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Absence of founder effect and evidence for adaptive divergence in a recently introduced insular population of white-tailed deer (*Odocoileus virginianus*)

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Abstract

Islands are generally colonized by few individuals which could lead to a founder effect causing loss of genetic diversity and rapid divergence by strong genetic drift. Insular conditions can also induce new selective pressures on populations. Here, we investigated the extent of genetic differentiation within a white-tailed deer (*Odocoileus virginianus*) population introduced on an island and its differentiation with its source mainland population. In response to their novel environmental conditions, introduced deer changed phenotypically from mainland individuals, therefore we investigated the genetic bases of the morphological differentiation. The study was conducted on Anticosti Island (Québec, Canada) where 220 individuals were introduced 120 years ago, resulting in a population size over 160,000 individuals. We used genotyping-by-sequencing (GBS) to generate 8,518 filtered high-quality SNPs and compared patterns of genetic diversity and differentiation between the continental and Anticosti Island populations. Clustering analyses indicated a single panmictic island population and no sign of isolation by distance. Our results revealed a weak, albeit highly significant, genetic differentiation between the Anticosti Island population and its source population (mean F_{ST} = 0.005), which allowed a population assignment success of 93%. Also, the high genetic diversity maintained in the introduced population supports the absence of a strong founder effect due to the large number of founders followed by rapid population growth. We further used a polygenic approach to assess the genetic bases of the divergent phenotypical traits between insular and continental populations. We found loci related to muscular function and lipid metabolism, which suggested that these could be involved in local adaptation on Anticosti Island. We discuss these results in a harvest management context.

KEYWORDS

genetic differentiation, genetic diversity, genetic drift, island rule, local adaptation, ungulate

1 | INTRODUCTION

The establishment of a new population from a mainland source into an isolated environment (e.g., islands) often leads to pronounced genetic divergence due to both restricted gene flow and genetic drift. As such, islands are remarkable natural laboratories to study the action of evolutionary mechanisms and their consequences for management and conservation (Warren et al., 2015). A special case of genetic drift, the founder effect, is the strongest process leading to drastic and rapid genetic differentiations between populations (Kolbe, Leal, Schoener, Spiller, & Losos, 2012). First proposed by Mayr (1954), the concept of founder effect refers to the random sampling of alleles brought by individuals from a source population to establish a new population (Nei, Maruyama, & Chakraborty, 1975). This random selection of introduced individuals leads to a genetic diversity that is not representative of the entire source population and which usually correlates with the number of introduced individuals and/or the number of introduction events (Allendorf, 1986; Blanchong, Sorin, & Scribner, 2013; Clegg et al., 2002). Because new populations are often founded by few individuals, especially on islands (Warren et al., 2015), they generally have low effective population size (N_e) which enhance genetic drift and consequently the loss of genetic diversity (Brambilla, Biebach, Bassano, Bogliani, & von Hardenberg, 2015; Frankham, 1995). Therefore, insular populations tend to have lower genetic diversity than mainland populations (Frankham, 1997), especially in mammals (Uller & Leimu, 2011). The lower genetic diversity of a population may reduce its capacity to adapt and, therefore, its chance to persist in time (Reed & Frankham, 2003; Wood, Yates, & Fraser, 2016). The rapid growth of a founder population can, however, decrease the rate of genetic diversity loss (Allendorf, 1986; Blanchong et al., 2013). In sum, the extant of loss of genetic diversity is guided by two partly independent variables: the number of founders (which determines the impact of the founder effect) and early population growth (which determines the intensity of the genetic drift).

Species introduced on islands often face novel abiotic conditions and biotic communities (Warren et al., 2015). In founder populations, initial genetic adaptations can occur rapidly from standing genetic variation (Barrett & Schluter, 2008; Crisci, Dean, & Ralph, 2016). Strong genetic drift in founder populations may, however, reduce standing genetic variation (Dlugosch & Parker, 2008; Luikart, Allendorf, Cornuet, & Sherwin, 1998), counteract selection, and hamper adaptive divergence (Agashe, Falk, & Bolnick, 2011; Swaegers et al., 2013). Rare alleles have more chance to be lost in such events (Clegg et al., 2002; Luikart et al., 1998), thus depriving founder populations of potential beneficial alleles in novel environments. Rapid population growth following a founder event, or founder-flush event, could however facilitate adaptive change (Doerner et al., 2005; Templeton, 2008).

Pronounced phenotypic changes, often in body size, occur commonly in insular populations (Meiri, Cooper, & Purvis, 2008). VanValen (1973) first proposed the island rule which states that species with small body size tend to get larger, while species with large body size tend to get smaller. This general pattern is explained by the novel selective pressures (i.e.: amount of resources available, intra- and interspecific interactions, etc.) faced by colonizing species which drive body size toward a new optimal state (Lomolino, 2005; Meiri et al., 2008; Runemark, Brydegaard, & Svensson, 2014). The limited resources available on islands increase competition which tends to benefit the smallest individuals of species with large body size because of their lower energy requirements (Lomolino, 2005). At the opposite, small species will be advantaged toward a larger body size due to the frequent absence of large predators and competitors in islands (Lomolino, 2005; Runemark et al., 2014). These phenotypic changes can occur over a few generations, including in mammals (Millien, 2006). Such rapid phenotypic changes may reflect a plastic response (adaptive or not) to environmental conditions (Ghalambor, McKay, Carroll, & Reznick, 2007; Lerp et al., 2014) or a genetically-determined adaptive response. Those genetic changes may result from either divergent selection (Grant, 2001; Price, Qvarnstrom, & Irwin, 2003) or genetic drift (Kolbe et al., 2012; Spurgin, Illera, Jorgensen, Dawson, & Richardson, 2014), and both of these evolutionary forces are more likely to occur in insular ecosystems than on the continent (Dlugosch & Parker, 2008; Funk et al., 2016; Prentice et al., 2017). Despite numerous studies conducted on island systems (Clegg et al., 2002; Grant, 2001; Warren et al., 2015), the link between genome-wide diversity and potential adaptive phenotypic changes considering the polygenic basis of traits has rarely been investigated.

The white-tailed deer (*Odocoileus virginianus* Zimmermann 1780) is one of the most widespread large mammals in North America and has been introduced in many areas because of its popularity for sport hunting (Little et al., 2016). Approximately 220 deer were introduced for this purpose on Anticosti Island (Québec, Canada) between 1896 and 1897 (Martin-Zédé, 1938; McCormick, 1982; L. Jobin, personal communication, May 30, 2018). The introduced deer were taken from the region of Montmagny on the southern shore of the St. Lawrence River, Québec, Canada (Martin-Zédé, 1938; McCormick, 1982). Because of the low abundance of predators on the island, the population quickly increased in number up to >160,000 individuals today. Intense browsing soon caused major impacts on the vegetation which were reported as early as 1934 (Côté et al., 2008). Phenotypic changes such as a reduction of body size, increased fat storage for fawns, increased leg length and increased antler spread were also documented (Lesage, Crête, Huot, & Ouellet, 2001; Simard, Huot, de Bellefeuille, & Côté, 2014). As reported in other studies, such rapid phenotypic divergence suggests a presence of genetic differentiation between Anticosti Island and mainland deer (Funk et al., 2016; Prentice et al., 2017) or could be attributed to phenotypic plasticity (Lerp et al., 2014). Evaluating the relative role of genetic drift and adaptive genetic divergence as drivers of phenotypic divergence in Anticosti deer requires documenting patterns of both neutral and potentially adaptive genetic variations between insular and mainland deer. To date, very few studies on wild mammals investigated both avenues even with the

increasing use of genome-wide SNPs (Funk et al., 2016; Galaverni et al., 2017; Pilot et al., 2014; Schweizer et al., 2016).

Our main goal was to document the patterns of genetic differentiation between white-tailed deer from Anticosti Island and their source population using genotyping-by-sequencing (GBS). We also compared divergence between the Anticosti Island deer population and a second continental population (Outaouais) located 400 km from the Montmagny source population which allowed putting the extent of neutral and adaptive genetic difference between Anticosti deer and its source population into perspective (Albert, 2007).

More specifically, we aimed to: (a) test the hypothesis that the founder effect led to a pronounced loss of genetic diversity of white tailed deer on Anticosti Island, as frequently reported in other studies; (b) test the hypothesis of a decreasing patterns of genetic diversity on Anticosti Island reflecting the colonizing process which began at the site of introduction located at the western end of the Island; and (c) test the hypothesis of a genotype-phenotype association for morphological traits that diverged between Anticosti and mainland deer, which would support an adaptive basis of differentiation. We then interpret and discuss our results in the context of harvest management.

2 | MATERIALS AND METHODS

2.1 | Study area

Deer were sampled from three areas: Montmagny (MON; 46°N 70°W), the continental source population, Outaouais (OUT; 46°N 76°W), a geographically distant outgroup (Figure 1), and on Anticosti Island (ANT; 49°N 62°W; 7,943 km^2). Deer harvested on Anticosti Island were sampled in one of the three main exploited zones: (a) Western Anticosti (W-AN); (b) Central Anticosti (C-AN), and (c) Eastern Anticosti (E-AN).

Anticosti Island is located in the Gulf of St. Lawrence, Québec (Canada) at the northern limit of white-tailed deer distribution. Climate is harsh with long, cold and snowy winters (mean of 406 cm of snow/year; Environment Canada, 2017). High deer density on the island (>20 deer/km^2 vs. <3 deer/km^2 in Montmagny and Outaouais; Huot & Lebel, 2012) has been maintained over the past nine decades, causing intense long-term browsing which resulted in the decline of most deciduous browse species such as *Sorbus americana* Marsh, *Amelanchier* sp., *Diervilla lonicera* P. Mill., and *Viburnum* spp. (Tremblay, Thibault, Dussault, Huot, & Côté, 2005). The forest is

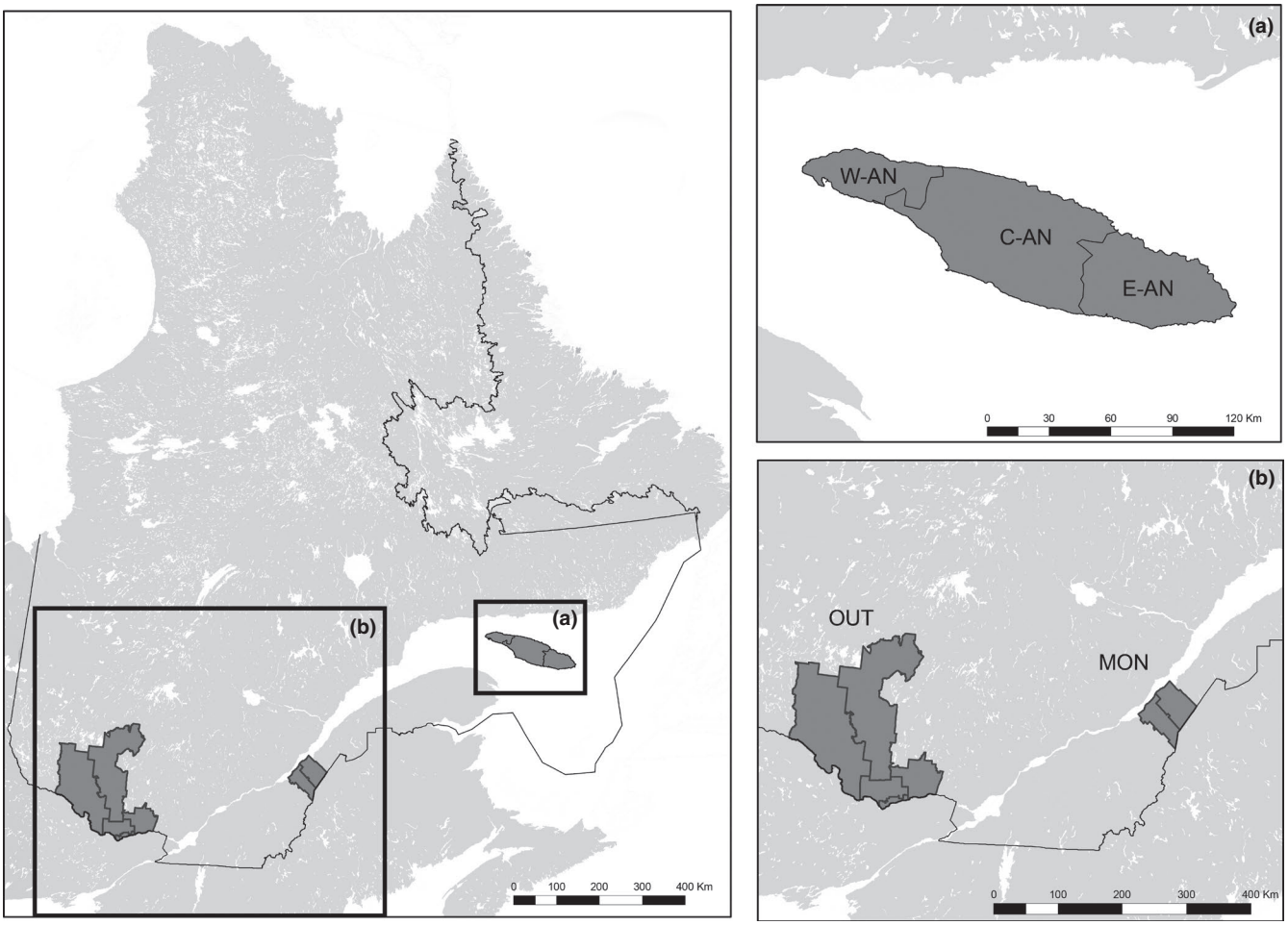

FIGURE 1 The three study areas (Québec, Canada). (a) Anticosti Island divided into three regions: western (W-AN), central (C-AN), and eastern (E-AN). (b) Montmagny-L'Islet (MON) and Outaouais (OUT)

mainly composed of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*), and is located in the balsam fir-white birch bioclimatic domain (Huot & Lebel, 2012). Montmagny is located in the balsam fir-yellow birch bioclimatic domain on the southern shore of the St. Lawrence River where winter can also be harsh (mean of 243 cm of snow/year; Environment Canada) and Outaouais is located in southwestern Québec on the northern shore of the St. Lawrence River which is an effective barrier for white-tailed deer (Albert, 2007). Outaouais is mostly characterized by the sugar maple-yellow birch bioclimatic domain where milder winter occurs (mean of 200 cm of snow/year; Environment Canada).

2.2 | Sampling and phenotypic measurements

A total of 571 individuals were sampled through sport hunting in the fall (Anticosti: 445 individuals (W-AN: 144, C-AN: 145, E-AN: 148), Montmagny: 54 and Outaouais: 72). Ear or muscle tissues were collected and preserved in 95% ethanol or kept frozen at −20°C for genomic analyses. We used a balanced sex ratio for Anticosti samples: W-AN (71 females: 73 males), C-AN (73F:72M), E-AN (74F:74M) collected during two periods: 2003 to 2005 and 2012 to 2014. Samples from Montmagny were mostly collected on males in 2013 (15F:39M), whereas samples from Outaouais were collected in 2006 and 2015 with a balanced sex ratio (39F:33M). Only adult individuals (>1.5 years) were used, their age was determined using cementum layers of teeth (Hamlin, Pac, Sime, DeSimone, & Dusek, 2000). Morphometric measures were only recorded on Anticosti Island. We recorded (a) eviscerated body mass; (b) total body length; (c) chest girth; (d) length of the left hind leg and the mass of its peroneus muscle which is a reliable estimator of protein mass (Crête, Huot, Nault, & Patenaude, 1993; Simard et al., 2014); (e) rump fat thickness which is used as an index of body fat reserves (Cook et al., 2010), and (f) antler spread for males. More details on morphometric measurements are in Simard et al. (2014).

2.3 | Genomic analyses

2.3.1 | DNA extraction and sequencing

We extracted genomic DNA from ear or muscle tissues with a phenol-chloroform-isoamyl protocol (Sambrook, Fritsch, & Maniatis, 1989). We checked sample concentration and quality by using a 1% agarose gel and a NanoDrop 2000 spectrophotometer (Thermo Scientific) and normalized the genomic DNA to obtain 20 ng/μl in 10 μl (200 ng) by the Biotium AccuClear protocol performed on a SPARK 10M (TECAN) 96-well plate. Genotyping-by-sequencing (GBS) libraries were prepared by the Institut de Biologie Intégrative et des Systèmes (IBIS) sequencing platform (Laval University) and sequenced on an Ion Torrent Proton with a two-enzyme GBS protocol (Mascher, Wu, St Amand, Stein, & Poland, 2013), using restriction enzymes *Nsi*I and *Msp*I. Individuals were barcoded with a unique sequence of six nucleotides. Each sample was sequenced a second time to reach a sufficient coverage per individual.

2.3.2 | Bioinformatic and quality filtering

FastQC was used to inspect raw reads for overall quality and presence of adaptors (http://www.bioinformatics.babraham.ac.uk/projects/fastqc/). Cutadapt (Martin, 2011) was used to remove adaptors. All the trimmed data were analyzed to identify loci and call genotypes using STACKS version 1.44 (https://github.com/enormandeau; Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013). Process_radtags was used to demultiplex the libraries and perform a quality trimming on the reads at a 80 bp length. Sequence reads were aligned on the reference genome of white-tailed deer (NCBI BioProject accession number PRJNA420098) with the aligner tool GSNAP version 2016-06-09 with default parameters but fixing minimum fraction of reads mapping of 90% ("—min-coverage") (Wu, Reeder, Lawrence, Becker, & Brauer, 2016). We extracted the stacks aligned to the reference genome and identified SNPs at each locus with a minimum depth coverage (m) of three (by default) using pstacks with model type snp and α of .05. A catalog with all putative tags was created with the default parameter (n = 1) with the module cstacks. The next step was applying the populations module of STACKS version 1.42 to define SNPs. Only loci with minimal depth (m) of 7 and SNPs present in at least 70% of the individuals were kept. Putative paralogs were excluded by rejecting SNPs with heterozygosity higher than 0.6 and a F_{IS} outside −0.4 and 0.4. Polymorphisms were kept with minor allele frequency (MAF) >0.05 for one location and >0.05 over all populations to removed potential biases inferred by low-frequency SNPs (Roesti, Salzburger, & Berner, 2012). The following filtering steps were performed with homemade PYTHON script (https://github.com/enormandeau/stacks_workflow; Catchen et al., 2013). Individuals with more than 20% of missing genotype were removed from the final data set. Missing data, representing approximately 2% of the data set, were filled based on the genotypes with a Random Forest approach implemented in the R package STACKR (Gosselin & Bernatchez, 2016). Imputations were computed by population (Anticosti Island, Montmagny and Outaouais) with 100 trees and 10 iterations as suggested by Gosselin and Bernatchez (2016). To minimize the impact of potential linkage disequilibrium, the first SNP of each locus was retained (Figure S1). Ultimately, the VCF file produced was converted into appropriate types of files by genomic_converter function of stackr package and VCFTOOLS (Danecek et al., 2011).

2.3.3 | Population clustering

Several methods were used to perform population clustering on the three sampling locations (Anticosti Island, Montmagny and Outaouais) to document the population structure. First, a *K*-means clustering analysis was run on GENODIVE 2.0b27 (Meirmans & Van Tienderen, 2004), which splits objects into groups to minimize the

within-group genetic diversity while maximizing it among-groups. An a priori assigned number (k) of groups from 1 to 8 was tested with 5,000 permutations. We used the Calinski-Harabasz pseudo-F-statistic (Caliński & Harabasz, 1974) to determine the optimal number of clusters. We then performed a discriminant analysis of principal components (DAPC) with the function find.clusters from the ADEGENET 2.0.1 package in R (Jombart, Devillard, & Balloux, 2010). Based on the lowest Bayesian Information Criterion (BIC), this function assesses the most likely number of genetic clusters among populations without prior information on individuals' provenance (Jombart et al., 2010). DAPC analysis used a discriminant analysis (DA) to maximize the difference between groups while overlooking variation within groups which make the method particularly efficient to detect weak genetic differentiation among populations.

2.3.4 | Population differentiation and genetic diversity

We estimated pairwise F_{ST} values of Weir and Cockerham (1984) implemented in GENODIVE 2.0b27 to quantify the extent of genetic differentiation among Anticosti Island, Montmagny and Outaouais. We performed 10,000 permutations to generate 95% confidence intervals around estimates. We also used GENODIVE 2.0b27 to quantify observed (H_o) and expected heterozygosity (H_e) as well as the degree of deviation from Hardy-Weinberg equilibrium (G_{is}). Inbreeding coefficients (F) were computed with VCFTOOLS on a per individual basis, thus we calculated an average for each population (Danecek et al., 2011). We used haplotypes to quantify the extent of nucleotidic diversity (π) and the overall proportion of polymorphic loci using the tidy_genomic_data function of the STACKR package in R. Effective population size over a generation (N_e) was estimated for each population with the program NEESTIMATOR version 2.01 (Do et al., 2014). The program was used with the linkage disequilibrium model, a random mating system and a minor allele frequency (MAF) threshold of 0.05 for N_e. For each population, all loci under putative selection found in the section "Outlier detection and genotype-phenotype association" were removed to obtain an unbiased N_e (Larson et al., 2014). Because age was known for deer from Anticosti Island, we split individuals into birth year cohorts. The harmonic mean of N_e among all cohorts was used for the Anticosti Island population since it has been shown to be a good estimate of demographic variation among cohorts (Kalinowski & Waples, 2002). For each cohort with more than 15 individuals (from 1995 to 2012), we estimated the effective number of breeders over a reproductive cycle ($N_{b_{LD}}$) with the linkage disequilibrium model and a random mating system. The MAF threshold was adjusted for each population according to sample size to reach an arbitrary minimal representation of four copies of the minor allele per locus per cohort. We then followed the calculations of Waples, Antao, and Luikart (2014) to correct the bias due to overlapping generations using adult life span and age at maturity:

$$N_b(\text{adj}) = \frac{N_b(\text{LD})}{1.103 - 0.245 \times \log(\text{AL}/\alpha)} \quad (1)$$

where $N_{b_{adj}}$ is an estimate of N_b adjusted for overlapping generations, AL is adult life span and α is age at maturity. We used AL = 3.5 and α = 1.5, adult life span was estimated as the median age of harvested females from Anticosti Island for which age was known (4,551 deer), because the median is less affected by a few long-lived individuals than the mean (Wiese & Willis, 2004). We only kept adult females, which are expected to be under weaker selection bias caused by hunting (relative to males with antlers) and were therefore assumed to be representative of the annual age structure of the adult population as used by Simard, Coulson, Gingras, and Côté (2010). It was then possible to estimate an effective deer population size ($N_{e_{adj}}$) for Anticosti Island (Ferchaud et al., 2016; Waples et al.., 2014).

$$N_e(\text{adj}) = \frac{N_b(\text{adj})}{0.485 + 0.758 \times \log(\text{AL}/\alpha)} \quad (2)$$

2.3.5 | Population assignment

We attempted to assign each individual to its respective population, the one that is the most similar, based on allele frequencies in the populations and individual's genotype. We randomly selected 70 individuals from Anticosti Island for this analysis to consider similar sample sizes across all populations. The analysis was performed on GENODIVE 2.0b27 with the home likelihood criterion. This statistic is more appropriate than the likelihood ratio because we only sampled parts of all possible source populations (Meirmans & Van Tienderen, 2004). We used a significant α-level threshold of .05 and, as suggested by Paetkau, Slade, Burden, and Estoup (2004), all the frequencies with a value of 0 were changed into .005 to avoid the calculation of numerous likelihoods of zero. The program used the Leave-One-Out (LOO) approach which consists in removing one individual from the reference sample when estimating allele frequencies of the source population as a cross-validation method to avoid bias. We used 5,000 permutations and no corrections were needed to avoid high-grading bias because we used all loci and not a subset (Anderson, 2010). Missing values were replaced by randomly picking alleles from the global allele pool as implemented in GENODIVE 2.0b27.

2.3.6 | Outlier detection

Genome scan analyses typically detect only loci with large effects (Lotterhos & Whitlock, 2015), but most phenotypic traits have a polygenic basis (Le Corre & Kremer, 2012; Pritchard, Pickrell, & Coop, 2010). Therefore, analyses searching for covariation among loci of small effects and phenotypic traits are more appropriate to identify markers associated with those traits and, consequently, combining genome scan analyses with genotype-phenotype associations are better suited to infer a genetic basis to local adaptation (Gagnaire & Gaggiotti, 2016; Laporte et al., 2016; Lotterhos & Whitlock, 2015; de Villemereuil, Frichot, Bazin, Francois, & Gaggiotti, 2014). Three genome scan analyses were used to detect SNPs under putative selection among populations. We used two F_{ST} based approaches; we

first ran the program BAYESCAN version 2.1 (Foll & Gaggiotti, 2008), using 10,000 iterations with 200,000 burnin length, a prior odds of 10 as default and a stringent false discovery rate of 0.01. We also used the R package OUTFLANK (Whitlock & Lotterhos, 2015) with the default option (LeftTrimFraction = 0.05, RightTrimFraction = 0.05, Hmin = 0.1) as conducted in Benestan et al. (2016). We then used a principal component approach (PCA) implemented in the R package PCADAPT (Luu, Bazin, & Blum, 2017) to detect outliers based on a correlation between genetic variation and the first *K* principal components. As suggested by Luu et al. (2017), the optimal *K* was found by the graphical approach based on the scree plot (Jackson, 1993). We then followed the Cattell's rule to keep the highest value of *K* before the straight line (Cattell, 1966). We used the default Mahalanobis method with an α threshold of .1. In order to investigate a potential signal of selection acting on the Anticosti Island population, we used independent comparisons between this population and each continental population in pairwise analyses (Lotterhos & Whitlock, 2015; Nosil, Funk, & Ortiz-Barrientos, 2009).

2.3.7 | Genotype-phenotype association

We used two analyses to perform genotype-phenotype associations. Analyses were performed on Anticosti Island population only since no phenotypic measures were available for mainland populations. We first used a latent factor mixed models (LFMM) analysis performed with the R package LEA (Frichot & François, 2015) as it provides the best compromise between detection of weak selection and low error rate compared to other analyses (Frichot, Schoville, Bouchard, & Francois, 2013; Rellstab, Gugerli, Eckert, Hancock, & Holderegger, 2015; de Villemereuil et al., 2014). LFMM uses an allele frequency approach to evaluate the correlation between allele frequencies and a continuous variable. In our case, we performed the LFMM separately for both sexes using phenotypic measures (rump fat thickness, peroneus muscle mass, body mass, hindfoot length, and antler spread for males only) as continuous variables. LFMM has previously been used to perform genotype-phenotype associations in other species (Mazzarella, Boessenkool, Ostbye, Vollestad, & Trucchi, 2016; Perreault-Payette et al., 2017). As recommended by Frichot et al. (2013), we ran LFMM with five repetitions, 10,000 cycles and 5,000 burnin. We also added a correction for population structure and adjusted the *p*-values with a lambda (λ) of .05 and applied a false discovery rate of .01 to select the associated markers.

We also used the random forest (RF) approach (Bureau et al., 2005) applied on the same traits. RF is a tree-growing algorithm that can handle several predictors and is therefore well suited for genomic associations (Brieuc, Ono, Drinan, & Naish, 2015; Holliday, Wang, & Aitken, 2012; Laporte et al., 2016). Phenotypic variation between individuals can be separated into genetic and environmental components (Hill & Mulder, 2010; Nussey, Wilson, & Brommer, 2007). The influence of environmental components on each phenotypic trait of female deer was assessed by Ayotte (2018) with mixed-effects models. We selected the following variables among those tested by Ayotte: date of harvest, deer density, lactation status, age of individuals, and year of harvest. We generated models for male traits with the same approach (Table S1). We then used the residuals of the models to isolate genetic influence on each phenotypic trait which includes the variation not explained by environmental variables (Hill & Mulder, 2010; Westneat, Wright, & Dingemanse, 2015). We used the RANDOMFOREST function from the RANDOMFOREST R package (Liaw & Wiener, 2002) with 100,000 trees and assessed the importance of predictors with the extractor function "importance" contained in the same package. We kept only the top 1% markers that best explained each phenotypic trait to remain conservative. We followed the polygenic score approach to quantify the phenotypic variation explained by those markers (Gagnaire & Gaggiotti, 2016). Briefly, we assigned a value from 0 to 2 to denote the total number of minor alleles in each marker (homozygote for the major allele = 0, heterozygote = 1 or homozygote for the minor allele = 2). If a locus showed a negative correlation with the expression of the trait, the value between the homozygote types were exchanged (major allele = 2, minor allele = 0). Finally, we summed all those values for each individual into a polygenic score and tested with a linear regression for a relationship between this score and the associated phenotypic trait.

We compared the extent of overlap between loci found by genome scan approach, LFMM and random forest. To assess the degree of overlap expected by chance, we performed permutation tests between three vectors with the same number of loci found by genome scan (67 loci), LFMM (1,339) and random forest (684) for 10,000 iterations.

2.3.8 | Gene ontology

All loci under putative selection detected by either genome scan or association methods were blasted against the white-tailed deer transcriptome (Seabury et al., 2011) to identify known biological functions. We kept the sequences with an e-value threshold of 1×10^{-6} and a homology of 75% on a minimum of 50 bp out of 80 bp. We blasted all significant sequences against the well annotated SWISS-PROT database (Bairoch & Apweiler, 2000).

3 | RESULTS

3.1 | SNP calling

A total of 1.7 billion reads after demultiplexing were obtained with an average of 3 million raw reads per individual and a mean depth coverage of 35 reads per locus. Seven individuals (1.2%) were removed due to an insufficient mean coverage (<10×). The catalogue contained 4,179,071 loci and a total of 365,311 SNPs located on 97,176 loci. Following the filtering steps, 13,420 SNPs were retained (Table S2). The first SNP of each locus was kept, leaving 8,518 SNPs for subsequent analyses. Five individuals with more than 20% of missing values were also removed from the final data set. Finally,

559 deer were used for genomic analyses and 437 from Anticosti Island were used for genotype-phenotypic analyses.

3.2 | Clustering analysis

The *K*-mean analysis indicated two groups (K = 2) as the optimal number of clusters for the three studied populations (not shown). BIC values decreased as the number of clusters increased (Figure S2) so an optimal number of clusters could not be identified with this analysis. Jombart and Collins (2015) suggested that in such situations there is no real true *K* but rather a range of plausible *K* summarizing the data. Therefore, K = 3 was used for DAPC analysis to represent the three main locations (Anticosti Island, Montmagny, Outaouais). The DAPC without prior information on group provenance (Figure 2) revealed three clusters despite a small overlap between two clusters (Anticosti Island and Montmagny). The three sectors of Anticosti Island (W-AN, C-AN and E-AN) overlapped into a single cluster even with a K = 5 (not shown). The first discriminant function (DA-1) explained 77% of the total genetic variation among individuals whereas DA-2 explained 12%. The DAPC with prior information on group provenance also showed three defined clusters (Figure S3). There was no overlap between the Montmagny and Anticosti Island clusters. The first and second eigenvalue explained 87% and 8% of the total genetic variation among individuals, respectively.

3.3 | Genetic diversity and structure

We observed low pairwise F_{ST} (mean = 0.0049 [0.0046–0.0053]) between Montmagny and Anticosti Island (Table 1) and extremely small, albeit statistically significant (thanks to the high number of markers), pairwise F_{ST} within Anticosti Island (mean F_{ST} = 0.0009 [0.0008–0.0010]). Given this extremely small F_{ST} value, we do not consider it as biologically significant. A more pronounced differentiation was observed between Anticosti and the Outaouais population (mean = 0.022 [0.021–0.022]), which was comparable to the differentiation between the two continental populations (F_{ST} = 0.0206 [0.0196–0.0214]). All pairwise comparisons were significant (p < .05).

Observed heterozygosity (H_o) was significantly higher (ANOVA F = 1,349, p < .001) in Anticosti (H_o = 0.129) compared to the two continental sites (H_o = 0.117 and 0.083, Table 2). The inbreeding coefficient (F) was significantly lower (ANOVA F = 1,927, p < .001) for Anticosti Island (F:0.085, 95 CI: [0.081–0.089]) compared to Montmagny (0.169 [0.158–0.180]), and Ouatouais (0.408 [0.399–0.417]), as was the inbreeding coefficient (G_{is}) (ANOVA F = 2.72, p = .07) for Anticosti Island (0.126 [0.123–0.130]) compared to Montmagny (0.143 [0.137–0.148]), and Outaouais (0.159 [0.153–0.165]). We observed pronounced temporal variation in the effective population size ($N_{e_{adj}}$) on Anticosti Island (Table S3). Similar variations were observed with the effective population size calculated over a reproductive cycle ($N_{b_{LD}}$) and the corresponding adjusted values ($N_{b_{adj}}$). With 14 cohorts on Anticosti Island, the harmonic mean effective population size ($N_{e_{adj}}$) was 1,587 [1,196–2,354] and ranged from 622 [572–682] (cohort 1998) to 4,384 [2,868–9,279] (cohort 2004). The Anticosti Island population had a larger effective size than the Montmagny population (1,412 [1,343–1,489]), but smaller than the Outaouais population (1,878 [1,753–2,023]).

We successfully assigned 93% of the individuals to their original location. All individuals harvested on Anticosti Island and in Outaouais were assigned to their respective genomic group. A total of 78% of the individuals from Montmagny were successfully assigned to their own genomic group while the remaining 22% were all attributed to the Anticosti Island genomic group.

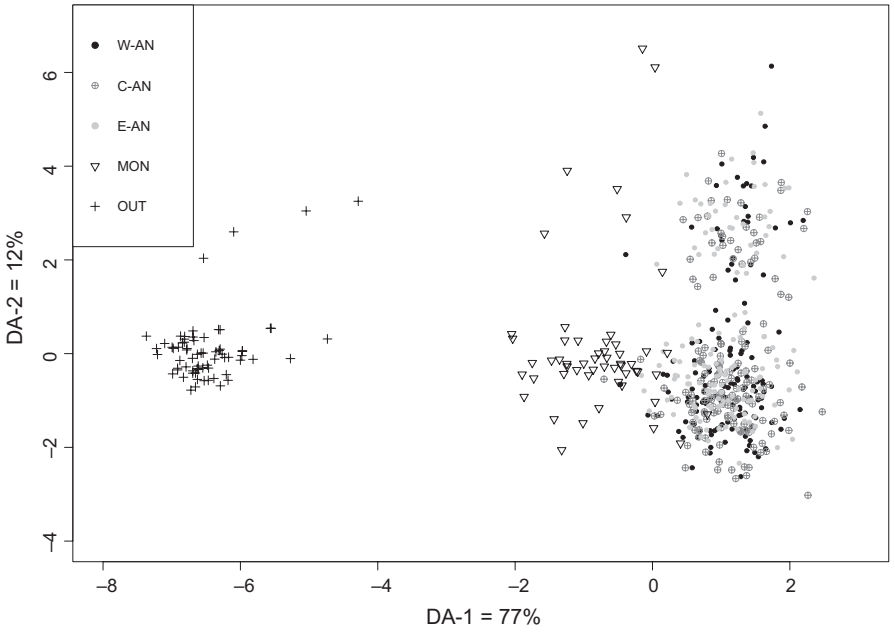

FIGURE 2 Discriminant analysis of principal components (DAPC) of the genetic variation of white-tailed deer without prior information on their group provenance: Western Anticosti (W-AN), Central Anticosti (C-AN), Eastern Anticosti (E-AN), Montmagny (MON) and Outaouais (OUT)

TABLE 1 Below main diagonal: Fixation index (F_{ST}) obtained with 8,518 SNPs among populations of white-tailed deer from western Anticosti Island (W-AN), central Anticosti Island (C-AN), eastern Anticosti Island (E-AN), Montmagny (MON) and Outaouais (OUT); above main diagonal: 95% confidence intervals

Locations	W-AN	C-AN	E-AN	MON	OUT
W-AN		0.0007–0.0009	0.0014–0.0017	0.0044–0.0051	0.0213–0.0225
C-AN	0.0008		0.0002–0.0005	0.0045–0.0051	0.0208–0.0220
E-AN	0.0015	0.0004		0.0049–0.0056	0.0212–0.0225
MON	0.0047	0.0048	0.0052		0.0196–0.0214
OUT	0.0218	0.0214	0.0219	0.0206	

TABLE 2 Descriptive genetic statistics of white-tailed deer populations obtained with 8,518 SNPs: observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficients (G_{is} and F), nucleotidic richness (π), number of polymorphic loci (N), effective population size (N_e), census population size (N_c) for Anticosti Island (ANT), Montmagny (MON) and Outaouais (OUT) populations

Populations	H_o	H_e	G_{is}	F	π	N	N_e	N_c
ANT	0.129	0.147	0.126	0.085	0.00270	8,518	1,587 (1,196–2,354)	>160,000 (Rochette & Gingras, 2007)
MON	0.117	0.136	0.143	0.169	0.00265	8,504	1,412 (1,343–1,489)	4,950 (Arithmetic mean of the zone 3; Huot & Lebel, 2012)
OUT	0.083	0.099	0.159	0.408	0.00241	8,193	1,878 (1,753–2,023)	14,000 (Huot & Lebel, 2012)

3.4 | Outlier detection with genome scan approaches

Overall, 67 different loci were identified as potentially under selection by the three different genome scan analyses performed among population pairs. OUTFLANK failed to detect any outliers between Anticosti Island and Outaouais, but 34 outliers were identified between Anticosti Island and Montmagny (Figure 3). A total of 35 outliers were identified with PCADAPT (optimal K = 2 according the scree plot) between Anticosti Island and Montmagny of which 29 were included in the 31 identified between Anticosti Island and Outaouais (Figure 3). Four outliers were common between PCADAPT and OUTFLANK. More details on the loci distribution are shown in Figure S4. BAYESCAN failed to detect any outliers between Anticosti Island and Montmagny and also between Anticosti Island and Outaouais.

3.5 | Phenotype-genotype associations

Considering the clustering analyses described above, we used K = 1 for the population structure of Anticosti in LFMM. LFMM identified 288 loci for females associated with fat reserves compared to 283 for males (Table S4). The analysis identified 288 loci for female associated with peroneus muscle mass and 291 loci for males. Moreover, 336 loci were associated with body mass for females and 299 loci for males. Hind foot length was associated with 207 loci for females and 263 loci for males (Figure 4). Finally, 42 loci were detected by LFMM as associated with antler spread (Table S4). More details on the loci distribution are shown in Figure S5. None of the detected loci were common between all phenotypic traits for a given sex even if high correlation between body mass, fat reserves and muscle mass was expected. However, between 5.7% and 9.5% of the loci of interest were shared between sexes (Figure S6) which is more than expected by chance (permutation test, p < .001). Overall, 1,339 unique loci were associated with different phenotypic traits.

For the random forest approach, 85 markers representing the top 1% were selected. More details on the importance rank for each locus are shown in Figure S7. The correlations between phenotypic traits (i.e., rump fat thickness, peroneus muscle mass, body mass, hind foot length, and antler spread) and polygenic score were variable but all statistically significant (Figure 5; p < .001). The correlations expressed the phenotypic variation explained by the

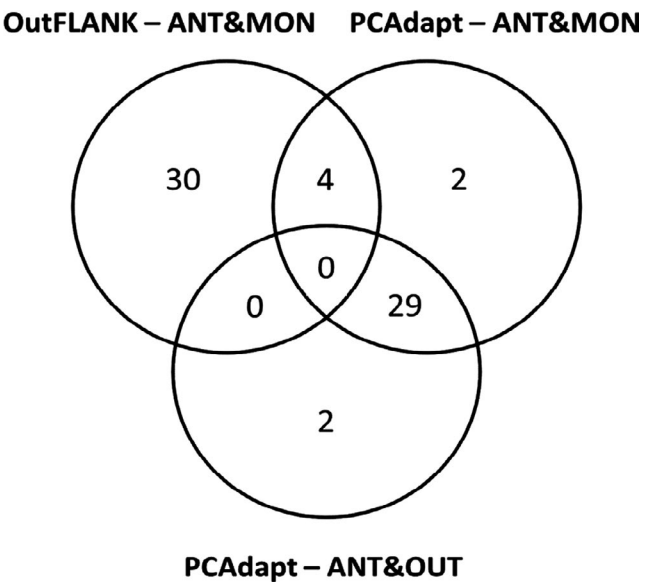

FIGURE 3 Venn diagrams (Oliveros, 2007–2015) of outliers detected by OUTFLANK and PCADAPT between white-tailed deer from Anticosti Island and Montmagny (ANT&MON), and between Anticosti Island and Outaouais (ANT&OUT)

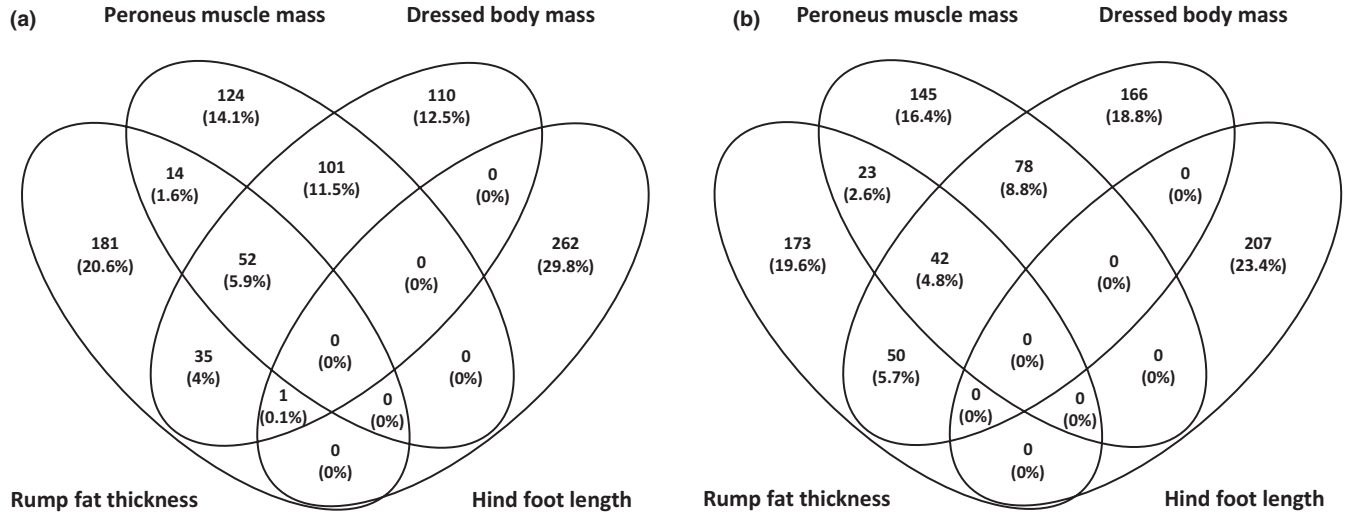

FIGURE 4 Venn diagrams (Oliveros, 2007–2015) of loci, detected by LFMM, associated with rump fat thickness, peroneus muscle mass, hind foot length and dressed body mass of (a) male and (b) female white-tailed deer from Anticosti Island

"important" loci, which also represent the genetic basis for a given trait. Different markers were obtained for the same traits in males and females. The variation explained by the different rump fat thickness markers was, however, similar for both sexes (Figure 5). The correlations for peroneus muscle mass, hind foot length, and dressed body mass were higher for females than males (Figure 5). Overall, 684 unique loci were associated with different phenotypic traits. Among the 1,339 loci detected by LFMM, 116 were in common with the 684 loci detected by random forest (Figure 6).

3.6 | Genetic basis of phenotypic differentiation

Overall, 1,959 unique loci were found by either genome scan approaches (OUTFLANK, PCADAPT) between populations (MON, OUT and ANT) or associative approaches (LFMM and random forest) performed on the Anticosti population only given that morphological data were not available for the continental populations. We looked for overlap between the loci under putative selection found by genome scan approach and the loci associated to the divergent phenotypic traits of Anticosti island deer to confirm a genetic basis for phenotypic traits potentially involved in local adaptation. Of the 29 loci common in the two PCADAPT analyses between Anticosti Island population and each continental population, only one was found among loci found by random forest, one was shared with loci found by LFMM, and another locus was shared with both associative approaches (Figure 6a). These three loci were only linked to male phenotypic traits namely hind foot length and peroneus muscle mass (Table S5). Of the 67 loci found by at least one genome scan approach, two were common with loci found by random forest. Also, the permutation test, which determines whether an overlap is due to chance, was not significant ($p = 1$), eleven in common with LFMM ($p < .001$), and two with both associative approaches ($p < .001$, Figure 6b). These 13 loci were linked to several phenotypic traits of both sexes found by all associative analyses (Table S5). Overall, 19% of the outliers found by genome scan were linked to a divergent phenotypic trait between the Anticosti and mainland populations, therefore suggesting an adaptive basis for phenotypic differentiation at these traits.

All 1,959 unique markers were blasted against the white-tailed deer transcriptome and 172 were linked to an annotated gene after quality filtering, but none of the 13 loci found by both genome scan and association analyses (Table S6). Of those 172, 120 are involved in a biological function potentially relevant for the adaptation of white-tailed deer on Anticosti Island (e.g., muscular protein expression, lipid metabolism and transport, and immune response see Discussion). Of the 120 loci, 55 were found by at least two different analyses.

4 | DISCUSSION

The context of the Anticosti Island white-tailed deer population provided the possibility to document the genetic impact of a recent insular introduction of a large mammal species. Previous studies conducted on a wild mammal, the Alpine ibex (*Capra ibex*), revealed a persistent genomic signature of their reintroduction history with a lower diversity, higher inbreeding in reintroduced populations and a high genetic differentiation with source populations (Biebach & Keller, 2009; Grossen, Biebach, Angelone-Alasaad, Keller, & Croll, 2018). Here, however, our results revealed a significantly higher genetic diversity in the Anticosti Island population and a weak (albeit significant) genetic differentiation from its source population, therefore revealing an absence of founder effect. The discrepancy between both studies is likely due to the relatively large group of founders followed by rapid population growth for Anticosti Island deer. Indeed, the Alpine ibex introductions started with a few decades individuals only, followed by a slow population growth (Grossen et al., 2018). We detected no significant genetic structure within the Anticosti Island population because the F_{ST} values were too weak,

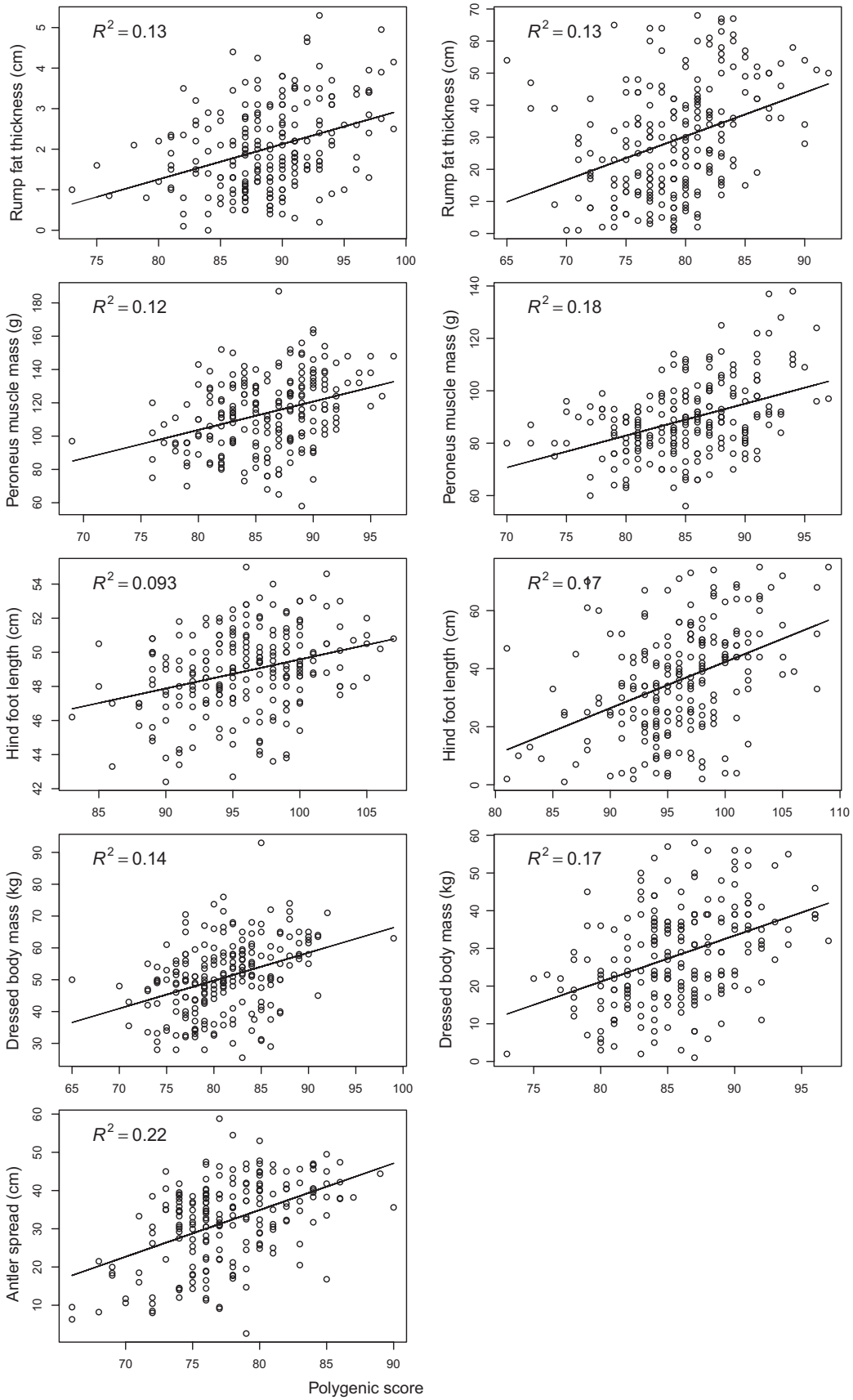

FIGURE 5 Correlations between the polygenic score and the corresponding phenotypic trait (rump fat thickness, peroneus muscle mass, hind foot length, dressed body mass, and antler spread) for male (Left) and female (Right) white-tailed deer from Anticosti Island. Correlation coefficients (R^2) are shown at the top of each plot. All correlations were significant ($p < .001$)

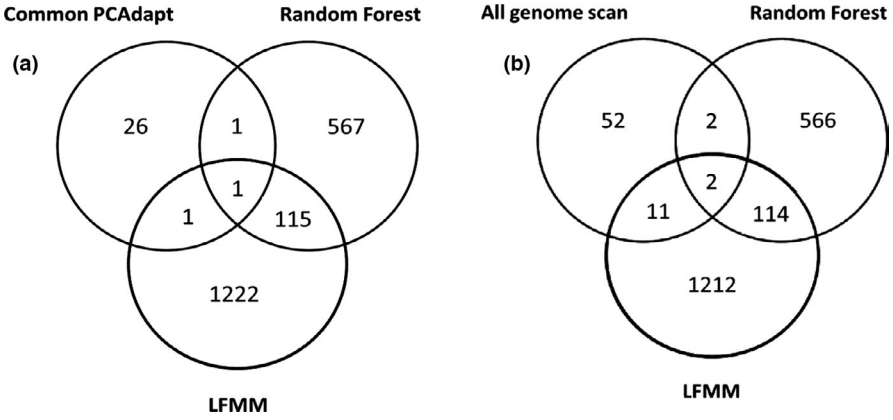

FIGURE 6 (a) Venn diagram (Oliveros, 2007–2015) of loci found in common by PCADAPT analyses between Anticosti Island and both mainland sites (Montmagny and Outaouais), compared to all loci found by random forest and LFMM analyses. (b) Venn diagram of loci found by all genome scan approaches (OUTFLANK and PCADAPT) among populations compared to all loci found by random forest and LFMM analyses

suggesting either pronounced connectivity over the whole insular landscape or insufficient time since population founding to reach migration-drift equilibrium. The identification of 13 loci found to be under putative divergent selection and associated with phenotypic traits that differed between the Anticosti Island population and the two mainland populations suggests that the insular population may be locally adapted.

4.1 | Genetic differentiation and structure of Anticosti Island deer

The modest, albeit highly significant F_{ST} index obtained between the two continental populations (Outaouais and Montmagny), along with high population assignment success confirmed that white-tailed deer on the northern shore of the St. Lawrence River are genetically differentiated from those on the southern shore, as previously shown by Albert (2007) using microsatellite loci. Further, the high assignment success of Anticosti Island deer to their own genetic group despite a small F_{ST} index provided evidence of significant genetic difference from the continental populations. However, the relatively weak (<1%) but highly significant differentiation between Anticosti Island and Montmagny suggests that (a) founding individuals were genetically representative of the allelic diversity of the source population thanks to the large number of founders (>200) and (b) genetic drift has been relatively modest since the insular population was founded. Yet, that the extent of differentiation is still sufficient to allow high population assignment success based on genetic differentiation is somewhat remarkable given the short timeframe involved (about 40 generations). The weak divergence we observed is in contrast with many previous studies in other organisms where strong genetic drift or strong selection likely explained the observation of a more pronounced divergence between an introduced population and its source even with a shorter period of isolation (Table S7).

Our second objective was to test for the occurrence of genetic structure within Anticosti Island. Because all white-tailed deer were introduced in the western part of Anticosti Island (Martin-Zédé, 1938; McCormick, 1982), we expected that small groups of individuals could have been isolated in the eastern part of the island during colonization. Genetic drift coupled with limited connectivity could have then led to a differentiation within the island (Clegg et al., 2002; Goodman et al., 2001). We found no indication of isolation-by-distance within the island and the results of the clustering analyses clearly indicate that the three regions formed a single cluster. F_{ST} values between the three regions of Anticosti Island were very low (F_{ST} < 0,001) with the values found between the continental populations. These results therefore confirm the presence of a single panmictic population within Anticosti Island. The high density of the population is a possible explanation for this lack of fine-scale genetic structure (Long, Diefenbach, Rosenberry, & Wallingford, 2008; Roy Yannic, Côté, & Bernatchez, 2012), as the dispersal rate of female deer increases with density (Lutz, Diefenbach, & Rosenberry, 2015). On Anticosti, forage quality and quantity are the main drivers for dispersal and could explain partially the high gene flow within the island (Coulombe, Côté, & Huot, 2008; Massé & Côté, 2012).

4.2 | Absence of a founder effect

Overall, genetic diversity was higher on Anticosti Island relative to the two mainland populations based on all measured metrics, and the effective population size was comparable among all three populations. The Anticosti Island population was isolated for a too short period (120 years) for new mutations to accumulate and be responsible for the higher genetic diversity observed. Also, the hypothesis of multiple introductions from several source populations has been discarded by reliable sources (Martin-Zédé, 1938; McCormick, 1982; L. Jobin, personal communication). These results combined with the moderate differentiation between the insular and continental populations confirm an absence of founder effect associated with the introduction of white-tailed deer on Anticosti Island.

Population growth rate may have a positive relationship with the genetic diversity retained after a bottleneck (DeYoung et al.., 2003; Groombridge, Raisin, Bristol, & Richardson, 2012; Murphy et al., 2015). On Anticosti Island, the population increased rapidly after the introduction, as shown by the impact of browsing on vegetation reported after less than 40 years of deer presence (Côté et

al., 2008), and by the contemporary effective population size that is far greater than the number of 220 founders. Mainland populations have progressively increased during the XIXth century but are maintained at low density by hunting pressure and harsh winters since the beginning of the XXth century (Huot & Lebel, 2012). Therefore, we suggest that the rapid population growth, helped by the large number of founders, is a key factor that led to the maintenance of high genetic diversity of white-tailed deer on Anticosti Island. The loss of heterozygosity within the island population could have also been limited by the long generation time and overlapping generations that characterize large mammals such as white tailed deer (Kaeuffer, Coltman, Chapuis, Pontier, & Reale, 2007; Lippé, Dumont, & Bernatchez, 2006).

We found a pronounced discrepancy between the census population size (N_c), estimated at >160,000 (Rochette & Gingras, 2007) and the estimated effective population size (N_e) 1,587 [1,196–2,354] for the Anticosti Island deer population (Table 2). The N_e/N_c ratio (0.01) for Anticosti is very low compared to Montmagny (0.29) and Outaouais (0.13). In Frankham (1995) meta-analysis, the average N_e/N_c ratio of natural populations was estimated at 0.1 and varied between 0.52 and 0.65 for white-tailed deer. The nature of most cervid mating systems, characterized by nonrandom mating, overlapping generations, highly variable reproductive success of males due to the polygamous breeding system and the possibility of females producing twins in favourable conditions (therefore contributing to increased variance in reproductive success), could partly explain this low N_e/N_c ratio (Kalinowski & Waples, 2002; Neuman, Newbolt, Ditchkoff, & Steury, 2016; Newbolt et al., 2017; Palstra & Ruzzante, 2008). For example, the large population of Sika deer (*Cervus nippon*) on Hokkaido Island (Japan) is estimated at 120,000 individuals with a N_e of 2,511 even though this population never faced a bottleneck event (Goodman et al., 2001). Low N_e/N_c ratios can also be found in populations with very large census size because of a substructuration of the population could possibly increase the probability of sampling related individuals (Luikart, Ryman, Tallmon, Schwartz, & Allendorf, 2010; Palstra & Ruzzante, 2008). In our case, we minimized the risk of substructuring the population by including individuals from the three regions of Anticosti Island in each cohort used to calculate the N_e. Other factors such as fluctuations of the N_c and sex ratio, and variance in family size could also lead to the small N_e/N_c ratio observed on Anticosti Island (Frankham, 1995; Perrier, April, Côté, Bernatchez, & Dionne, 2016). The harsh climate of Anticosti island and the strong competition for resources within the deer population causes highly variable mortality rates, reaching as much as 38% during winter and leading to large fluctuations of the population size from year to year (Potvin, Breton, & Gingras, 1997; Simard, Côté, Weladji, & Huot, 2008; Taillon, Sauve, & Côté, 2006). We also detected variation in the number of breeders and the effective population size of the Anticosti population (Table S3).

Overall, our results suggest that the introduction of approximately 220 individuals on Anticosti Island provided a good representation of the genetic diversity of mainland populations and resulted in a genetically variable and viable population. While a loss of genetic diversity can affect fitness-related traits following inbreeding depression as shown in ungulate populations (Brambilla et al., 2015; Zachos, Althoff, von Steynitz, Eckert, & Hartl, 2007), this apparently does not apply to Anticosti deer. Indeed, Anticosti Island introduction was based on more founders compared to most other cases introduction examples (Table S7) which likely explains the absence of a decrease in genetic diversity. Uller and Leimu (2011) meta-analysis also concluded that genetic diversity in introduced populations can be retained and even increased with large number of founders and multiple introductions. The number of individuals introduced on Anticosti Island was probably a key aspect of its success because introduction of ungulates are often based on few individuals and have generally resulted in a decreased genetic diversity (Broders, Mahoney, Montevecchi, & Davison, 1999; Côté et al., 2002; Hundertmark & Van Daele, 2010; Kekkonen, Wikström, & Brommer, 2012).

4.3 | Adaptation on the Island

We found several loci putatively under divergent selection for Anticosti Island deer that may be involved in local adaptation since they were also associated with divergent traits, but none were linked to a known gene. Thus, 67 loci identified by genome scan approaches (PCADAPT and OUTFLANK) were associated with 11 traits of males and 16 traits of females. Among the 29 markers common to both PCADAPT analyses, three were only linked to traits of males suggesting stronger selective pressures for males than females (Table S5). A stronger selection on males could be explained by the influence of winter conditions which affect them most (Conradt, Clutton-Brock, & Guiness, 2000; Rose, Clutton-Brock, & Guiness, 1998) or by the sexual selection and/or behaviour of males during the rut (Clutton-Brock, 2017; Strickland, Jones, Demarais, & Dacus, 2017). Sexual selection increases with intraspecific competition and promotes desirable sexually selected traits (Martin, Festa-Bianchet, Coltman, & Pelletier, 2016; Newbolt et al., 2017). It has been shown that the antler spread of males increases with deer density (Simard et al., 2014). Therefore, males seem to invest more in antler size than body mass at high deer density possibly as an adaptation to sexual competition which could explain the association of the most conservative markers with male traits only.

Among the 120 loci involved in a biological function potentially relevant for the adaptation of white-tailed deer on Anticosti Island, 55 were found by at least two different analyses (Table S6). The biological functions of the loci were mostly found by associative approaches and directly linked to the phenotypic trait used in the association. For example, antler spread was linked to the gene calcium/calmodulin dependent protein kinase II gamma (CAMK2G) involved in calcium transportation, the principal component of antler formation. We found three genes involved in several muscular functions among the 55 identified candidates. The genes collagen type XIX alpha 1 chain (COL19A1), alpha-1A adrenergic receptor,

and sarcospan (SSPN) respectively act in skeletal muscular development, muscle contraction, and cardiac muscle contraction. All these loci were not found by genome scan analyses but were correlated with peroneus muscle mass of both sexes and with hind foot length of males. Association with peroneus muscle mass suggests that selection may have favoured increased protein reserves which are critical for winter survival because they are used as last resort energy sources (Monteith et al., 2013). Several markers were linked to the variation of hind foot length (Table S5) which supports Lesage et al. (2001) suggestion that the relatively longer legs of fawns from Anticosti Island could be an adaptation to the harsh winter conditions on the island. Two genes involved in lipid, glycosphingolipid, and oligosaccharide biosynthetic processes were also among the candidates found by multiple associative analyses: lipase G endothelial type (LIPG) and ST6 N-acetylgalactosaminide alpha-2,6-sialyltransferase 5 (ST6GALNAC5). Fat reserves are a determinant factor of winter survival of white-tailed deer and are mostly influenced by environmental conditions, reproductive status and population density (Simard et al., 2014; Taillon et al., 2006). Our results suggest that variation in this trait could also have a genetic basis and support another suggestion of Lesage et al. (2001) that the relatively high fat reserves found in Anticosti Island fawns could be an adaptation to the harsh winter conditions. Body mass is likely under strong selection because it integrates the weight of multiple structures: muscles, fat, bones, and antlers for males (Figure 4). This explained why we found several associations with markers potentially under selection for body mass. Taillon et al. (2006) also showed that body mass is a key factor for overwinter survival of fawns on Anticosti Island. Because this high-density population faces harsh winter conditions, our results indicate a stronger selection toward individuals of high body mass compared to the mainland but the poor-quality diet limits body mass reached on the Island.

Among the loci linked to a known function (Table S6), two genes were involved in embryonic body morphogenesis and nervous system development: pleckstrin homology like domain family B member 1 (PHLDB1) and rap guanine nucleotide exchange factor 5-like. These genes were located in regions under putative selection between Anticosti Island and Montmagny deer which suggests that differences in body morphology of Anticosti Island deer could occur early during the development.

Phenotypic differences between populations may result from (adaptive or maladaptive) plasticity and/or local adaptation (Schmid & Guillaume, 2017; Volis, Ormanbekova, & Yermekbayev, 2015). These processes are not exclusive since selection can act on phenotypic variance generated by plasticity (Pfennig et al., 2010; Zalewski & Bartoszewicz, 2012). Plasticity is also beneficial for invasive species in novel environments (Price et al., 2003; Uller & Leimu, 2011) and for northern ungulates facing wide ranges of weather conditions (Courbin, Dussault, Veillette, Giroux, & Côté, 2017; Lesage et al., 2001). White-tailed deer are known to be plastic (Boucher, Crete, Ouellet, Daigle, & Lesage, 2004; Jones et al., 2010; Little et al., 2016), including on Anticosti Island where the population remained at high density despite low-quality diet by adjusting their life-history traits such as body size, reproductive rate, and behaviour (Courbin et al., 2017; Lesage et al., 2001; Simard et al., 2008). High density had a negative impact on body mass as illustrated by the increase of 30% in the body mass of fawns kept in enclosures at low density (Giroux, Tremblay, Simard, Yoccoz, & Côté, 2014). The polygenic approach indicated a genetic basis of phenotypic traits, and based on the genome scan approach, some of these loci found to be associated with a phenotype also shown to be outliers between the Island and continental populations (Table S5) (Lesage et al., 2001). Therefore, we propose that phenotypic plasticity alone is not responsible for all phenotypic differences of the Anticosti Island population but acts jointly with genetically based adaptation. Common garden and transplant experiments would be required to rigorously distinguish the relative role of phenotypic plasticity and local genetic adaptations (de Villemereuil, Gaggiotti, Mouterde, & Till-Bottraud, 2016; but see Bérénos et al., 2015 for a high-density SNP-based approach in a wild population). As such, the white-tailed deer population of Anticosti Island brings another example of rapid genetic and morphological changes following range expansion (Kays, Curtis, & Kirchman, 2010; Monzon, Atkinson, Henn, & Benach, 2016; Monzon, Kays, & Dykhuizen, 2014). Among the numerous outlier loci found between the Anticosti Island and mainland deer populations with the genome scan approach, 19% were significantly linked to divergent phenotypic traits, this provides some support for adaptive divergence in this population. We suspect that the particular conditions of Anticosti Island (i.e., long harsh winters, low abundance of predators, low-quality forage and high population densities leading to strong intraspecific competition) may have been among the selective agents promoting genetic divergence between Anticosti and continental populations (Lomolino, 2005; Pérez-Gonzalez & Carranza, 2009; Runemark et al., 2014; Simard et al., 2014). Given such strong selective pressures, the influence of divergent selection is more likely to have led to the small genetic differentiation of the Anticosti Island deer population than the weak genetic drift we documented.

4.4 | Limitations

We identified markers linked to phenotypic traits known to differ between Anticosti Island and mainland deer populations. Because many of these markers have unknown functions, especially the 13 loci found in common between genome scan and associative analyses, a better understanding of these genome regions will be required to obtain a more complete portrait of the adaptation of deer on Anticosti Island. It remains possible that the genetic variation of important markers may also be partially linked with unmeasured phenotypic traits. More importantly, GBS protocol consists in a reduction of genome complexity by looking at thousands of short sequences reads randomly distributed throughout the genome. Therefore, some important regions under selection have certainly been missed and cautious interpretations must be made

when assessing which phenotypic traits are under selection. Under these circumstances, it is recommended to use polygenic models, as we did, especially when focusing on complex adaptive phenotypes. We found more markers with LFMM than with PCADAPT and OUTFLANK suggesting that polygenic selection might be involved in the genetic and morphological differentiation of the Anticosti island population (Rellstab et al., 2015). Small overlap between the genome scan and associative approaches is not unusual and in fact expected given the conceptual and analytical differences between these analyses (Frichot et al., 2013; Rellstab et al., 2015; de Villemereuil et al., 2014).

4.5 | Management implications

Given its geographic isolation, the designation of the Anticosti Island deer population as a geographic management unit is obvious (Cronin, 2003), and our study revealed that it is sufficiently genetically distinct to allow population assignment based on individual genotypes with high success. As such, we showed that this population differs by both neutral and presumably adaptive loci from the mainland source population. This genetic divergence added to their morphological divergence from the mainland deer previously shown (Bonin, Tremblay, & Côté, 2016; Lesage et al., 2001; Simard et al., 2008) supports the uniqueness of Anticosti Island deer population. Their persistence in this unique place located at their northern distribution limit has given rise to local adaptation which supports the distinct contribution that this population bring to the species. Population structure analyses and the absence of biological differences also suggest that Anticosti Island deer form a single panmictic population across the three main regions of the island, which can be considered as genetically healthy given its higher genetic diversity relative to continental populations. Our study thus supports the designation of the Anticosti Island white-tailed deer population as a distinct population that should be managed accordingly.

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AUTHOR CONTRIBUTIONS

The study represents the master's project of J.F. J.F. did the laboratory work, analyzed the data and wrote the manuscript. A.N.F., and M.L. assisted in data analysis and writing. J.L. performed the genotyping. T.B.D. shared the reference genome that he assembled. S.D.C. conceived the study, provided the funding and samples, helped in data analysis and editing the manuscript. L.B. provided part of the funding, helped in data analysis and editing of the manuscript. All authors have read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The genomic data (filtered markers) and morphological data used for this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bk3j9kd6j. Raw demultiplexed sequences are available on the Sequence Read Archive (SRA) on the study accession number: PRJNA577977.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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