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Effects of Religion, Economics, and Geography on Genetic Structure of Fogo Island, Newfoundland*

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ABSTRACT The population structure of Fogo Island, Newfoundland is described using geography, religious affiliation, economic factors (such as the presence of a fish-packing plant), and genetic markers. Five different analytic methods, R-matrix analysis, r_{ij} vs. mean per locus heterozygosity, predicted kinship (ϕ), mean first passage time, and Mantel matrix comparisons, were applied to the Fogo Island genetic and demographic data. The results suggest that geography plays a role on Fogo Island in the distribution of genes, while religion, ethnicity, and economic factors play less significant roles. The communities with fish-packing plants and tourism serve as migratory "sinks" for Fogo islanders seeking employment. Reproductively, the most isolated village on Fogo Island is Tilting, and this is reflected in its genetic uniqueness, initially caused by Irish settlement and subsequently the action of stochastic processes. © 1995 Wiley-Liss, Inc.

Most studies on the structure of human populations focus either on historical demography or on blood genetic distributions within subdivided populations. In much of the world this focus is necessitated by the paucity of accurate demographic records and/or reliable historical documents. The few studies that combined both the demographic and genetic features of populations were focused on European agricultural communities such as Aland Islands (Jorde et al., 1982), the Northumberland region of Northern England (Roberts and Rawling, 1974), the Hutterites of Alberta (Morgan et al., 1982), and the Mennonites of the Plains of Kansas and Nebraska (Crawford et al., 1989). To date, there is little information available on the relationship between the predicted kinship (based on migration patterns) and genetic distributions in highly isolated fishing communities.

Parent-offspring migration patterns have been utilized to measure the rates of gene exchange between population subdivisions in three distinct regions of Newfoundland (Baer et al., 1987). The genetic effects of the predicted kinship (based upon the migration patterns) were not ascertained. However,

the population structure of Ramea Island, Newfoundland (subdivided into native, and short-term and long-term migrants) was investigated utilizing blood genetic data. This study revealed that under the influence of systematic evolutionary forces, population structures have short "memories" and the original gene pool was swamped by migration (Devor et al., 1983). Thus, the observed interaction of the genetic and demographic structures of populations provides a fuller "glimpse" of the evolutionary dynamics of human aggregates.

The majority of population structure research has been focused on the relationship between genetics and geography, and migration and geography (Jorde, 1980). Less is known about the genetic consequences of religious and economic factors that may influence mate selection and migration patterns between population subdivisions. The most

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common studies of the influences of religion on population genetics are on isolates such as the Amish of Pennsylvania (McKusick et al., 1964), the Jews of Rome (Dunn and Dunn, 1957), the Mennonites of Kansas and Nebraska (Crawford et al., 1989), and the Samaritans of Israel (Bonne, 1963). All of these studies view religion as a reproductive isolating mechanism that subdivides populations into smaller entities, which are influenced by stochastic processes. The unique history of Newfoundland offers an opportunity to examine the interactions of migration, geography, religion, and economic factors on the observed genetic variation in fishing villages. Koertvelyessy et al. (1988), using the repeated-pairs approach (RP), documented an excess of observed over random surname repetitions, most likely a result of religious subdivisions of Fogo Island.

POPULATIONS

Newfoundland was selected for this study because of its unique historical, geographical, and ecological characteristics. Because some of the best cod fishing in the world was located along the jagged coast of the island, England carefully protected Newfoundland from massive colonialization. In 1699, the British Parliament prohibited settlement of the island, except as necessary to maintain cod fishing. This remained the basic British policy governing Newfoundland for more than 150 years. During the 17th and 18th centuries, population growth necessitated the appointment of a naval governor and a court of law; however, both remained on the island only during the fishing season. Following the establishment of a permanent government in 1855, a number of prosperous British fishermen settled as merchants. Currently, the majority of resident fishermen in the villages dotting the island coast are primarily English, tracing their ancestry to the four southwestern counties of Devon, Dorset, Somerset, and Cornwall.

Irish Catholic laborers were settled during the early to middle 19th century. Initially, the Irish were employed primarily in the canneries and they resided in urban centers. Later, they expanded from the towns, and some of Irish descent founded fishing villages apart from the Anglicans. Fogo Island, the primary focus of this study, consists of a series of Irish Catholic, English Anglican, and combined villages. United Methodists and Evangelical groups can be found in sev-

eral of the villages. Fogo Island (Fig. 1) is located off the northeast coast of mainland Newfoundland, with its population subdivided into 14 settlements, of which 10 outports were of moderate size, ranging in size from 100 to approximately 1,000 persons. The island has been relatively isolated geographically until the 1950s, when seasonal ferry service was established.

The initial settlement of Fogo Island in 1690 was unlawful, and its small population was involved primarily in cod fishing. During the 1800s, fish-processing plants were established and Fogo became a major exportation center. Its population grew to a total of 3,526 inhabitants by 1884, but then declined slightly in 1891 because of a depression in the fish market, followed by outmigration. Since 1945, the island's population size has remained relatively stable, hovering around 4,000 persons. This population is subdivided by religion with 41% Anglican and with the Catholic and Methodist minorities each constituting 29% of the total.

MATERIALS AND METHODS

Fieldwork on Fogo Island was conducted with the collaboration of the Canadian Red Cross. The Anglican, Roman Catholic, and Methodist Church matrimonial records for Fogo Island from 1900 to 1983 were microfilmed. The Catholic records began from 1911 onwards, while both the Anglican and Methodist marriages were recorded from 1900. A total of 1,689 marriages were registered for members of the three denominations. Of the total number of marriages recorded, 795 were Anglican, 514 were Catholic, and 380 Methodist.

A similarity matrix of religious preference was constructed for each of the Fogo Island villages from the contemporary residents who participated in this study. The proportions of Catholics, Anglicans, Evangelical, United Churches, and Salvation Army in each village were used to compute religious "distances" between the subdivisions.

Blood specimens were collected by the Canadian Red Cross from 360 volunteers from isolated communities who were participating in an ongoing program of blood typing for medical reasons. These specimens were packed in ice and shipped to St. Johns for blood group analyses. Unfortunately, several of the smallest villages on Fogo Island could not be included in the analysis because of insufficient samples. Standard demographic

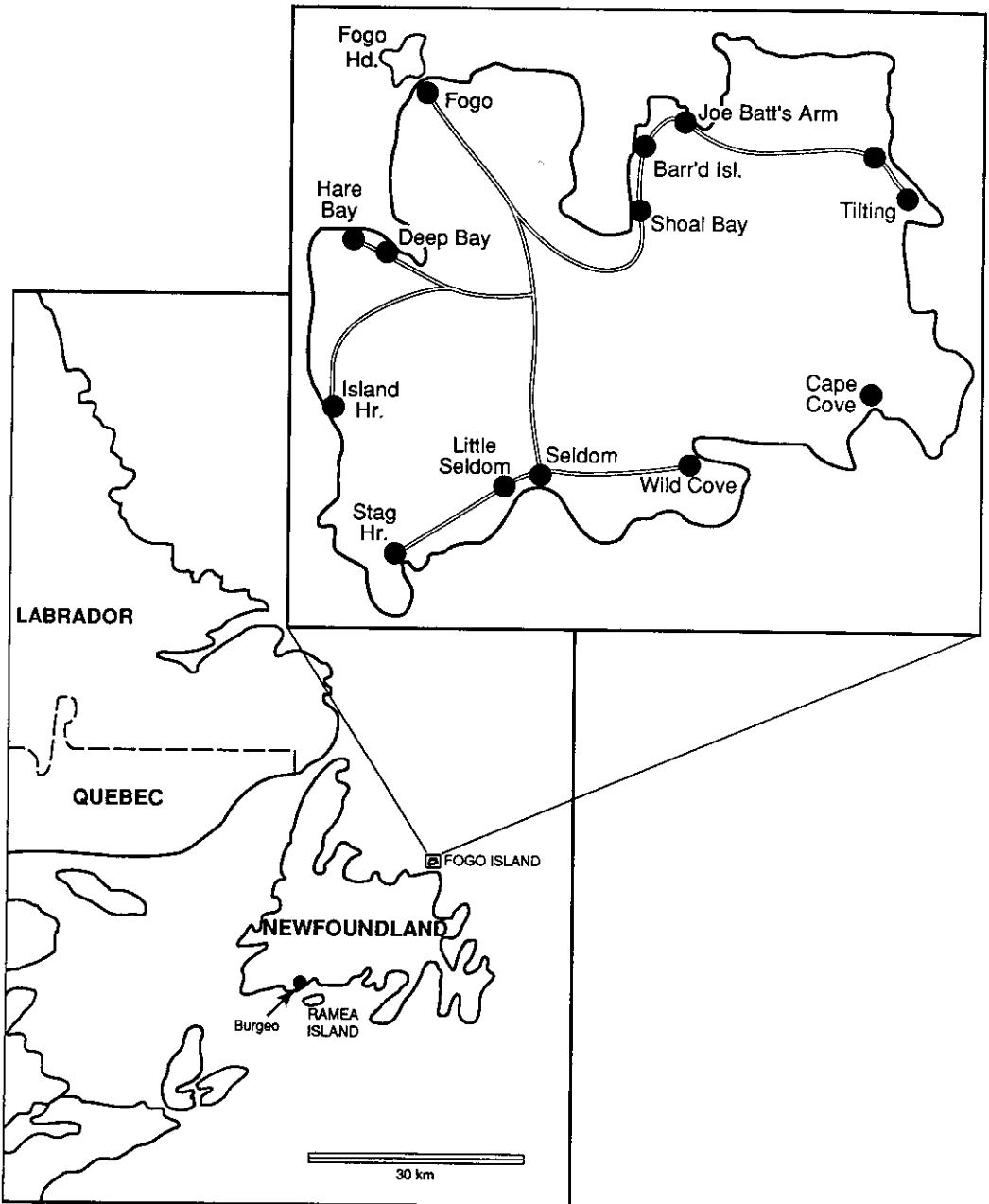


Fig. 1. Map of Newfoundland and Fogo Island indicating the locations of the populations sampled in this study.

pro formae were administered to all participants from nine villages of Fogo Island. Gene frequencies were computed using maximum likelihood procedures and were summarized together with the genotypic frequencies by Martin et al. (1995).

Analytical methods

Five analytical methods were employed for the analysis of the gene frequencies and migration matrices of the subdivisions of Fogo Island.

R-matrix. This method, devised by Harpending and Jenkins (1973), has been widely utilized for generating pseudo two- or three-dimensional least-square plots of synthetic variables between subdivisions of populations. Two genetic maps based on 10 polymorphic loci and 14 alleles (ABO*A, ABO*B, RH*R1, RH*R2, RH*R, MN*M, Ss*S, LU*B, P*P1, JK*A, LE*A, LE*B, K*k, FY*A) were constructed. The first "genetic map" analyzed the genetic variation in five settlements of Fogo Island. The samples for other communities were too small to be used in this analysis. The second genetic map contrasted the five settlements from Fogo Island with two communities from the southern coast of Newfoundland, Burgeo, and Ramea.

R_{ij} vs H . The diagonal element of the R-matrix, R_{ij} , was regressed against the mean per locus heterozygosity (H) for the subdivisions. This method, developed by Harpending and Ward (1982), provided some indication of the relative roles of systematic (persistent evolutionary force such as migration or natural selection) vs. nonsystematic forces (the action of stochastic processes) on the genetic microdifferentiation of subdivided populations.

Predicted kinship matrix. The predicted kinship matrix estimated genetic similarity among Newfoundland populations and theoretically denoted the probability of genetic identity by descent (Imaizumi et al., 1970). The diagonal elements, ϕ_{ii} , of the matrix provided the probability that two random genes in a population were identical by descent and denoted local kinship (Morton, 1973). The off-diagonal elements, ϕ_{ij} , were measures of the genetic relationship between any two populations, i and j . High values denoted population affinity, while low values suggested the existence of little genetic resemblance.

Matrix comparisons. Matrices (e.g., genetic distances vs. geographic distances) were compared using two techniques: MATFIT and Mantel correlation of matrix elements. The MATFIT method rotated one matrix to maximum congruence and provided a correlation between the elements (Schonemann and Carroll, 1970; Lalouel, 1973). However, this method failed to test the significance of the correlations. Matrices were compared by the Mantel method, which performed product-moment correlations and assessed their significance based on Mantel's permutations (Relethford, 1990; Smouse and Long, 1992).

Mean first passage time. This method depicted the asymmetric movement of migrants among the various subdivisions of human populations. An assumption was made that migration between the communities was approximated by a first-order discrete Markov process. Because there was interest in indirect as well as direct flow between the subdivisions, this measure of orientation was used. Mean first passage time was initially utilized with migration data (Brown and Horton, 1970; Lalouel and Langaney, 1976; Mielke, 1982; Pitkanen et al., 1988). Mean first passage time, f_{ij} , can be interpreted as the mean time in generations necessary for a gene from node i to reach j for the first time. The computational methods were initially described in Kemney and Snell (1960) and Isoifescu (1980).

RESULTS AND DISCUSSION

Table 1 contains the matrimonial migration matrix for nine villages of Fogo Island. In addition, the computed effective breeding sizes (N_e) are provided for the various subdivisions. The N_e was computed on the basis of the number of males and females of reproductive age taken from the current census of Fogo Island. However, several villages were not included in this census, and the effective sizes were estimated by taking the average percentage of males and females 14–44 years of age for the known populations and multiplying it with the total population size of the groups not included in the census. Thus, the average ratio of N_e/N was used to estimate N_e in those populations in which age/sex structure was unknown.

The frequency of village endogamy and the systematic pressure (migration) from outside Fogo are summarized in Table 2. Tilting (an Irish Catholic village) is reproductively

TABLE 4. Mean first passage time between five villages of Fogo Island (in generations)

| | Population subdivisions | | | | |
|---------------|-------------------------|--------|---------|----------|--------------|
| | Fogo | Seldom | Tilting | Isl. Hrb | J. Batts Arm |
| Fogo | 2 | 26 | 63 | 34 | 13 |
| Seldom | 6 | 9 | 65 | 34 | 12 |
| Tilting | 13 | 34 | 8 | 30 | 17 |
| Island Harbor | 7 | 27 | 61 | 13 | 12 |
| J. Batts Arm | 3 | 28 | 59 | 33 | 4 |
| Ne | 245 | 115 | 75 | 56 | 180 |

TABLE 5. Allelic frequencies used in the creation of the R-matrix for Ramea, Burgeo and five settlements of Fogo Island

| System/ Allele | Populations | | | | | | |
|-------------------|-------------|-------|-------|--------|---------|----------|--------|
| | Burgeo | Ramea | Fogo | Seldom | Tilting | Isl. Hrb | J.B.A. |
| ABO*A | 0.331 | 0.340 | 0.189 | 0.217 | 0.070 | 0.238 | 0.266 |
| ABO*O | 0.605 | 0.630 | 0.772 | 0.697 | 0.884 | 0.738 | 0.681 |
| RH*R2 | 0.157 | 0.271 | 0.147 | 0.117 | 0.149 | 0.044 | 0.077 |
| RH*R1 | 0.412 | 0.427 | 0.407 | 0.357 | 0.440 | 0.302 | 0.410 |
| RH*R | 0.359 | 0.274 | 0.383 | 0.408 | 0.315 | 0.488 | 0.513 |
| MNS | | | | | | | |
| M | 0.662 | 0.633 | 0.642 | 0.555 | 0.664 | 0.616 | 0.513 |
| S | 0.322 | 0.260 | 0.324 | 0.391 | 0.336 | 0.267 | 0.232 |
| LU*B | 0.975 | 0.989 | 0.945 | 0.944 | 0.977 | 0.924 | 0.906 |
| P*1 | 0.579 | 0.575 | 0.476 | 0.643 | 0.633 | 0.285 | 0.608 |
| JK*A | 0.426 | 0.508 | 0.521 | 0.515 | 0.571 | 0.469 | 0.541 |
| LE*A | 0.165 | 0.217 | 0.166 | 0.092 | 0.167 | 0.063 | 0.375 |
| LE*B | 0.419 | 0.332 | 0.419 | 0.595 | 0.450 | 0.567 | 0.525 |
| KELL | | | | | | | |
| k | 0.925 | 0.946 | 0.946 | 0.945 | 0.925 | 0.884 | 0.936 |
| FY*A | 0.419 | 0.387 | 0.394 | 0.421 | 0.438 | 0.352 | 0.359 |

within the nine populations of 0.00537 is comparable to the values observed in the Aland Islands (Mielke, 1982). As expected, Tilting, which is reproductively the most isolated community, also displays the highest predicted kinship, three times higher than in the next highest community. Tilting also exhibits high values with Joe Batts Arm and Island Harbor, its geographic neighbors that are connected by road. Tilting residents have the lowest probability of genetic relatedness to Stag Harbor, located diagonally at the other end of the Island.

Mean first passage time

The mean first passage time (functional association) between the various villages of Fogo Island, Newfoundland are summarized in Table 4. Lower values of f_{ij} , with respect to the other values in the matrix, indicate that the flow from i to j is more significant and the association is greater. On the other hand, values of large magnitude indicate that the flow is weaker and that there is less functional association between communities.

The f_{ij} values for Fogo Island indicate that the village of Fogo is acting as a "sink"; that is, there is more movement into Fogo village than out. This suggests that Fogo is a "central place" on Fogo Island. The attraction to the town of Fogo is primarily economic, because it contains a fish-processing plant and some tourism-related industry. The relatively low f_{ij} values for Joe Batts Arm suggest that it is acting as a secondary sink and attracts workers to the fish-processing plant. The extremely high values for Tilting indicate that it is functionally the most isolated village of Fogo Island. This finding is confirmed demographically by the high endogamy rates and the low outside migration level for Tilting. Its geographic and religious isolation (being the sole Catholic village on this island) have contributed to its reproductive isolation. The lower f_{ij} values also reflect population structure. Those communities with the lowest f_{ij} values exhibit the largest effective sizes, whereas those villages with the highest f_{ij} values have smaller effective population sizes.

Table 5 summarizes the allelic frequencies

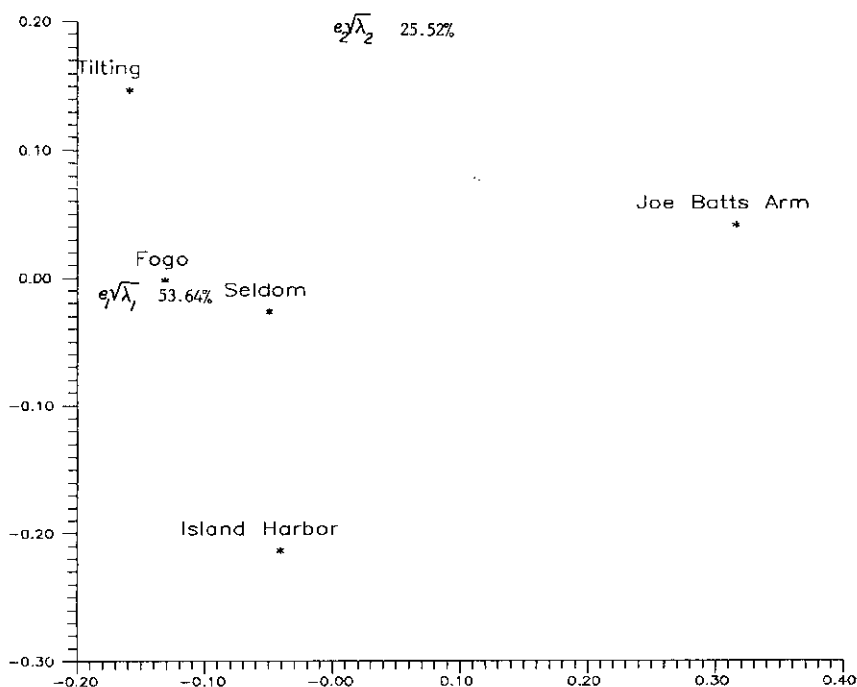


Fig. 2. Least squares reduction "genetic map" of five subdivisions of the population of Fogo Island based upon 10 polymorphic loci and 14 alleles.

used in the creation of the R-matrix for the five settlements of Fogo Island plus Burgeo and Ramea, coastal villages from southern Newfoundland. The methodology, connected with data collection, sampling, and the laboratory techniques used for blood grouping, are described in another paper (Martin et al., 1995). Gene frequencies were computed for only five of the nine Fogo communities. The sample sizes of four of the settlements in this study were too small to warrant such computations. The allelic frequency distributions exhibited by the subdivisions of Fogo Island are similar to those expected for hybrid British/Irish groups.

R-matrix analysis

Figure 2 compares (through a least squares reduction of the R-matrix and a total of 14 allelic frequencies) the five villages from Fogo Island. The first two scaled eigen-vectors plotted in this figure account for 79.16% of the total variance. The first axis separates the Catholic village of Tilting from the other communities, with Joe Batts Arm, Seldom, and Fogo being most proximal and

Island Harbor the most distant. The second axis separates Joe Batts Arm from the other populations. The separation of Joe Batts Arm and Tilting is most likely a function of religious isolation, because geographically they are adjacent. The two largest towns (Fogo and Seldom) in which both Catholics and Anglicans reside are closest to the centroid of distribution.

The distribution of alleles that separate the five populations of Fogo Island is shown in Figure 3. Joe Batts Arm is distinguished from the other populations on the basis of the high frequency of its LE*A allele. Island Harbor has a high frequency of RH*R and relatively high ABO*A. Tilting has a high frequency of P*1, low ABO*A, and exceptionally high ABO*O.

Figure 4 compares the five populations of Fogo Island with two outlier communities from the southern coast of Newfoundland, Ramea, and Burgeo. With the addition of these two populations to the R-matrix analysis, there is a slight reduction in the amount of variation explained by the first two eigen-vectors, from 76% to 64%. The first eigenvec-

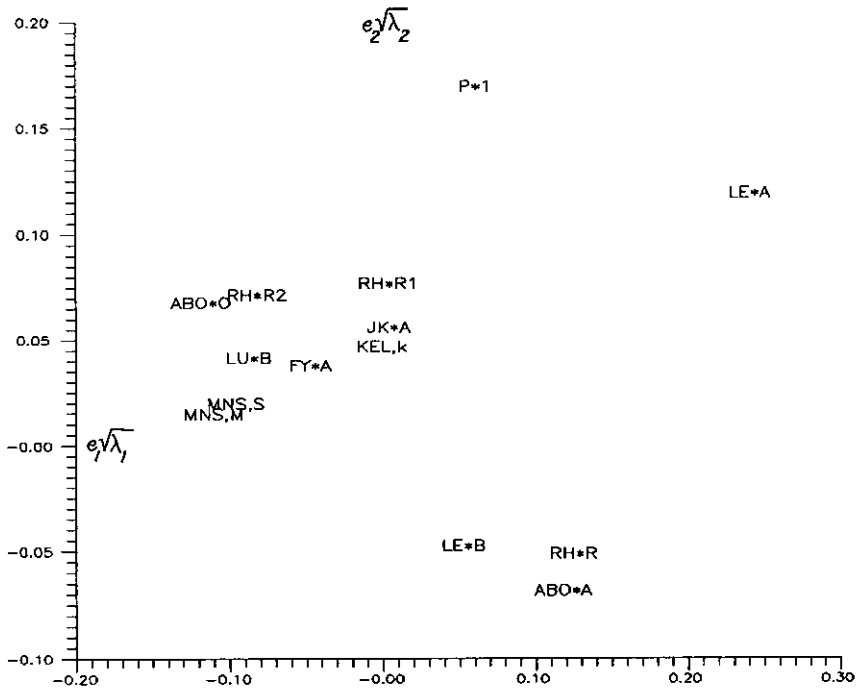


Fig. 3. Least squares reduction "genetic map" of the 14 alleles, corresponding to the "map" in Figure 2.

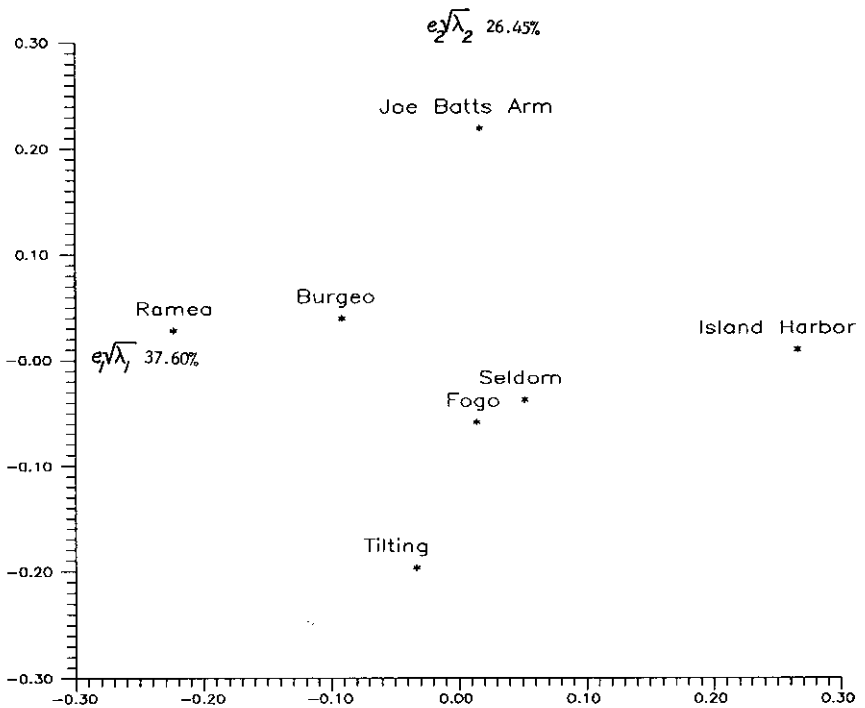


Fig. 4. "Genetic map" based upon 14 alleles comparing the five subdivisions of Fogo Island with two outports of southern Newfoundland.

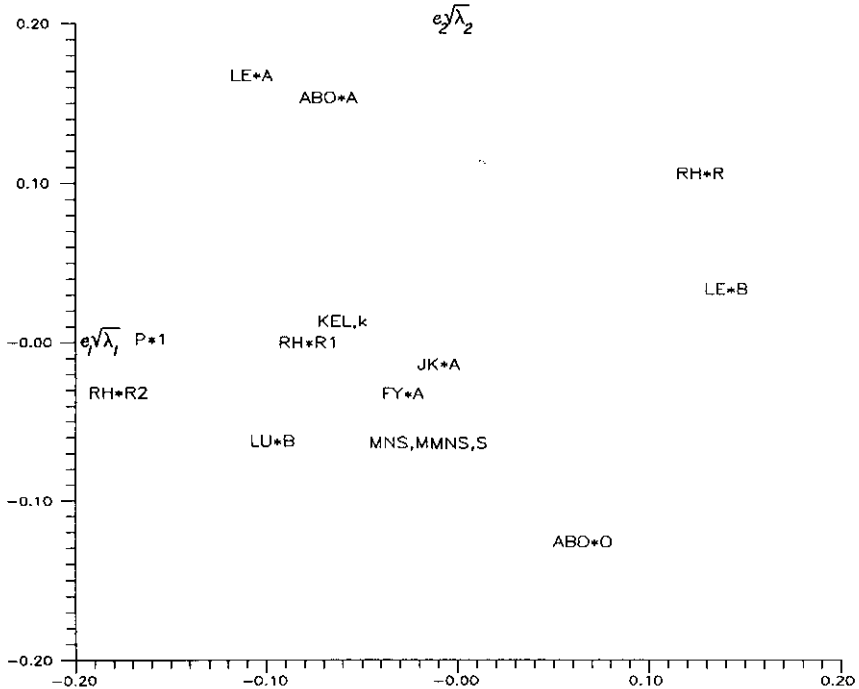


Fig. 5. Plot of the alleles contributing to genetic relationship among the seven population subdivisions shown in Figure 4.

tor explains 37.6% of the variation and separates two villages from Fogo (Joe Batts Arm and Tilting). The two outports of southern Newfoundland are separated from Fogo Island groups along the second axis. Along this axis, Ramea (a small isolated island of approximately 1,000 residents) and the village of Island Harbor on Fogo Island (281 residents) appear to be the most genetically divergent populations. As in Figure 2, Seldom and the town of Fogo appear to be closest to the centroid of distribution.

Figure 5 provides a plot of the distribution of alleles that are responsible for the dispersion of populations shown in Figure 4. In addition to the high incidence of ABO*O, Tilting has a high frequency of MN*M that separate it from the other populations. Island Harbor is distinguished from the other subdivisions by a unique combination of LE*B and RH*R alleles. Joe Batts Arm is separated from the other groups by high frequencies of ABO*A and LE*A alleles.

The weighted mean of diagonal elements r_{ii} of an R-matrix provides an estimate of F_{st} . The F_{st} values obtained for the five Fogo

communities is 0.0195, a value of moderate magnitude indicating relative heterogeneity among the subpopulations of this island. With the addition of two genetically heterogeneous southern coastal populations, Ramea and Burgeo, the F_{st} values (as expected) increased to 0.0253. This latter calculation was made with the assumption that all populations were of equal size. This assumption was necessitated by the unavailability of accurate census figures for the two communities.

Figure 6 contains a plot of the theoretical regression between mean per locus heterozygosity and the distance from the centroid of distribution for five Fogo Island communities. It describes the functional association between heterogeneity and distance r_{ii} of the region from the gene frequency centroid. As expected, Tilting has the lowest heterozygosity and a moderate r_{ii} . These data suggest that Tilting experienced the most reproductive isolation and the action of nonsystematic pressures. These conclusions are supported by the data from the mean first passage time and the mean predicted kin-

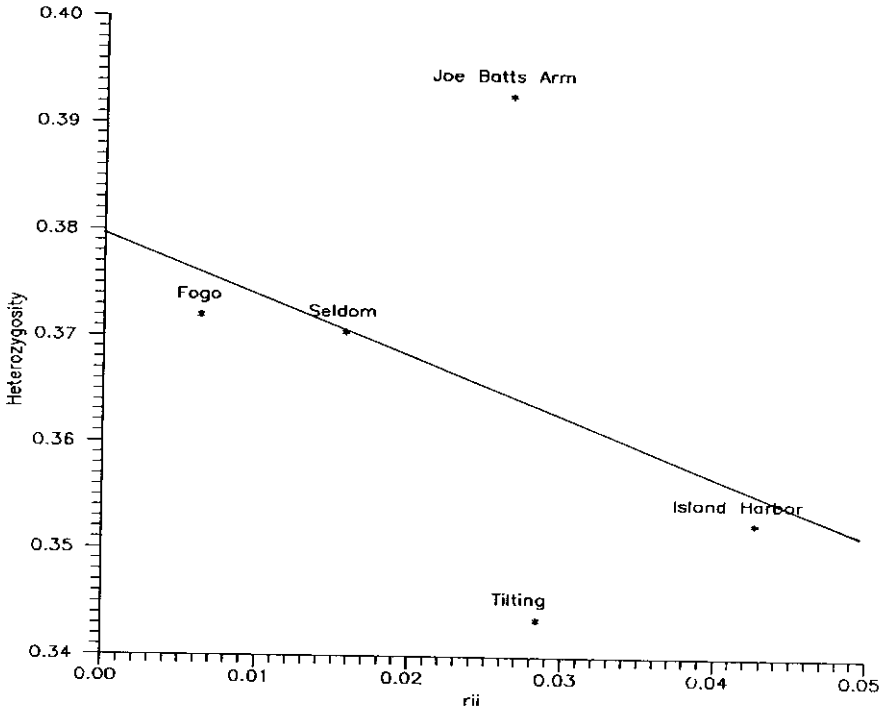


Fig. 6. Plot of mean per-locus heterozygosity (H) against distance from the centroid r_{ii} of the relationship matrix from the five subdivisions of Fogo Island.

ship coefficient. Functionally, Tilting is the most isolated village on Fogo. It also has the highest predicted kinship, which is three times higher than in the next highest community. Island Harbor has the lowest r_{ii} and a relatively low level of heterozygosity, slightly higher than Tilting. This is suggestive of the action of nonsystematic pressures acting on this small village. Joe Batts Arm has the highest level of mean per locus heterozygosity and has a moderate migration rate (8.4%) from the outside (see Table 2). Fogo town and Seldom exhibit the lowest levels of r_{ii} and an intermediate level of heterozygosity. Seldom has a migration rate from outside of 13%.

Figure 7 provides a genetic map of four Fogo Island religious subdivisions. The total sample from Fogo was grouped on the basis of religion, that is, each individual was coded for religious preference. Gene frequencies were calculated for each of the four religious groups, namely, Catholics, Anglicans, Evangelical, and United Methodists (see Table 6). All four groups were given equal weights

in the R-matrix analysis because a census based upon religious preference was unavailable. In comparison to the plot based upon geography (Fig. 2), in which 79% of the variation was explained, a subdivision of Fogo population by religion accounts for almost 73% of the total variation. The first eigenvector separates the Catholics and Evangelicals from the Anglicans and the United Churches, while accounting for 50.36% of the variation. The second eigenvector (22.44% of the variation) separates the Catholics and United Methodists from the Anglicans and Evangelicals.

Figure 8 provides a plot of the distribution of alleles that contribute to the population dispersion of Fogo population, subdivided by religion. The Catholics of Fogo have high frequencies of the ABO*O, LU*B, RH*R1, and RH*R2 genetic markers. The Evangelicals can be distinguished by high frequencies of K*k, Ss*S, and P*P1. The Anglicans are separated from the other denominations by high frequencies of RH*R, ABO*A, JK*A, and LE*A. The

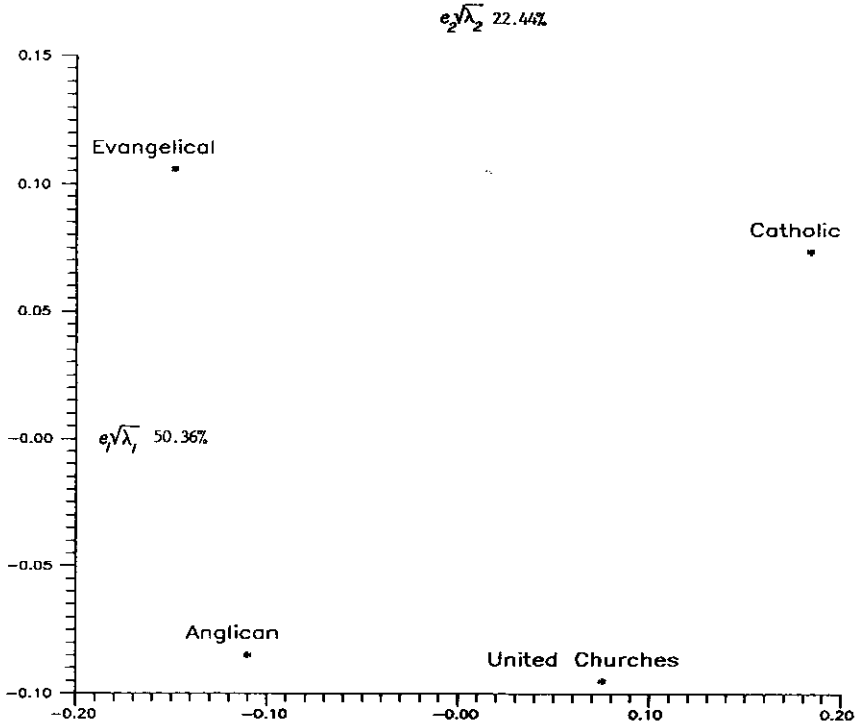


Fig. 7. "Genetic map" of Fogo Island population subdivided by four religious preferences.

TABLE 6. Allelic frequencies used in the creation of the R-matrix for Fogo Island religious subdivisions

| System/Allele | Religious subdivisions | | | |
|---------------|------------------------|----------|-------------|-----------------|
| | Anglican | Catholic | Evangelical | United Churches |
| ABO*A | 0.276 | 0.148 | 0.246 | 0.208 |
| ABO*O | 0.672 | 0.809 | 0.710 | 0.732 |
| RH*R2 | 0.121 | 0.160 | 0.130 | 0.114 |
| RH*R1 | 0.354 | 0.456 | 0.348 | 0.374 |
| RH*R | 0.454 | 0.316 | 0.441 | 0.392 |
| MNS | | | | |
| M | 0.583 | 0.670 | 0.522 | 0.674 |
| S | 0.337 | 0.311 | 0.435 | 0.384 |
| LU*B | 0.945 | 0.972 | 0.953 | 0.915 |
| P*1 | 0.483 | 0.539 | 0.639 | 0.597 |
| JK*A | 0.541 | 0.472 | 0.500 | 0.512 |
| LE*A | 0.147 | 0.128 | 0.106 | 0.109 |
| LE*B | 0.420 | 0.499 | 0.493 | 0.629 |
| KELL | | | | |
| k | 0.944 | 0.920 | 0.978 | 0.919 |
| FY*A | 0.441 | 0.394 | 0.326 | 0.456 |

United Methodists exhibit high frequencies of FY*A, LE*B, and MN*M.

Figure 9 shows how the religious subdivisions of Fogo Island relate to two south coast populations, Ramea and Burgeo. The addi-

tion of these two distant outliers adds a geographic component to the comparison and slightly raises the total variation explained by the first two axis from 73% (dispersion based entirely on religion) to 76.12%. The

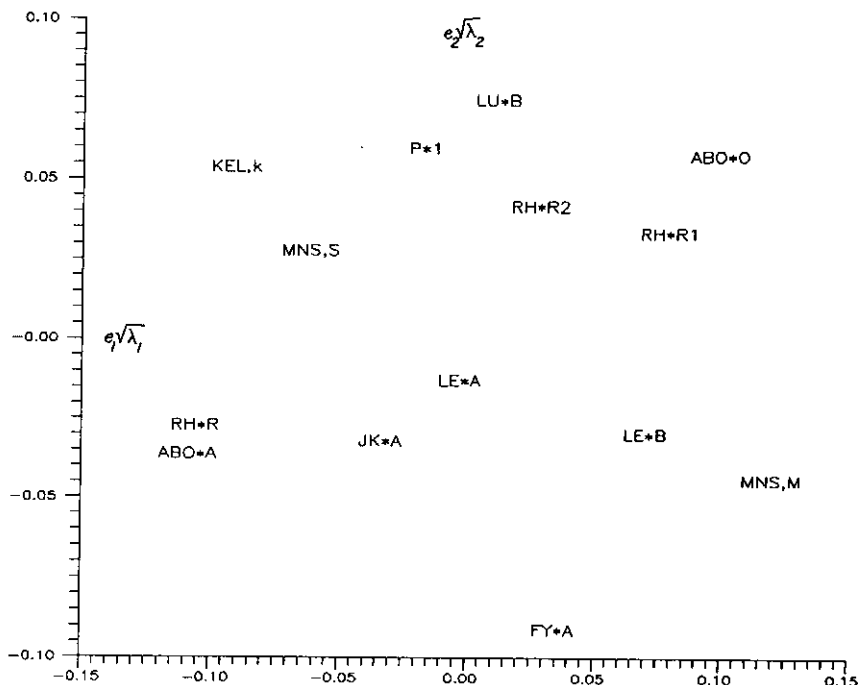


Fig. 8. Distribution of the alleles contributing to the dispersion of the four religious subdivisions of Fogo Island.

first axis (52.83% variation) separates the Catholics from the Protestants and the two southern outports (with a majority of Protestants residents). The second axis represents geography and separates Ramea and Burgeo from the religious denominations of Fogo. Religious subdivisions of Fogo Island are critical in understanding the population structure of Newfoundland communities. The relatively high frequencies of ABO*A, LE*A, LU*B, and RH*R2 in Ramea and Burgeo are associated with their separation from the religious subdivisions of Fogo Island (Fig. 10).

Genetic and geographic distances were compared in order to assess the influence of geography on the distribution of genetic variation in Newfoundland (Table 7). The MATFIT rotation of a genetic distance matrix around a geographic distance matrix for maximum congruence yields a correlation between the matrices of $r_c = 0.676$. This high correlation is suggestive that geography plays a major role in the population affinities between Fogo aggregates. However, Mantel correlations between genetics and geography reveal that these correlations are not

significant ($r = -0.249$; $P = 0.798$). Even with the addition to our analysis of Ramea and Burgeo (both populations of considerable geographic distance from Fogo, approximately 400 Km), no significant fit was observed between geography and genetics ($r = 0.163$; $P = 0.226$).

The relationship between religious and genetic distances was measured using the Mantel permutation test for Fogo Island villages. A subdivision of Fogo into nine villages and the three most common religions (Catholic, Anglican, and Salvation Army) yielded a correlation between religious and genetic distances of $r = -0.0876$; $P = 0.66870$, that is, not significant. Similarly, when the villages were subdivided by five religions (i.e., United Churches and Evangelical were added to the analysis), $r = -0.1948$ and $P = 0.8630$, that is, not significant.

CONCLUSIONS

No simple population structure model can explain the gene frequency distributions observed in the subdivided human aggregates of Newfoundland. For example, while geo-

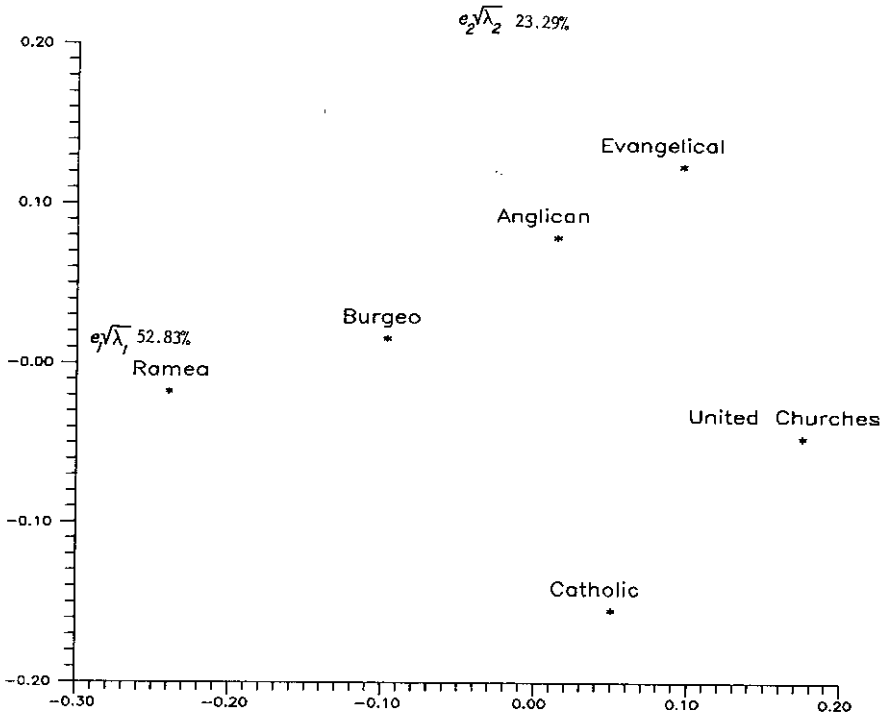


Fig. 9. Least squares reduction of an R-matrix that compares the population subdivisions of Fogo Island with two outports from the southern coast of Newfoundland.

graphic distances do contribute to the systematic pressures acting on Fogo Island and the South coast of Newfoundland, economic factors and religion also play roles in the settlement and movement of people. The presence of employment opportunities in towns with fish-processing plants or tourist industries create "sinks," into which migrants "flow" disproportionately. Similarly, village endogamy is fairly low in some small villages, yet high in others, such as the Catholic community of Tilting.

This reproductive isolation is documented by the predicted kinship, ϕ_{ij} , mean first passage time, r_{ij} vs. mean per locus heterozygosity, and R-matrix plots. Tilting is the only all Irish Catholic community and is the most endogamous (Koertvelyessy et al., 1988). Although reproductive isolation due to religious affiliation is diminishing, the decline in endogamy rates among the Catholics of Fogo is significantly less than among the Protestant groups. At the turn of the century, the endogamy rates in all three denominations approached 100% but diminished rapidly from the 1940s onward (Koertvelyessy

et al., 1988). The larger communities of Fogo Island, such as the town of Fogo, are subdivided by religion and have Catholic, Anglican, and Methodist parishes.

The relationship between religion and genetics proved not to be statistically significant when tested by Mantel tests. Such a relationship was expected because the Catholic/Anglican dichotomy should reflect genetic differences between the Irish and English ethnicities. However, there may be sufficient "noise" resulting from the recent conversions of individuals from either Catholicism or Anglicanism to the Evangelical religions, such as the Salvation Army or United Churches. The presence of converts obscures the genetic differences between the Irish and the English ethnicities of Newfoundland.

The settlement of Newfoundland was stimulated primarily by economic factors, the availability of cod for the earliest English fishermen and fish-packing opportunities for the later Irish immigrants. In this study, the genetics, demography, economics, and history all form a complicated "mosaic" of

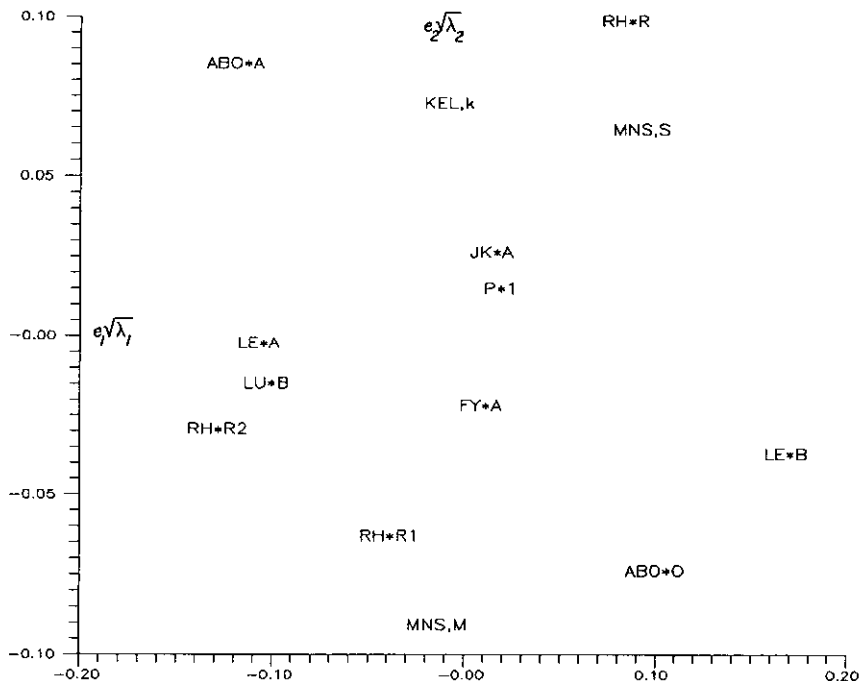


Fig. 10. Plot of the alleles that contribute to the dispersion of the seven population subdivisions displayed in Figure 9.

TABLE 7. A comparison of geographic distances (km) with genetic distances (d_{ij}) of Fogo population subdivisions

| | Geographic distances (KM) | | | | | | |
|-----------------------------|---------------------------|-----------|----------|------------|-------------|---------------|---------------|
| | Burgeo (B) | Ramea (R) | Fogo (F) | Seldom (S) | Tilting (T) | Isl. Hrb (IH) | J. Batts (JB) |
| B | 0 | 24 | 419 | 413 | 429 | 406 | 424 |
| R | 37 | 0 | 423 | 417 | 432 | 410 | 428 |
| d_{ij} $\times 10^2$ F | 52 | 80 | 0 | 16 | 20 | 14 | 10 |
| S | 65 | 137 | 55 | 0 | 16 | 12 | 15 |
| T | 125 | 144 | 45 | 85 | 0 | 26 | 11 |
| IH | 143 | 242 | 88 | 115 | 74 | 0 | 20 |
| JB | 123 | 164 | 107 | 120 | 177 | 185 | 0 |

Upper triangle consists of geographic distances in kilometers. Lower triangle consists of genetic distances ($d_{ij} \times 10^2$).

the interactions of biology and culture in the evolution and microdifferentiation of subdivided populations.

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