-year variation in ice concentrations.

Our primary suite of predictor variables therefore included Proportion of Vegetation, Ruggedness, Proportion of Glacier, Distance to Trail, and Inverse Fall Sea Ice Concentration (Figure 4). For the Baffin Island group, given the relatively high number of communities, we also tested Distance to Community (independently of Trails). Here, communities were primarily coastal and ranged in size from 482 to 7543 residents (Nunavut Department of Health 2016).

3.1.3 Multi-surface Resistance Optimization - Using multi-surface optimization in ResistanceGA, we optimized various combinations of our predictors, and we ranked our models to identify which composite surface best explained genetic differentiation across our two study areas (High Arctic group, Table 1; Baffin Island group, Table 2).

For the High Arctic group, our best composite model included Distance to Trail, Proportion Glaciers and Inverse Fall Sea Ice Concentrations. The marginal and conditional R^2 for this model were 10.1 % and 26.5 %, respectively (Table 1). Inverse Fall Sea Ice Concentration contributed most to the optimized resistance surface (41.9%), followed by Distance to Trail (39.3%) and Proportion Glacier (18.8%). Response plots for Sea Ice show that resistance increased when transitioning from land to sea ice and continued to rise with declining sea ice concentrations (shown here as inverse values; Figure 4). For Trails, proximal areas had the highest resistance (i.e., maximum value = 222), declining steeply towards 0 for approximately 100 km (Figure 4). Lastly, while low proportions of glacier created little resistance, resistance increased steeply when proportions of glacier (per cell) were high (i.e., 0.8-1; Figure 4). Overall, the slope of the model was positive (global beta; b = 0.024, SE = 0.001), indicating that genetic distance and effective resistance were positively correlated. Our bootstrap analysis, with subsampling at 75%, strongly supported the identified top model for the High Arctic group, as well as identifying the same 5 best models (Table 2).

In contrast, for the Baffin Island group, we found that the statistical Null model (intercept-only model) ranked first (Table 3); that is, Barren-ground caribou appeared panmictic and gene flow uninhibited by any of the landscape features investigated here, including geographic distance (no IBD) for individuals distant up to 1200 km apart.

For the High Arctic group, varying our approach to penalize model complexity (k = category 2 vs k = category 4) did not alter our top-ranked model. However, for the Baffin Island group, the composite model — Distance to Community and Inverse Fall Sea Ice Concentration — was best when k values were limited to the number of surfaces plus the intercept. Although only marginally better than the statistical Null model based on AICc, this result was supported by both the highest log-likelihood and marginal R2 (Table 3; see also Supplemental Information).

3.1.4 Functional Connectivity - Maps of current density illustrated heterogeneous patterns of caribou connectivity across the High Arctic Islands with current values varying between 0.01 and 169.4 (Figure 5). Probability of movement generally appeared greater on land than sea ice, while in the eastern High Arctic, glaciers appeared to funnel terrestrial movements. Additionally, connectivity across sea ice appeared to be greater where land was proximal, and trails were absent.

4.0 DISCUSSION

Understanding how landscape features govern functional connectivity is critical for conservation as anthropogenic forces extend even to the most remote areas of the globe (Huntington et al. 2007, Post et al. 2009, Humphries and Huettmann 2014, Pizzolato et al. 2016, Leihy et al. 2020). In the Canadian Arctic, this is complicated by the natural fragmentation of terrestrial habitat via seasonally dynamic sea ice (Meier et al. 2014, Jenkins et al. 2016). Still, by using an individual approach, applying simultaneous multi-surface optimization, and testing discrete genetic groups, we found evidence of both IBR or panmixia with absence of IBD, depending on the genetic group considered. In line with our prediction, we found that habitat discontinuity — related to glaciers and reduced sea ice concentration — inhibited functional connectivity, that intact sea ice was an important platform for inter-island movement, and that trails impeded gene flow — but only for the High Arctic group. For the Baffin Island group, our models suggested that gene flow has been unrestricted by the natural and anthropogenic features tested here. These divergent results emphasize that organism-landscape relationships can vary across space.

Indeed, context is important (Robertson et al. 2018). Spatial differences in environmental characteristics can lead to regional discrepancies in the drivers of functional connectivity (Yannic et al. 2018, LaCava et al. 2021). In the Arctic Archipelago, our findings varied starkly by genetic group, a feature parallel to other studies that focused on large, heterogeneous spaces such as those occupied by mule deer (Wyoming, USA; LaCava et al. 2021), bobcat (California, USA; Kozakiewicz et al. 2019), or caribou (Holarctic, Yannic et al. 2018). While the two subareas of our study shared many natural and anthropogenic features, we were able to capture considerable spatial variation in land- and sea-scape structure. For example, the High Arctic and Baffin groups differed in the extent and fragmentation of land, heterogeneity in elevation and glaciers, and degree of anthropogenic disturbance (Figure 4). Our contrasting results — for example, that sea ice influences gene flow in the fragmented habitat of the High Arctic but not in the more continuous terrestrial landscape of Baffin Island — emphasizes the immense variety in island size (<1 km^2 to >500,000 km^2) and sea ice fragmentation in the Canadian Arctic Archipelago.

Sea ice is a dominant feature in the Arctic, and despite its importance to many species (caribou, Jenkins et al. 2016, Peeters et al. 2020; polar bear, Regehr et al. 2016, Laidre et al. 2018, Johnson et al. 2020; arctic fox, Geffen et al. 2007, Noren et al. 2011, Fuglei and Tarroux 2019; Ivory Gull, Gilg et al. 2016), movement across sea ice can be risky (Poole et al. 2010, Dumond et al. 2013). We found that sea ice connectivity in the High Arctic caribou group was most prominent between neighbouring patches of land (Figure 5), particularly areas with intact sea ice. Disturbance by trails impedes connectivity in the southern portion of this region, even on sea ice; contrasting with the extreme north. Indeed, Peary caribou rely on sea ice to move among islands (Miller et al. 2005, Jenkins et al. 2016) and to disperse — a finding supported in our analysis by admixed individuals and the mixing of genetically distinct individuals across space (Figure 2S). Still, our results reveal that this critical movement platform also impedes movement, particularly where sea ice is more dynamic (Figure 4).

On land, perennial ice can similarly influence the distribution and movement of wildlife (Rosvold 2016, Jenkins et al 2020, Peeters et al. 2020). Although glaciers provide important habitat to many organisms (Rosvold 2016), areas with high proportions of glacier (at elevation) were an obstacle to caribou gene flow. Glaciers represent a similar hindrance for Svalbard reindeer in the Norwegian Arctic (Peeters et al. 2020), and, based on species distribution models, they represent low habitat suitability for Peary caribou and muskoxen in this region (Jenkins et al. 2020). Nevertheless, caribou do travel across glaciers but apparently only rarely (Hemming 1971, Hansen et al. 2010, Rosvold 2016). Crevasses, high elevations, and limited food availability on terrestrial ice (Huston and Wolverton 2009) may discourage such movement given its higher energetic costs and travel risks (Hansen et al. 2010). Our connectivity maps (Figure 5) highlight this barrier effect of glaciers; it also identifies important movement corridors that skirt glaciers and thus facilitate connectivity. Such areas are of high conservation value, to be preserved as a priority, particularly as human pressures escalate (Venter et al. 2016).

Human activity and infrastructure are increasing in the Arctic (Sherwin and Bishop 2019), and at the same time, a long-established and enduring network of trails connect settlements, and settlements with sites of cultural and social significance (Freeman 1976a,b,c, Aporta 2004, 2009). Travel routes over land and sea ice are testament to multigenerational land use of Inuit (Aporto 2009, 2011), and demonstrate remarkable continuity across time (Aporta 2011). Today, air travel and shipping routes are increasing in many of these same areas (Figure 1). Although our predictions recognized the potential for anthropogenic impacts, our finding that trails significantly influenced caribou connectivity was somewhat surprising. Still, remote roads and unpaved linear features (i.e., hiking trails and tracks) have similarly imposed high resistance to the movement of female mouflon (Ovis gmelini) – identified as a behavioural response to non-barrier features versus a physical response to structures (Portanier et al. 2018). Indeed, a growing body of literature highlights the spatial response of wildlife to human disturbance (Nellemann et al. 2001, Cushman et al. 2010, Bötsch et al. 2018, Boulanger et al. 2021, Ghoddousi et al. 2021). For caribou, such disturbances include snowmobiles (Seip et al. 2007), linear features (ATV trails, Newton et al. 2015; roads, Leblond et al. 2013) and ice breaking (Dumond et al. 2013). Notably, northern trails are commonly associated with hunting (Freeman 1976abc, Aporta 2004, 2009, 2011, Taylor 2005), an activity with marked impacts on the movement and range use of harvested species (Plante et al. 2018, Doherty et al. 2021, Ghoddousi et al. 2021, McNamara et al. 2021). Our study region is open and treeless, and the impacts of humans occur over greater distances in these environments (Benitez-Lopez et al. 2010). Because trails are moderately correlated with other human features (i.e., communities [and associated airports], shipping routes), we cannot discount that this pattern may be amplified by these associations and reflect cumulative anthropogenic forces. Indeed, it can be challenging to tease apart the potential compounding effects of human infrastructure and the sensory disturbance associated with their use (Colman et al. 2017; Bötsch et al. 2018).

Anthropogenic alterations can have powerful influences on patterns of genetic diversity and differentiation (Ghoddousi et al. 2021, this study). Yet, for the Baffin Island group, an area with 11 communities and over half of Nunavut's human population (Nunavut Department of Health 2016), caribou gene flow appears unrestricted by both anthropogenic (i.e., trails) and natural factors – a surprising result. Here, caribou were widely dispersed over 500,000 km^2 of almost continuous terrestrial space with extensive, suitable habitat (Jenkins et al. 2021), characterized by high coverage of vegetation (Figure 4). Because trails were positively related to vegetation (as distance to trails increases, the proportion of vegetation decreases; r = -0.24) it is possible that the negative effect of trails, as we detected in the High Arctic, was counteracted here by the benefits of well-connected quality habitat — in other words, a trade-off between risk and resources (Marchand et al. 2015). Historic radio-collar observations also confirm some overlap and potential mixing of caribou (from north and south Baffin) on the central Baffin calving grounds and small proximal islands (Government of Nunavut, unpublished data), although observations are limited. Notably, substantial population declines and likely range retraction (Jenkins et al. 2012, Campbell et al. 2015), along with recent mining roads (proposed railroad), multiple mining camps, airstrips, shipping ports, open-pit mining, resource exploration, and increased access (Nunavut Impact Review Board, Mary River Project; nirb.ca/project/123910), may create the conditions for future isolation on Baffin Island. Landscape genetic analyses, such as ours, are unlikely to detect recent changes to landscape connectivity (Landguth et al. 2010, Yannic et al. 2021).

Worldwide, the fragmentation and loss of terrestrial and marine habitat are recognized as a grave threat to biodiversity (IPBES 2019). The impacts are far reaching. The loss of population connectivity can increase isolation, reduce fitness and threaten population persistence (Pavlova et al. 2017, Thatte et al. 2018, Zacarias and Loyola 2018). In response, the protection and restoration of ecological connectivity has emerged as a fundamental planning objective (Hilty et al. 2020, Lemieux et al. 2021) — a goal emphasized in the post-2020 global biodiversity framework (CBD 2020). In the Arctic, planning initiatives such as the Northern Marine Transportation Corridors project (NMTC; Chénier et al. 2017), the Canadian Arctic Marine Priority Areas for Conservation (2021), the Pan-Canadian Approach to Transforming Species at Risk Conservation in Canada (Environment and Climate Change Canada, 2018) and the Nunavut Land Use Plan (draft 2021) are likely to influence the long-term persistence of Arctic caribou. Such plans can serve as tools for the protection of caribou habitat, functional connectivity, and the critical ecosystem processes they confer. Yet, scientific data on the connectivity of terrestrial wildlife across both land and sea, particularly genetically informed functional connectivity, are largely overlooked – likely exacerbated by the conventional terrestrial-marine dichotomy, lack of clarity among jurisdictions, reliance on sparse movement data, and the complexity of modeling this process. Importantly, this study highlights how landscape genetics can inform conservation planning and protection, by revealing multiple generations of movement and gene flow across even the most remote areas of the Arctic.

For species of conservation concern, understanding and conserving connectivity are vital — supporting demographic and genetic rescue (Jangjoo et al. 2016), recolonization (Hemmingmoore et al. 2020), and potential range shifts under climate change (Littlefield et al. 2019 [review], Marrotte et al. 2020). For threatened island-dwelling caribou, an ecologically important and especially remote species, the current influence of ice and human trails, coupled with the prospects of rapid environmental change, emphasize connectivity is a conservation priority. If missed, the long-term consequences could be significant – the breakdown of metapopulation structure, the extirpation of island populations, and the loss of genetic diversity and adaptive potential

(Colella et al. 2020). The conservation implications of our study are clear: protect extant habitat and connectivity, plan for redundancy to provide animals with spatial flexibility in habitat and movement pathways (Wolf et al. 2015), and address climate change with strong limits on greenhouse gases (IPCC 2021).

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6.0 FIGURES

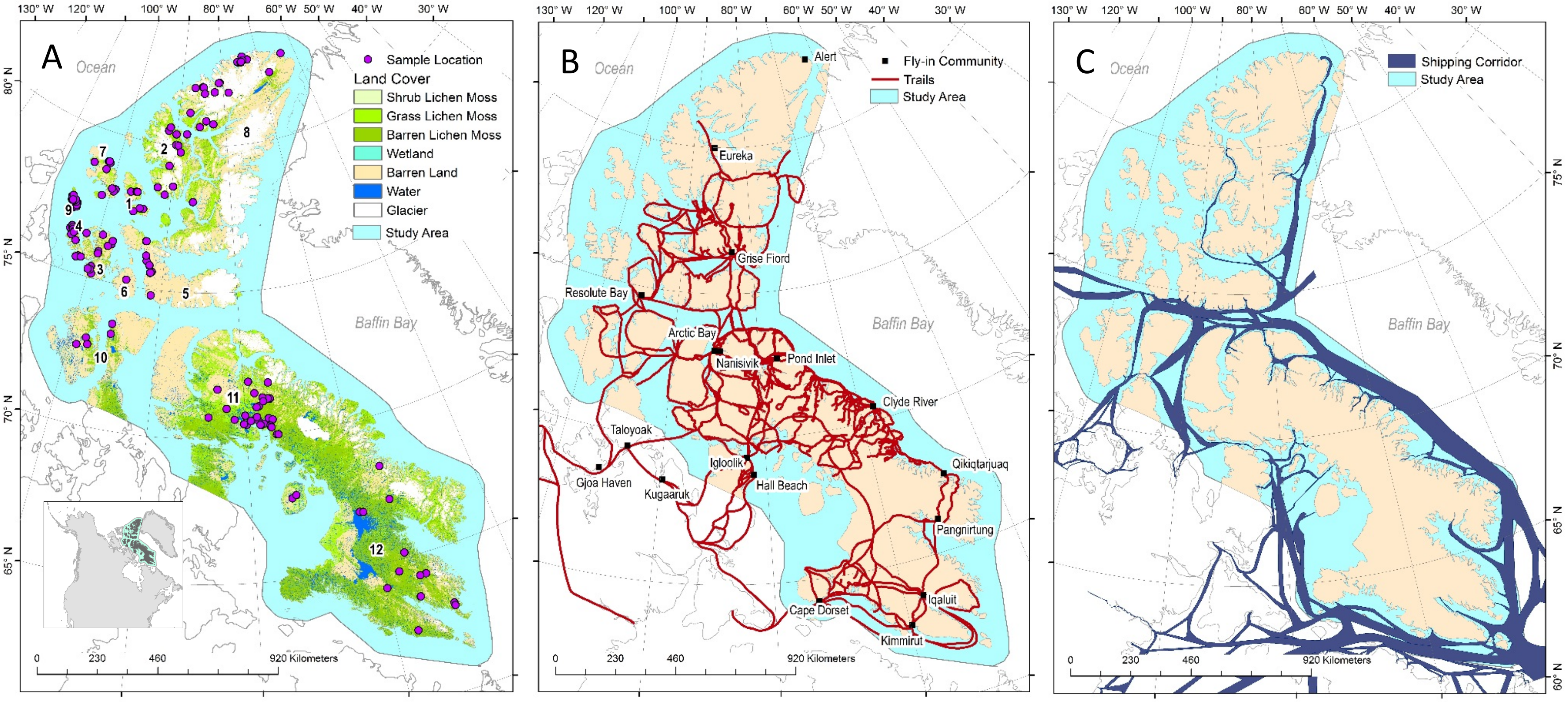

Figure 1. (A) The study area illustrating the land cover types, sample locations, and major islands: (1) Amund Ringnes and Cornwall, (2) Axel Heiberg, (3) Bathurst, (4) Cameron, (5) Devon, (6) Cornwallis, (7) Ellef Ringnes and King Christian, (8) Ellesmere, (9) Lougheed, (10) Prince of Wales and Somerset, (11) north Baffin, and (12) south Baffin; (B) Trails (Aporta 2004, 2009, Table 2S) and communities, including three weather stations, and (C) Shipping corridors (The PEW Charitable Trusts 2016, Chenier et al. 2017, Dawson et al. 2020).

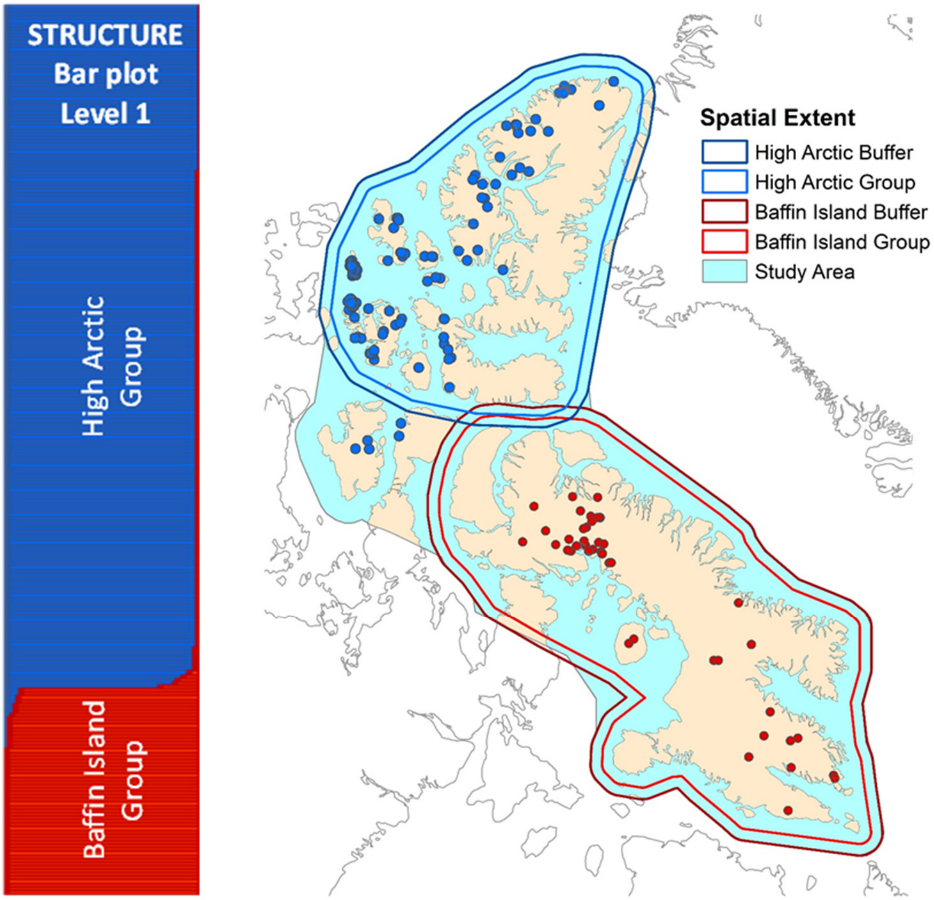

Figure 2. Two genetic clusters of caribou in the Canadian Arctic inferred with a Bayesian cluster analysis on 252 caribou genotypes — High Arctic Island (blue) and Baffin Island (red) groups — and the spatial extent used for the landscape genetic analysis. Buffers (70 km) for each group are also depicted.

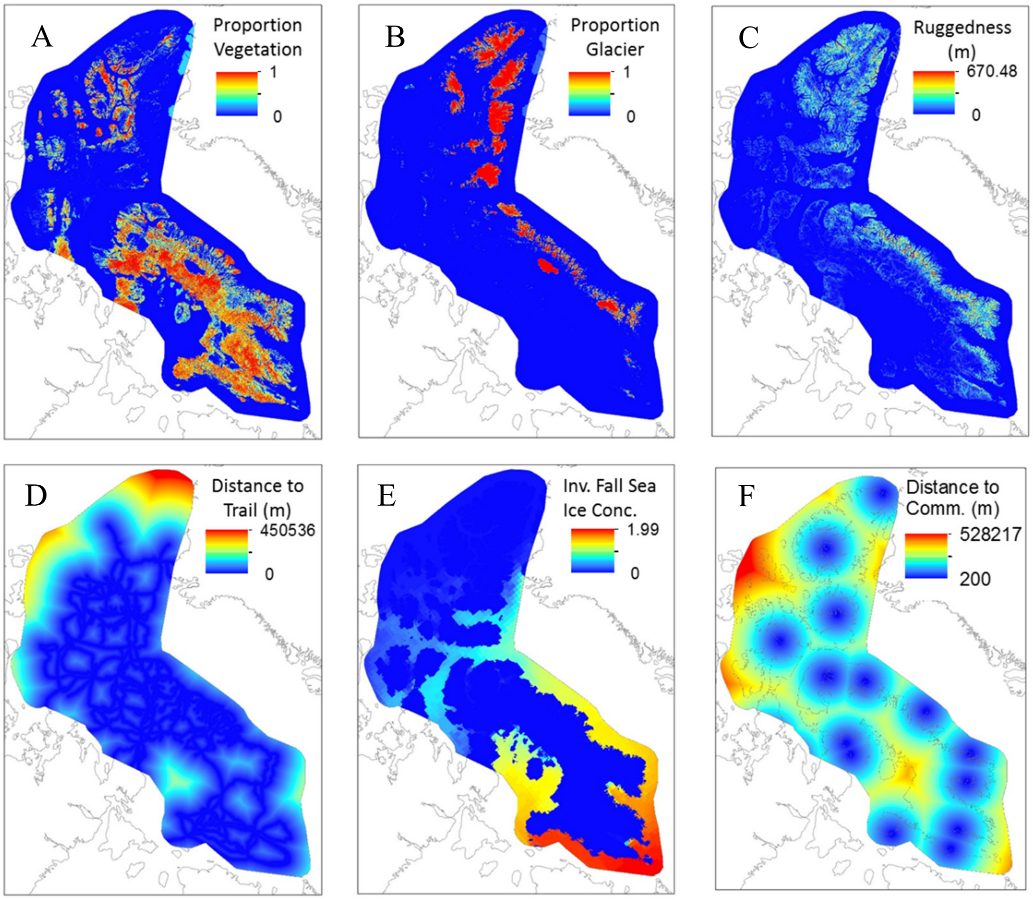

Figure 3. Description and extent of environmental variables used in the landscape genomic analyses. The six environmental features represented as continuous raster layers (1-km resolution). These variables included: (A) Proportion Vegetation, (B) Proportion Glacier, (C) Ruggedness, (D) Distance to Trail, (E) Inverse Fall Sea Ice Concentration, and (F) Distance to Community. See Table 2S for raster details.

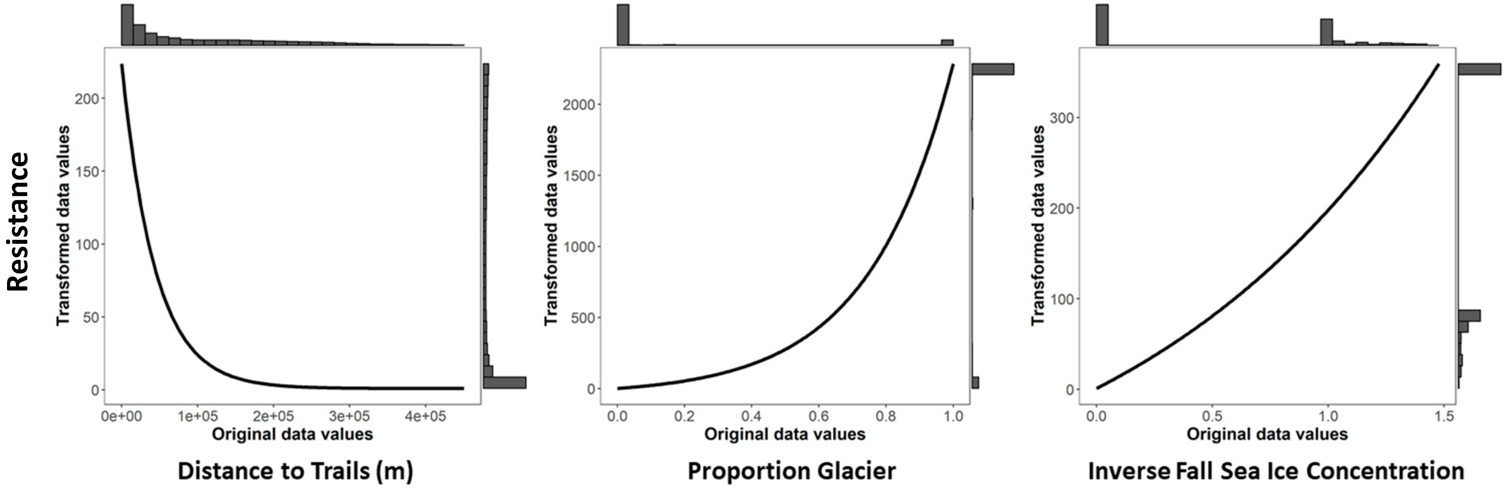

Figure 4. Response plots for each variable retained in the top ranked model (e.g., Trails, Glaciers and Fall Sea Ice) for the High Arctic group, illustrating the transformation of original data to resistance values. The frequency distribution of the original data values and the transformed cost values are illustrated on the side of each plot.

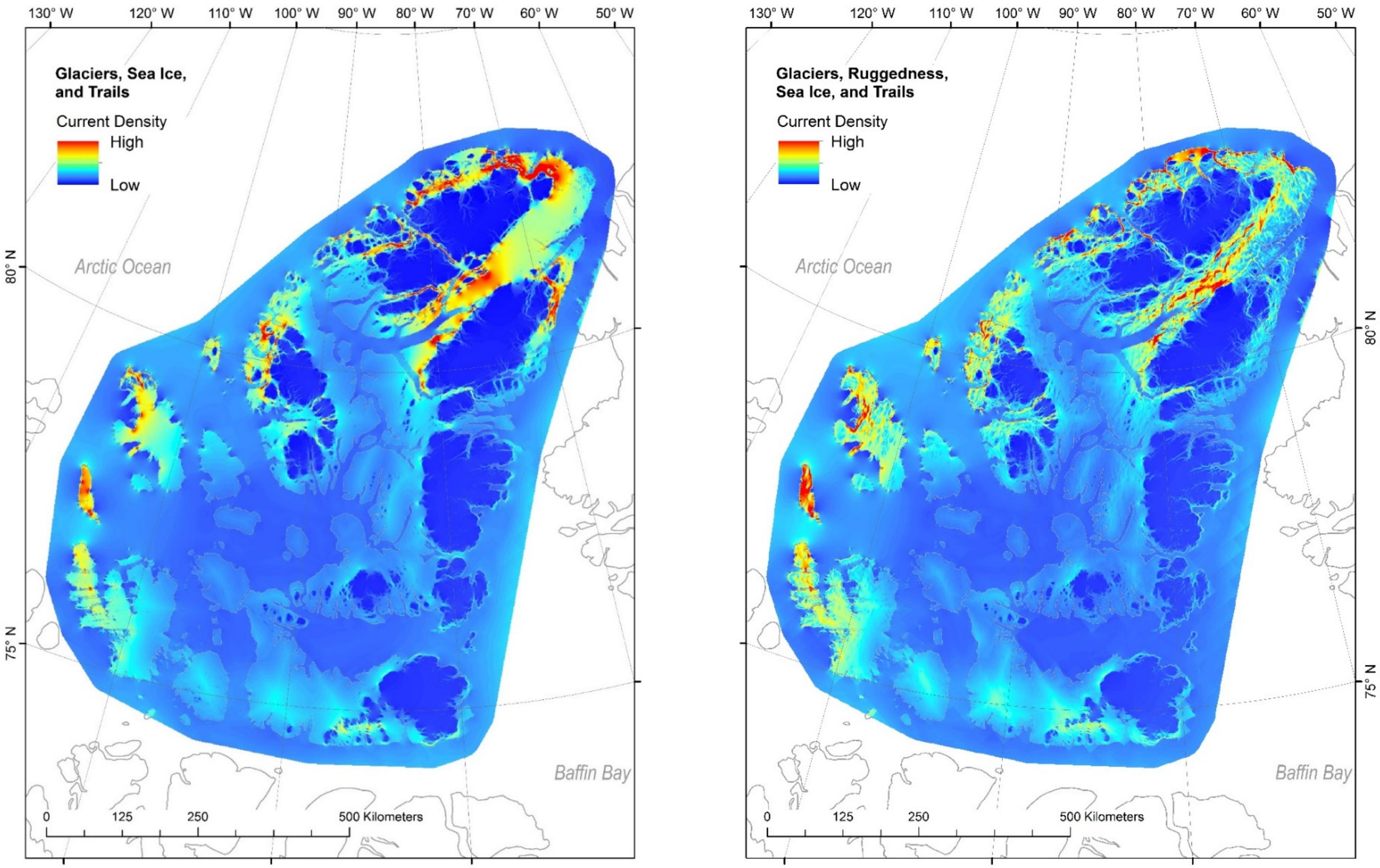

Figure 5. Functional connectivity maps for High Arctic Island [or Peary] group derived from the top two models (Table 1) at a 1-km resolution. Cell values can be interpreted as the probability of use by a moving animal (McRae et al. 2008, Koen et al. 2014).

7.0 TABLES

Table 1. Model selection results of High Arctic Island group based on AICc (k-category 2). Marginal R^2 (R^2m) and conditional R^2 (R^2c) reveal the percent variation explained by fixed effects, and fixed effects plus random effects, respectively. Log likelihood (LL) provides a measure of model fit. For comparison, AICc (k-category 4), where k is the number of surfaces plus the intercept.

Model	k 2	k 4	AICc (k 2)	AICc (k 4)	R^2m	R^2c	LL
DisTrail.Glacier.FallSeaIce	10	4	-16010.82	-16024.62	0.1012	0.2652	8016.4983
DisTrail.Glacier.Ruggedness.FallSeaIce	13	5	-16004.21	-16023.36	0.1133	0.2784	8016.9643
DisTrail.Glacier.Veg.FallSeaIce	13	5	-16001.52	-16020.67	0.0986	0.2640	8015.6167
DisTrail.Ruggedness.FallSeaIce	10	4	-16000.44	-16014.24	0.1066	0.2694	8011.3092
DisTrail.FallSeaIce	7	3	-15994.64	-16003.50	0.0938	0.2572	8004.8596

* DisTrail = Distance to Trail (m), Glacier = Proportion Glacier, Veg = Proportion Vegetation, Ruggedness = Ruggedness (m), FallSeaIce = Inverse Fall Sea Ice Concentration

Table 2. Pseudo boot-strap results for High Arctic group based on 5000 iterations.

Model	k	Average AICc	Average Weight	Average Rank	Average R^2m	Average LL	Percent Top Model
DisTrail.Glacier.FallSeaIce	10	-8926	0.655	1.16	0.099	4474	88.30
DisTrail.Ruggedness.FallSeaIce	10	-8920	0.059	3.49	0.104	4471	1.14
DisTrail.Glacier.Ruggedness.FallSeaIce	13	-8917	0.012	3.78	0.106	4474	0.00
DisTrail.FallSeaIce	7	-8920	0.133	4.27	0.092	4468	4.46
DisTrail.Glacier.Veg.FallSeaIce	13	-8916	0.007	4.56	0.097	4474	0.00

*DisTrail = Distance to Trail (m), Glacier = Proportion Glacier, Veg = Proportion Vegetation, Ruggedness = Ruggedness (m), FallSeaIce = Inverse Fall Sea Ice Concentration

** k is the number of parameters in each model based on category 2; Average AICc is the Average AIC values corrected for k and the sample size; Average Weight is the Akaike weight of the model; Average Rank is the average rank of models during boot strap analysis based on AICc; Average R^2m is the average marginal R^2 value across iterations; Average LL is the average log-likelihood across iterations; Percent Top Model is the frequency a model was the best.

Table 3. Model selection results of Baffin Island group based on AICc (k-category 2), where AICc is calculated based on the number of parameters optimized plus the intercept. Marginal R^2 (R^2m) and conditional R^2 (R^2c) reveal the percent variation explained by fixed effects, and fixed effects plus random effects, respectively. Log likelihood (LL) provides a measure of model fit. For comparison, AICc (k-category 4), where k is the number of surfaces plus the intercept.

Model	k 2	k 4	AICc (k 2)	AICc (k 4)	R^2m	R^2c	LL
Null	1	1	-3148.32	-3148.32	0.0000	0.2878	1575.2052
Distance	2	2	-3146.15	-3146.15	0.0000	0.2876	1575.2082
DisComm.FallSeaIce	7	3	-3138.49	-3148.74	0.0460	0.2961	1577.6440
DisTrails.FallSeaIce	7	3	-3133.80	-3144.06	0.0012	0.2866	1575.3021
Ruggedness.FallSeaIce	7	3	-3133.63	-3143.89	0.0001	0.2879	1575.2166

* DisTrail = Nearest Distance to Trail (m), Ruggedness = Ruggedness (m), FallSeaIce = Inverse Fall Sea Ice Concentration

Supplemental Information

Landscape connectivity among island-dwelling caribou – where ice and human activity amplify habitat discontinuity

Jenkins et al. 2021

This file contains additional information on Methods and Results

2. METHODS (Supplemental)

2.2 Genetic Database, Diversity and Structure

Our samples were primarily fecal pellets acquired from aerial and ground surveys (Jenkins 2009a, Jenkins et al. 2011, 2012), tissue (i.e., ear punch, hair, muscle, antler) from field studies during roughly the same period (Gunn and Dragon 2002, Jenkins 2009b) and archived samples where caribou are rare (Cornwallis Island) or near extirpation (Prince of Wales and Somerset; Gunn et al. 2006). Despite the large study area, our sampling captured the heterogeneous landscape, while representing both the low abundance of caribou and remoteness (Table 1S).

Samples were genotyped at 18 microsatellite loci, including NVHRT16 and NVHRT30 (reinde*er, R.t. tarandus;* Røed and Midthjell, 1998), BL42, BM4513, BM6506 (bovine; Bisho et al., 1994), BMS745, BMS1788 (bovine; Stone et al., 1995), CRH (bovine; Moore et al., 1992), FCB193 (ovine; Buchanan et al. 1994), OhemD, OhemQ (deer; Jones et al., 2000), and Rt1, Rt5, Rt6, Rt7, Rt9, Rt24, Rt27 (caribou; Wilson et al., 1997). All genotyping was performed by Wildlife Genetics International Inc. (D. Paetkau: Nelson, BC, Canada).

For each island herd, we estimated the number of alleles, allelic richness (based on rarefaction), heterozygosity, and inbreeding coefficient using diveRsity package (Keenan et al. 2013) in R. We screened for Hardy-Weinberg Equilibrium and linkage disequilibrium using GENEPOP v4.2 (Raymond and Rousset 1995, Rousset 2008) and estimated p-values with a Markov Chain algorithm (10000 batches, 10000 iterations per batch: Rousset 2008). We applied Bonferroni correction (family-wise $\alpha = 0.05$) to account for multiple tests.

To visualize genetic variation at the individual level, we performed a principal components analysis using R package ‘adegenet’ (Jombart 2008) and reduced our genetic data into uncorrelated principal components. We also estimated hierarchical population structure using individual-based non-spatial Bayesian Cluster Analysis, implemented in Structure 2.3.4 (Pritchard et al. 2000). We performed 50 independent runs to test K= 1 to K = 10, with a burn in of 100,000 iterations followed by 500,000 iterations for data collection (Jenkins et al. 2018). For each K, we retained the top 10 runs based on highest likelihood. We aligned and averaged these runs in CLUMMP using the Greedy algorithm and 10,000 permutations (Jakobsson and Rosenburg, 2007).

Additionally, we used Structure Harvester v0.6.94 (Earl and vonHoldt, 2012) to generate mean likelihood scores for each K and implemented the ΔK Evanno method (Evanno et al. 2005). We used these results to build plots of individual membership coefficients (q), assign individuals to clusters, and identify the most likely number of genetic clusters across the study area. To assign individuals to clusters, we used the highest percentage of membership (q) and a cut-off of $q \geq 0.5$ (Jenkins et al. 2018, Yannic et al. 2021). Individuals characterized $q < 0.5$ were considered admixed.

Finally, to evaluate the possibility of substructure, we used the outcome from our first-level Structure analysis and ran separate Bayesian cluster analysis for each of the identified clusters (second-level analysis). This process continued until no additional substructure was identified (here, third-level analysis).

3. RESULTS (Supplemental)

Genetic diversity and structure - Briefly, the number of alleles per locus ranged from 7-15 for our island herds and totalled 196 across loci. Mean expected and observed heterozygosity were 0.76 (SD = 0.07) and 0.71 (SD = 0.08), respectively (Table 5S). We found no significant deviations from Hardy-Weinberg equilibrium and no evidence of linkage disequilibrium after sequential Bonferroni corrections.

Adjusted allelic richness ranged between 3.40--3.95, and observed heterozygosity from 0.634 to 0.753. Significant inbreeding coefficients, from -0.03 to -0.24, were found for central and southern island herds (Table 5S).

The PCA revealed two genetic clusters: a High Arctic group and a Baffin Island group (Figure 1S). These clusters corresponded to caribou in separate designatable units (units of conservation applied by the Committee on the Status of Endangered Wildlife in Canada [COSEWIC; Green 2005]), Peary caribou (DU1) and Barren-ground caribou (DU3: COSEWIC 2011). Individuals in these groups did not overlap in ordination or geographic space (Figure 2S).

Similarly, Bayesian Cluster Analysis in STRUCTURE revealed two genetic clusters (as above), at the first level of analysis (k=2, Evanno Table 6S, Figure 2S). For each cluster, the average membership coefficient (q) was 0.99. Second and third-level analyses revealed a total of four clusters (k) among the High Arctic group (Table 7S), while no substructure was identified for the Baffin Island group (k=1).

At the first level, membership plots and mapping indicated that caribou clusters were genetically and spatially disjunct. Conversely, at the second and third level, genetic groups were not spatially discrete. As well, evidence of admixture indicated dispersal and gene flow between High Arctic clusters (Figure 2S). Thus, we conducted our landscape genetics analyses within each of the level 1 genetic clusters (i.e. the High Arctic and Baffin Island groups; Figure 2S) after thinning the genotypes to address sample period and reduce spatial autocorrelation. Notably, we eliminated historical samples for Prince of Wales and Somerset, as well as Cornwallis Island, despite them belonging to the same western Peary caribou genetic clusters. We retained one sample on Cornwallis Island (collected 1993) to supported geographic coverage.

3.3.3. Multi-surface Resistance Optimization (Supplemental)

Approaches to model selection vary and we used AICc to balance complexity and model fit. Marginal R^2 values offer an alternative but can be biased towards models of greater complexity (Row et al. 2017). By testing different estimates of k when calculating AICc, we show that model selection was robust for the High Arctic group; valuable given that there is little advice on how to estimate k (Peterman 2017). For the Baffin Island Group, our results using k = category 4, highlight the possible influence of communities and sea ice on gene flow, although the Null model ranked highest using AICc and k= category 2. Notably, the log-likelihood and marginal R^2 values were the highest for the Community/Fall Sea Ice model and not the Null. Indeed, human activity is already prevalent in this region with nearly half of Nunavut's population (49.6%; Nunavut Department of Health, 2016) and growing industrial development and infrastructure (not tested here due to recent time period).

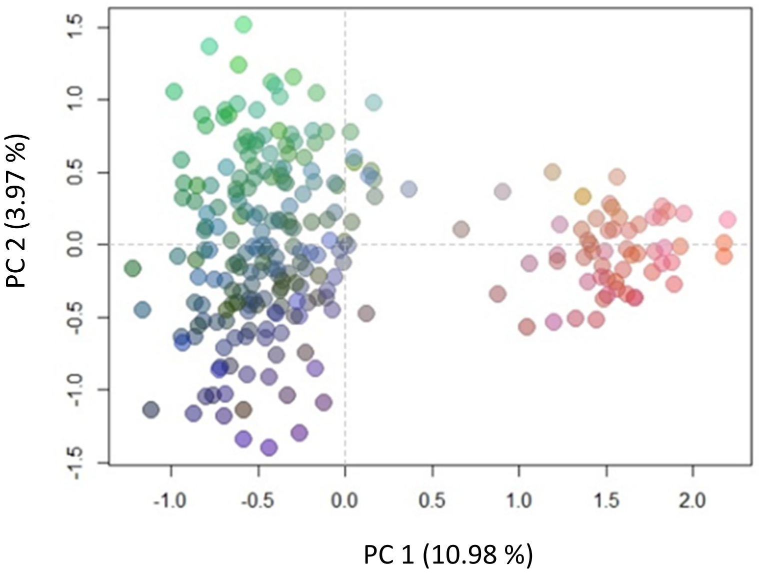

Figure 1S. The first two axes (PC) of principal component analysis of all caribou (n=252), highlighting two primary clusters: High Arctic Peary caribou (blue-green) and Baffin Island Barren-ground caribou (red); greater distances apart and greater differences in colour represent larger genetic differences. Numbers in parentheses denote the fraction of total variation captured by each axis.

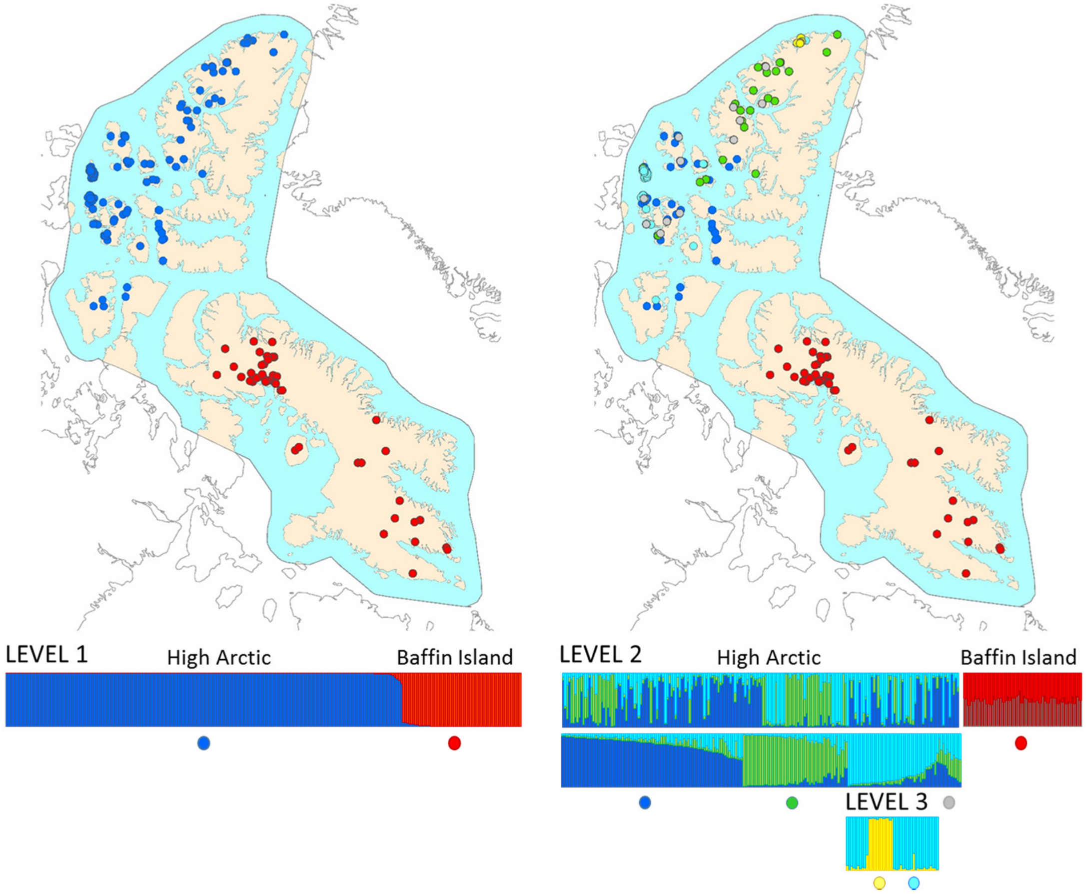

Figure 2S. On the map, the Hierarchical Bayesian cluster analysis of 252 caribou genotypes. First-level analysis reveals two genetic clusters, separating High Arctic Island caribou (blue) from the Baffin Island group (red; maps and bar plots). Second- and third-level analyses identified substructure among High Arctic caribou for a total of four clusters (blue, green, yellow, and turquoise) plus an admixed group (grey).

Table 1S. Location and sample period for tundra-wintering Arctic Island caribou. The map ID corresponds with Figure 1, and the number of animals is denoted as n.

Map ID	Sample Unit	n	Subspecies	Longitude* (°W)	Latitude* (°N)	Sample Period
1	Amund Ringnes/Cornwall islands	6	Peary	96.17	78.11	2007
2	Axel Heiberg Island	20	Peary	91.20	79.75	2007
3	Bathurst Island Complex	20	Peary	99.80	75.81	2000-03
4	Cameron Island	22	Peary	103.91	76.48	1998-2003
5	Devon Island	10	Peary	88.33	75.16	2002-03
6	Cornwallis Island	4	Peary	94.92	75.13	1993
7	Ellef Ringnes/King Christian islands	16	Peary	102.22	78.57	2007
8	Ellesmere Island	41	Peary	82.19	79.43	2006
9	Lougheed Island	42	Peary	105.29	77.38	2007
10	Prince of Wales/Somerset islands	13	Peary	96.62	72.89	1975
11	north Baffin Island	36	Barren-ground	80.83	71.39	2008-13
12	south Baffin Island	22	Barren-ground	70.16	66.71	2009-12

* Latitude and longitude represent the center of the island, or island group.

The values were generated in ArcGIS using the National Topographic Database layers at 1:250,000

Table 2S. Suite of environmental layers (original in grey and derived in white) considered for landscape genetic analysis of caribou in the Canadian Arctic Archipelago.

Environmental variable	**Grain**	**Thematic scale**	**Source**	**Rational**
Elevation	~1 km	Continuous; elevation above mean sea level.	National Centers for Environmental Information. Hastings et al. 1999.	Elevation can be an important predictor of suitable habitat for caribou (Jenkins et al. 2020) with suitability decaying with increases in elevation.
Ruggedness (Terrain Ruggedness Index)	1 km	Mean of the absolute differences between a cell and its 8 surrounding cells (Wilson et al. 2007)	Derived from elevation using raster package in R; following Wilson et al. (2007).	Caribou may select for varied terrain (Nellemann and Thomsen 1994, Nellemann and Fry 1995), but as Terrain Ruggedness increases, steep and uneven terrain may increase energetic costs and impede movement (Fullman et al. 2017).

Land cover	30 m	Categorical	2010 Land Cover Map of North America - available for Natural Resources Canada (Latifovic et al. 2017).	Natural and anthropogenic land cover is an important predictor of caribou distributions. For large Arctic herbivores, vegetation communities that included lichen-moss were important predictors of caribou distributions while glaciated areas represent unsuitable habitat (Jenkins et al. 2020). Due to crevasses, high elevations and the lack of forage, glaciers are likely a barrier to movement (Jenkins et al. 2018). There are few observations of caribou moving over glaciers.
Vegetation	1 km	Continuous; Proportion of grass and barren lichen moss per cell		Grassland-lichen moss and Barren-lichen moss were combined based on Jenkins et al. 2020, which showed their relationship to high habitat suitability for caribou.
Barren land	1km	Continuous; Proportion of Barren Land		Large areas - but positively correlated with ruggedness and negatively correlated with sea ice. We used vegetation instead (above) as shown to be important. Not considered further.
Wetland	1km	Continuous; Proportion of Wetland		Not considered further - Jenkins et al. 2020

Fresh Water	1 km	Continuous; Proportion of fresh water		Caribou movement across freshwater bodies is influenced by ice availability vs open water; caribou avoid the later but cross ice (Leblond et al. 2016). Large areas of water may be avoided due to high energy cost of swimming but inland water is frozen for much of the year. Not considered further.
Snow and Ice	1 km	Continuous; Proportion of Glacier		Glaciers impede movement (Hansen et al. 2010, Rosvold 2016, Peeters et al. 2020)
Trails	Linear feature	Shape File	We digitized the linear Pan-Arctic travel routes from Freeman (1976), Aporta (2009), and maps published on Pan Inuit Trails site (paninuittrails.org; co-directed by Claudio Aporta, Michael Bravo, and Fraser Taylor) after request to Dr. Claudio Aporta (personal communication, February 2020).	Human disturbance and infrastructure, including communities, roads, vehicle and jet traffic, and construction, can disrupt wildlife movement and influence distributions (Mahoney and Schaefer, 2002, Seip et al. 2007, Newton et al. 2015). In the High Arctic, roads are limited but a network of snowmobile and ATV trails facilitates movements by people (Freeman 1976, Aporta 2009).
Distance to Trail	1 km	Continuous; Distance to nearest Trail		

Communities	Points	Shape File		Caribou tend to avoid centres of human activity. Human development and activities include communities, military bases, industrial camps, roads, and seismic lines (Vistnes and Nellemann, 2008, Polfus et al. 2011, Boulanger et al. 2021). Impacts on caribou movement diminish with distance from these features (Johnson et al. 2005, Polfus et al. 2011, Newton et al. 2015)
Distance to Community	1 km	Continuous; Distance to nearest Community.	Inuit Communities Location, Government of Canada https://open.canada.ca/data/en/dataset/2bcf34b5-4e9a-431b-9e43-1eace6c873bd	
Sea Ice	Polygon shape file	Originally shape files identify sea ice extent with polygons no less than 25 km^2	Sea Ice Index, National Snow and Ice Data Center 1979-2015.	Sea and lake ice are important platforms for caribou movement (Jenkins et al. 2016, LeBlond et al. 2016). The absence of ice can be a barrier to movement (Dumond et al. 2013, Jenkins et al. 2018, Peeters et al. 2020).
Average March Sea Ice Concentration	1 km	Categorical; as Sea Ice is continuous		

(March, 1979-2015)		across all years.		
Average Spring Sea Ice Concentration (April - May - June, 1979-2015)	1 km	Continuous		
Average Fall Sea Ice Concentration (Sept-Oct-Nov, 1979-2015)	1 km	Continuous		
Shipping - Low Impact Shipping Corridors	Polygon		The PEW Charitable Trusts 2016, Chenier et al. 2017, Dawson et al. 2020.	Shipping is increasing in the Arctic, and distance travelled by vessels has nearly tripled over a 25 year period - 1990 to 2015 (Dawson et al. 2018).
Distance to Low Impact Shipping Corridor	1 km	Continuous		Not considered in MLPE models – but evaluated to identify potential spatial relationship(s) with other human features.

Table 3S. Correlation matrix of candidate environment layers for the High Arctic Group

Layer	**Glacier**	Elevation	Distance to Community	**Distance to Trail**	**Ruggedness**	**Vegetation**	SIC March	SIC Spring	**SIC Fall**
Glacier	1.000	0.803	-0.118	-0.002	0.326	-0.153	-0.443	-0.441	-0.437
Elevation	0.803	1.000	-0.193	0.031	0.501	0.001	-0.615	-0.613	-0.608
Distance to Community	-0.118	-0.193	1.000	0.274	-0.191	-0.117	0.267	0.262	0.217
Distance to Trail	-0.002	0.031	0.274	1.000	0.022	-0.092	0.078	0.063	0.021
Ruggedness	0.326	0.501	-0.191	0.022	1.000	0.124	-0.570	-0.569	-0.564
Vegetation	-0.153	0.001	-0.117	-0.092	0.124	1.000	-0.399	-0.397	-0.394
SIC March	-0.443	-0.615	0.267	0.078	-0.570	-0.399	1.000	0.997	0.988
SIC Spring	-0.441	-0.613	0.262	0.063	-0.569	-0.397	0.997	1.000	0.993
SIC Fall	-0.437	-0.608	0.217	0.021	-0.564	-0.394	0.988	0.993	1.000

Table 4S. Correlation matrix of candidate environment layers for the Baffin Island Group.

Layer	**Glacier**	Elevation	**Distance to Community**	**Distance to Trail**	**Ruggedness**	**Vegetation**	SIC March	SIC Spring	**SIC Fall**
Glacier	1.000	0.649	-0.116	-0.069	0.320	-0.130	-0.207	-0.207	-0.201
Elevation	0.649	1.000	-0.212	-0.170	0.520	0.275	-0.570	-0.569	-0.552
Distance to Community	-0.116	-0.212	1.000	0.367	-0.213	-0.057	0.084	0.083	0.117
Distance to Trail	-0.069	-0.170	0.367	1.000	-0.161	-0.246	0.330	0.324	0.381
Ruggedness	0.320	0.520	-0.213	-0.161	1.000	0.223	-0.412	-0.412	-0.402
Vegetation	-0.130	0.275	-0.057	-0.246	0.223	1.000	-0.690	-0.690	-0.670
SIC March	-0.207	-0.570	0.084	0.330	-0.412	-0.690	1.000	0.999	0.969
SIC Spring	-0.207	-0.569	0.083	0.324	-0.412	-0.690	0.999	1.000	0.971
SIC Fall	-0.201	-0.552	0.117	0.381	-0.402	-0.670	0.969	0.971	1.000

Table 5S. Estimates of genetic diversity, number of genotypes (N), number of alleles across loci (Na), allelic richness - based on rarefaction (AR_R), observed heterozygosity (H_o), expected and unbiased expected heterozygosity (H_e, uH_e), and inbreeding coefficient (Fis).

ID	Sample Unit	N	Na	AR_R	H_o	H_e	uH_e	F_{is}	
1	Amund Ringnes/Cornwall islands	6	72	3.58	0.667	0.654	0.713	-0.032	
2	Axel Heiberg Island	20	103	3.738	0.672	0.697	0.715	0.037	
3	Bathurst Island Complex	20	98	3.719	0.753	0.707	0.725	-0.06	*
4	Cameron Island	22	96	3.643	0.747	0.702	0.719	-0.065	*
5	Cornwallis Island	4	62	3.444	0.736	0.59	0.675	-0.245	*
6	Devon Island	10	82	3.475	0.65	0.638	0.672	-0.03	*
7	Ellef Ringnes/King Christian islands	16	87	3.399	0.634	0.639	0.66	0.002	
8	Ellesmere Island	41	93	3.504	0.671	0.678	0.687	0.009	
9	Lougheed Island	42	103	3.573	0.735	0.698	0.706	-0.055	*
10	Prince of Wales/Somerset islands	13	100	3.742	0.73	0.681	0.709	-0.076	*
11	north Baffin Island	36	157	3.951	0.722	0.696	0.706	-0.033	*
12	south Baffin Island	22	137	3.935	0.685	0.697	0.713	0.013	

Table 6S. Level 1, Evanno Method implemented on top 10 of 50 runs in STRUCTURE. For each K (number of clusters; #K), we present the mean log probability of the data (LnP[K]) and standard deviation (Stdev LnP[K]; also described as the mean likelihood), the rate of change of the likelihood distribution (Ln'[K]), the absolute value of the second order rate of change (|Ln"[K]|) and delta K (which is |Ln"[K]| divided by Stdev LnP[K]). The most likely number of clusters (in bold) is identified based on the highest Delta K.

# K	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
1	-15217.47	0.07	—	—	—
2	**-13907.29**	**0.14**	**1310.18**	**1137.31**	**8299.57**
3	-13734.42	0.32	172.87	41.30	129.46
4	-13602.85	0.64	131.57	51.58	80.18
5	-13522.86	0.75	79.99	22.90	30.65
6	-13465.77	0.87	57.09	48.07	55.22
7	-13456.75	2.80	9.02	10.53	3.76
8	-13458.26	2.35	-1.51	14.07	6.00
9	-13473.84	6.97	-15.58	6.76	0.97
10	-13496.18	5.72	-22.34	—	—

Table 7S. Level 2, Evanno Method implemented on top 10 of 50 runs in STRUCTURE for High Arctic Caribou. For each K (number of clusters; #K), we present the mean log probability of the data (LnP[K]) and standard deviation (Stdev LnP[K]; also described as the mean likelihood), the rate of change of the likelihood distribution (Ln'[K]), the absolute value of the second order rate of change (|Ln"[K]|) and delta K (which is |Ln"[K]| divided by Stdev LnP[K]). The most likely number of clusters (in bold) is identified based on the highest Delta K.

# K	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
1	-10435.57	0.0483	—	—	—
2	-10311.62	0.9211	123.95	35.4	38.431874
3	**-10223.07**	**1.9172**	**88.55**	**120.59**	**62.898927**
4	-10255.11	30.1839	-32.04	16.11	0.533728
5	-10271.04	28.5821	-15.93	89.77	3.140782
6	-10376.74	58.9981	-105.7	142.12	2.40889
7	-10340.32	22.25	36.42	146.99	6.606282
8	-10450.89	26.9748	-110.57	138.97	5.151849
9	-10700.43	22.8431	-249.54	73.26	3.207097
10	-10876.71	77.0212	-176.28	—	—

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CHAPTER 6

SYNTHESIS

Central to wildlife conservation and management is the need for refined, spatially explicit knowledge on the diversity and distribution of species and the factors that drive those patterns (Soulé et al. 2004, Cushman et al. 2013). The aim of my research was to determine the influence of land- and sea-scape heterogeneity on the spatial patterns of genetic differentiation, diversity, and broad-scale distribution of Arctic ungulates — patterns that are fundamentally driven by the movement of wildlife and their genes. By uniting biogeographical theoretical principles, extensive field observations, and a mosaic of statistical tools and predictive models, my research provides insights on contemporary population structure below the species level, the natural and anthropogenic drivers of this structure, and broad-scale estimates of functional connectivity —in other words, "how a species responds to patterns of landscape structure" (Taylor et al. 1993). By forecasting sea-ice change through time, I also highlight the vulnerability of caribou to isolation in the absence of actions to curb climate change. Further, we reveal contemporary abiotic and biotic predictors of caribou and muskoxen distributions and identify highly suitable habitat, in addition to functional connectivity, for protection in the face of anthropogenic stress. Importantly, our research provides fundamental baselines and mapped outputs for conservation planning and management while advancing our understanding on the array of wildlife responses to a naturally fragmented and increasingly dynamic landscape.

MY THESIS IN SUMMARY

In chapter 2, we asked whether genetic differentiation among island populations of Peary caribou was different from continental migratory caribou and whether genetic exchange among Peary caribou island populations was limited by the availability of sea ice. Our results were clear. We found that differentiation among both groups was best explained by geodesic distance; we revealed sea ice as an effective platform for Peary caribou movement and gene flow. When we projected sea ice extent based on moderate to high greenhouse gas concentration trajectories (RCP4.5 and RCP8.5 forecasting scenarios; IPCC 2014, Yuan et al. 2021), we found that future sea ice extent could be substantially reduced by 2086, likely increasing resistance to movement, most severely through the summer and fall. Collectively, these findings point to mounting obstacles, such as interference with seasonal inter-island migrations, dispersal, and escape from severe weather (Miller et al. 2005); such movements are of ecological and evolutionary significance (Webster et al. 2002, Lowe and Allendorf 2010, Tucker et al. 2018). Furthermore, sea ice can be regarded as an element of critical habitat for Peary caribou, requiring protection against anthropogenic disturbance (i.e. sea ice breaking for shipping; Macias-Fauria and Post 2018) through measures to conserve species (i.e., Species at Risk Act) and prompt reductions in greenhouse gas emissions (Peeters et al. 2020).

In chapter 3, we expanded our study area across the far north, to evaluate population structure and diversity of caribou below the species level. Initially, we found low to moderate genetic differentiation among continental and island populations. In keeping with Island Biogeography Theory (MacArthur and Wilson 1967) and Central Marginal Hypothesis (Eckert et al 2008), island-dwelling caribou displayed lower genetic diversity compared to mainland and mainland migratory herds. At the individual level, we found that island size/range size positively influenced genetic diversity, while distance-to-mainland and fall ice-free coastlines negatively influenced genetic diversity. Further, we found that caribou were hierarchically structured: High Arctic caribou (Peary caribou subspecies) grouped separately from other island and mainland barren-ground caribou. In particular, we found substructure within the Peary and barren-ground groups, and we identified Baffin Island caribou as insular, genetically distinct, and likely of evolutionary significance due to unique adaptations. Overall, these findings highlight important units of diversity below the species level; such knowledge can inform conservation planning (e.g. Peary caribou Recovery Strategy, Environment and Climate Change Canada 2021).

Notably, population structure signifies the disruption of gene flow (Frankham 2005, McManus et al. 2015). Such knowledge highlights the need to better understand species-environment relationships and the features that influence dispersal. In Chapters 4 and 5, we turned to these questions.

In chapter 4, we shifted our focus to the terrestrial landscape and explore the elements governing caribou-environment relationships. To help resolve the long-standing question of interspecific interactions, we include muskoxen in these analyses. Specifically, to model winter distributions and estimate the response of caribou and muskoxen to *abiotic* versus *abiotic + biotic* predictors, we used species distribution models and included distance to heterospecifics as a predictor. In keeping with a growing body of literature (Atauchi et al. 2018, Palacio and Girini 2018), we found that models that included biotic predictors, specifically the proportion of grass-lichen-moss and barren-lichen-moss, outperformed models with abiotic predictors alone. These biotic predictors were the most important when identifying habitat suitability for both ungulate species, while distance to heterospecifics, a proxy for competitive interactions, was minor. Notably, we found that areas of high habitat suitability for caribou and muskoxen were largely disjunct, limited in extent, and mainly outside protected areas. The implications for conservation are clear.

Finally, in chapter 5, we applied our findings from the previous chapters to estimate functional connectivity among two genetically and spatially disjunct groups of island-dwelling caribou – High Arctic Peary caribou and Baffin Island caribou. Using an individual-based landscape genetics approach and both natural and anthropogenic predictors, we found that connectivity among Peary caribou was impeded by sea ice, glaciers, and human trails. For Baffin Island caribou, in contrast, we failed to find any relationship between caribou genetic structure and the landscape, although our results bring attention to human communities, where proximity to communities may impede caribou connectivity. Overall, however, caribou on Baffin Island were panmictic — demonstrating random mating across the massive island and small proximal islands. These results provide a pre-development baseline in an area of growing industrial interest. Together, our work underscores the enduring influence of sea ice and the vulnerability of insular caribou to anthropogenic impacts.

CONSERVATION IMPLICATIONS

Taken together, the chapters of my dissertation demonstrate the strong influence of land- and sea-scape heterogeneity on the genetic diversity, differentiation, and distribution of caribou and muskoxen. Because conservation planning is 'inherently spatial' (Evans et al. 2011) and often applied across broad scales (Coristine et al. 2018, Cameron and Hargreaves 2020, WWF-Canada 2021), our landscape approach provides refined geo-spatial knowledge to inform the conservation and recovery of these iconic Arctic species. The ramifications of my thesis for conservation are manifold.

Diversity below the species level - Conserving the variety of life on Earth requires an understanding of intra-specific diversity (Moritz 2002). Our hierarchical approach, to identify biodiversity below the species level (Chapter 3), recognizes that ecological patterns can change with scale – a premise essential to conservation (Johnson 1980, Levin 1992, Mayor et al. 2009). Notably, by starting at a broad extent and using individual-based analysis, we identified multiple subunits of diversity; these biologically relevant units (populations, subpopulations, local populations) and areas (i.e. population range, subpopulation range), represent the fundamental units of conservation (Chapter 3; Yannic et al. 2016). We highlight threatened Baffin Island caribou for consideration as a separate conservation unit (i.e. Designatable Unit, COSEWIC 2011). Genetically distinct and spatially disjunct, these barren-ground caribou uniquely occupy the Northern Arctic and Arctic Cordillera ecozones and spend the entire year above the tree line. Indeed, Baffin Island caribou may represent an irreplaceable component of caribou diversity in Canada (Green 2005, COSEWIC 2011).

Sea ice as habitat - In my thesis, a recurrent theme is the importance of sea ice. Indeed, for caribou, sea ice is a unique and often overlooked component of their habitat. Nonetheless, by quantifying its role in connectivity (Chapter 2, 5), and highlighting a relationship between genetic diversity and intact sea ice (Chapter 3), our research draws attention to sea ice as critical habitat for High Arctic caribou. The designation of ice as critical habitat [or not] has profound consequences for conservation action planning and recovery.

Sea ice and climate change - Understanding the vulnerability of arctic biota and sea ice habitat to anthropogenic change is a crisis discipline (Macias-Fauria and Post 2018). Our projections of sea ice under different climate change scenarios forecast the loss of sea ice (and hence, a loss of habitat), and the likely erosion of summer and fall dispersal and migration pathways [over ice]. The consequences are likely substantial: the isolation of island caribou, loss of connectivity to critical terrestrial habitat, and the restriction of gene flow (Post et al. 2013, Peeters et al. 2020). As the future of self-sustaining island-dwelling caribou may be contingent on intact sea ice (Chapter 2-3), our research points to sea-ice conservation alongside the protection of extant terrestrial habitat as key measures to protect this species.

Limiting factors – The abundance and distribution of species are a reflection of population limiting factors (Hamilton and Murphy 2018); conservation and management efforts that reduce their adverse effects are essential to recover species (Hamilton and Murphy 2018). At broad scales, limiting factors are hypothesised to be the most substantial for species to overcome (Rettie and Messier 2000). Working at the landscape level allowed us to identify the factors governing the distribution of caribou and muskoxen in the Arctic Archipelago. For both ungulates, vegetation cover (a proxy for forage) was the most important predictor of winter distributions (Chapter 4) – an unsurprising result given that Arctic vegetation is patchy (Latiflovic et al 2017) and that forage quality and quantity are generally lowest during the winter (Hobbs et al. 1983, Schaefer and Messier 1995, Gustine et al. 2017)

Notably, heterospecifics were not important predictors in our models. This result suggests that muskoxen are not a limiting factor for caribou – at least in winter and at the landscape scale. Instead, our models reveal the spatial and ecological separation of High Arctic muskoxen and caribou. To my knowledge, this is the first time where these patterns have been demonstrated through large-scale predictive models. Although the mechanisms are unclear without experimentation (Sinclair 1991), our findings mimic the classic work of Diamond (1975) who documented the ecological separation of birds on islands of the Bismarck Archipelago.

Area-Based Conservation - Safeguarding habitat while also conserving movement corridors that ensure access to habitat patches (functional connectivity; Chapter 5) is a clear conservation response (Brennan et al. 2021, Lemieux et al. 2021). This is critical for species of conservation concern, such as endangered Peary caribou (Mallory and Boyce 2019) and threatened barren-ground caribou, both of which have been identified as priority species under the new Pan-Canadian Approach to Transforming Species at Risk Conservation in Canada (Environment and Climate Change Canada 2018).

Area–based conservation is foundational to the protection and recovery of biological diversity (Maxwell et al. 2020). Broad-scale spatial models can reveal important species-habitat relationships and areas of conservation value (Lawler et al. 2011, Guisan et al. 2013). Our predictive models of species distributions (Chapter 4) and landscape functional connectivity (Chapters 2, 5) identified highly suitable late-winter habitat for both caribou and muskoxen, and regions of high [and low] functional connectivity for mobile caribou. These findings support the conservation of key areas, (Maxwell et al. 2020) by generating biogeographical layers with continuous scores of habitat suitability and functional connectivity — layers directly applicable to conservation planning for threatened species.

An area-based conservation approach is of national and international interest, supporting legal obligations for terrestrial and marine protection through the Convention on Biological Diversity (Glowka et al. 1994, Convention on Biological Diversity 2011, Convention on Biological Diversity 2018) and the Pan-Canadian approach to transforming species-at-risk conservation in Canada (Environment and Climate Change Canada 2018). The new Pan-Canadian approach to conservation has identified 11 priority places and 6 priority species, including barren-ground and Peary caribou. Notably, these priority places do not include Arctic caribou range, which highlights a lack of congruence, but also an opportunity for our research to help address this. Indeed, highly suitable late-winter habitat of Arctic Island caribou and muskoxen is largely outside existing protected areas (Chapter 4; Jenkins et al. 2021-in progress) and vulnerable to current and future human disturbance such as trails, shipping, and overall land-use change; Chapter 5.

Opportunities and Challenges - In practice, efforts for evidenced-based, biologically informed conservation have fallen short (Lemieux et al. 2019, Maxwell et al. 2020). Our research highlights the Arctic – particularly the Northern Arctic ecozone – as underrepresented in the national protected areas network, particularly given that habitat is important to the long-term persistence of Arctic ungulates. By mapping critical habitat, including functional connectivity, our research underscores areas of conservation value

(Guisan et al. 2013, Huang et al. 2018, Hameed et al. 2020), which if applied, would help protect the corridors that facilitate the movements of one of the most mobile pedestrians on earth (Kelt and Van Vuren 2001, Hein et al. 2012, Joly et al. 2019)

A Region on the Cusp of Change - The future of Arctic caribou will be governed by today's environmental decisions. Of immediate relevance are the draft Nunavut Land Use Plan (Nunavut Planning Commission 2021), the draft Peary caribou Recovery Strategy (Environment and Climate Change Canada 2021), and the Northern Low-Impact Shipping Corridors (NLISC) initiative (https://www.dfo-mpo.gc.ca/about-notre-sujet/engagement/2021/shipping-corridors-navigation-eng.html). Such plans can serve as tools for the protection of caribou habitat, landscape connectivity, and the critical ecosystem processes these areas confer. If missed, the consequences could be significant and long term.

Yet, scientific data on terrestrial wildlife connectivity across land and sea ice are largely absent from these projects — likely exacerbated by the conventional terrestrial-marine dichotomy, jurisdictional or mandate issues, reliance on movement data, and the complexity of modelling distributions and connectivity. For example, the NLISC project aims to concentrate ship travel into 'low impact shipping corridors' to advance navigation safety and to focus infrastructure and reduce risks to the environment and biodiversity (Chénier et al. 2017). While the initiative relies on the integration of several existing environmental layers (i.e. ecologically and biologically significant marine areas, National Parks, and Marine Conservation Areas; Chénier et al. 2017), it has largely overlooked connectivity corridors that support terrestrial wildlife migration and gene flow. In such areas, ice-breaking would have detrimental consequences for inter-island movements. To address key information gaps, the Arctic Corridors Research Project (arcticcorridors.ca) emerged to engage Inuit and capture Inuit Knowledge (Porta et al. 2017). In complement, my thesis highlights how landscape genetics and species distribution modelling can help to inform conservation planning, by spatially revealing highly suitable habitat and multiple generations of movement and gene flow across even the most remote areas of the Arctic islands and ice.

Temporal Mismatches in Applied Conservation - Human decision-making and the application of conservation measures [or not] can take time - time that is not in sync with the speed of anthropogenic change and biodiversity loss (Wilson et al. 2015, Ferreira et al. 2019). Currently, no terrestrial habitat has been identified for protection under the draft Recovery Strategy for Peary caribou (Environment and Climate Change Canada 2021) and Nunavut's Draft Land Use Plan leaves large gaps in the protection of terrestrial and sea ice habitat for island-dwelling caribou (Nunavut Planning Commission 2021).

These deficiencies are concerning, particularly given the long times and delays associated with Land Use Planning, species assessments under COSEWIC, the listing of species under the Species at Risk Act (S.A.R.A.; Turcotte et al. 2021), and recovery planning (Ferreira et al. 2019). Such extensive time-frames leave caribou and their habitat vulnerable to rapid anthropogenic change and may exacerbate the decline of these imperiled species (Ferreira et al. 2019). Indeed, the mismatch between the speed of typical conservation and legislative timeframes, versus the speed and extent of anthropogenic change, is concerning. This issue is increasingly obvious and recommendations to remedy such mismatches are growing (Ferreira et al. 2019, Bolliger et al. 2020, Turcott et al. 2021).

THE FUTURE

Through this study, we uncovered opportunities and priorities for future research and monitoring. Firstly, we were able to estimate species-environment relationships and map important habitat for caribou and muskoxen using species distribution models (SDMs; Chapter 4). Recognizing the ongoing threat of anthropogenic change and the potential alteration of wildlife habitat and distributions, we have proposed SDMs to forecast potential future distributions and climate refugia under multiple scenarios of climate warming. Because our research highlights the importance of biotic interactions (Chapter 4), large-scale projections of biotic features will be necessary to build robust forecasts of ungulate distributions — a complicated but emerging area of research (Stewart et al. 2018). Indeed, vegetation cover, especially in light of climate change, continues to occupy much attention from ecologists (Pearson et al. 2013, Phoenix and Bjerke 2016, Pecl et al. 2017, Jenkins et al. 2020, Taylor et al. 2020).

Secondly, re-estimating contemporary models on an iterative basis (i.e., in five to ten years), to integrate new information and to identify the effects (or lack thereof) of recent conservation initiatives, will be critical (Sofaer et al. 2019). This includes using targeted field sampling with updated predictive layers that recognize environmental change (i.e., biotic [vegetation land cover] and abiotic [climate, human land use]; Sofaer et al. 2019). Such iteration is particularly constructive as our research provides an invaluable baseline (i.e., for habitat suitability and spatial distributions) for measuring changes in the distribution of wildlife and their optimal habitat (Durner et al. 2019). Hand-in-hand, contemporary models and forward projections will help inform immediate area-based conservation, including likely climate refugia.

Thirdly, our research on the functional connectivity of island-dwelling caribou provides spatially explicit recommendations for connectivity conservation and a powerful baseline for testing proposed developments (Fullman et al., 2021). Still, evaluating functional connectivity in relation to anthropogenic features has been challenging. Large-scale spatial layers for anthropogenic features, including military operations, flight zones, exploration and development sites, and even human trails, are limited or lacking. To incorporate trail networks, for instance, we carefully digitized existing data but information on the intensity of trail use, for example, was not available. Thus, to better understand the impacts of anthropogenic drivers on northern wildlife, efforts to quantify, map, and monitor anthropogenic features and activity are required.

Finally, our research uncovered the impact of anthropogenic features on caribou movement and gene flow. Still, due to the timing of sample collection and the lag time in genetic signatures (Landguth et al. 2010), connectivity models did not include large, albeit recent, developments (e.g. Baffinland Iron Mine). The effect of anthropogenic features on individuals and populations is likely to accumulate over time, and our results provide both a powerful baseline and knowledge of the influence of natural and anthropogenic features on functional connectivity. Still, given the magnitude of recent anthropogenic developments and the threatened status of Baffin Island caribou, a priority for research is to address these changes. Because simple maps of biophysical elements (i.e. roads) generally overlook human activity and disturbance (i.e. snowmobile use, noise, hunting), capturing these influences as “anthropogenic resistance” (Ghoddousi et al. 2021), along with the physical features, could be very informative. Shedding light on the impact of human activity, for example, may lead to practical outcomes, including targeted management and conservation efforts that reduce disturbance and support recovery (Ghoddousi et al. 2021).

CLOSING

Caribou are an irreplaceable component of the Canadian Arctic Archipelago. Although causes for decline are not always clear (Mallory et al. 2020), conservation measures to protect caribou habitat and their connectivity in the Canadian Arctic Archipelago will be vital to their long-term persistence. Extensive refugia from anthropogenic perturbations, including exploration, development, and even hunting, will likely be necessary to secure habitat, arrest population declines, and support recovery.

My thesis identifies pockets of genetic diversity for planning, highlights unique populations for special conservation consideration, and advances explicit spatial information to conserve important habitat and connectivity. Delays in the application of area-based conservation and other recovery measures will be detrimental to the species. Such delays portend a future of potentially small, unsustainable populations that require continual human intervention for their persistence. In a remote and harsh environment, healthy, well-connected populations with ample quality habitat must be the focus.

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