

When Genetics and Genealogies Tell Different Stories—Maternal Lineages in Gaspesia

Claudia Moreau¹, H  l  ne V  zina^{2,3,4}, Mich  le Jomphe^{2,3,4},   ve-Marie Lavoie^{2,3,4}, Marie-H  l  ne Roy-Gagnon^{1,5} and Damian Labuda^{1,6*}

¹Centre de Recherche, CHU Sainte-Justine, Universit   de Montr  al, 3175, C  te Sainte-Catherine, Montr  al (Qu  bec), Canada H3T 1C5

²D  partement des sciences humaines, Universit   du Qu  bec    Chicoutimi, 555, boulevard de l'Universit  , Chicoutimi (Qu  bec), Canada G7H 2B1

³Projet BALSAC, Universit   du Qu  bec    Chicoutimi, 555, boulevard de l'Universit  , Chicoutimi (Qu  bec), Canada G7H 2B1

⁴Groupe de recherche interdisciplinaire en d  mographie et   pid  miologie g  n  tique-GRIG, Universit   du Qu  bec    Chicoutimi, 555, boulevard de l'Universit  , Chicoutimi (Qu  bec), Canada G7H 2B1

⁵D  partement de m  decine sociale et pr  ventive, Universit   de Montr  al, Pavillon 1420 Mont-Royal, 1430 boul. du Mont-Royal, Outremont (Qu  bec), Canada H2V 4P3

⁶D  partement de p  diatrie, Universit   de Montr  al, 3175, C  te Sainte-Catherine, Montr  al (Qu  bec), Canada H3T 1C5

Summary

Data from uniparentally inherited genetic systems were used to trace evolution of human populations. Reconstruction of the past primarily relies on variation in present-day populations, limiting historical inference to lineages that are found among living subjects. Our analysis of four population groups in the Gasp   Peninsula, demonstrates how this may occasionally lead to erroneous interpretations. Mitochondrial DNA analysis of Gaspesians revealed an important admixture with Native Americans. The most likely scenario links this admixture to French-Canadians from the St. Lawrence Valley who moved to Gaspesia in the 19th century. However, in contrast to genetic data, analysis of genealogical record shows that Native American maternal lineages were brought to Gaspesia in the 18th century by Acadians who settled on the south-western coast of the peninsula. Intriguingly, within three generations, virtually all M  tis Acadian families separated from their nonadmixed relatives and moved eastward mixing in with other Gaspesian groups, in which Native American maternal lines are present in relatively high frequencies. Over time, the carriers of these lines eventually lost memory of their mixed Amerindian-Acadian origin. Our results show that a reliable reconstruction of population history requires cross-verification of different data sources for consistency, thus favouring multidisciplinary approaches.

Keywords: mtDNA, genealogy, genetic ancestry, admixture, Native American, Quebec population

Introduction

European 17th-century settlements along the St. Lawrence Valley led to the foundation of New France, later renamed Canada with its French-speaking province of Quebec (Charbonneau et al., 1987; Charbonneau et al., 2000). The Gasp   Peninsula is situated at the entrance to the Valley, south of the St. Lawrence Estuary (Fig. 1). Stable European col-

onization of this region of Eastern Quebec began only in the middle of the 18th century at the time of the British conquest of New France (Desjardins et al., 1999). The earliest Gaspesian settlers were descendants of French pioneers from Acadia (present-day Nova Scotia, Prince Edward Island and New Brunswick—Fig. 1) who escaped the British deportation campaign that started in 1755 (Arsenault, 1994). In 1784, Acadians were followed by Loyalists from the US, who preferred to remain under British rule after the Declaration of Independence (Rees, 2000). In the 19th century, the developing fishing industry attracted French-Canadians from the lower St. Lawrence Valley and newcomers from Europe, including Channel Islanders from Jersey and

*Corresponding author: Damian Labuda, Pediatrics Department, Universit   de Montr  al, Sainte-Justine Hospital Research Center, Room B-607 b, 3175 C  te Sainte-Catherine, Montr  al (Qu  bec), Canada H3T 1C5. Tel: 514 345-4931 Ext. 3586 [Sec.: 3282]; Fax: 514 345-4731; E-mail: damian.labuda@umontreal.ca

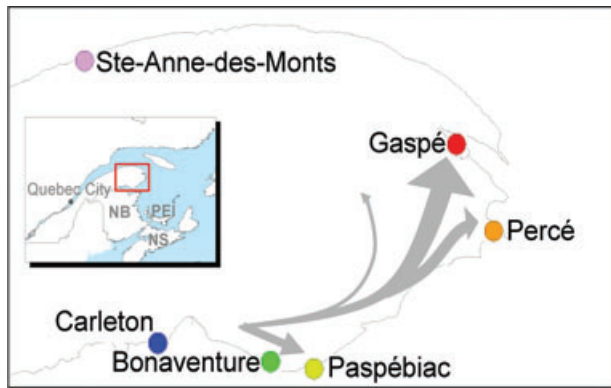


Figure 1 Map of the Gaspé Peninsula and Acadia. Historical Acadia included the banks of the Bay of Fundy between New Brunswick (N.B.) and Nova Scotia (N.S.), south of the Baie-des-Chaleurs and extended farther to Prince-Edward Island (P.E.I.). Arrows indicate the migration of Métis families over generations.

Guernsey (Desjardins et al., 1999). Recently, the maternal and paternal lineages of these four population groups were compared based on the analysis of mitochondrial DNA (mtDNA) and Y-chromosome diversities (Moreau et al., 2009). This analysis revealed an important presence of maternal lineages representing Amerindian haplogroups. They were especially preponderant among self-declared French-Canadians (13%) and Channel Islanders (18%), and much less so among Loyalists (7%) and Acadians (1%). Most parsimoniously, the origin of these lineages could be explained by only three admixture events and, given the high population frequencies of these lineages, the admixture should have occurred early, at the beginning of the colony.

Their distribution among the four Gaspesian groups suggested that they were brought to the Gaspé Peninsula by French-Canadian settlers from the St. Lawrence Valley whose female descendants frequently married immigrants from Jersey and Guernsey (Desjardins et al., 1999). In this paper, we show that this simple interpretation of the genetic data needs to be revised in light of the genealogical evidence and the reconstructed maternal genealogies in particular.

Results and Discussion

Genetic and Historical Evidence

Gaspesian subjects were grouped based on their self-declared ancestral affiliation (Fig. S1) (Moreau et al., 2009). Genomic samples of the four groups were analyzed by sequencing the hypervariable regions I and II (*D-loop* segment) and by genotyping three positions in the coding region of their

Table 1 Distribution of the Amerindian mtDNA haplogroups A, C and D among Gaspesian populations (compiled from Table S4 of Moreau et al. (2009)).

Group	n_{total}	A	C	D
Acadians	102		1	
Channel Islanders	93	3	12	2
French-Canadians	105	1	12	1
Loyalists	92	1	4	1

mtDNA (Moreau et al., 2009). Among the 394 Gaspesians analyzed, 38 carried Amerindian mtDNA sequences (Table 1) (Torroni et al., 1993; Lorenz & Smith, 1996; Malhi et al., 2001). The Amerindian haplogroup C was present in 29 individuals who all shared the same *D-loop* haplotype. Five carriers of haplogroup A shared four identical haplotypes and one differed from them by one mutational step only. Out of four D haplogroup copies, three haplotypes were identical and one differed again by a single mutation only. This pattern of mutations was observed in samples that belong to multigenerational pedigrees, which reflects a high rate of mutation in the *D-loop* (Heyer et al., 2001). Therefore, taking into account the diversity of the maternal lineages within Amerindian groups (Torroni et al., 1993; Lorenz & Smith, 1996; Malhi et al., 2001; Malhi et al., 2002; Bolnick & Smith, 2003), three independent admixture events may be sufficient to explain the presence of Amerindian mtDNA sequences in our Gaspesian sample. In the absence of selection, the age of a new allele is related to its population frequency (Kimura & Ohta, 1973; Griffiths & Tavaré, 1998). Therefore, relatively high population frequencies of these three groups of haplotypes indicate their early introduction, presumably at the beginning of the colony. This is consistent with the earlier supposition that these samples were interconnected through multigenerational genealogies, which explains two singleton mutations. In comparison, the remaining 356 maternal lines represent all major European haplogroups and 172 distinct *D-loop* haplotypes (Moreau et al., 2009), thereby revealing the much greater diversity of the European founders who continued to colonize Gaspesia over its entire history since the first European settlements. The greatest concentration of Amerindian lines among French-Canadians and Channel Islanders, their lower proportion among Loyalists and their virtual absence among Acadians (Table 1) led to a conclusion that French-Canadian founders introduced Amerindian maternal lines into Gaspesia. Without additional data there was no reason to invoke a possibility of a frequency shift that changed the proportion of maternal lines between Gaspesian groups, especially over a period of a few generations. It was natural to apply a simple frequentist interpretation and assign the place/population of origin of an allele where it is most prevalent. Moreover, French-Canadians who moved to Gaspesia from the St. Lawrence Valley can be

traced back to the 17th-century founders of Nouvelle France. At that time, there was a shortage of women among European settlers, which could have favoured marriages between men of European descent and Native American women. Likewise, in 19th-century Gaspesia, most immigrants from Jersey and Guernsey were fishermen (Desjardins et al., 1999). These men often married French-Canadian women, which could plausibly explain the high frequency of the same Amerindian maternal lines among the Channel Islanders. This is the scenario of the origin and history of the maternal Amerindian lineages in the Gaspesian populations that emerges from the analysis of our genetic data and colonization history. Nevertheless, this likely interpretation should be revisited and amended given the genealogical data.

Genealogical Data

Ascending genealogies of all the participants were reconstructed using the BALSAC population database, the Early Quebec Population register and complementary sources, such as marriage repositories and family dictionaries. They were used to determine the time and place of marriage of all ancestors, as far as the sources allowed and when possible up to the first marriage on Quebec territory. Although the Amerindian origin of spouses was sometimes mentioned in marriage records, it was certainly under-reported. Other historical sources (see list of Internet resources) had to be consulted, but information was not always available and was often uncertain or ambiguous.

Haplogroup C maternal lineages (i.e., female-only genealogical lines) form two large pedigrees as shown in Figure 2A and B. The two haplogroup C pedigrees and the maternal line of one other C haplotype carrier could not be connected. Nevertheless, all of these individuals carry identical haplotypes determined by D-loop polymorphisms and suggest a common origin. Three carriers of haplogroup A, including the one separated from the others by a single mutation, form a single pedigree, whereas only two carriers of D haplotypes could be connected (Fig. 2C). In three instances, one in each of the haplogroups, maternal lines end in the 19th century. All the others could be traced back to before the middle of the 18th century.

Contrasting our inferences above, Amerindian maternal lines do not originate in the St. Lawrence Valley, as we tentatively deduced based on their frequency distribution among the Gaspesian groups. Instead, the most remote traceable ancestors of these lines were from either France or Acadia or passed through Acadia because their carriers married there. The Acadian connection is well established in the large C pedigree shown in Figure 2A, with two top ancestors married in Acadia and another Acadian marriage in the middle

of the genealogy. Even though ancestral lines could not be connected, it is likely that the remaining C lineages carrying an identical maternal haplotype belong to the same family (Fig. 2A and B). Obviously, an independent origin of the Figure 2B family cannot be completely excluded. Yet, the odds of a sequence of such events are very slim. This would require an independent admixture with a carrier of the same *D-loop* C haplotype as the founder of the Figure 2A genealogy and the settlement of her descendants at the same time and in the same region of Gaspesia. Yet even within the same Native American community maternal lines are not homogenous and represent different haplogroups and haplotypes (Lorenz & Smith, 1996; Scozzari et al., 1997; Malhi et al., 2001; Malhi et al., 2002; Bolnick & Smith, 2003). Furthermore, the reproductive success of these different founders would have had to be similar with the resulting distinct families (Fig. 2A and B) coincidentally settling in the same neighbourhood, in spite of the unprecedented dispersion of the deported Acadians to Louisiana, Europe and various islands in the Atlantic (Arsenault, 1994; Jobb, 2005). In contrast, Acadian families tended to settle together and to reunite after forceful dispersal. All this makes a common origin of the C genealogies from Figure 2A and B all the more likely. In addition, the oldest marriage among our C lineages, before the families moved to Acadia, was traced to Carleton (known as Tracadieche at the time) in the Baie-des-Chaleurs region of Gaspesia around 1705 (Fig. 2A). Perhaps, these Gaspesian roots led their descendant great-grand-daughters to choose this part of Quebec when leaving Acadia to escape deportation by the British. Importantly, the Acadian origin appears again in the pedigree connecting three haplogroup A carriers (Fig. 2C). The most remote ancestors were in Acadia and their grand-daughter married in the Percé region in 1748. This again suggests that Acadian families who settled in Gaspesia following the deportation had earlier connections and knowledge of this region. In the D lineages as well, two carriers share a common female ancestor married around 1740 either in France or in Acadia, based on conflicting historical sources, but again pointing to Acadian origins because of the unlikely presence of Amerindians in France. Not all of the ancestral maternal lines of Amerindian haplogroup carriers could be traced back to Acadia. However, given all the arguments presented above, it is very unlikely that the identical or almost identical (one mutation removed) haplotypes observed in Gaspesia with origins traceable to Acadia could have originated elsewhere and coincidentally settled in Gaspesia.

Métis Migration

In summary, the genetic and genealogical evidence combined (Fig. 2) points to a common origin of all Amerindian lineages

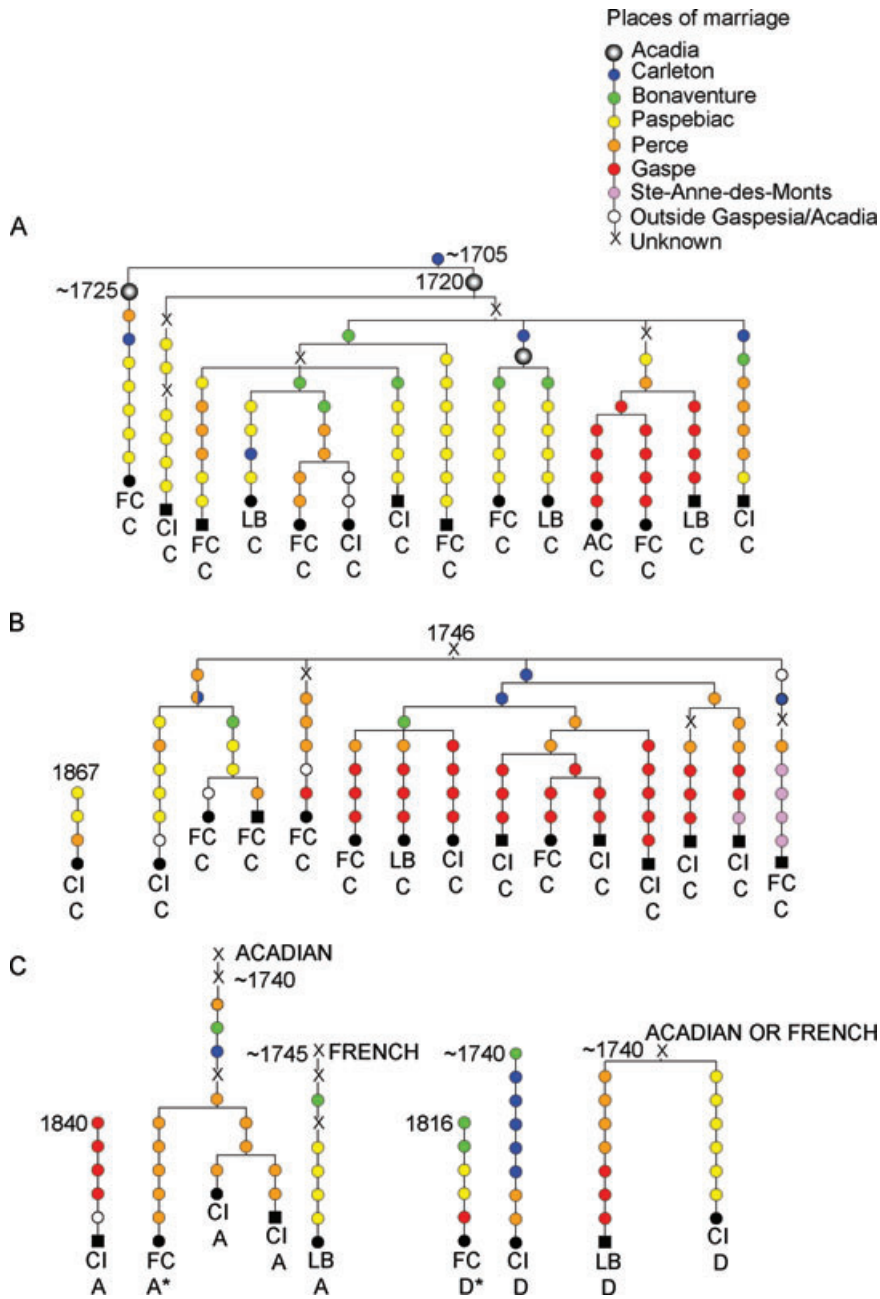


Figure 2 Maternal lineage genealogies of haplogroup A, C, and D carriers. In the genealogy, participants are in black (squares for males and circles for females) with the population group with which they identified indicated directly below: FC, French-Canadian; LB, loyalist; AC, Acadian and CI, Channel Islander; the lowest letter denotes mtDNA haplogroup. Numbers indicate a year or approximate year of marriage at the top of the genealogies. The regional location of the place of marriage is colour coded as indicated. Note the same colour code is used in Figure 1 and 3. Known ancestral origin of pedigree founders is indicated in capital letters.

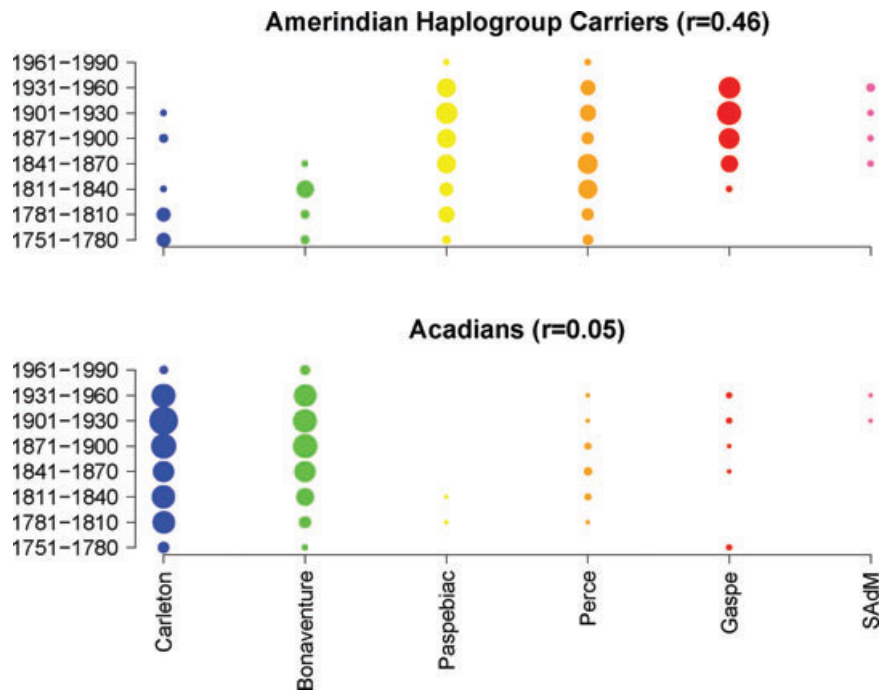


Figure 3 Bubble graphs of the frequency of marriage of maternal ancestors of carriers of Amerindian haplotypes (upper) and of Acadians (lower) in six regional subdivisions of Gaspesia over eight time periods. The circle size is proportional to the frequency of marriages per time period per locality using the total number of marriages within the analyzed group as the denominator (186 and 435 in Amerindian and Acadian maternal lines, respectively). The Pearson correlation coefficient r , indicated in parentheses, was calculated between the region of marriage (coded as integers from 1 to 6 starting at Carleton and following the coastal line of the Peninsula up to Ste-Anne-des-Monts) and the time period (coded as integers from 1 to 8 in chronological order, that is, 1 = 1751–1780, ..., 8 = 1961–1990). SAdM – Ste-Anne-des-Monts.

going back to Acadia or evokes an Acadian connection. This raises a puzzling issue. Why did all these Amerindian maternal lines, which were present among Gaspesian-Acadians more than two centuries ago, disappear from contemporary individuals declaring Acadian ancestry? Did the separation between admixed and nonadmixed Acadians take place at the time of initial settlement in the Gaspé Peninsula or was it an ongoing process? Could it have happened only by chance? To shed light on these questions, we traced all the places of marriage of the maternal ancestors of the carriers of the Amerindian mtDNA haplotypes and of the remaining participants in each of the four groups. Places of marriage, available in the BALSAC database, were used as a proxy for places of residence, dividing the Gaspesian territory into six regions named after the localities where the highest concentration of marriages was observed. These six localities are colour coded in the map shown in Figure 1 and the same colour code is used in Figure 2 and Figure 3. The regional grouping of the surrounding parishes followed that of the diocese of

Gaspé. It reflects historical affinities between different population groups that colonized Gaspesia. It also represents the geographic partition of these groups along the interconnecting natural coastal route, eastward into the Baie-des-Chaleurs, then north and back westwards into northern Gaspesia along the banks of the St. Lawrence River.

Bubble graphs in Figure 3 represent the distribution of marriages among these regions over 30-year time periods, which approximate the time span of a single generation (Tremblay & Vezina, 2000; Fenner, 2005). The graphs compare marriages of the maternal ancestors of carriers of Amerindian haplotypes (Métis families) with marriages of the maternal ancestors of contemporary Acadians. The latter remained in their initial 18th-century settlements of Carleton and Bonaventure (Fig. 3). In contrast, their admixed relatives carrying Amerindian maternal lines, who initially also settled in Carleton and Bonaventure, left these regions within a period of three generations (Fig. 3) and moved eastward/northward (see arrows in Fig. 1).

To evaluate these observations quantitatively, we calculated Pearson's correlation coefficient " r " between the region of marriage (coded as integers from 1 to 6 starting at Carleton and following the coastal line of the Peninsula up to Ste-Anne-des-Monts) and the time period (coded as integers from 1 to 8 in chronological order, that is, 1 = 1751–1780, . . . , 8 = 1961–1990). A spatial–temporal correlation coefficient of 0.05 of stationary Acadians contrasts with $r = 0.46$ obtained for the carriers of Amerindian haplogroups. An almost identical correlation coefficient of 0.48 was obtained from a matrix comprising the marriages of the whole set of descendants of the Amerindian founders present in the genealogies reconstructed in this study (Fig. S2). We used multinomial logistic regression models to formally test the hypothesis that the migration patterns differed between carriers of Amerindian lineages and the maternal ancestors of self-declared contemporary Acadians. We investigated migration patterns by examining the region where the marriages occurred. Multinomial logistic regression is appropriate to model outcomes consisting of unordered categorical data, in this case the six regions where marriages occurred. Specifically, each region is compared with the Carleton region in terms of the odds of an ancestor's marriage occurring in a given region as opposed to the Carleton region. We investigated the effect of time period and lineage identity (i.e., Amerindian or Acadian) on the odds of a marriage being away from Carleton (in another region). We were mostly interested in the interaction between time period and lineage identity, which allows the odds of a marriage location to vary between the two lineage identities over time periods. We found a significant interaction effect ($P < 0.0001$ from a likelihood ratio test comparing the models with and without an interaction term), which indicated significantly different marriage locations (migration patterns) over time between the two lineage identities.

Split

The split between nonadmixed Acadians and Métis families was most pronounced in the regions of Carleton and Bonaventure. It occurred over a time span of about three generations. After 1840, practically no more marriages of the Amerindian mtDNA carriers were observed in these regions (Fig. 3). The same pattern was seen among all other descendants of the admixed maternal founders who were present in the analyzed genealogies (Fig. S2). What could have happened to drive Métis families out of their original settlements in the Acadian Gaspesian "fief" of Carleton and Bonaventure?

During the 17th and 18th centuries, Acadian bonds with Mikmaqs, their Native American hosts were particularly friendly. They were marked by frequent intermarriage creating familial ties, reinforcing the egalitarian and communal

nature of their society and favouring Mikmaq conversion to Catholicism. Furthermore, the complementary economies of the nomadic Mikmaqs and sedentary Acadian farmers were conducive to collaboration and a common stand against the British further cemented their alliance (Arsenault, 1994; Jobb, 2005). This thriving cohabitation in historical Acadia (today Nova Scotia, Prince Edward Island and New Brunswick) ended between 1755 and 1763 when more than 10,000 people were deported by the British. Among those who settled in Gaspesia, about one third belonged to admixed families, based on our data on 65 marriages pertaining to Acadian and 35 to Amerindian maternal lines in the time period between 1751 and 1810. Was the separation of admixed and nonadmixed Acadians a direct consequence of the permanent establishment of British rule in Canada? The British way of parceling out land likely led to competition between deported Acadians and the Gaspesian Mikmaqs, whose territory shrank to an area west of the Baie-des-Chaleurs. Other factors such as an increase in population density, changes in lifestyle and social attitudes or personal choices could also have led to a disruption in friendly cohabitation with Native American hosts, driving Métis families eastward (Arsenault, 1994; Desjardins et al., 1999; Jobb, 2005).

Eastward migration of the descendants of the settlers of Carleton and Bonaventure was not limited to Métis families (Figs. S3 and S4). However, Métis founders carrying Amerindian mtDNA haplogroups contributed proportionally much more to population groups that gained in importance in Gaspesia throughout the 19th century, while practically no trace of their maternal lines is now found in contemporary Acadians. It should be noted that the family of the only C haplogroup carrier who remembered her Acadian roots (Fig. 2A) had lived in the Gaspé region for six generations. An analysis of the matrices of the paternal lines of Acadians, Channel Islanders and Loyalists is also revealing. A comparison of the places of residence of the participants (Fig. S1) and places of marriages of their paternal ancestors (Fig. S4) confirms the tendency to self-identification following the paternal identities, whether related to the family name or other cultural traditions (Poloni et al., 1997). Both the graphs and the correlation coefficients clearly illustrate the correspondence between self-declared identity and the paternal lineages that remained in the original settlement (Fig. S4) and the tendency of those who moved to mix in with the dominant group, represented in Gaspesians by French-Canadians (paternal lineages: $r = 0.46$).

Data Complementarity

We were able to reconstruct the genetic history of Gaspesian groups by combining knowledge of ascending genealogies

with genetic data and historical facts. Neither genealogical nor genetic data alone would have allowed us to perform this historical reconstruction. The origin of the founders, especially those of non-European descent, is often missing and unreported, which leads to a patchy and incomplete picture of Amerindian contribution. On the genetic side, some lost lineages can be genetically retraced if their DNA was lucky enough to be preserved (Rasmussen et al., 2010). Others, such as the lost Amerindian lines of Gaspesian Acadians survived in other populations. However, in the absence of genealogical records that retrace their historical pathways, learning about their geographical distribution would require much more extensive genetic surveys of the whole population of Quebec. This emphasizes the complexity of human migration history and that of particular genetic lineages. It also emphasizes the pitfalls of inferring origins from uniparentally inherited markers (King et al., 2007).

Clearly, in addition to the female founders of New France who came from France, some of whom are known as the “Filles du Roi” (Charbonneau et al., 1987), the Native American “Filles de Godasiyo” (a legendary woman chief from the East) also made a significant genetic contribution to the Quebec population and can be traced in the genealogical record. Both arrived early and significantly contributed to the peopling of a new territory. Curiously, the carriers of Amerindian lines virtually disappeared from the population group that still identifies itself with its Acadian ancestors. Could we attribute this to allele surfing (Edmonds et al., 2004; Klopstein et al., 2006; Excoffier et al., 2009), whereby a genetic variant gains in frequency in a population during its expansion into a new territory, while remaining modestly represented in its place of origin. Indeed, during the colonization of a new territory, pioneer families always have a chance to contribute more alleles to future generations than later migrants, which leads to founder effects (Labuda et al., 1996; Labuda et al., 1997). At the same time, a small number of pioneers in such an advancing population may often increase genetic drift, the chance of extinction and also the frequency of some initially rare alleles (Excoffier et al., 2009). The addition of other phenomena, such as a correlation in family size over generations, which amounts to inheritance of fertility, even if it can be also due to social selection, would further tend to reinforce the impact of a founder effect (Austerlitz & Heyer, 1998). This has been particularly well studied in Eastern Quebec in the region of the Charlevoix and Saguenay (Bouchard & DeBraekeleer, 1991; Scriver, 2001). An unprecedented abundance of maternal lines of Amerindian origin in Gaspesia, particularly among French-Canadians and Channel Islanders, provides insight into possible mechanisms that reinforce a surfing effect (Klopstein et al., 2006). In addition to chance, there are other contributory factors: (i) Amerindian line carriers were among the first settlers (as in the forefront of a migration wave), (ii) a shortage

of women among subsequent immigrants favoured the early mtDNA variants (Bedoya et al., 2006), and (iii) to reinforce it all, these particular settlers enjoyed great reproductive success (Fig. 2), a characteristic of the whole territory of New France (Austerlitz & Heyer, 1998; Livi-Bacci, 2001). On the other hand, neither chance nor embracing Gaspesian newcomers can explain the selective disappearance of Métis families from Carleton and Bonaventure (Fig. 3 and Fig. S2), which left behind the settlers who continued to preserve their Acadian identity. This requires a separate historico-sociological analysis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Figure S1** Place of residence of the Gaspesian participants.
- Figure S2** Distribution of the frequency of marriages, over time and across six Gaspesian regions (see text and Fig. 1), among all descendants of the Gaspesian founders carrying an Amerindian haplogroup, considering only the descendants found within the genealogies of the participating Gaspesians.
- Figure S3** Distribution of the frequency of marriages of the maternal ancestors in four Gaspesian groups, excluding carriers of the Amerindian maternal lines.
- Figure S4** Distribution of the frequency of marriages of the paternal ancestors in four Gaspesian groups.

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