

Integrating ecological and genetic structure to define management units for caribou in Eastern Canada

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Abstract Genetic diversity is a key parameter to delineate management units, but many organisms also display ecological characteristics that may reflect potential local adaptations. Here, we used ecological and genetic information to delineate management units for a complex system involving several ecotypes of caribou (*Rangifer tarandus*) from Québec and Labrador, eastern Canada. We genotyped 560 caribou at 16 microsatellite loci and used three Bayesian clustering methods to spatially delineate and characterize genetic structure across the landscape. The different approaches employed did not converge on the same solution, and differed in the number of inferred genetic clusters that best fit the dataset but also in the spatial distribution of genetic variation. We reconciled variability among the methods using a synthetic approach that considers the sum of the partitions obtained by each of them and retrieved six genetically distinct groups that differ in their spatial extent across the range of caribou in the study area. These genetic groups are not consistent with

the presently defined ecological designations for this species. Combining both genetic and ecological criteria, we distinguished eight independent management units. Overall, the management units we propose should be the focus of conservation and management actions aimed to maximize genetic and ecological diversity and ensure the persistence of caribou populations inhabiting increasingly disturbed landscapes.

Keywords Bayesian assignment clustering · Genetic diversity · Management unit · Spatial structure · Ecotype · *Rangifer tarandus* · Effective population size

Introduction

Large herbivores are fundamental to the structure and functioning of ecosystems (Côté et al. 2014; Legagneux et al. 2014) and are of economic and cultural importance (Gordon et al. 2004). Yet, several large herbivore populations are declining across the world and some are at risk of

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extirpation (Vors and Boyce 2009; Ripple et al. 2015). The situation prompts actions for the conservation of various herbivore species. A long-standing goal of conservation biology is to delineate and prioritize intraspecific conservation units that should be preserved due to their ecological or evolutionary importance (Waples 1991; Fraser and Bernatchez 2001). The term evolutionarily significant unit (ESU) was first proposed by Ryder (1986) to define such conservation units. While many definitions of ESU have been proposed, they are usually defined as populations that present reproductive isolation because of their long-term evolutionary divergence and as such represent a significant evolutionary component of the species (Ryder 1986; Moritz 1994; Crandall et al. 2000; Fraser and Bernatchez 2001; Frankham et al. 2002; Funk et al. 2012). The conservation of several ESUs is then crucial to maximize the adaptive potential of species facing environmental changes. Moreover, many countries legally recognized and protected ESUs, for example the USA under the Endangered Species Act. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) proposed the concept of Designatable Unit (DU) as a pragmatic and applicable alternative to ESU (Green 2005). The DUs are unique in having a two-part validation system requiring first an establishment of discreteness, for example significant differences in nuclear or mitochondrial DNA sequences, followed by the demonstration of evolutionary significance, where a DU should represent an irreplaceable component of Canada's biodiversity (COSEWIC 2009). Designatable Units have been assessed in several species, e.g., the lake whitefish species complex *Coregonus* spp. (Mee et al. 2015) and the Polar bear *Ursus maritimus* (Thiemann et al. 2008).

In Canada, most caribou *Rangifer tarandus* (L., 1758) populations from Newfoundland to Yukon are declining (Vors and Boyce 2009; Festa-Bianchet et al. 2011; Gunn et al. 2011). Thus, a better understanding of variability below the species level is necessary to inform and prioritize conservation actions. COSEWIC proposed 12 DUs for caribou, that may be assessed and potentially receive protection under the Species at Risk Act (COSEWIC 2011). In addition, caribou populations are found in a variety of ecosystems, from boreal forests to the High Arctic, and have accordingly been classified into multiple ecological designations (ecotypes) (Hummel and Ray 2008). COSEWIC (2002) defines ecotypes as groups of populations adapted to different landscapes or environments as reflected primarily by behavior (migratory *versus* sedentary), without any requirement in terms of genetic diversification. Therefore the delineation of DUs for caribou was challenging because of a lack of correspondence between taxonomy, ecotype designation, phylogeography and genetic structure of populations (Serrouya et al. 2012; Weckworth et al. 2012; Yannic et al. 2014a).

Yet at smaller spatial scales, managers and policy makers often deal with local populations that are managed as distinct units because of their independent demographic dynamics. These units are termed Management units (MU) (Moritz 1994, 2002) and are considered as demographically independent because their dynamics primarily depends on local growth rates rather than on dispersal and gene flow among units. MUs are thus fundamental for the short-term management of populations while the previously defined ESUs focus on the historical divergence among populations (Fraser and Bernatchez 2001). A single ESU may then be subdivided into several MUs. The delineation of MUs is particularly needed to assess the effects of harvesting, anticipate the consequences of potential threats (e.g. habitat fragmentation, climate change and disease outbreaks), and establish appropriate management practices that take into consideration the dynamics and evolutionary trajectories of populations (Frankham 2005).

The delineation of demographically independent populations based on genetic data is a widely accepted parameter to assess MUs (Moritz 1994; Palsbøll et al. 2010), for example in Scandinavian brown bear *Ursus arctos* (Manel et al. 2004) or harbour seal *Phoca vitulina* (Olsen et al. 2014). Several authors also argued that the demographic independence of units should be properly addressed when delineating management units from population genetic data (Waples and Gaggiotti 2006; Palsbøll et al. 2007; Lowe and Allendorf 2010). Specifically, Waples and Gaggiotti (2006) proposed to apply a “10 % migration criterion” based on the detection of genetic migrants to consider two populations as demographically independent. The temporal scale addressed by a population genetics approach allows the detection of ongoing demographic and micro-evolutionary processes that are highly useful to complement the information provided by classical (phylogeographic) analyses focused on the delineation of historical evolutionary lineages (Waser and Strobeck 1998; Moritz 2002; Wang 2010). The discriminatory power of multilocus data generally employed in population genetics can help to disentangle contemporary processes, a necessary step to delineate management units and characterize their distinctive features such as effective population sizes, dispersal and demography that constitute baseline information to guide management practices. It is therefore essential to take into account the spatial distribution of genetic diversity in a landscape context to define management units, particularly considering that the landscape is the scale at which conservation agendas and policies most often implement management strategies (Funk et al. 2012).

For a more rigorous definition of MUs, patterns of neutral genetic variation should also be complemented with information on ecological differences, such as movement

and space use (Wakefield et al. 2013), life history traits and demographic analyses (Olsen et al. 2014), phenotypic variation and ecological niches (Zannese et al. 2006; Barata et al. 2012; Cicero and Koo 2012; Wood et al. 2014), behavior (Coulon et al. 2008) or isotope data (Rundel et al. 2013). Thus, the integration of genetic and ecological data is likely to better account for possible adaptive differentiation among MUs that may not be captured by analyses of genetic structure generally relying on neutral markers.

Based on the above considerations, we combined information yielded by genetic and ecologic data to delineate MUs from four of the 12 proposed DUs for caribou in eastern Canada (Fig. 1). These four DUs correspond to (1) Migratory Tundra caribou of northern Labrador, Québec, Ontario, and Manitoba (DU4), (2) Boreal caribou, which resides in the boreal forest throughout Canada (DU6), (3) Torngat Mountains caribou of Northern Québec and Labrador (DU10), and (4) Atlantic-Gaspésie caribou, the only caribou herd south of the St. Lawrence River (DU11) (Fig. 1). DUs identification was based on multiple lines of evidence but mainly on movements, behavior, distribution and, when available, genetic information in the study area (Courtois et al. 2003; Boulet et al. 2007). Despite their considerable longitudinal distribution, Boreal caribou were all assigned to the same DU (DU6; COSEWIC 2011). This DU, however, comprised multiple “local populations”, defined as a demographically independent group of animals that live and breed together where the population dynamic is mainly driven by local demographic rates with limited exchange among adjacent populations (Environment Canada 2008, 2011; Équipe de rétablissement du caribou forestier du Québec 2013). While this definition is similar to the MU definition based on genetic criteria (Palsbøll et al. 2007), the “local population” demographic independence is primarily based on the spatial distribution range of populations determined from telemetry data rather than on genetic information (Environment Canada 2008, 2011). The delineation of “local populations” is, moreover, uncertain in Québec and Labrador where a single local population broadly extends throughout the entire range of the boreal forest and includes the range of other local populations (Environment Canada 2011, 2012). Therefore the delineation of local populations for Boreal caribou deserves further investigation.

Here, we assessed genetic structure of caribou using neutral loci and different Bayesian clustering methods—some integrating the spatial location of genetic samples in their models. The demographic independence of genetic clusters was assessed applying the “10 % migrant criterion” proposed by Waples and Gaggiotti (2006). To make our approach transparent and repeatable, we present in Fig. 2 how we integrated the different sources of

information to spatially delineate MUs. Specifically, we combined (1) microsatellite data to identify genetic clusters and (2) ecotype designation, the location of calving grounds, and space use to delimit ecological units.

Materials and methods

Study area and species

The study area covers several ecosystems in Québec and Labrador, eastern Canada, including boreal forest, mountain habitat and Arctic tundra, over $\sim 1,365,000$ km² (Yannic et al. 2014b). Three ecotypes of caribou are present in the study area: the Migratory Tundra caribou, the Mountain caribou, and the Boreal forest caribou (Bergerud 2000) (Fig. 1). Migratory Tundra caribou herds can be large and formed of hundreds of thousands of individuals (Bergerud 2000) (Table 1). Migratory Tundra caribou are gregarious on calving grounds and undertake seasonal migrations over long distances (often >1000 km) between wintering areas in the boreal forest and summer range in the tundra (Dalziel et al. 2015). Boreal forest caribou are sedentary and inhabit the boreal forest throughout the year. Several animals undertake short seasonal migrations within their home-range of hundreds or thousands of km² (Schaefer et al. 2000; Faille et al. 2010). They live alone or in small groups. The Mountain caribou performs altitudinal migration associated with food availability and predation avoidance between seasonal ranges (up to 100 km) (Boulet et al. 2007).

Sample collection

We analyzed 560 caribou representative of the three caribou ecotypes found in Québec and Labrador, all belonging to the North-Eastern American lineage (Yannic et al. 2014a), and mainly to the haplogroup A1 and to a lesser extent to haplogroup A3 defined by Klütsch et al. (2012) ($n = 30$; data not shown). The sampling included the two Migratory Tundra herds of the Ungava Peninsula: the Rivière-George (RGH; $n = 71$) and the Rivière-aux-Feuilles (RFH; $n = 77$) herds (Table 1). Although these two herds are genetically similar (Boulet et al. 2007), they are managed as different populations because they use separate calving grounds and show contrasting population dynamics (Taillon et al. 2012). We analyzed Mountain caribou from the Torngat ($n = 23$) and Gaspésie populations ($n = 29$), and sedentary boreal forest caribou ($n = 331$, including 25 caribou from the disconnected Val d’Or herd) ranging over ca. 500,000 km² of boreal forest (Table 1; Fig. 1). We also included 29 individuals from the Charlevoix herd (CHARL), which was founded in the late

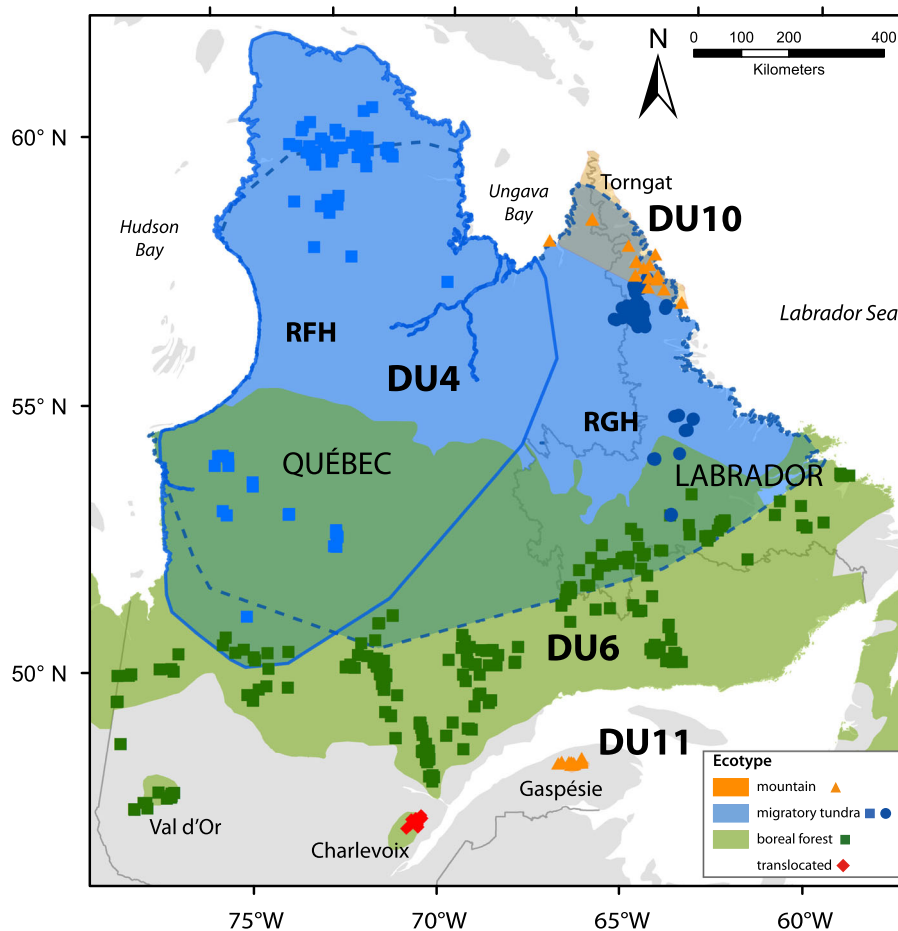


Fig. 1 Distribution of caribou sampled for DNA analyses in Québec and Labrador, eastern Canada. 1 *Blue squares* Rivière-aux-Feuilles Migratory Tundra herd (RGH), 2 *dark blue dots* Rivière-George Migratory Tundra herd (RFH), 3 *green squares* Boreal caribou ecotype, 4 *orange triangles* the Mountain caribou of Gaspésie and Torngat Mountains, 5 *red diamonds* translocated caribou herd of Charlevoix. The range of designatable units (DU) adopted for caribou in Canada is also shown by colored polygons. The four DUs present in the study area and correspond to DU4: Migratory Tundra caribou of northern Labrador, Québec, Ontario, and Manitoba, DU6: Boreal

caribou which resides in the boreal forest throughout Canada, DU10, Torngat Mountains caribou of northern Québec and Labrador, and DU11: Atlantic-Gaspésie caribou, the only caribou herd south of the St. Lawrence River. The range of DU4 (eastern Migratory Tundra) and DU6 (Boreal) extend beyond the study area and only parts of their range are thus studied here. The annual ranges of migratory herds are delineated by *solid and dashed contour lines* for RFH and the RGH, respectively. Annual ranges are 100 % Minimum Convex Polygons based on ARGOS locations. The spatial overlap between ecotypes is indicated by intermediate *shading*

1960s from 48 individuals translocated from the continuous distribution area of boreal forest caribou and captured along the Québec–Labrador border (St-Laurent and Dus-sault 2012).

Tissue samples were mostly collected between 1999 and 2010, and consisted of blood clots, ear punches and hair obtained during field research studies or muscle from euthanized animals (Taillon et al. 2011). Sedentary Boreal forest and Migratory Tundra caribou ranges overlap during certain periods of the year (e.g., in winter). When caribou were captured in overlapping areas, we ensured ecotype assignment through the evaluation of movement patterns using a satellite-tracking system [Ministère des Forêts, de la Faune et des Parcs (MFFP)]. Animal manipulations

followed guidelines of the Canadian Council on Animal Care.

DNA extraction and microsatellite genotyping

DNA was extracted from dried blood and muscle according to the salt extraction protocol of Aljanabi and Martinez (1997). We extracted DNA from hair and fresh blood samples using DNeasy™ Tissue and Blood Kits (Qiagen, Inc., Valencia, CA, USA), respectively. We followed the manufacturer's protocol, with minor modifications for hair samples. Up to 15 guard hair roots were first incubated in tubes containing 180 µl of ATL buffer, 20 µl of proteinase K (20 mg/ml) and 30 µl of dithiothreitol (10 mg/ml).

Fig. 2 Workflow for delineating Management Units (MU) in caribou. White caribou represent fictitious individual sampling locations, *1 blue outlines* represent the genetic delineation, *2 yellow outlines* represent the ecological delineation, and *3 red outlines* are MUs obtained from the combination of genetic and ecological delineation criteria

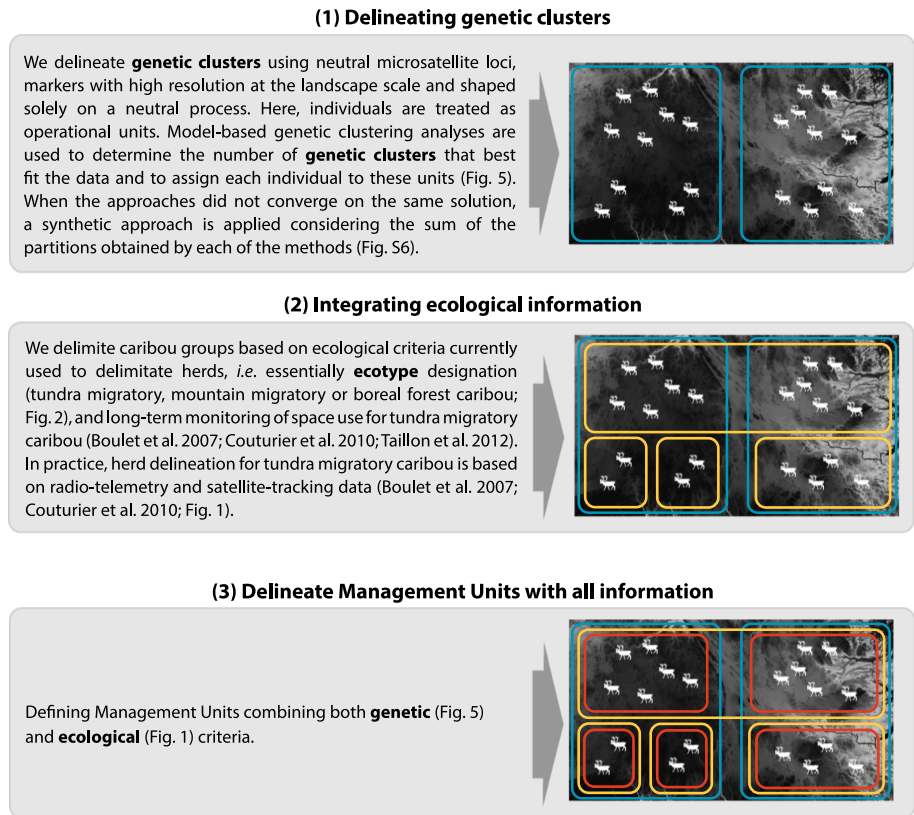


Table 1 Population parameters for all caribou herds analyzed; including name (Herd), herd abbreviation (abbr.), number of individuals sampled for genetic analysis (*N*) and census population size (*N_c*; when available, 90 % confidence intervals (CI 90 %) are provided)

Ecotype	Herd	abbr.	<i>N</i>	<i>N_c</i>	<i>A</i>	<i>A_r</i>	<i>H_O</i>	<i>H_E</i>	<i>F_{IS}</i>
Migratory Tundra	Rivière-George	RGH	71	14,200 ± 710 (2014) ^a	11.2	8.5	0.70	0.76	0.083
	Rivière-aux-Feuilles	RFH	77	430,000 ± 98,900 (2011) ^a	11.6	8.6	0.71	0.75	0.059
Boreal forest	Continuous range	Boreal	306	~ 10,000 (2000 s) ^{b,c}	13.0	7.8	0.68	0.75	0.101
	Val d’Or	VaOr	25	<20 (2012) ^b	3.8	3.7	0.58	0.57	−0.006
	Charlevoix	CHARL	29	84 (2008) ^b	6.0	5.8	0.69	0.71	0.036
Mountain	Gaspésie	GASP	29	103 (2012) ^d	4.4	4.2	0.56	0.61	0.084
	Tornat Mountains	TORN	23	930 ± 312 (2014) ^e	8.9	8.8	0.73	0.77	0.053
Total			560						

A mean number of alleles per locus, *A_r* allelic richness averaged over loci based on minimum sample size of 22 diploid individuals, *H_O* observed heterozygosity, *H_E* expected heterozygosity, *F_{IS}* inbreeding coefficient

^a Ministère des Forêts, de la Faune et des Parcs, Québec. unpublished data

^b Équipe de rétablissement du caribou forestier du Québec (2013)

^c Schmelzer et al. (2004)

^d Lalonde and Michaud (2013)

^e Couturier and Mitchell Foley (2014)

Samples were incubated overnight at 37 °C and the remaining steps followed the manufacturer’s protocol.

Optimized microsatellite markers were used in multiplex PCRs, totaling 16 microsatellite markers: Nvhrt16 and Nvhrt30 (Røed and Midthjell 1998), Rt1, Rt5, Rt6, Rt7, Rt9 s, Rt24 and Rt27 (Wilson et al. 1997), BL42, BM4513

and BM6506 (Bishop et al. 1994), BMS745 and BMS1788 (Stone et al. 1995), FCB193 (Buchanan and Crawford 1993) and OheQ (Jobin et al. 2008) (Table S1). Individuals were genotyped in 10-μl multiplex reactions containing 3 μl of DNA (5–50 ng/μl) and 1 × Multiplex PCR MasterMix (Qiagen, Valencia, CA, USA). One primer pair was

fluorescently labeled (fluorescent tags: 6-FAM, PET, NED or VIC) and primer concentrations ranged from 0.08 to 0.4 μM . The PCR profile consisted of an initial denaturing of 15 min at 95 °C, followed by 35 cycles at 94 °C for 45 s, 54 °C for 90 s, 72 °C for 1 min, and a final extension at 72 °C for 30 min. Multiplexes 1 and 2 were pooled after PCR (Table S1). All PCR products were ran on an ABI 3130xl Genetic Analyzer 16 capillary system (Applied Biosystems, Forster City, CA, USA) and sized with internal lane standard (500 LIZ; Applied Biosystems) using the program GENE Mapper 4.0 (Applied Biosystems).

Standard population genetic analyses

Genetic diversity across all samples and within each cluster (determined by the 60 % threshold assignment; see genetic clustering analyses below) was assessed by determining the number of alleles (A), observed (H_O) and expected (H_E) heterozygosity (Nei 1973) using GENALEX 6.2 (Peakall and Smouse 2006). Allelic richness (A_r) was estimated using the rarefaction method implemented in FSTAT 2.9.3 (Goudet 1995). FSTAT was also used to test for linkage disequilibrium, and significance was tested with 10,000 permutations. We tested for deviation from Hardy–Weinberg equilibrium (HWE) using the exact test in GENEPOP 4.0 (Rousset 2008). Individual heterozygosity was estimated as the proportion of heterozygous genotypes for each individual with the R function “GENHET” (Coulon 2010). Spatial interpolation of genetic diversity was then plotted using a thin plate spline method, implemented in the R package “fields”.

We estimated genetic differentiation among clusters from F_{ST} values calculated with FSTAT, with 10,000 random permutations to assess significance. We estimated the effective population size (N_e) for each inferred genetic cluster using the linkage disequilibrium method in LDNE (Waples and Do 2008). Allele frequencies <0.02 were excluded from analyses and 95 % confidence intervals estimated by Jackknife (Waples and Do 2010).

Genetic clustering analyses

We investigated genetic structure using three Bayesian clustering methods, because different methods have been shown to provide somewhat different results (Latch et al. 2006; Chen et al. 2007), see Ball et al. (2010) for an example on boreal caribou in central Canada. Thus, we adopted a conservative approach combining the results of methods with alternative properties. We first used analyses implemented in STRUCTURE version 2.3.3, considered as the standard reference software for such analyses (Pritchard et al. 2000; Falush et al. 2003). Second, we used two alternative approaches that integrate spatial coordinates of

samples as implemented in TESS version 2.3 (Chen et al. 2007) and GENELAND version 4.0.3 (Guillot et al. 2005a). This can provide a more reliable inference of genetic clusters by incorporating spatial information. In this case, individuals are assigned to the most likely cluster based on their genotype, but also on their geographic location such that boundaries among populations may be identified more clearly than with STRUCTURE analyses (Coulon et al. 2006). For Migratory Tundra caribou that migrate long distances between winter areas and calving and summer grounds, we used sampling points for the two spatially explicit Bayesian analyses (TESS and GENELAND; Fig. 1). Procedures are detailed in Electronic Supplementary Material. Individuals were subsequently assigned to their most likely cluster using an arbitrarily defined threshold of 0.60 that ensures that at least 60 % of an individual’s genome is assigned to one cluster (e.g., Coulon et al. 2008). Increasing the value for this arbitrary threshold resulted in a higher proportion of individuals unassigned to any cluster, but the global conclusions of our study remained the same (data not shown). We plotted the assignment results on interpolated maps using the Kriging method implemented in the “fields” R package. We estimated the range of each genetic cluster with minimum convex polygons (95 % MCPs) using the “adehabitatHR” R package (Calenge 2006).

Isolation by distance vs clustering

Bayesian clustering methods can detect a spurious number of genetic clusters when uneven sampling is performed along a genetic cline or under isolation by distance (IBD) (Frantz et al. 2009; Blair et al. 2012; Landguth and Schwartz 2014). To alleviate this problem, we compared the results of spatially explicit and non-spatial clustering methods (GENELAND and TESS versus STRUCTURE; see below), together with the detection of IBD as suggested by Guillot et al. (2009), to accurately assess the genetic structure of populations. To do so, we explored IBD at different levels. First we investigated the spatial genetic structure at the individual level. Genetic distance a (Rousset 2000) was computed between pairs of caribou (Fig. 1) using the program SPAGeDi 1.4c (Hardy and Vekemans 2002), and geographic distances among individuals were calculated using the great circle distance among their original location of capture using the R package ‘geosphere’ 1.3-11 (Hijmans 2014), and the ‘Vincenty (ellipsoid)’ method. Second, we explored the relationship between the logarithm of geographic distances and the pairwise genetic distances ($F_{ST}/(1 - F_{ST})$) (Rousset 1997) among clusters obtained for the three Bayesian clustering methods and the synthetic clustering approach. Geographic distances among clusters were estimated using the great circle distances between their 95 % MCP centroids.

Finally, we investigated IBD at the individual level within each cluster, i.e., the relationship between the genetic distance a (Rousset 2000) and the great circle distance among the locations of capture. The relationships between geographical and genetic distances were tested with Mantel tests (Mantel 1967) implemented in the R package ‘*ecodist*’ 1.2.9 (Goslee & Urban 2007), and significance assessed with 10,000 permutations.

Delineation of management units (MU) in caribou

To delineate MUs for caribou in eastern North America, we employed the workflow detailed in Fig. 2. We first delineated genetic clusters using the model-based genetic clustering analyses described above. The results obtained with the three methods may differ in the number of inferred genetic clusters (see “Results” section). Thus, in order to reconcile the variability among the employed model-based methods, we adopted a comparative synthetic approach, where we considered each of the genetic partitions obtained by the methods (Results and Fig. S6). Then, we plotted the results of the assignments on a map and we delimited the areas including the individuals assigned to the same genetic groups. This map was then compared to the map of ecotypes and herd delineation provided on Fig. 1. With the superposition of genetic clustering (Figs. S7, 5) and ecological information (Fig. 1), we delineated MUs boundaries for caribou in eastern North America.

Demographic independence

We assessed the demographic independence of each genetic cluster and each management unit using the “10 % migrant criterion” (Waples and Gaggiotti 2006). According to this criterion, a population is considered as demographically independent if contemporary migration rate is below a 10 % threshold. The proportion of migrants within each genetic cluster was estimated using the “detection of first-generation migrants” model implemented in *GENECLASS 2* (Piry et al. 2004). We estimated the likelihood of migration rate ($L = L_{HOME}/L_{MAX}$) using the Bayesian criteria of Rannala and Mountain (1997) and significance was assessed by the resampling method of Paetkau et al. (2004), based on 10,000 simulated individuals.

Results

Population genetic analyses using all samples

The mean number of alleles per locus was 15 ± 8 SD, ranging from 9 to 43, the maximum number being on locus

BM4513 (Table S2). Global F_{IS} was 0.063 and heterozygote deficiency was significant ($P = 0.001$) (Table S2), likely due to three loci (BM4513, NVHRT30 and Rt5). There was no significant linkage disequilibrium after multi-test adjustment. We observed a latitudinal gradient of genetic diversity, with the proportion of heterozygous loci in an individual increasing with latitude (linear regression: $F_{1,558} = 25.3$, $R^2 = 0.05$, $P < 0.001$; Fig. 3).

Bayesian genetic clustering

STRUCTURE analyses

STRUCTURE identified four distinct genetic clusters (Fig. S2). The mean likelihood $L(K)$ reached a plateau at $K = 4$, but was still slightly increasing for higher values of K for which the variance among runs increased. This is a commonly observed phenomenon once the true K is reached (e.g., Evanno et al. 2005). A histogram of individual assignment scores for $K = 4$ (Fig. 4) and the spatial interpolated map (Fig. S4) show a clear geographic delineation of the inferred genetic clusters. Cluster#1 was confined to the Gaspésie Peninsula, south of the St. Lawrence River. Cluster#2 had a northerly distribution and encompassed the two Migratory Tundra caribou herds, the Torngat Mountains caribou and the Boreal forest caribou from Labrador and the north shore of the St. Lawrence River. Cluster#3 had a more westerly distribution, south of James Bay along the Ontario border, and it also included the translocated herd in the Charlevoix massif. Finally, Cluster#4 included boreal forest caribou inhabiting the area centered on the Saguenay/Lac St-Jean region. The ΔK method indicates that the study area encompasses two main genetic clusters (Fig. S2). The two clusters are geographically well defined and correspond to (i) all individuals from the north and the east of the Ungava Peninsula (Cluster#2) and (ii) individuals in the south of the study area (Cluster#1). Hierarchical analyses performed on each cluster for $K = 2$ distinguished the same four clusters retrieved using the original procedure of Pritchard et al. (2000).

TESS analyses

TESS algorithm, that integrates spatial information on sampling points suggested that the data set was likely composed of five genetic clusters. *TESS* runs with the smallest deviance information criterion (DIC) values were obtained for a number of clusters $K_{max} \geq 5$ (Fig. S3). With number of clusters $K_{max} > 5$, we detected the same five genetically distinct clusters. The clustering was very similar to results obtained with *STRUCTURE* (Figs. 4, S4). The main difference is the split of the most westerly cluster

Fig. 3 Spatially interpolated values of genetic diversity for 560 caribou of Québec and Labrador, eastern Canada, defined as the proportion of heterozygous loci in an individual based on 16 microsatellite loci: lower genetic diversity values are illustrated in *blue* while higher genetic diversity values are in *red*

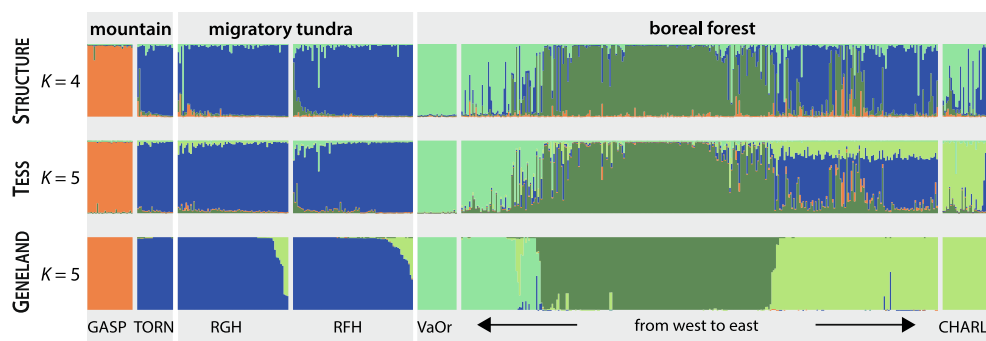
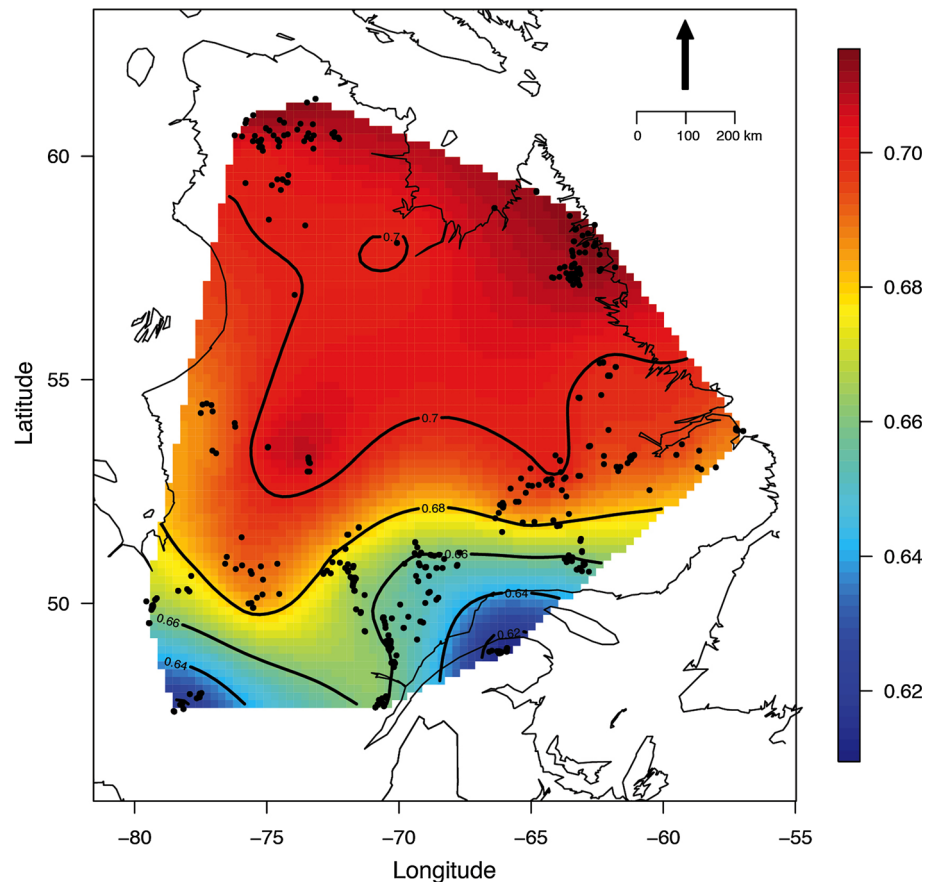


Fig. 4 Individual clusters assignment (q [0, 1]) using the three clustering methods (STRUCTURE, TESS and GENELAND) for 560 caribou of Québec and Labrador, eastern Canada. Clusters were ordered by ecotype and by longitudinal location for the Boreal forest caribou ecotype. *GASP* Mountain caribou of Gaspésie, *TORN* Mountain

caribou of Torngat Mountains, *RFH* Rivière-aux-Feuilles Migratory Tundra herd, *RGH* Rivière-George Migratory Tundra herd, *VaOr* Boreal caribou of Val d'Or, *CHARL* translocated caribou herd of Charlevoix

inferred by STRUCTURE in two independent clusters; (i) the translocated herd of Charlevoix (Cluster#5) and (ii) the Val d'Or and western boreal forest caribou (Cluster#3). As with STRUCTURE, Cluster#2 corresponds to the two Migratory Tundra caribou herds, the Torngat Mountains caribou and the boreal forest caribou from Labrador and the north shore of the St. Lawrence River. Cluster#4 includes boreal forest

caribou around the Saguenay/Lac St-Jean region and Cluster#1 corresponds to the population from Gaspésie.

GENELAND analyses

GENELAND analyses revealed the presence of 5 genetic groups (K) for nine of the ten runs and the remaining run

estimated a modal value of $K = 6$. The run with the highest mean posterior density was obtained for $K = 6$, but the 6th cluster corresponded to a “ghost” cluster (Guillot et al. 2005b), i.e. a cluster for which no individual was assigned. This is a common result with GENELAND, which likely originates from departure from the model assumptions (e.g., panmixia within cluster) (Guillot et al. 2005b). While GENELAND inferred the same number of clusters as TESS ($K = 5$), the two methods differed in the partitioning of genetic clusters. The main difference corresponded to the split between the group composed of the two Migratory Tundra caribou herds (RGH and RFH) and the Torngat Mountains caribou (Cluster#2), and the group formed by the boreal forest caribou from Labrador, the north shore of the St. Lawrence River and the Charlevoix herd (Cluster#5; Figs. 4, S4). The later was originally composed of caribou translocated from the Québec-Labrador border grouped with caribou of its source area according to GENELAND, whereas it formed an independent cluster according to TESS analyses (TESS Cluster#5; Figs. 4, S4). The three remaining clusters corresponded to the same genetic groups previously detected by STRUCTURE and TESS.

Population genetic analyses on the inferred populations

The clusters with lower genetic diversity were located in the southern part of the study area (Fig. 3; Table S2). Among clusters, the lowest genetic diversity was observed in Gaspésie (Cluster#1): $H_o = 0.56$, $A_r = 4.31$ and $A_p = 0$. F_{IS} values for most clusters were positive and significant, suggesting population deviation from HWE due to non-random mating (Tables 2, S2). Global F_{ST} values were similar and significant for analyses comparing the genetic clusters inferred with all Bayesian clustering methods (STRUCTURE $K = 4$: 0.060; TESS $K = 5$: 0.067; and GENELAND $K = 5$: 0.051; $P < 0.0001$). Pairwise comparisons between clusters identified by STRUCTURE $K = 4$ (pairwise F_{ST} values 0.035–0.138), TESS $K = 5$ (pairwise F_{ST} values: 0.048–0.162) and GENELAND $K = 5$ (pairwise F_{ST} values: 0.016–0.140) were all significant (Table S4). Largest values were observed between the Gaspésie herd (Cluster#1 in all analyses) and all other clusters: pairwise F_{ST} range [0.130–0.138] with STRUCTURE, [0.128–0.162] with TESS and [0.126–0.140] with GENELAND (Table S4). Gaspésie caribou also have the smallest range (320 km²) and a low effective population size (N_e ; Tables 2, S3).

For all clustering methods, >90 % of individuals were assigned to a single genetic cluster using the threshold of 0.60 (Table S3). A number of individuals were not assigned to any cluster using this threshold: STRUCTURE $n_{ADMIXED} = 44$, TESS $n_{ADMIXED} = 57$ and GENELAND $n_{ADMIXED} = 9$ out of 560 caribou (Fig. S5). These

admixed individuals were distributed throughout the study area (Fig. 5), but mostly concentrated along the zones of contact between the Migratory Tundra ecotype and the Boreal forest caribou ecotype, suggesting genetic exchanges among ecotypes across the landscape.

Reconciling genetic clustering approaches

The results obtained with the three methods differed in the number of genetic clusters that best fit the dataset. Among the different results, those of GENELAND are the most biologically plausible, as they grouped caribou of the Charlevoix Massif with boreal forest caribou of eastern Québec and Labrador. Given our sampling design, we have no biological reason to consider that the genetic clusters detected by a particular method provides a better picture of the real genetic structure than others (Chen et al. 2007). Then, we reconciled variability among the employed model-based methods using a synthetic approach (Fig. S6).

The methods differed mainly on the position of the translocated Charlevoix herd and the boreal caribou from eastern Québec and Labrador (Figs. 4, S4). These caribou (i) grouped with Migratory Tundra and Torngat Mountains caribou according to STRUCTURE (cluster#2), (ii) in different clusters according to TESS (cluster#2 and cluster#5), and (iii) formed an independent genetic group from Migratory Tundra and Torngat Mountains caribou according to GENELAND (cluster#5). We considered the translocated Charlevoix herd and the boreal caribou from eastern Québec and Labrador as independent genetic clusters following Fig. S6. Although differences are apparent, the results obtained with each genetic clustering method nevertheless showed some consistent patterns. For each of the methods, cluster #1, cluster #2 and cluster #4 were consistently detected and grouped individuals of the same area (Figs. 4, S4).

Overall, 499 out of 560 caribou were assigned to a genetic cluster (Table 2). Accordingly, we distinguished six genetic clusters in Québec and Labrador: (i) the Gaspésie genetic cluster (cluster #1); (ii) the Migratory Tundra and Torngat Mountains caribou cluster (cluster #2), (iii) the western boreal forest group of Québec (cluster #3); (iv) the central boreal forest genetic group of Québec (cluster #4); (v) the eastern boreal forest genetic group of Labrador (cluster #5); and (vi) the translocated herd of Charlevoix (cluster #6) (Fig. 5; Table 2). Descriptive statistics for each of the inferred clusters obtained with this synthetic approach are presented in Table 2 and pairwise F_{ST} among clusters in Table 4.

Isolation by distance

We observed an overall low but significant relationship between geographic distance and genetic distance among

Table 2 Estimates of genetic diversity, spatial extent and effective population size of caribou clusters obtained by our synthetic approach based on different Bayesian clustering methods

	N	A	Ap	Ar	H _O	H _E	F _{IS}		Area (km ²)	N _e (95 % CI)	Mantel' r (P value)	Herd/locality
Cluster#1	29	4.4	0.00	4.31	0.56	0.61	0.084	NS	3.20 × 10 ⁺²	46.4 (27.6; 108.8)	−0.111 (P = 0.64)	GASP
Cluster#2	167	13.4	1.31	9.06	0.71	0.76	0.068	*	6.46 × 10 ⁺⁵	+∞ (1838.0; +∞)	0.058 (P = 0.001)	RGH, RFH and TORN
Cluster#3	64	8.1	0.47	6.65	0.64	0.69	0.076	*	5.26 × 10 ⁺⁴	36.1 (30.8; 42.7)	0.082 (P = 0.001)	Western Boreal forest of Québec; VaOr
Cluster#4	153	10.1	0.61	7.15	0.66	0.73	0.098	*	1.64 × 10 ⁺⁵	185.5 (148.9;240.2)	0.026 (P = 0.06)	Central Boreal forest of Québec
Cluster#5	61	9.8	0.58	7.76	0.71	0.75	0.055	NS	1.15 × 10 ⁺⁵	286.7 (181.9; 620.1)	0.017 (P = 0.50)	Eastern Boreal forest of Labrador
Cluster#6	25	6.0	0.18	5.94	0.69	0.71	0.036	NS	3.15 × 10 ⁺²	37.7 (26.9; 58.7)	0.111 (P = 0.08)	CHARL

See Table 1 for herd/locality designation

N sample size, *A* mean number of alleles per locus, *Ap* mean number of private alleles per locus, *Ar* allelic richness averaged over loci based on minimum sample size of 25 diploid individuals, *H_O* observed heterozygosity, *H_E* expected heterozygosity, *F_{IS}* inbreeding coefficient and p-value based on 1600 randomizations (*significant, NS not significant), *N_e* Effective population size with 95 % confidence intervals (CIs), *Mantel' r* Mantel correlation between pairwise genetic distance a (Rousset 2000) and geodesic distance among individuals within each cluster

Area range size for each cluster (in km²), based on a minimum convex polygon estimated with 95 % of the animal locations

pairs of caribou (Mantel's *r*: 0.06, *P* = 0.001; genetic distance = $1.17 \times 10^{-2} + 1.66 \times 10^{-5}$ geographic distance, adjusted-*R*²: 0.004; Fig. S1). We detected a low effect of geographic distance on genetic differentiation, but with a high statistical power due to the high number of data points (*n* = 560 caribou; 156,520 pairwise distances) (Luximon et al. 2014). In addition, a significant IBD was also observed among forest-dwelling caribou along the continuous boreal forest (*n* = 306 caribou; Mantel's *r*: 0.02, *P* = 0.005). Low but significant correlations between geographic and genetic distances were observed at the individual level within some genetic clusters (Tables 2, S3). We did not observe significant correlations between geographic and genetic distances among the inferred clusters: STRUCTURE (*K* = 4, Mantel's *r*: −0.12, *P* = 0.75), TESS (*K* = 5, Mantel's *r*: −0.20, *P* = 0.81), and GENELAND (*K* = 5, Mantel's *r*: −0.23, *P* = 0.88), as well as for the synthetic clustering approach (*K* = 6, Mantel's *r*: −0.33, *P* = 0.53).

Effective population size of the inferred clusters

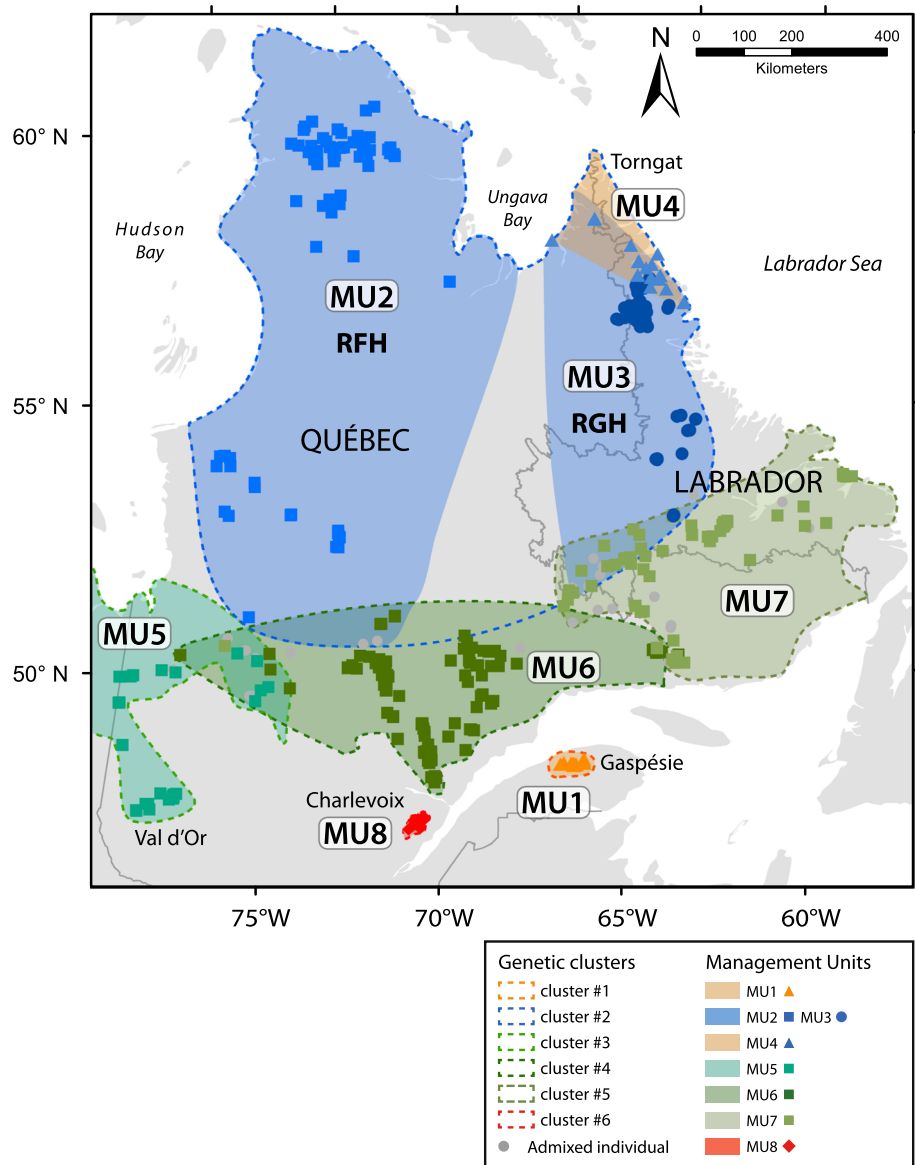
Overall, *Ne* was low for most clusters and much lower than *Nc* (Tables 2, S3; Fig. S8). *Ne* were <50 for genetic clusters #1, #3 and #6 and <500 for genetic clusters #4 and #5. *Ne/Nc* ratio ranged from 0.03 to 0.45 (mean ± SD = 0.24 ± 0.19) if we exclude the *Ne* estimate for cluster#2. Estimate of *Ne* was indeed unclear for cluster#2 (i.e., Migratory Tundra RGH and RFH and Tornгат Mountains herd) with 95 % CIs spanning from 1800 to

infinity (Table 2). This was the most imprecise estimate. Despite changes in the recent time, RGH and RFH population sizes (*Nc*) are still large (Table 1). Estimating effective size with precision is, however, very difficult in large populations (i.e., *Ne* ≥ 1000 or larger) even when the number of individuals sampled for genetic analysis is high (Waples and Do 2010).

Demographic independence

GENECLASS2 identified 32 first-generation migrants among the 499 animals assigned to a genetic cluster using the synthetic approach (Table 3). Applying the “10 % migrant criterion” of Waples and Gaggiotti (2006) to evaluate the demographic independence of each cluster, we found five out of six genetic clusters as demographically independent. The proportion of first-generation migrants was particularly high in the boreal caribou from eastern Québec and Labrador (cluster#5: 16 %). The ten first-generation migrants detected by GENECLASS in cluster#5 were all originating from cluster#2, i.e. the cluster including the Migratory Tundra herds RFH and RGH and the Tornгат caribou. We also estimated the proportion of first-generation migrants for the different clusters identified by each of the three Bayesian clustering approaches (STRUCTURE, TESS and GENELAND). Fifteen (STRUCTURE), fourteen (TESS) and forty-eight (GENELAND) caribou were detected as immigrants at the 5 % probability threshold (data not shown). Then, 4/4 (STRUCTURE), 5/5 (TESS) and 4/5 (GENELAND) genetic clusters

Fig. 5 Delineation of management units (MU) for caribou in Québec and Labrador, eastern Canada, based on genetic and ecological information. Caribou assigned to the same genetic clusters are depicted by the same color and genetic cluster are delineated by *dashed lines* (see Fig. S7). *Grey dots* correspond to caribou not assigned to any of the inferred clusters at the threshold $q_i > 0.6$. Colored polygons represent management units based on genetic information and ecotype and demographic designation



were considered demographically independent according to the “10 % migrant criterion”, respectively (Table S3).

Delineation of management units (MU) in caribou

Integrating information from Bayesian genetic clustering analyses (step 1) and ecological knowledge on caribou (step 2), we distinguished eight management units (step 3) (Fig. 2): (i) the Gaspésie Mountain caribou herd (MU #1); (ii) the Rivière-aux-Feuilles Migratory Tundra caribou herd (MU #2); (iii) the Rivière-George Migratory Tundra caribou herd (MU #3); (iv) the Torngat Mountains herd (MU #4); (v) the western Boreal forest caribou unit of Québec (MU #5); (vi) the central Boreal forest caribou unit of Québec (MU #6); (vii) the eastern Boreal forest caribou

unit of Labrador (MU #7); and (viii) the translocated Charlevoix herd (MU #6) (Fig. 5). The different MUs are not always genetically demographic independent using the “10 % criteria” (Table 3).

Discussion

We integrated genetic and ecological information to accurately detect spatial boundaries of management units for caribou in eastern Canada, a critical step to inform effective management actions. In order to delineate genetic boundaries, we used different Bayesian clustering methods available in three computer programs, STRUCTURE, TESS and GENELAND, which are known to outperform other

Table 3 Detection of first-generation migrants within each genetic cluster defined using the synthetic approach and within each Management Unit (MU; Fig. 5)

Genetic cluster	MU	Herd/locality	<i>N</i>	mig	%mig
Cluster #1	MU #1	GASP	29	0	0.00
Cluster #2		RGH, RFH, TORN	167	12	0.07
	MU #2	RGH	68	10	0.15
	MU #3	RFH	76	11	0.14
	MU #4	TORN	23	3	0.13
Cluster #3	MU #5	Western Boreal forest of Québec; VaOr	64	6	0.09
Cluster #4	MU #6	Central Boreal forest of Québec	153	6	0.04
Cluster #5	MU #7	Eastern Boreal forest of Labrador	61	10	0.16
Cluster #6	MU #8	CHARL	25	0	0.00

N, the number of animals within each cluster; mig and %mig, respectively the number and the proportion of animals in each cluster detected as first-generation migrant by GENECLASS 2, at the 5 % probability threshold to be originating from another cluster. See Table 1 for Herd/locality designation

approaches (Blair et al. 2012). Hence, we first distinguished six genetic clusters in Québec and Labrador. Five of these six genetic clusters were considered as demographically independent when applying the “10 % migrants criterion” (Waples and Gaggiotti 2006). Integrating genetic and ecological information as summarized in Fig. 2, we further distinguished eight management units: (i) the Gaspésie Mountain caribou herd (MU #1); (ii) the Rivière-aux-Feuilles migratory caribou herd (MU #2); (iii) the Rivière-George migratory caribou herd (MU #3); (iv) the Torngat Mountains herd (MU #4); (v) the western Boreal forest caribou unit of Québec (MU #5); (vi) the central Boreal forest caribou unit of Québec (MU #6); (vii) the eastern Boreal forest caribou unit of Labrador (MU #7); and (viii) the translocated Charlevoix herd (MU #6) (Fig. 5). Each management unit presents unique genetic membership and/or ecological characteristics that make them valuable candidates for management consideration (Table 4).

The Migratory Tundra and Torngat Mountains caribou genetic cluster represents the core area for caribou, with large panmictic herds that exhibit the highest levels of genetic diversity. Our results also confirm previous study that found that the two Migratory Tundra and Torngat caribou herds were not genetically distinct (Boulet et al. 2007). The genetic results also clearly showed that populations in the continuous range of the boreal forest were separated in three distinct entities (central and western boreal forest units of Québec; and eastern boreal forest unit of Labrador). The three genetic clusters correspond to true discontinuities in the range of the Boreal forest caribou that can be explained by landscape discontinuities, e.g. by boreal forest logging, and habitat preferences of the species (Vors et al. 2007; Leclerc et al. 2012; Weckworth et al. 2013; Leclerc et al. 2014; Yannic et al. 2014b; Losier et al. 2015). Then, as previously shown in other portions of its range (e.g., Ball et al. 2010), Boreal forest caribou does not

form a continuous panmictic population along the boreal forest of Québec and Labrador.

Higher number of genetic clusters in the southern part of the study area may reflect historical and ongoing habitat fragmentation and population isolation (Équipe de rétablissement du caribou forestier du Québec 2013). In accordance with the “central-marginal” model (Eckert et al. 2008), caribou populations are likely to be genetically impoverished and highly differentiated at the edge of their distribution (Yannic et al. 2014a). This was particularly evident for the Gaspésie herd, the only caribou population south of the St. Lawrence River, and for herds located in the southwestern portion of the study area and part of the western boreal forest group of Québec. Genetic diversity should also increase with effective population size (Frankham 1996). Accordingly, the Val d’Or herd (cluster #3) was estimated at <20 caribou (Équipe de rétablissement du caribou forestier du Québec 2013) and showed

Table 4 Pairwise F_{ST} among pairs of genetic clusters inferred by the synthetic approach, using a 60 % individual assignment threshold to a cluster (below diagonal)

	#1	#2	#3	#4	#5
Cluster #1		*	*	*	*
Cluster #2	0.140		*	*	*
Cluster #3	0.143	0.047		*	*
Cluster #4	0.128	0.051	0.070		*
Cluster #5	0.150	0.010	0.054	0.048	
Cluster #6	0.161	0.054	0.070	0.057	0.053

The synthetic approach is based on the spatial interpolation of admixture individual proportion to the different clusters identified with the three Bayesian clustering approaches (STRUCTURE, TESS and GENELAND). The significance of F_{ST} was tested by permuting individuals 10,000 times among samples (above diagonal). Asterisks indicate F_{ST} significantly different than zero after correction for multiple testing (Bonferroni correction)

lower diversity, whereas Migratory Tundra herds from the north of the peninsula were composed of several hundred thousands caribou in recent decades (Couturier et al. 2010) and had higher genetic diversity (Fig. 3).

The values of N_e are of concern for most genetic clusters (Fig. S8). Inbreeding and loss of genetic diversity are unavoidable in small and closed populations, and accumulate in a ratchet-like manner over generations for diploid random mating populations (Wright 1969). The 50/500 rule often cited by conservation practitioners (e.g., Jamieson and Allendorf 2012), and recently revised to $\geq 100/1000$ (Frankham et al. 2014) postulates that a minimum of 100 for N_e is necessary to avoid inbreeding depression, but that an $N_e \geq 1000$ is required to maintain evolutionary potential (Frankham et al. 2014). N_e/N_c ratio ranged from 0.03 to 0.45 (mean \pm SD = 0.24 ± 0.19) if we exclude the estimate of N_e for genetic cluster#2, i.e., Migratory Tundra and Torngat Mountains herd genetic cluster ($+\infty$ [1838.0 – $+\infty$]). Given the small effective population sizes for most of the populations we studied, management strategies should target connectivity among caribou herds to protect them. In a landscape genetic perspective, effective dispersal among populations is influenced by landscape variables that separate them but also by environmental conditions experienced by individuals locally (Wang et al. 2013). Weckworth et al. (2013) studied the effect of N_e on the genetic structure of woodland caribou in west-central Alberta. They found that some landscape features (e.g., selected habitat, human features or predation risk from wolves *Canis lupus*) and effects of local demographic status (i.e., N_e) were the best predictors of genetic structure among caribou populations. This indicates the need to consider both the effects of local conditions and landscape matrix among sampling locations to properly assess effective dispersal among them and to develop appropriate conservation strategies (Pflüger and Balkenhol 2014).

The results from the three Bayesian clustering methods consistently grouped caribou in genetic clusters irrespective of their assigned ecotype. Therefore, in contrast to a previous study that found correspondence between genetic and ecotype designation (Courtois et al. 2003), our results suggest that caribou ecotypes do not match neutral genetic differences. In eastern North America, ecotypes are not necessarily distinct genetically for neutral markers (e.g., Torngat and Migratory Tundra herds) and each ecotype may be represented by multiple genetic entities (e.g., Boreal caribou). Such discrepancies have already been observed in the same area (Boulet et al. 2007) or elsewhere throughout the caribou range in North America (Cronin et al. 2005; Serrouya et al. 2012; Weckworth et al. 2012). The overlap of genetic clustering and ecotype designation highlights the importance of differentiating groups defined using genetic

criteria from those defined using ecological criteria (Cronin et al. 2005). For caribou, genetic clusters should be defined using genetic criteria whereas ecotypes and herds within genetic clusters should be defined using ecological criteria for management purposes. It is, however, worth noting that this conclusion is based on neutral genetic variation and a natural next step would be to explore adaptive genetic differences among ecotypes as well as increasing sample sizes for some locations (e.g., the Torngat Mountains herd), which may potentially redefine in the future some of the management units delineated in this study.

Across their circumpolar range, many caribou and reindeer populations are declining (Vors and Boyce 2009; Festa-Bianchet et al. 2011). This encourages the development and application of recovery strategies at different jurisdictional levels (e.g., for woodland caribou; Environment Canada 2012; Équipe de rétablissement du caribou forestier du Québec 2013). Given the incompatibility between intensive anthropogenic land use and viability of caribou populations (Environment Canada 2011; Festa-Bianchet et al. 2011), habitat protection (e.g., Taillon et al. 2012; Lesmerises et al. 2013) is often considered the most adequate strategy for the conservation of the species (see also Mosnier et al. 2008; Beauchesne et al. 2014 for a discussion on predator control) and biologists need objective and unambiguous criteria to characterize management units that require distinct management plans. Yet several “local populations” have been defined for Boreal caribou in the study area based on radio-telemetry data (Environment Canada 2011; Équipe de rétablissement du caribou forestier du Québec 2013). The delineation of “local populations” in the continuous range of boreal forest is, however, difficult because it requires an extensive longitudinal monitoring of caribou populations in order to determine accurately their demographic independence. The MUs we proposed for Boreal caribou encompass several of these “local populations”, e.g., Val d’Or herd included in the western Boreal forest caribou unit of Québec (MU #5) or the eastern Boreal forest caribou unit of Labrador (MU #7) that includes three well-recognized Boreal caribou herds, Lac Joseph, Red Wine Mountains and Mealy Mountains (Schmelzer et al. 2004). Our analyses constantly grouped these local populations in the same demographically independent genetic clusters whereas they are treated as independent local populations elsewhere (Environment Canada 2008). On a genetic basis, this suggests that they could be managed as a whole rather than as separated units. The MUs we delineated could then be the units on which management actions should be implemented to locally maximize genetic and ecological diversity and ensure the persistence of highest DU numbers and caribou overall.

Most conservation efforts are either directly or indirectly aimed at preserving the evolutionary integrity of a species

via the maintenance of genetic variation and its adaptive potential. As demonstrated in caribou, the delineation of MUs on which to focus management and recovery efforts is often predicted upon evolutionary significance as assessed by a combination of genetic data (variation at neutral genetic markers) and the uniqueness of the habitat occupied with respect to the species' distribution. Finally, moving beyond the caribou perspective, our study illustrates the importance of integrating ecological data and genetic approaches in a landscape context for objectively delineating populations and management units.

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