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4 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 extirpation (Vors & 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 & 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 & 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 & 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 & 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 & 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). Several authors also argued that the demographic independence of units should be properly addressed when delineating management units from population genetic data (Waples & Gaggiotti 2006; Palsbøll et al. 2007; Lowe & 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 (e.g., Olsen et al. 2014). 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 & 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 & 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.

Material 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 ~ 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 >1000s 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 100km) (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 and Fig. 1). We also included 29 individuals from the Charlevoix herd (CHARL), which was founded in the late 1960s from 48 individuals translocated from the continuous distribution area of boreal forest caribou and captured along the Québec–Labrador border (St-Laurent & Dussault 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

202 DNA was extracted from dried blood and muscle according to the salt extraction protocol of
Aljanabi & Martinez (1997). We extracted DNA from hair and fresh blood samples using
204 DNeasyTM 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
206 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). Samples were incubated
208 overnight at 37°C and the remaining steps followed the manufacturer's protocol.

Optimized microsatellite markers were used in multiplex PCRs, totaling 16
210 microsatellite markers: Nvhrt16 and Nvhrt30 (Røed & Midthjell 1998), Rt1, Rt5, Rt6, Rt7,
Rt9s, Rt24 and Rt27 (Wilson et al. 1997), BL42, BM4513 and BM6506 (Bishop et al. 1994),
212 BMS745 and BMS1788 (Stone et al. 1995), FCB193 (Buchanan & Crawford 1993) and
OheQ (Jobin et al. 2008) (Table S1). Individuals were genotyped in 10-µL multiplex reactions
214 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
216 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
218 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
220 capillary system (Applied Biosystems, Forster City, CA, USA) and sized with internal lane
standard (500 LIZ; Applied Biosystems) using the program GENEMAPPER 4.0 (Applied
222 Biosystems).

224 **Standard population genetic analyses**

Genetic diversity across all samples and within each cluster (determined by the 60% threshold
226 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 & 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 & Do 2008). Allele frequencies < 0.02 were excluded from analyses and
95% confidence intervals estimated by Jackknife (Waples & 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 & Schwartz 2014). To alleviate this problem, we compared the results of spatially explicit and non-spatial clustering methods (GENELAND and TESS vs 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 & 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 (Results). 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
(Fig. S7 and Fig. 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 & 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 39, 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

i) 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
 328 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
 330 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
 332 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
 334 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
 336 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
 338 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
 340 (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).

342 **ii) TESS analyses**

344 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
 346 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.
 348 The clustering was very similar to results obtained with STRUCTURE (Fig. 4 and Fig. S4). The
 main difference is the split of the most westerly cluster inferred by STRUCTURE in two
 350 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.

iii) GENELAND analyses

GENELAND analyses revealed the presence of 5 genetic groups (K) for 9 of the 10 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; Fig. 4 and Fig. 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; Fig. 4 and Fig. 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 and 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 and 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 and 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 (Fig. 4 and Fig. 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 (Fig. 4 and Fig. 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 and 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 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 (Table 2 and Table 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, N_e was low for most clusters and much lower than N_c (Table 2, Table S3 and Fig. S8). N_e were < 50 for genetic clusters #1, #3 and #6 and < 500 for genetic clusters #4 and #5. N_e/N_c ratio ranged from 0.03 to 0.45 (mean $\pm$ SD = 0.24 ± 0.19) if we exclude the N_e estimate for cluster#2. Estimate of N_e was indeed unclear for cluster#2 (*i.e.*, Migratory Tundra RGH and RFH and Torngat 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 (N_c) are still large (Table 1). Estimating effective size with precision is, however, very difficult in large populations (*i.e.*, $N_e \geq 1000$ or larger) even when the number of individuals sampled for genetic analysis is high (Waples & 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 herd RFH and RGH and the Torngat 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 were considered demographically independent according to the “10% migrant criterion”, respectively (Table S3).

Delineation of Management Units (MU) in caribou

Integrating information (Fig. 2) from Bayesian genetic clustering analyses (step 1) and ecological knowledge on caribou (step 2), we distinguished eight management units (step 3): 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 #8) (Fig. 5). The different MUs are not always genetically demographic independent using the “10% criteria” (Table 3).

476

Discussion

478 We integrated genetic and ecological information to accurately detect spatial
boundaries of management units for caribou in eastern Canada, a critical step to inform
480 effective management actions. In order to delineate genetic boundaries, we used different
Bayesian clustering methods available in three computer programs, STRUCTURE, TESS and
482 GENELAND, which are known to outperform other approaches (Blair et al. 2012). Hence, we
first distinguished six genetic clusters in Québec and Labrador. Five of these six genetic
484 clusters were considered as demographically independent when applying the “10% migrants
criterion” (Waples & Gaggiotti 2006). Integrating genetic and ecological information as
486 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
488 #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
490 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
492 presents unique genetic membership and/or ecological characteristics that make them valuable
candidates for management consideration.

494 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
496 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
498 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
500 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 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 & 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 populations 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 & 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
552 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.
554 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
556 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.

558 Across their circumpolar range, many caribou and reindeer populations are declining
(Vors & Boyce 2009; Festa-Bianchet et al. 2011). This encourages the development and
560 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).
562 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.,
564 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; and Beauchesne et al. 2014 for a
566 discussion on predator control) and biologists need objective and unambiguous criteria to
characterize management units that require distinct management plans. Yet several “local
568 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
570 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
572 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
574 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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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. See Table 1 for Herd/Locality designation.

	<i>N</i>	<i>A</i>	<i>Ap</i>	<i>Ar</i>	<i>HO</i>	<i>HE</i>	<i>FIS</i>	Area (km ²)	<i>N_e</i> (95% <i>CI</i>)	<i>Mantel'</i> <i>r</i> (<i>P</i> -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 (<i>P</i> =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 (<i>P</i> =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 (<i>P</i> =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 (<i>P</i> =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 (<i>P</i> =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 (<i>P</i> =0.08)	CHARL
<i>N</i>	Sample size											
<i>A</i>	Mean number of alleles per locus											
<i>Ap</i>	Mean number of private alleles per locus											
<i>Ar</i>	Allelic richness averaged over loci based on minimum sample size of 25 diploid individuals											
<i>HO</i>	Observed heterozygosity											
<i>HE</i>	Expected heterozygosity											
<i>FIS</i>	Inbreeding coefficient and p-value based on 1600 randomizations (*=significant, NS=not significant)											
Area	Range size for each cluster (in km ²), based on a minimum convex polygon estimated with 95% of the animal locations											
<i>N_e</i>	Effective population size with 95% confidence intervals (CIs).											
<i>Mantel'</i> <i>r</i>	Mantel correlation between pairwise genetic distance a (Rousset 2000) and geodesic distance among individuals within each cluster											

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

RGH, RFH, TORN

Genetic cluster	MU	Herd/Locality	<i>N</i>	<i>mig</i>	<i>%mig</i>
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

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). 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 (Bonferonni correction).

	#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

946 **Figure legends**

948 **Fig. 1** Distribution of caribou sampled for DNA analyses in Québec and Labrador, eastern
Canada. 1) Blue squares: Rivière-George Migratory Tundra herd (RGH); 2) blue dots:
950 Rivière-aux-Feuilles Migratory Tundra herd (RFH); 3) green squares: Boreal caribou ecotype;
4) orange triangles: the Mountain caribou of Gaspésie and Torngat Mountains; 5) red
952 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
954 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
956 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
958 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
960 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
962 between ecotypes is indicated by intermediate shading.

Fig. 2 Workflow for delineating Management Units (MU) in caribou. White caribou represent
964 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
966 from the combination of genetic and ecological delineation criteria.

968 **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.

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.

(1) Delineating genetic clusters

We delineate **genetic clusters** using neutral microsatellite loci, markers with high resolution at the landscape scale and shaped solely on a neutral process. Here, individuals are treated as operational units. Model-based genetic clustering analyses are used to determine the number of **genetic clusters** that best fit the data and to assign each individual to these units (Fig. 5). When the approaches did not converge on the same solution, a synthetic approach is applied considering the sum of the partitions obtained by each of the methods (Fig. S6).

(2) Integrating ecological information

We delimitate caribou groups based on ecological criteria currently used to delimitate herds, *i.e.* essentially **ecotype** designation (tundra migratory, mountain migratory or boreal forest caribou; Fig. 2), and long-term monitoring of space use for tundra migratory caribou (Boulet et al. 2007; Couturier et al. 2010; Taillon et al. 2012). In practice, herd delineation for tundra migratory caribou is based on radio-telemetry and satellite-tracking data (Boulet et al. 2007; Couturier et al. 2010; Fig. 1).

(3) Delineate Management Units with all information

Defining Management Units combining both **genetic** (Fig. 5) and **ecological** (Fig. 1) criteria.