

# ECOGRAPHY

## Research

### Linking genetic and ecological differentiation in an ungulate with a circumpolar distribution

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Genetic differentiation among populations may arise from the disruption of gene flow due to local adaptation to distinct environments and/or neutral accumulation of mutations and genetic drift resulted from geographical isolation. Quantifying the role of these processes in determining the genetic structure of natural populations remains challenging. Here, we analyze the relative contribution of isolation-by-resistance (IBR), isolation-by-environment (IBE), genetic drift and historical isolation in allopatry during Pleistocene glacial cycles on shaping patterns of genetic differentiation in caribou/reindeer populations *Rangifer tarandus* across the entire distribution range of the species. Our study integrates analyses at range-wide and regional scales to partial out the effects of historical and contemporary isolation mechanisms. At the circumpolar scale, our results indicate that genetic differentiation is predominantly explained by IBR and historical isolation. At a regional scale, we found that IBR, IBE and population size significantly explained the spatial distribution of genetic variation among populations belonging to the Euro-Beringian lineage within North America. In contrast, genetic differentiation among populations within the North American lineage was predominantly explained by IBR and population size, but not IBE. We also found discrepancies between genetic and ecotype designation across the Holarctic species distribution range. Overall, these results indicate that multiple isolating mechanisms have played roles in shaping the spatial distribution of genetic variation across the distribution range of a large mammal with high potential for gene flow. Considering multiple spatial scales and simultaneously testing a comprehensive suite of potential isolating mechanisms, our study contributes to understand the ecological and evolutionary processes underlying organism–landscape interactions.

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#### Introduction

Understanding the factors and processes structuring genetic variation in natural populations is a long-standing goal in ecology and evolution. It is acknowledged that both geographic distance and landscape features are major drivers of genetic



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differentiation among populations (Wright 1943, Manel et al. 2003) and special attention has been devoted to this topic in recent literature (Holderegger and Wagner 2006, Sork and Waits 2010, Petren 2013, Sommer et al. 2013). Geographically distant populations may experience 'isolation-by-distance' (hereafter IBD) (Wright 1943), for which genetic differentiation increases with geographic distances separating populations. The IBD model predicts an increase of genetic differentiation among populations when dispersal is spatially limited, so that the effects of genetic drift are stronger than those resulting from gene flow among geographically separated populations (Slatkin 1993, Rousset 1997). Besides geographical distances, landscape features can also have a strong impact on the spatial genetic structure of natural populations (Manel et al. 2003, Segelbacher et al. 2010). Landscape genetics is a synthetic discipline that allows explicitly testing the influence of different landscape features on gene flow in a spatially explicit framework (Manel et al. 2003, Segelbacher et al. 2010). This approach primarily aims at quantifying the resistance of landscape features to movement in order to determine genetic connectivity among populations, identify corridors and barriers to gene flow, and infer dispersal routes (i.e. isolation-by-resistance, IBR; McRae 2006, McRae and Beier 2007).

Geographic distance and landscape composition are not the only factors that can affect gene flow among populations (Shafer and Wolf 2013, Sexton et al. 2014, Wang and Bradburd 2014). Spatially varying local selective pressures linked to particular environmental conditions and the evolution of locally adapted traits that confer fitness advantages can also shape gene flow and genetic differentiation (Nosil et al. 2005, Shafer and Wolf 2013). Disruption of gene flow among populations may arise when spatially varying selection leads to a higher relative fitness for locally adapted genotypes than for immigrants originating from populations experiencing contrasted environmental conditions (Kawecki and Ebert 2004, Wang and Bradburd 2014). Thus, environmental heterogeneity can influence the evolutionary and demographic trajectories of populations by imposing varying selective pressures and limiting migration and/or realized gene flow, a process termed 'isolation-by-environment' (hereafter IBE) (Bradburd et al. 2013, Shafer and Wolf 2013, Sexton et al. 2014, Wang and Bradburd 2014). Different and not mutually exclusive ecological and evolutionary processes can generate IBE (reviewed by Wang and Bradburd 2014). IBE may arise when 1) biased dispersal preferences for particular environments or habitats that are determined by individual's genotype, phenotype or behavior occur, 2) selection acts negatively against immigrant genotypes that are adapted to their original local environments, 3) sexual selection reduces the reproductive success of dispersers with divergent sexual traits or mate choice preferences, or 4) hybrids between native and immigrant individuals adapted to different environmental conditions have reduced fitness, for example due to selection against intermediate and maladaptive traits (Wang and Bradburd 2014). Thus, IBD, IBR

and IBE encapsulate key pathways in which geographic distance and landscape heterogeneity influence genetic differentiation among populations (Wang et al. 2013). Disentangling the relative importance of IBD, IBR and IBE can help to understand the landscape features limiting neutral gene flow and how populations are adapted to local environments and may cope with major environmental changes (e.g. global climate changes), which has strong evolutionary implications and can inform conservation and management actions, e.g. translocation programs (Fraser and Bernatchez 2001, Funk et al. 2012).

Central to landscape genetics is the necessity to understand how the results obtained in one region can translate into other areas (Short Bull et al. 2011, Hand et al. 2016). The relative importance and consistency of the different factors and processes shaping genetic divergence can only be tested through the study of different landscape areas representing sets of exchangeable populations. This can help to determine whether contrasting results in diverse regions are due to differences in the range of variability of landscape attributes or to the biology of the study organism in various portions of its range (Segelbacher et al. 2010, Short Bull et al. 2011, Trumbo et al. 2013). Hence, recent studies have suggested that considering different geographic regions may help to identify more accurately the most important factors affecting gene flow (Short Bull et al. 2011, Trumbo et al. 2013). Nearly all past studies on landscape genetics have either considered a single landscape replicate or disregarded the potential impact of spatial scale and the few exceptions taking into account these important aspects have not analyzed the role of isolation-by-environment (i.e. IBE) in structuring spatial genetic variation (Short Bull et al. 2011, Trumbo et al. 2013).

A good candidate species to address the issue of scale is the caribou and reindeer, *Rangifer tarandus* (hereafter termed caribou) because of its extensive Holarctic distribution encompassing a broad variety of environmental conditions (Klüttsch et al. 2012, Weckworth et al. 2012, Yannic et al. 2014b). Caribou inhabit several biomes and ecosystems that include temperate and mountain forests, taïga and sub-arctic, arctic or alpine tundra. These climatic diversities correspond to differences in habitat preferences, space-use, and migratory behavior, which have led to different ecotype designations for caribou (Mallory and Hillis 1998). Glacial-interglacial cycles of the Pleistocene have greatly influenced the evolutionary history of caribou (Flagstad and Røed 2003, Yannic et al. 2014b, Polfus et al. 2017). Previous genetic investigations divided caribou populations into two major phylogeographic lineages that probably originated from diversification in glacial refugia from Eurasia (i.e. the Euro-Beringia lineage) and south of the Laurentide Ice Sheet in North America (i.e. the North American lineage) (Flagstad and Røed 2003, Cronin et al. 2005, Weckworth et al. 2012, Yannic et al. 2014b). The Euro-Beringia lineage covers a vast region from Eurasia to northwestern America, including Fennoscandia, Greenland, Svalbard and the Arctic

archipelagos of Russia and Canada (Flagstad and Røed 2003, Yannic et al. 2014b). The North American lineage is now restricted to the north-eastern part of North America (Yannic et al. 2014b). At finer scales, studies have further documented genetic subdivisions within the two large divisions described above (Røed et al. 2008, Klütsch et al. 2012, Serrouya et al. 2012, Weckworth et al. 2012, Yannic et al. 2016, Polfus et al. 2017). While there is great environmental and ecological diversity among caribou populations, the current taxonomy fails to integrate all the diversity below the species level that is relevant to its evolutionary legacy (COSEWIC 2011, Serrouya et al. 2012, Yannic et al. 2016). Therefore, a worldwide picture of the links between genetic differentiation, environmental dissimilarity, and ecotype designation is required to determine whether observed regional and range-wide patterns of genetic divergence among caribou populations have resulted from morphological, life history, and behavioral adaptations to different ecological constraints.

In this study, we first examine the relative contribution of environment and geography to spatial patterns of genetic differentiation in caribou populations sampled throughout the entire species range, after accounting for the effects of population size and historical isolation during Pleistocene glacial cycles. Second, we address this question following a hierarchical structure analysis, from range-wide to regional landscapes, to understand whether past evolutionary history, demography or the species dispersal capacity influenced the relative importance of environment and geography in the spatial structure of genetic variation among populations. Disentangling the roles of gene flow and genetic drift on genetic differentiation is particularly challenging because the two processes are acting simultaneously (Prunier et al. 2015). Here, we tested the influence of population size on genetic differentiation to assess the contribution of drift on population genetic differentiation (i.e. isolation-by-drift; Serrouya et al. 2012, Mager et al. 2014, Prunier et al. 2015). Third, we consider landscape replication from the two independently evolved lineages of caribou in North America (Yannic et al. 2014b), which allows us determining the generalization of obtained inferences in different geographic regions (Wang and Bradburd 2014). Finally, we examine the congruence between genetic variation and ecotype designation across the entire species distribution range.

## Material and methods

### Study system

Caribou are distributed throughout the northern Holarctic region in North America and Eurasia, including Greenland, the Svalbard Archipelago and the Canadian Arctic Archipelago (Fig. 1). While different classification and taxonomy schemes exist through the species range, they are not always consistent between conservation agencies. Therefore, we refer throughout this study to the ecotype

terminology common to caribou and reindeer proposed by the Arctic Council (2001) and Hummel and Ray (2008) (Fig. 1). Migratory barren-ground ecotype herds can be large and consist of several thousand caribou (Bergerud 2000). Migratory barren-ground caribou are gregarious on traditional calving grounds and undertake seasonal migrations over long distances (up to 2500 km) between wintering ranges in the boreal forest and summer areas in the tundra (Dalziel et al. 2015). The Mountain caribou performs altitudinal migration associated with food availability and predation avoidance between seasonal ranges (up to 100 km). Mountain caribou usually stay in the same alpine area and calve at high altitudes. Further distinctions have been recognized within the mountain caribou ecotype in western Canada (COSEWIC 2014), but these are all designated as mountain ecotype in this study. Boreal forest caribou are sedentary and inhabit the boreal forest all year-round. Animals undertake short seasonal migrations within their home range of hundreds or thousands of km<sup>2</sup> (Schaefer et al. 2000, Faille et al. 2010). They live alone or in small groups. Arctic forms include the Peary caribou *Rangifer tarandus pearyi* and reindeer of Svalbard *Rangifer tarandus platyrhynchus*. Arctic ecotypes are adapted to the arctic environmental conditions, generally characterized by cold temperature, little precipitation, and a short growing season (Flagstad and Røed 2003, Festa-Bianchet et al. 2011). Herd sizes are generally small for Peary caribou and reindeer of Svalbard and post-calving groups generally only consist of tens of animals (Flagstad and Røed 2003, Festa-Bianchet et al. 2011). Arctic ecotype migratory behavior varies from short migrations between seasonal home ranges to year-round occupation of relatively small home ranges (Côté et al. 2002, Festa-Bianchet et al. 2011).

### Database and microsatellite analyses

We reanalyzed a dataset of 1297 caribou and reindeer genotyped at 16 nuclear microsatellite markers (Yannic et al. 2014b). Samples were obtained from 57 sites located across the entire circumpolar native species' range, including Alaska, Canada, Greenland, Svalbard, Norway, Finland, and the Russian Federation (Fig. 1 and Supplementary material Appendix 1 Table A1). Samples were collected over the last decade and consisted of blood clots, ear punches and hair handfuls obtained during field studies or muscle acquired from hunted individuals. The dataset included semi-domestic herds from Russia and Scandinavia, because at the scale of our study the wild and semi-domestic co-distributed herds generally have a similar genetic composition (Røed et al. 2008). We also analyzed samples from a herd established in Iceland with individuals originally introduced from Norway. The introduction of domestic reindeer in Alaska in the past and its interbreeding with local caribou populations is likely to have a negligible impact on our results. Indeed, only a small proportion of wild individuals from Alaska have been found to show signs of introgression (< 3%; Mager et al. 2013, Colson et al. 2014).

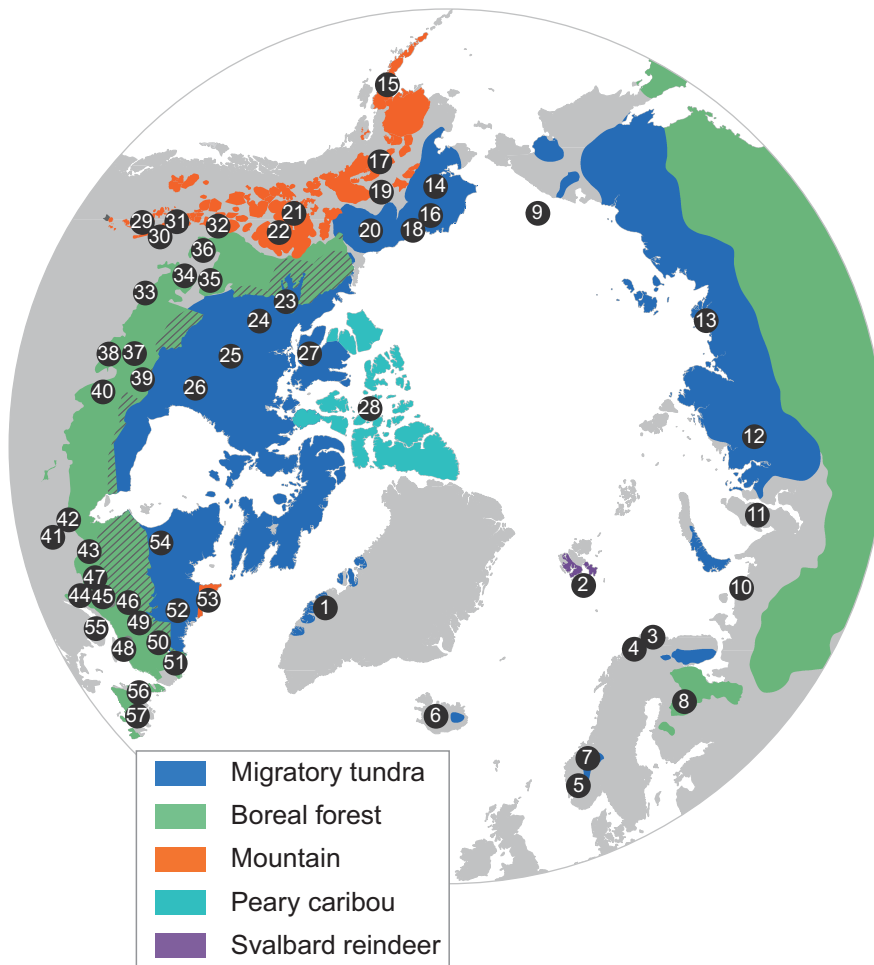


Figure 1. Distribution of caribou and reindeer *Rangifer tarandus* herds and ecotypes across the species' Holarctic distribution. Sampling locations are indicated by black dots. Spatial overlaps between ecotypes are indicated by hatching. Information on ecotype distribution was retrieved from map 2.11 of Hummel and Ray (2008) and from map no. 28 of the Conservation of Arctic Flora and Fauna (CAFF) (Arctic Council 2001).

Genetic distances between pairs of populations were estimated as  $F_{ST}$  according to Weir and Cockerham (1984) and Cavalli-Sforza chord distance  $D_c$  (Cavalli-Sforza and Edwards 1967).  $F_{ST}$  and  $D_c$  were computed using Genodive 2.0b27 (Meirmans and Van Tienderen 2004). A neighbor-joining unrooted tree based on pairwise  $D_c$  was obtained with the package 'ape' in R 3.3.1 (R Development Core Team).

We used a Bayesian Markov chain Monte Carlo clustering analysis as implemented in the software Structure 2.3.3 (Pritchard et al. 2000) to assess genetic structure and admixture among populations and ecotypes, without considering information about the geographic origin of individuals. We assumed an admixed model with correlated allele frequencies (Falush et al. 2003). Fifty independent runs for  $K=1$  to  $K=10$  were performed using 250 000 iterations with the first 50 000 removed as a burn in. The 10 runs having the highest likelihood were averaged using Clumpp 1.1.1 (Jakobsson and Rosenberg 2007). We used the Greedy algorithm with random input order and 10 000 permutations to align runs from the same  $K$  and the  $G'$  pairwise matrix

of genetic similarity. We used a hierarchical procedure by repeating Structure analyses within each of the two major lineages with the same methods as described above (Yannic et al. 2014b). The apportionment of genetic variation within and between lineages was assessed by hierarchical AMOVAs using the software Arlequin 3.1 (Excoffier and Lischer 2010). The total variance is partitioned into covariance components due to differences between lineages ( $F_{CT}$ ), among populations within lineages ( $F_{SC}$ ) and among all populations ( $F_{ST}$ ). AMOVAs were based on conventional  $F$ -statistics (i.e. using allelic frequencies without accounting for distances between alleles) and  $R$ -statistics (i.e. an estimator of genetic structure based on the variance in allele size). Significance was assessed by 10 000 permutations. Hierarchical Bayesian analyses with Structure and AMOVA were performed excluding herds that could not be assigned to any of the two lineages with a probability higher than 0.8 according to the initial Structure analyses including all populations. The threshold value of 0.80 was arbitrarily chosen to ensure that at least 80% of an individual's genome is assigned to one cluster (Manel

et al. 2002, Basset et al. 2006). All excluded herds are from the contact zone of the two lineages located in Manitoba (Fig. 2).

### Geographical distances

We calculated the geodesic geographic distance among each pair of populations based on great circle distances using the package ‘geosphere’ 1.2-27 implemented in R. To make the distance among populations more reflective of current caribou dispersion patterns, we also measured cost-weighted distances along paths connecting populations considering that animals did not generally cross large bodies of open water, but can walk hundreds of kilometers on fresh water or sea ice (up to 380 km) (Miller et al. 2005, Jenkins et al. 2016, Leblond et al. 2016). Then, we weighted the seawater resistance for the occurrence of sea ice over the 1979–2010 period, retrieving monthly Arctic sea ice extents available at the National Snow and Ice Data Centre (Univ. of Colorado, Boulder, USA) (Supplementary material Appendix 1). Isolation-by-resistance models were estimated using circuit theory, which simultaneously consider all possible pathways connecting population pairs (McRae 2006). Landscape resistance was calculated on resistance surfaces using the ‘commuteDistance’ function implemented in the ‘gdistance’ 1.1-4

R package (Supplementary material Appendix 1). ‘commuteDistance’ function was also used to calculate distances among populations on a completely ‘flat landscape’ to test the effect of IBD based on a raster layer in which all cells were given an equal value (resistance: landmass = 1 and seawater = 1). This approach is more appropriate for comparison with alternative models based on cost-weighted distances (Noguerales et al. 2016). Because model supports were higher for IBR than for IBD models, and because the cost-weighted distances are ecologically more realistic than flat landscapes, we only reported IBR results based on circuit theory (Supplementary material Appendix 1 Table A3–A4) (see also Yannic et al. 2014a).

### Environmental data

We used a total of 22 environmental, ecological and topographical variables among those most frequently used in similar ecological studies (Wang et al. 2013, Noguerales et al. 2016) and thought to influence caribou habitat selection (Environment Canada 2008). We extracted environmental information from 19 bioclimatic variables (bioclim), two variables related to the vegetation [net primary productivity (npp) and tree cover (tree)], and elevation (Supplementary material Appendix 1 Table A2).

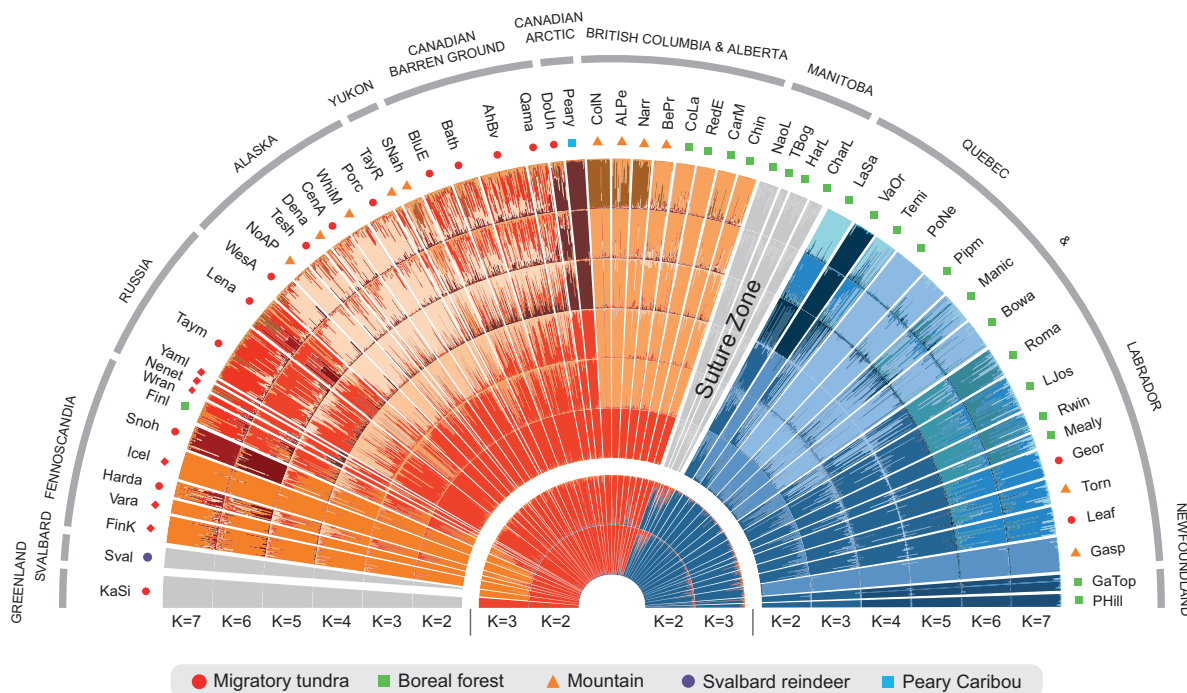


Figure 2. Genotype-based assignments of 1297 caribou and reindeer based on Structure Bayesian clustering analyses of 16 microsatellite loci without any prior information about the geographic origin of individuals. Each individual is represented by a thin vertical line that is partitioned into  $K$  colored segments that indicate the proportional assignment of each individual to the clusters with that color. Individuals are grouped into main regions and herds (see Supplementary Table 1 for further information). The two lower central charts include all samples [ $K=2$  and  $K=3$ ]. The upper outlying charts correspond to hierarchical analyses on each of the two main clusters (upper left: Euro-Beringia,  $K=2$  to  $K=7$ ; upper right: North-America,  $K=2$  to  $K=7$ ). Samples located in the suture zone between the two main lineages and the most geographically and genetically isolated herds of Greenland and Svalbard were not included in the hierarchical analyses. Red diamonds correspond to introduced or semi-domestic migratory caribou-reindeer.

We performed a principal components analysis (PCA) on environmental variables with the ‘dudi.pca’ function in R package ‘ade4’ and used the resulting first three PC axes to calculate environmental dissimilarity between localities and test the effect of IBE (Wang 2013, Wang et al. 2013, Papadopoulos et al. 2014, Nogueras et al. 2016). Then, we calculated dissimilarity matrices among populations for 5 environmental variables separately (Papadopoulos et al. 2014): 1) npp, 2) tree; 3) elevation; 4) and 5) corresponding to the first and second axes of a PCA performed on bioclimatic data.

### Measures of population size

Small and isolated populations are particularly sensitive to genetic drift (Allendorf and Luikart 2007). Accordingly, population size has been shown to influence population genetic differentiation and diversity in caribou (Serrouya et al. 2012, Weckworth et al. 2013, Mager et al. 2014, Yannic et al. 2014b, Prunier et al. 2015). The relative effect of genetic drift on genetic differentiation can be assessed using census population size (Supplementary material Appendix 1 Table A1) considering that genetic distances among population pairs are mainly driven by genetic drift in the smallest ones and that census population size is positively correlated to effective population size (Prunier et al. 2015, Yannic et al. 2016). We calculated the harmonic mean of population size (hereafter  $N_c$ ) between each pair of populations as an estimate of genetic drift. Theoretically,  $N_c$  decreases disproportionately with decreasing population sizes (Supplementary material Appendix 1 Fig. A2), so that we expected greater genetic differentiation among populations due to drift as  $N_c$  decreases.

### Phylogeographic origin: Euro-Beringian vs North American lineages

The possible impacts of historical processes on genetic differentiation among herds was taken into account considering their phylogeographic origin, i.e. whether they belong to the North American lineage or to the Euro-Beringian lineage (Yannic et al. 2014b). We calculated a categorical matrix with 0s and 1s for pairs of populations belonging to the same or different lineages, respectively (King 1987).

### Effects of IBR, IBE, $N_c$ and phylogeographic origin on genetic differentiation

We used an information theoretic approach (Burnham and Anderson 2002) to quantify the relative contributions of IBR, IBE,  $N_c$ , and phylogeographic origin on genetic differentiation. We evaluated the effect of each explanatory variable on genetic differentiation using model averaging (Burnham and Anderson 2002) as implemented in the ‘MuMIn’ R package (Bartoń 2016). For each dataset and each response genetic matrix ( $F_{ST}$  and  $D_c$  distance), we calculated parameter estimates from models including all possible combinations of predictor variables obtained with

the function ‘dredge’ (Bartoń 2016). Specifically, we estimated effect sizes, unconditional standard errors and 95% confidence intervals (95% CI) for each independent variable by averaging the coefficients from models in which each predictor factor appears and weighting estimates according to the models’ Akaike information criterion weight ( $\omega_{AICc}$ ) (Burnham and Anderson 2002) (see Papadopoulos et al. 2014 for a similar approach). Effect sizes were considered significant when 95% CIs did not overlap zero (Grueber et al. 2011). Analyses were performed using 1) four matrices: IBR, IBE,  $N_c$  and lineage as explanatory variables; and 2) eight matrices: IBR, environmental dissimilarity (npp, tree, elevation, bioclim PC1 and PC2),  $N_c$ , and lineage. We standardized all continuous variables to facilitate comparison of model parameter estimates. Prior to analysis, we ensured that there was no strong multicollinearity among explanatory variables, i.e. that the correlation coefficient between predictor variables  $|r| < 0.7$  (Dormann et al. 2013) and by calculating variance inflation factors (VIF) using the package ‘usdm’ implemented in R. Multicollinearity begins to affect parameter estimates when the VIF values are  $> 10$  (Zuur et al. 2010). Collinearity diagnostic tests for all models revealed no multicollinearity problems: the highest VIFs were 2.3 when environmental dissimilarity was amalgamated into a single distance measure and 2.8 when each environmental variable was included as a separate predictor.

Information theory is increasingly used in landscape genetics (Wang 2009, Phillipsen and Lytle 2013, Papadopoulos et al. 2014), although its limitations have been discussed elsewhere because of the pairwise nature of the distance data (Balkenhol et al. 2016). Therefore, to account for the matrix nature of our data, we repeated the analyses using a multiple matrix regression approach (Legendre et al. 1994, Lichstein 2007). We specifically used a modified version of the ‘Multiple Matrix Regression with Randomization’ function (MMRR; Wang 2013) implemented in R, with 10 000 permutations to assess significance.

All analyses were performed on different datasets and at different scales, from worldwide to regional scales (Table 2). We expected that IBR, IBE and phylogeographic membership would increase and then have a positive relationship with genetic distance, while  $N_c$  was expected to be negatively correlated with genetic differentiation. Specifically, we tested the alternative hypothesis  $H_a$  that  $\beta_{IBR}$ ,  $\beta_{IBE}$  ( $\beta_{npp}$ ,  $\beta_{tree}$ ,  $\beta_{elev}$ ,  $\beta_{pc1}$ , and  $\beta_{pc2}$ ), and  $\beta_{Lineage}$  were significantly  $> 0$  and  $\beta_{N_c}$  significantly  $< 0$ . Therefore, we used one-tailed hypothesis test (Ruxton and Neuhäuser 2010, Berkman et al. 2013), using both the rejection region approach (one-sided 95% confidence intervals) and the p-value approach ( $\alpha = 0.05$ ; MMRR) for making statistical decisions regarding the null hypothesis of no effect of independent variables on genetic differentiation.

We also used MMRR to test whether populations that belong to the same ecotype – coded with 0s and 1s for pairs of populations belonging to the same or different ecotypes, respectively – tend to inhabit similar environments, controlling for the effects of IBR and phylogenetic origin.

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.f971b>> (Yannic et al. 2017).

## Results

### Worldwide genetic structure

The studied populations split into two major genetic clusters (Fig. 2), which correspond to the two lineages previously described for caribou, i.e. the Euro-Beringian lineage and the North American lineage (Flagstad and Røed 2003, Yannic

et al. 2014b). The pattern of genetic split in two lineages was also apparent on the neighbor-joining tree based on  $D_c$  genetic distances (Fig. 3), but the cut-off between the two lineages was less clear in comparison to Structure results. The secondary contact zone between the two lineages is located in central Canada (Alberta, Manitoba and Ontario) and occurred about 8 kyr BP (Yannic et al. 2014b), which corresponds to the final deglaciation of North America (Clark et al. 2009) (Fig. 2). Herds from Manitoba displayed intermediate assignment values to both lineages, with average probabilities of membership that were below the  $q_i = 0.80$  assignment threshold considered to assign a given population to any of the two lineages: NaoL  $q_{\text{Euro-Beringia}} = 0.17 \pm 0.15$  [mean  $\pm$  SD], TBog  $q_{\text{Euro-Beringia}} = 0.25 \pm 0.15$ ,

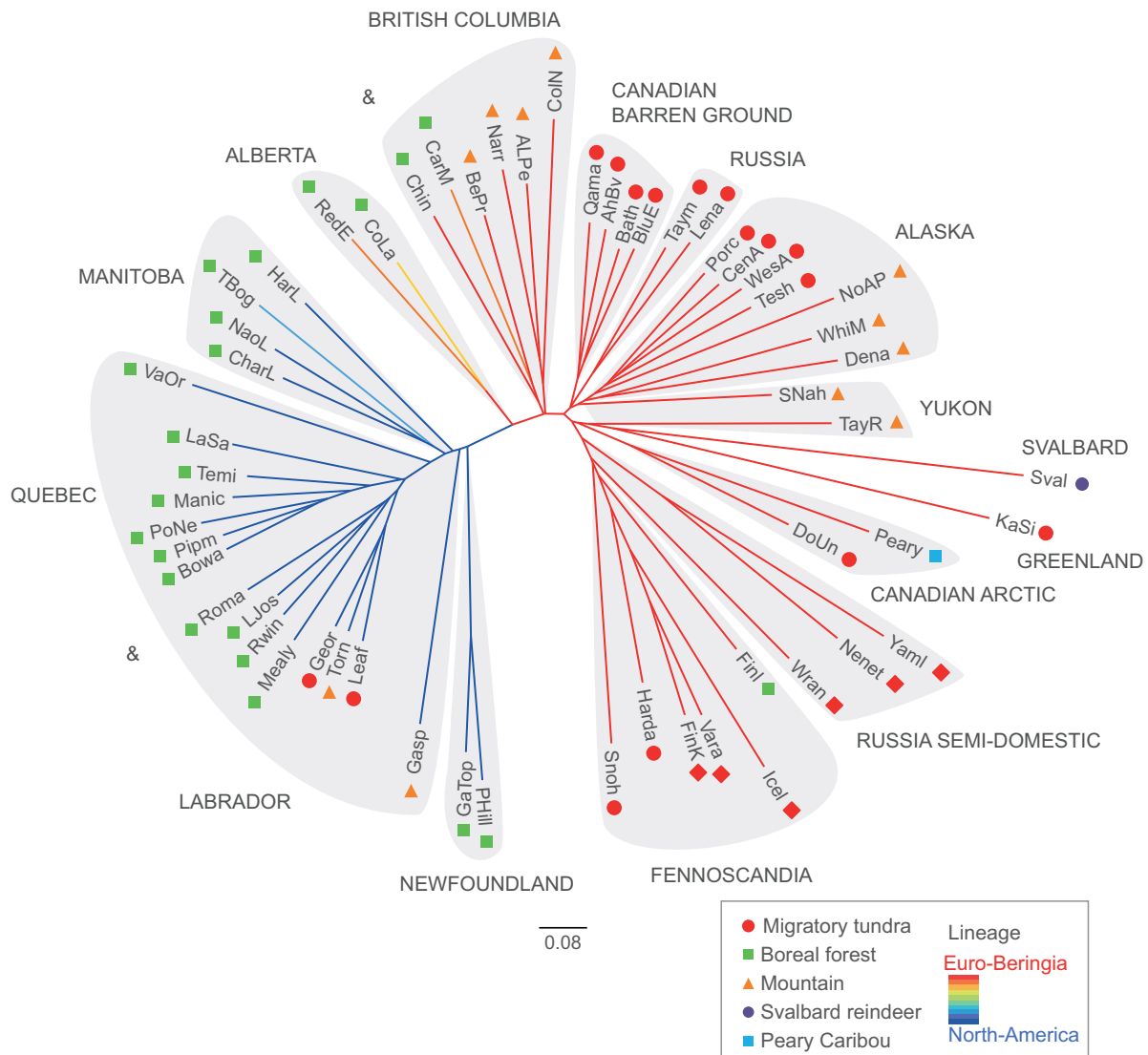


Figure 3. Neighbor-joining tree based on Cavalli-Sforza chord distance  $D_c$  among 57 populations of caribou and reindeer *Rangifer tarandus* herds and ecotypes across the species' Holarctic distribution.  $D_c$  were computed with the program Populations 1.2.31 (Langella 1999) based on 16 microsatellites (see Methods). The length of the branches is proportional to the genetic distance between herds and colors correspond to the Bayesian membership of each population to the North American (blue) and Euro-Beringian (red) lineages, respectively, obtained with Structure for  $K=2$ . Red diamonds correspond to introduced or semi-domestic migratory caribou-reindeer.

Table 1. Analysis of molecular variance between and within caribou lineages across the species' Holarctic distribution. Asterisks indicate significant values for the estimators: \*\*\* $p < 0.001$  for both conventional  $F$ -statistics ( $F_{CT}$ ,  $F_{SC}$  and  $F_{ST}$ ) and when allele size or the distances among alleles were taken into account ( $R_{CT}$ ,  $R_{SC}$ ,  $R_{ST}$ ).

	F-statistics		R-statistics	
	%		%	
Between lineages	6.7	$F_{CT} = 0.16^{***}$	12.5	$R_{CT} = 0.22^{***}$
Among populations within lineages	9.0	$F_{SC} = 0.10^{***}$	9.1	$R_{SC} = 0.10^{***}$
Within populations	84.2	$F_{ST} = 0.07^{***}$	78.4	$R_{ST} = 0.12^{***}$

HarL  $q_{\text{Euro-Beringia}} = 0.19 \pm 0.16$  and CharL  $q_{\text{Euro-Beringia}} = 0.17 \pm 0.17$ . These populations represent the suture zone depicted on Fig. 2. Therefore, these herds were excluded from subsequent hierarchical analyses performed with Structure and AMOVA.

AMOVA analyses based on  $F_{ST}$  and  $R_{ST}$  produced comparatively similar results. For the two estimators, most of the variation was found within populations and a much smaller proportion of variance was explained by differences between lineages or among populations within lineages (Table 1).

### Genetic differentiation and ecotype designation

Bayesian clustering analysis with Structure (Fig. 2) and  $Dc$  distance NJ tree (Fig. 3) on microsatellites data indicated the co-occurrence of similar ecotypes in different genetic clusters and lineages. Hierarchical analyses performed with Structure within each of the two lineages indicated regional substructure of genetic diversity ( $K=2$  to  $K=7$  within each lineage; Fig. 2). Note that because of their high genetic differentiation, the herds from Greenland and Svalbard were excluded from hierarchical analyses. Regional genetic structure in caribou has been discussed elsewhere (McDevitt et al. 2009, Serrouya et al. 2012, Weckworth et al. 2012), but notable results emerged from our global analyses. Across the circumpolar distribution of the species, we observed strong genetic clustering of herds that belong to different ecotypes, even at small spatial scales. Mountain herds of Alaska are, for example, closely related to neighbor migratory tundra herds (Fig. 2, 3), the exact same situation is observed among migratory tundra herds and the Torngat mountain herd from Québec and Labrador. Conversely, along the continuous range of boreal forest in Canada, a major genetic break was observed. The so-called forest-dwelling or boreal ecotype is composed of two highly divergent genetic lineages that came into secondary contact in Manitoba where genetic admixture between them is observed (Fig. 2).

### Multivariate analyses on environmental data

Principal component analyses performed on the environmental variables indicated that the first two axes explained between 78 and 84% of the total variance depending on the dataset considered (Supplementary material Appendix 1

Table A6). Specifically, the first axis retained between 52.3 and 65.6% of the total inertia and the second axis between 17.3 and 31.1%. Precipitation variables had a predominant impact on the variance of axis 1 and temperature and vegetation variables had a higher weight on axis 2 (Supplementary material Appendix 1 Fig. A4). Populations that belong to the same ecotype tend to group together according to environmental criteria (Fig. 4 and Supplementary material Appendix 1 Fig. A5b), an association that was significant after controlling for the effects of landscape resistance and phylogeographic origin (MMRR Ecotype  $\sim$  IBE + IBR + lineage:  $\beta_{\text{IBE}} \pm \text{SE} = 0.048 \pm 0.005$ ,  $t = 10.41$ ,  $p = 0.001$ ;  $\beta_{\text{IBR}} \pm \text{SE} = 0.041 \pm 0.012$ ,  $t = 3.32$ ,  $p = 0.020$ ;  $\beta_{\text{lineage}} \pm \text{SE} = 0.050 \pm 0.022$ ,  $t = 2.29$ ,  $p = 0.060$ ;  $R^2 = 0.13$ ).

### Landscape genetic analyses

The relative importance and significance of explanatory factors for genetic differentiation among caribou herds depended on the genetic metric used ( $F_{ST}$  or  $Dc$ ) and the spatial scale of the study (Table 2 and Fig. 5). Overall, models explained a moderate to high proportion of genetic variance ( $R^2$  ranged between 0.40 and 0.71) and models based on  $F_{ST}$  and  $Dc$  as dependent genetic distances had on average a similar fit (e.g. similar  $R^2$ , Table 2).

At large geographical scale (worldwide or continental), lineage membership had a significant effect on genetic differentiation in all datasets that included this predictive factor (Table 2 and A, B, C, and D on Fig. 5). Genetic differentiation ( $F_{ST}$  and  $Dc$ ) was positively associated with resistance distance (IBR based on circuit theory) in all cases, whereas environmental distance (IBE) presented significant effects only in some datasets and for models based on  $Dc$  distance (B, C, and D; Fig. 5).  $Nc$  had a limited effect on genetic differentiation at the largest spatial scales (Table 2 and Fig. 5).

At regional scales, we obtained contrasting results (E, F, and G on Fig. 5). Effect sizes of IBE and IBR differed between the North American lineage and the Euro-Beringian lineage in America (i.e. their two-sided respective 95% CIs did not overlap). IBE explained a significant proportion of genetic variance ( $Dc$  and  $F_{ST}$ ) among herds within the Euro-Beringian lineage in North America, whereas IBR had a limited effect in this dataset and only reached significance in the model based on  $Dc$ . In contrast, IBE had no significant effect for the North American lineage and genetic differentiation within this lineage was mostly explained by a strong effect of IBR. At this scale,  $Nc$  had a significant and negative effect on genetic differentiation in all datasets, i.e. genetic differentiation decreased when harmonic mean population size between pairs of herds increased (Table 2 and Fig. 5).

When the different environmental variables were included separately in the analyses, we obtained results broadly consistent with those obtained considering a global estimate of environmental dissimilarity. However, signals of IBE were more widespread and there were differences in selected environmental variables for some datasets (Supplementary material Appendix 1 Table A6 and Fig. A6). IBR was



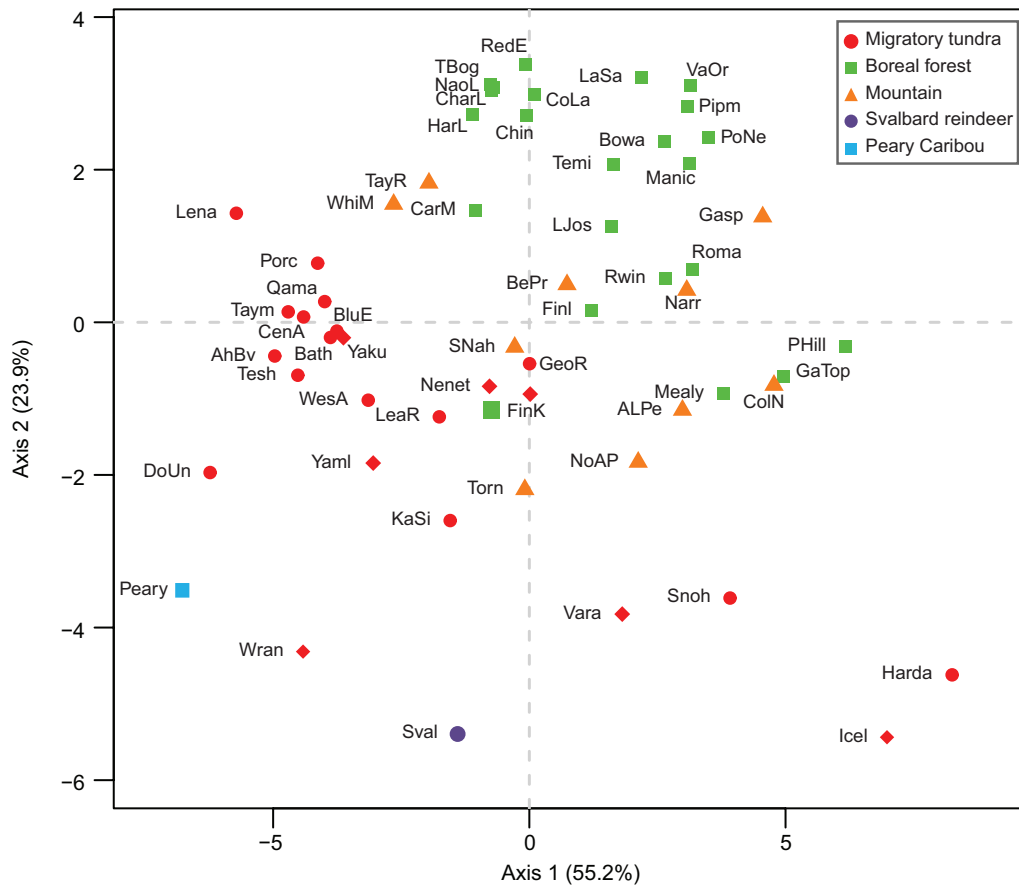


Figure 4. Scatterplots of a principal component analysis representing coefficients for each locality sorted according to ecotype designation for the studied populations of caribou and reindeer *Rangifer tarandus* across the species' Holarctic distribution. Red diamonds correspond to introduced or semi-domestic migratory caribou-reindeer.

significant in 6 and 7 datasets when  $F_{ST}$  and  $Dc$  were the dependent variables, respectively. IBE driven by at least one environmental variable had a significant effect in all datasets but within the whole Euro-Beringian lineage in Eurasia and America. However, the effects of the environmental predictors varied greatly between the two estimates of genetic differentiation ( $F_{ST}$  or  $Dc$ ). Differences in elevation between populations and environmental dissimilarity on the 2nd axis (bioclim pc-2) of the bioclimatic variables (mainly explained by precipitation; Supplementary material Appendix 1) were the most common sources of IBE for models based on  $Dc$ . Conversely, elevation had no significant effect in any model based on  $F_{ST}$ , while npp and bioclim pc-2 were positively associated with genetic distance in some instances, both at worldwide and regional scales (Supplementary material Appendix 1 Table A6, Fig. A6).

## Discussion

### Disentangling the mechanisms driving genetic structure

Hierarchical analyses of genetic structure across the entire circumpolar distribution of caribou revealed considerable

genetic subdivision both at range-wide and regional spatial scales. At larger scales, genetic variation is geographically structured in two main caribou lineages, one originating from and confined to northeastern America, the other originating from Euro-Beringia but also currently distributed in western North America. Such dual origin is a major driver of genetic differentiation among herds (Yannic et al. 2014b). Our results support also the findings of previous local and regional studies indicating that caribou populations show remarkable genetic differentiation despite the high dispersal potential of the species (Courtois et al. 2003, Boulet et al. 2007, Weckworth et al. 2012, Mager et al. 2013, 2014, Colson et al. 2014, Gubili et al. 2017). This suggests the presence of mechanisms behind genetic isolation other than geographical distance, such as physical barriers to dispersal, predation risk avoidance or isolation by environment (Serrouya et al. 2012, Weckworth et al. 2013, Mager et al. 2014, Yannic et al. 2014b, Gubili et al. 2017).

Disentangling the relative importance of the mechanisms driving spatial genetic divergence is an evolutionary question that has received considerable attention in the last few years (Shafer and Wolf 2013, Wang et al. 2013, Sexton et al. 2014, Wang and Bradburd 2014). Here, we used an information theoretic approach and multiple matrix regressions

Table 2. Model-averaged parameter estimates ( $\beta$ ) with their unconditional standard errors (SE) and 95% confidence intervals (95% CI) quantifying the effects of isolation-by-resistance (IBR), isolation-by-environment (IBE), harmonic mean of population size (Nc), and lineage membership (Lineage) on genetic differentiation of caribou and reindeer *Rangifer tarandus* herds and ecotypes across the species' Holarctic distribution. Analyses are presented for the complete dataset (Worldwide), excluding the isolated populations from Greenland and Svalbard and focusing on certain populations according to their membership to different geographic regions, main genetic lineages or ecotype designations. Continuous variables were standardized to a mean of zero and a standard deviation of one. The number of herds in each dataset is also indicated. Adjusted  $R^2$ -squared were obtained from multiple linear regression models including the four predictive factors. Estimates were considered as significant (bold type) when the one-sided 95% CI did not overlap zero and by randomization tests performed with MMRR.

	n	IBR			95% CI			IBE			95% CI			Nc			Lineage			95% CI		
		$R^2$	$\beta$	SE	lower	upper	lower	upper	$\beta$	SE	lower	upper	lower	upper	$\beta$	SE	lower	upper	$\beta$	SE	lower	upper
$F_{ST}$																						
A: worldwide	53	0.40	<b>0.61</b>	<b>0.03</b>	<b>0.57</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B: worldwide without Greenland and Svalbard	51	0.65	<b>0.60</b>	<b>0.02</b>	<b>0.57</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C: ecotype (migratory. Forest and mountain)	43	0.60	<b>0.42</b>	<b>0.03</b>	<b>0.38</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D: among North American herds	39	0.59	<b>0.45</b>	<b>0.03</b>	<b>0.41</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E: within North American lineage	17	0.52	<b>0.86</b>	<b>0.08</b>	<b>0.73</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F: within Euro-Beringian lineage in America	22	0.36	0.22	0.07	0.11	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G: within Euro-Beringian lineage	34	0.59	<b>0.75</b>	<b>0.03</b>	<b>0.70</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
$D_C$																						
A: worldwide	53	0.59	<b>0.59</b>	<b>0.02</b>	<b>0.56</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B: worldwide without Greenland and Svalbard	51	0.64	<b>0.53</b>	<b>0.02</b>	<b>0.50</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C: ecotype (migratory. Forest and mountain)	43	0.69	<b>0.39</b>	<b>0.03</b>	<b>0.35</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D: among North American herds	39	0.71	<b>0.46</b>	<b>0.03</b>	<b>0.41</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E: within North American lineage	17	0.58	<b>1.00</b>	<b>0.11</b>	<b>0.82</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F: within Euro-Beringian lineage in America	22	0.47	<b>0.28</b>	<b>0.05</b>	<b>0.20</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G: within Euro-Beringian lineage	34	0.40	<b>0.51</b>	<b>0.03</b>	<b>0.45</b>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

with randomization to quantify the relative contribution of environment and geography in driving population genetic differentiation. We found that environmental dissimilarity, as a single metric or included as specific environmental gradients, contributes to increase genetic differentiation among caribou populations across different spatial scales and portions of the species range after taking into account the effects of geography (IBR), population size ( $N_c$ ) and phylogeographic origin (lineage membership) (Fig. 5 and Supplementary material Appendix 1 Fig. A6). In a first step, we combined environmental variables into a single measure of environmental dissimilarity and observed a consistent effect of IBE only among populations that belong to the Euro-Beringian lineage in North America (Table 2 and Fig. 5). It is remarkable that the relative importance of IBR and IBE considerably differed between the datasets for the North American lineage and the Euro-Beringian lineage in America (i.e. two-sided 95% CIs obtained for IBR and IBE in the two datasets did not overlap). Within the Euro-Beringian lineage in North America, we observed significant effects of IBE on genetic variation that explained a higher proportion of genetic differentiation than IBR. This is a highly surprising result given that most studies have generally found that environmental dissimilarity explains less variation in genetic divergence than geographical distances (Wang et al. 2013). In contrast, genetic differentiation within the North American lineage was mostly explained by IBR, whereas IBE had no significant effect (Table 2 and Fig. 5). In a second step, we analyzed individual environmental variables and found that some of them (e.g. temperature and vegetation) had significant effects at both large and regional scales that were not detected when combining all environmental parameters in a single metric (Supplementary material Appendix 1 Fig. A6).

Collectively, our results demonstrate that environment can be an important driver of genetic differentiation in caribou populations, highlighting its prominent role as an evolutionary force behind population subdivision, even in a species with high dispersal capacity and a worldwide distribution (Shafer and Wolf 2013, Sexton et al. 2014, Wang and Bradburd 2014). Our analyses also showed that the effects of a particular set of environmental variables may become masked by analyses based on a single combined variable. This indicates that exploring the effects of specific parameters should be considered in studies aimed to understand the role of environment in structuring genetic variation of natural populations (Wang et al. 2013, Papadopulos et al. 2014). Finally, our study also highlights the importance of considering multiple replicates (i.e. sets of exchangeable populations) and different spatial scales to get a better understanding of organism-landscape interactions (Short Bull et al. 2011).

### Potential mechanisms of isolation-by-environment in caribou

IBE is a pattern that can be generated by a variety of non-mutually exclusive processes, including biased dispersal preferences for particular habitats or environments, natural and

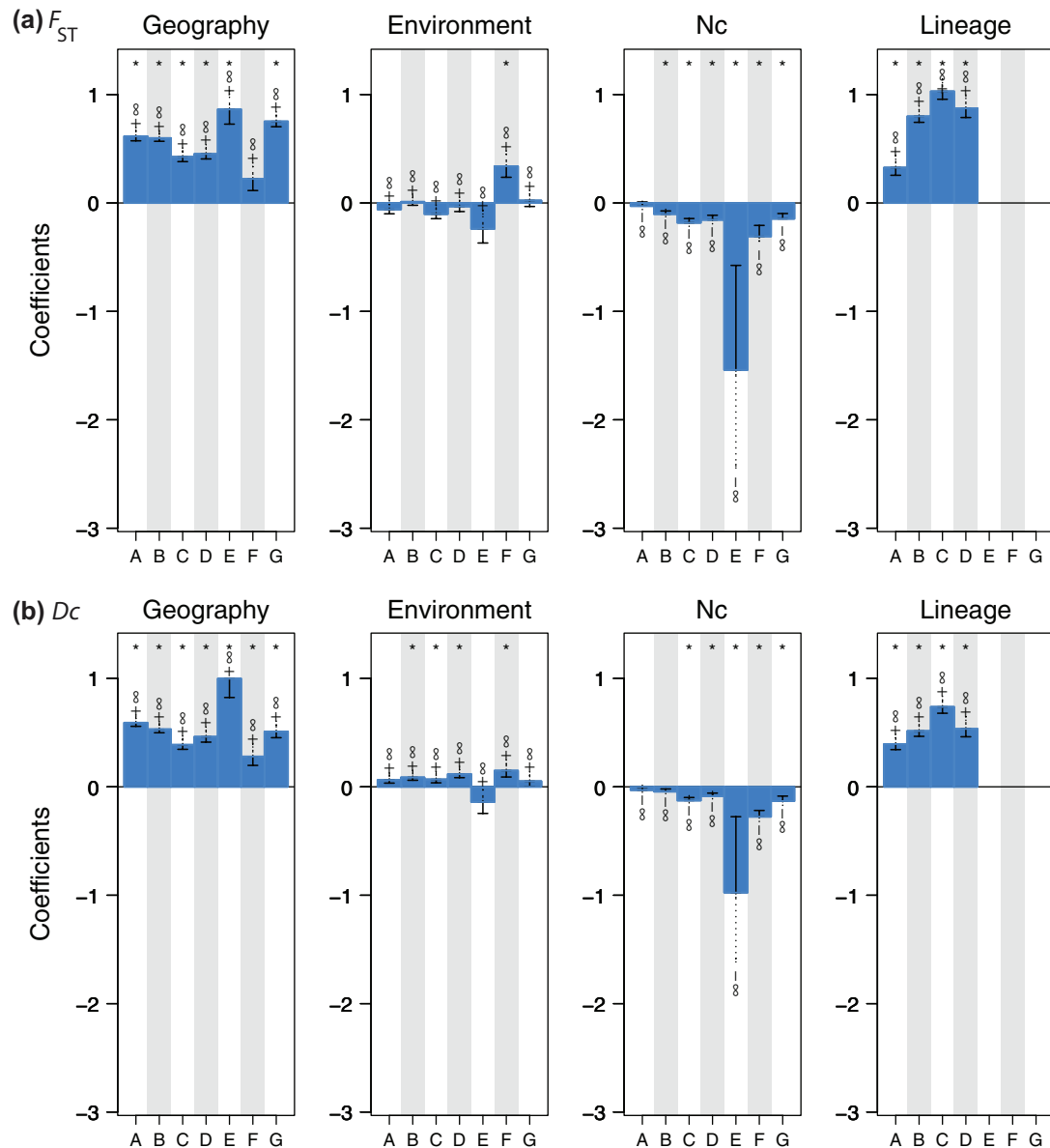


Figure 5. Relative contributions of geography (isolation-by-resistance, IBR), environment (isolation-by-environment, IBE), harmonic mean of population size ( $N_c$ ), and lineage membership (lineage) to genetic differentiation of caribou and reindeer *Rangifer tarandus* herds and ecotypes across the species' Holarctic distribution. The dependent variables are (a)  $F_{ST}$  and (b)  $D_c$  chord distance. A: at worldwide scale; B: excluding herds from Greenland and Svalbard; C: considering only migratory tundra, mountain and boreal forest ecotypes; D: considering all North American herds; E: within the North American lineage; F: within the Euro-Beringian lineage in North America; and G: within the Euro-Beringian lineage. Barplots depict effect sizes and one-sided 95% confidence intervals (95% CI) for each parameter. Estimates were considered as significant (asterisk) when the 95% CI did not overlap zero and by randomization tests performed with MMRR.

sexual selection against immigrants adapted to different environmental conditions, or reduced fitness of hybrids resulting from crosses between immigrant and local individuals (Wang and Bradburd 2014). Caribou are found in a broad variety of ecosystems from the temperate and mountain forest biome to arctic or alpine tundra, spanning a wide latitudinal range. Acclimation to local environmental conditions can be indirectly estimated by evaluating the fitness of individuals translocated to other habitats (Kawecki and Ebert 2004). In

the past decades, caribou translocation has been proposed as a conservation strategy to support declining populations or to reestablish extirpated herds (Compton et al. 1995, Stronen et al. 2007, Decesare et al. 2011, St-Laurent and Dussault 2012). At the end of the 1980s, woodland caribou from two herds in British Columbia were translocated to northern Idaho (USA), respectively at 750 and 250 km south from their native sites (Warren et al. 1996). Translocated individuals retained movement and foraging behavior of the source

herds (Warren et al. 1996), leading to the death by starvation of most of them. These observations point to an ecological specialization of caribou populations for movement and foraging behavior and the action of natural selection against immigrants, which can contribute to maintaining genetic differentiation among populations (Mager et al. 2014).

Available data on introduced individuals from domesticated herds offer a different picture. Studies found that domestic reindeer introduced in different regions can survive (e.g. in Alaska, Greenland or Sub-Antarctic Islands) and successfully reproduce with their wild relatives when living in sympatry (Jepsen et al. 2002, Mager et al. 2013, Colson et al. 2014). The survival of reindeer introduced in Alaska from domestic Siberian herds and their hybridization with local caribou populations were first expected to be limited due to differences in the peak of reproductive timing, behavior, or body size (Finstad et al. 2002). However, the presence of genetically introgressed individuals within wild caribou herds, decades after the introduction, suggests that at least some domestic reindeer were able to survive and reproduce with local caribou in the wild (Mager et al. 2013, Colson et al. 2014). This may be due to feral reindeer populations experiencing similar environmental conditions (e.g. temperature and vegetation) in Alaska than in their native range in Siberia. Selection of different traits during the domestication process may have also resulted in a competitive advantage for feral reindeer, a situation that can greatly differ from the evolutionary history and demography of wild populations.

At regional scales, satellite-tracking data have shown that migratory caribou undertake excursions into the forest-dwelling caribou range, suggesting possibilities of gene flow between adjacent migratory and boreal forest caribou herds (Boulet et al. 2007). Densities in forest-dwelling herds are, however, usually very low (Boulet et al. 2007 and references therein). The probability that a migratory caribou encounters a boreal forest caribou, furthermore of the opposite sex and at the right time of the year, may be very low (Boulet et al. 2007). In addition, satellite-tracking data indicated that range overlap occurs mainly in winter and ecotypes use distinct areas during the rutting period and differ in the peak of reproductive timing. Some studies have reported, however, possible cases of emigration of sedentary forest-dwelling female caribou to adjacent migratory herds, where females adopted the migratory behavior of local females (Hinkes et al. 2005). Gene flow among adjacent herds that belong to different ecotypes and inhabit different habitats may thus occur via herd switching.

### Ecotype designation and genetic differentiation

Worldwide caribou herds are broadly classified into major ecotypes that are shared by Eurasian and North American populations. This study assessed the current genetic differentiation among caribou populations and ecotype designation across the worldwide species distribution. Using a comprehensive number of sampling locations across the species range ( $n = 57$ ;  $\sim 1300$  genotyped animals), we found

multiple discrepancies between ecotype and nuclear genetic designation. Using mitochondrial markers and a reduced number of sampling locations, a weak relationship between genetic variation and ecotype characteristics has already been found among caribou populations (Flagstad and Røed 2003). At finer spatial scales, incongruence between genetic and ecotype designation was also reported using mitochondrial DNA, nuclear microsatellite markers or a combination of both (Cronin et al. 2005, Serrouya et al. 2012, Weckworth et al. 2012, Yannic et al. 2016, Polfus et al. 2017). For example, the sedentary forest-dwelling ecotype is found in Finland and North America, each belonging to distinct evolutionary lineages. Conversely, in Quebec–Labrador, migratory tundra herds, sedentary forest-dwelling herds, and sedentary mountain herds are ecologically very different but all belong to the same North American genetic lineage and are closely related at neutral genetic markers (Fig. 3) (Boulet et al. 2007, Yannic et al. 2016). These results suggest that similar environmental constraints in different portions of the caribou range have led to similar behavioral responses across the entire species circumpolar distribution (Arendt and Reznick 2008, Losos 2011). Convergent behavior in caribou probably evolved in allopatry, after colonization of the different regions, rather than through ancient divergence predating the separation of lineages (i.e. 300 kya [95% highest posterior densities 184: 430]; Yannic et al. 2014b).

A recent study discussed the possibility that the migratory tundra ecotype within the North American lineage originated during the late Pleistocene as a result of genetic introgression from migratory tundra caribou of the Euro-Beringian lineage (Klütsch et al. 2016). Our study did also detect genetic admixture in the area of contact among migratory caribou that belong to the two lineages (Fig. 2). However, our study based on neutral microsatellite markers as well as that of Klütsch et al. (2016) did not measure adaptive introgression that could explain the migratory behavior within the North American lineage. In addition, the large confidence interval around the date of introgression estimated by Klütsch et al. (2016) about 6.8 kya [95% CI: 1.7–17.0 kya; microsatellite loci and mtDNA haplotypes combined] makes it difficult to establish whether the introgression event was linked with the timing of deglaciation of North America (Dyke et al. 2002) when the two lineages got into geographical contact (Yannic et al. 2014b). Finally, introgression between lineages could not explain alone the scattered distribution of forest-dwelling and mountain ecotypes across the species range, where adaptive introgression was unlikely to occur.

### Ecological and conservation implications

Our results indicate that conservation policies aimed to preserve caribou-reindeer populations should carefully consider the characterization of the ecological and environmental niche envelop of the different herds, particularly when management practices involve translocations or reintroductions of individuals that belong to different phylogeographic lineages or populations adapted to specific local

environmental conditions. This is specifically the case of the threatened boreal caribou ecotype in North America that suffer high anthropogenic pressures (Environment Canada 2012), but could be extended to all ecotypes. Any program of reinforcement of declining boreal caribou populations should consider that two distinct independent evolutionary lineages are living in close vicinity in the continuous range of the boreal forest and source populations for translocations should be carefully selected (Yannic et al. 2016).

Caribou inhabit a wide variety of ecosystems (e.g. boreal forest, alpine tundra, or Arctic environments) spanning about 40° latitudinal range and the species is one of the last remnants of Late Quaternary megafauna that survived the glacial-interglacial cycles of the Pleistocene (Lorenzen et al. 2011). Yet, current global climate change is taking place rapidly and severely at high latitudes (IPCC 2007). Caribou, as most species adapted to cold environments, is facing the effects of climate warming (Altizer et al. 2013, Post et al. 2013), and it is expected to experience considerable range reductions (Sharma et al. 2009, Yannic et al. 2014b). At the species level, caribou is thought to be tolerant to changing environments due to some adaptive capacity and phenotypic plasticity (Joly et al. 2011, Lorenzen et al. 2011). While our work provides some indications of local adaptation in caribou, additional information is required to understand how the unprecedented speed of human-induced environmental change will affect its levels of genetic diversity and the capacity of the populations to cope with environmental changes (Bell and Gonzalez 2011, Lindsey et al. 2013).

Overall, our study illustrates the benefit of large-scale approaches to properly assess intraspecific variation and understand the interplay between ecological, ecotype and genetic information in caribou, an essential step to guide conservation and management programs aimed at maximizing the species' diversity and evolutionary potential (Barrett and Schluter 2008). It should be considered that we have estimated genetic divergence at putative neutral markers, which remains a surrogate to estimate environment-driven selection. Populations in different environments should thus have higher differentiation at loci under local selection than for neutral markers (Soria-Carrasco et al. 2014). An extension of our approach aimed at identifying loci potentially under ecologically-driven selection is the logical next step. Such genomic approach may improve our understanding of the effects of environment and local adaptation on genetic and ecotype divergence in caribou (see Schweizer et al. 2016 for an example in grey wolf *Canis lupus* ecotypes), while providing refined predictions of the future responses of this iconic species to global change (Harrisson et al. 2014).

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Supplementary material (Appendix ECOG-02995 at <[www.ecography.org/appendix/ecog-02995](http://www.ecography.org/appendix/ecog-02995)>). Appendix 1.