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Integration involves a trade-off between fertility and status for World War II evacuees

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Understanding how refugees integrate into host societies has broad implications for researchers interested in intergroup conflict and for governments concerned with promoting social cohesion. Using detailed records tracking the movements and life histories of Finnish evacuees during World War II, we find that evacuees who intermarry are more likely to be educated, work in professional occupations, marry someone higher in social status and remain in the host community. Evacuees who intermarry before the war have fewer children, whereas those who marry into their host community after the war have more children. These results indicate that life-history and assimilation outcomes depend on key differences between pre-war environments—when migrants are living in their own communities—and post-war environments—when migrants are living in the host community. Overall, this suggests that integration involves a trade-off between reproduction and status such that evacuees who integrate gain social status, whereas those who maintain stronger bonds with their natal communities have higher fertility. We discuss these results within the framework of social capital, intergroup conflict and life-history theory and suggest how they can inform our understanding of evolutionary adaptations that affect tribalism.

Examining how migration affects the relationship between natal groups and dispersers is crucial for gaining insight into how intraspecies competition and cooperation affect evolution[1]. In mammals, dispersal is seen to provide benefits by both reducing inbreeding and offering advantages in mate competition[2], and overall dispersal is favoured whenever the fitness costs of remaining in one's birth area outweigh the costs of migrating[3]. In humans, competition and cooperation between groups has been shown to drive dispersal patterns[4], which, in contemporary societies, are frequently characterized by mass exoduses resulting from war, natural disasters or disparate economic opportunities between host and emigrant countries[5]. Although these migrations have enormous effects on both host and immigrant populations, there is considerable disagreement across disciplines about how these events affect life-history outcomes and overall social cohesion[6]. Various theoretical frameworks have been proposed to understand the underlying causes of cooperation and conflict between individuals and groups. Evolutionary biologists, for example, focus on kinship[7] and reciprocity[8], whereas economists examine markets and externalities[9] and sociologists and social psychologists tend to be concerned with factors influencing intergroup tolerance and integration[10]. However, researchers across disciplines often reference 'social capital'—the norms, networks and transactions marked by reciprocity and trust that enable people to act collectively and are beneficial to the common good[11]—when seeking to understand the effects of immigration on society (see Supplementary Information: Social Capital) and there is widespread agreement that social capital has important effects on integration and social cohesion[12].

Although there is a broad consensus that social capital affects relationships within and between groups, there is considerable disagreement about how immigration affects social capital. For instance, the 'contact hypothesis', first proposed by G.W. Allport, posits that higher rates of contact with people from different backgrounds will tend to increase tolerance of other groups under specific conditions, such as equal status between the immigrant and host populations[13] (see Supplementary Information: The Contact Hypothesis). In this view, immigration will promote social solidarity and build trust as contact with different types of people with diverse backgrounds increases. Although there is some evidence that increasing the number of positive contacts between host and immigrant populations reduces anti-immigrant attitudes in Europe, these attitudes were found to be largely dependent on conditions and context[14]. Alternatively, the 'conflict hypothesis' makes the distinction between bonding social capital—the relationships, ties and networks among people who share a culture and similar background—and bridging social capital—the connections between groups that transcend cultural differences[15] (see Supplementary Information: Social Capital). Examples of bonding social capital include the language, dialects, rituals and traditions specific to a certain community, whereas bridging capital is often characterized by social networks that transcend these differences, such as membership in organizations that have people from diverse backgrounds. This viewpoint purports that the increased diversity resulting from immigration exacerbates conflict between immigrants and hosts by reducing bridging social capital and increasing bonding social capital (that is, in-group solidarity)[12,16]. It predicts that the more we are brought into physical proximity with people from another culture or ethnic background, the more we stick to our own groups and the less we trust people who are different from us. In short, competition between the immigrant and the host populations is thought to reduce tolerance and impede integration.

However, the contact and conflict hypotheses are not mutually exclusive and there is considerable evidence that individual characteristics can affect rates of integration. For example, whereas younger immigrants[17] and immigrants from higher social classes[18] are expected to integrate more quickly, lower social classes are expected to: (1) compete more with the host population over resources; (2) form tighter within-group social networks and (3) be less likely to integrate[19]. Attitudes of the host population may also affect integration. For example, lower education[20], rural residence[21] and the perceived threat and size of the immigrant population[20] are known to be some of the best predictors of hostile attitudes

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towards immigrants. There is also evidence that the social networks of younger, urban and more-educated individuals are more likely to bridge group boundaries, whereas the networks of older, rural and less-educated individuals are more restricted to their own in-group[22]. Families with more education in Britain are seen to be more upwardly mobile because of their ability to form connections with a more diverse group of people[23]. An important type of bridging social capital is intermarriage, which has been shown to increase employment opportunities, raise income and result in the greater social integration of immigrants. This is often due to both selection effects (that is, immigrants who are more integrated are also more likely to intermarry) and positive effects of the marriage on further integration and the generation of additional bridging social capital[24]. Internal migration within a country can also have effects on both migrants and hosts. Boustan et al.[25] found that, although internally displaced migrants in the United States during the Great Depression had no effect on overall wages, these migrants did cause many longer-term residents to leave and substantially reduced the work hours of those who remained. This research suggests that internal migrants can have just as disruptive of an effect on labour markets as immigrants from other countries. Overall, the demographic characteristics of the migrants, competition over resources and the social networks that connect hosts with migrants are all expected to affect economic outcomes and the rate of integration.

However, the benefits accrued by one group may come at a cost to another, and although increased bonding within immigrant groups can reduce overall social cohesion and inhibit integration, it may still provide direct benefits to the immigrant population. In particular, the mere act of moving through space together has been experimentally shown to increase group solidarity[26], and stronger within-group social bonds have been shown to increase reproductive outcomes in many species[27]. In addition, evolutionary simulations have demonstrated that enhanced bonding with in-group members can be adaptive[28]. Kulu et al.[29], for example, have shown that, although the descendants of immigrants to European countries often have fertility rates that are similar to those of the native population in their respective countries, the host society and the minority subculture both exert strong influences on these birth rates. Sweden, for example, had the lowest fertility variation across ethnic groups and the authors of the paper attributed this to low levels of residential segregation and high labour market integration in Nordic countries[24]. Other researchers have argued that the strength of social networks within immigrant and minority populations can affect fertility outcomes[30]. Higher educational achievement—especially among females[31]—intergroup marriages[29], further cultural distance from the host population[30,32], increased opportunities for social and economic mobility and a desire for acculturation have all been shown to reduce fertility[33]. At the same time, greater access to close kin[34], resistance to assimilation and concern with group preservation have been shown to increase reproductive output[35]. Integration can also entail risks of ostracism from one's in-group and there is good evidence for both parochialism[28] and mobility traps—the opportunities gained by joining a new group conflict with opportunities for upward mobility within one's former group[36]—in humans. In this way, developing bridging connections can weaken key social connections and create stress by forcing individuals to deepen their commitment to their new group while cutting off connections with their old communities[37]. Because many anthropologists contend that support from non-parents is critical to offspring survival[38] and decisions to reproduce[39], increasing these bridging social connections may adversely affect reproductive outcomes if they interfere with or replace weaker bridging ties.

Despite evidence showing that the demographic characteristics of individuals and populations have important effects on the relationship between immigrants and host populations, it remains unknown how these factors interact to affect both integration and life-history outcomes. Exploring these interactions has been challenging for several reasons. First, accessing longitudinal data sets that contain the marriage records, reproductive histories, birthplaces, occupations and movements of an entire population across decades is exceptionally rare. Second, it is difficult to analyse how bonding and bridging social capital affect integration and reproduction when we do not know who would return to their natal community if given the opportunity. This is important because there is evidence showing that groups that are more easily able to return home are less likely to build strong bonding social networks within their host communities than those whose exit is blocked[40]. Last, we are rarely able to directly compare the integration and life-history outcomes of those who chose to return to their natal communities from those who remained because they are effectively different populations existing in separate locations.

Here, we use an unusually well-documented data set of the marriages, reproductive histories, movements and occupations of a population of evacuees from Karelia, Finland, during World War II, to test whether integration involves a trade-off between status and reproduction by examining the effects that age at migration, population size, education, social class and in-group bonding have on marriage, migration patterns and reproductive outcomes. On 30 November 1939, the Soviet Union invaded Finland, which started the Winter War. Four months later, in March 1940, the southern portion of Finnish Karelia—approximately 10% of Finnish territory—was ceded to the Soviet Union and approximately 410,000 individuals (12% of the population of Finland) had to flee west[41] (see Fig. 1a–c). Although the Finnish government played an important role in organizing the exodus and attempted to keep evacuees from the same towns together (see Supplementary Information: The Influence of the Finnish Government on the Evacuations) and to distribute them widely and evenly among the resident population (see Supplementary Information: Evacuations and the Proportion of Migrants to Hosts), the evacuations were frequently chaotic. The evacuees spoke a Karelian dialect of Finnish. Before urbanization took place in Finland in the 1950s and 1960s[42], this difference was especially notable (for relative differences between dialects of Finnish about 100 years ago, see ref. [43]; figures 12 and 13) and the Karelian dialect was easily distinguished. In addition to cultural differences, these linguistic differences contributed to Karelians facing discrimination owing to their ethnic background (see Supplementary Information: Prejudices Against Evacuees). Government-enforced land sales to accommodate the evacuees also fuelled resentment against Karelians. A short peace followed until June 1941 when Finland joined Germany's attack on the Soviet Union. This resulted in the Continuation War, and 3 months after it began, Finland had recaptured all of the lost territories. For the next 3 years, from August 1941 until the spring of 1944, Finland once again controlled the Karelian territories and more than half of the evacuees returned home. However, by August 1944, the Soviet Union had recaptured Karelia and those who had returned were once again evacuated; this time, their ability to return was permanently blocked. This unique historical situation provides a quasi-natural experiment that allows us to analyse some of the factors that distinguished the people who remained in western Finland from those who returned home, and presents an extraordinary opportunity to investigate differences in social integration and life-history outcomes between these two groups. By comparing the marriages and reproductive histories of the evacuees who returned to Karelia with those who did not, we are able to assess how natal philopatry—preferences for returning to one's birthplace—affects later integration and reproduction.

Intermarriage is used to assess social integration (for example, individuals who marry non-Karelian Finns are seen as more socially integrated), whereas the number of offspring is used to assess reproductive outcomes. In this study, we aim to analyse the

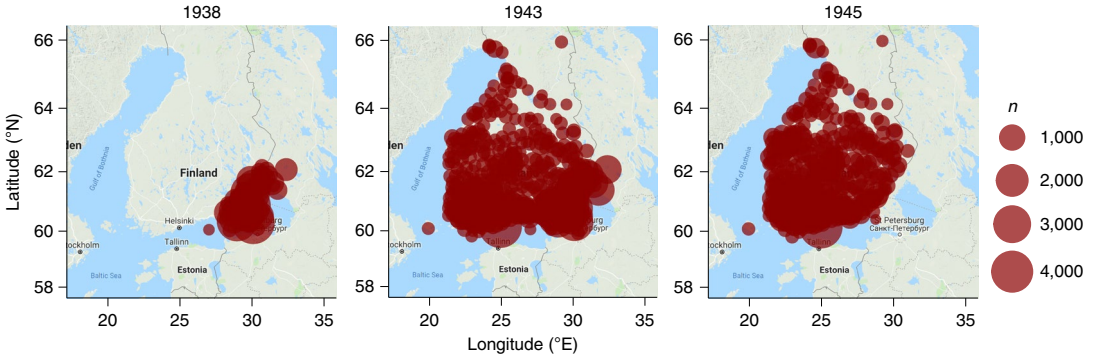

Fig. 1 | Evacuee locations before (1938), during (1943) and after (1945) the war. The Karelian region, located in southeastern Finland, was ceded to the Soviet Union twice during the war. The first evacuation took place in 1939–1940, followed by a resettling in Karelia starting in 1941 and a second evacuation occurring in 1944. For an animation of Karelian moves over time, please see: https://www.helsinki.fi/en/projects/learning-from-our-past/data#section-60700.

effect of bonding and bridging social capital on integration and life-history outcomes. We model how decisions to return to Karelia or remain in western Finland have an effect on how likely evacuees are to intermarry and how many children they have in the pre-war and post-war environment. First, we hypothesize that younger immigrants will assimilate more quickly with a host population than older migrants and predict: (P1a) younger people will be more likely to marry into the host population after the war. Second, we hypothesize that evacuees who prefer to return to their place of birth will be less likely to integrate and predict: (P1b) those who return to Karelia during the war will be less likely to marry into the host population both before and after the war. Third, we hypothesize that the risks of integration will be partly offset by increased economic opportunities and predict: (P1c) evacuees who intermarry will gain social or economic benefits of integration by being more likely to marry someone from a higher social class both before and after the war. Fourth, in a test of the 'contact hypothesis', we hypothesize that individuals living in areas with a higher population density will have had more interactions with people from different backgrounds, will be better able to transcend regional and cultural differences between groups and will therefore be more likely to integrate. Specifically, we predict: (P1d) evacuees who are from areas of high population density in Karelia will be used to interacting with people who are different from them and will be more likely to intermarry both before and after the war. Fifth, in a test of the 'conflict hypothesis', we predict that more-educated Karelians will be more capable of transcending group boundaries and will be more welcomed by the host community. Specifically, we predict: (P1e) more-educated evacuees will be more likely to intermarry both before and after the war. Last, to test the effect of bonding social capital on integration and life-history outcomes, we hypothesize that individuals who return to Karelia and those who marry other Karelians will both reap reproductive benefits by maintaining stronger cultural bonds with their natal community. Specifically, we predict: (P2a) Karelians across all social classes, birth cohorts and occupations who marry other Karelians will have more children than those who marry resident Finns, and (P2b) Karelians across all social classes, birth cohorts and occupations who return to Karelia during the war will have more children than those who remain in the rest of Finland.

Overall, many of the same factors that increase the probability of integration have a negative effect on fertility. Error bars and raw data for all variables used in this study can be accessed with this interactive app: https://www.helsinki.fi/en/projects/learning-from-our-past/data#section-60700. We found support for the prediction that younger evacuees (P1a) were more likely to marry into the host population after the war. Evacuees who eventually marry resident Finns after the war are an average of 2.8 years younger at the time of the first evacuation. The mean age of evacuees who intermarry after the war is 21.4 years (±0.09 (s.e.)), but is 24.2 years (±0.20 (s.e.)) for evacuees who marry other Karelians. The model predicts that an average (see Supplementary Information: Model validity, effects and specifications), unmarried evacuee who is 15 years of age in 1939 (at the time of the first evacuation) is predicted to have an 89% (95% highest density interval (HDI): 87–91%) probability of eventually marrying a resident Finn, which decreases to 48% (95% HDI: 43–52%) for an unmarried evacuee who is 30 years of age in 1939. Evacuees who marry another Karelian before the war are also, perhaps unsurprisingly, more likely to return to Karelia. The model predicts that Karelians who return have an 18% (95% HDI: 16–20%) chance of being married to someone from western Finland, whereas those who do not have a 38% (95% HDI: 34–41%) chance of being married to someone from western Finland (P1b). At the same time, an average evacuee who marries after the war and remains in western Finland (P1b) is also more likely to intermarry (68%; 95% HDI: 65–71%) than someone who returns to Karelia (58%; 95% HDI: 55–62%).

To test the prediction that evacuees receive social or economic benefits through integration (P1c), we tested whether evacuees who intermarry are more likely to marry someone from a higher social class both before and after the war. If a Karelian marries someone from a higher social class (see Methods: Predictor variables) before the Soviet Union invasion, the model predicts that the probability that their spouse is from western Finland is approximately 26% (95% HDI: 24–28%), which falls to 22% (95% HDI: 20–25%) if they marry someone from a lower social class (see Figs. 2a and 3). For these pre-war marriages, the relationship between hypergamy and intermarriage, as well as the overall probability of intermarriage, is nearly identical for men and women. After the war ends, intermarriage is also positively associated with marrying up. Evacuees who marry someone from a higher social class have a 66% (95% HDI: 63–69%) chance of marrying into the host population and this falls to 57% (95% HDI: 53–61%) if they marry someone from a lower social class (see Fig. 3). Although, overall, women are predicted to be more likely to intermarry after the war—74% (95% HDI: 71–77%) for women versus 50% (95% HDI: 46–54%) for men—the relationship between hypergamy and intermarriage after the war is driven more by men (see Fig. 2a and Supplementary Table 1). Men are more likely to have a wife who is from a higher social class if they marry into the host population—55% (95% HDI: 51–58%) chance of intermarriage if their wife is from a higher social class and a 45% chance (95% HDI: 41–49%) if she is from a lower social class versus women who have a 78% (95% HDI: 75–80%) chance of

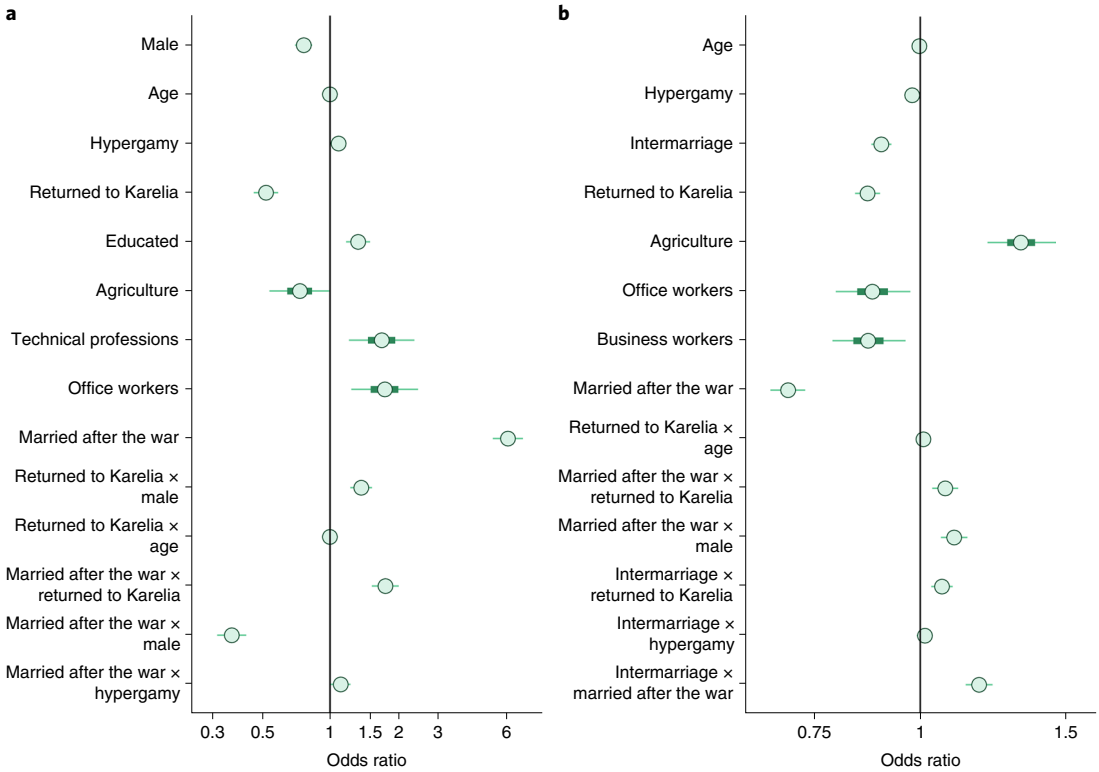

Fig. 2 | Posterior distribution credibility intervals for factors affecting the probability of intermarriage and the number of children for all evacuees. **a**, Factors affecting the probability of intermarriage. **b**, Factors affecting reproductive outcomes. The distributions display the proportional change in the outcome (that is, relative effect) induced by each predictor. Only fixed effects and interactions with 95% HDIs that do not overlap with 0 are shown (see Supplementary Table 1 for mean estimates and 95% HDIs for all parameters entered into the model, Supplementary Table 5 for mean differences in the number of children of evacuees contingent on who they married (that is, resident Finn or Karelian) and Supplementary Table 7 for percentages and sample sizes of social status differences between spouses who married resident Finns and those who married fellow Karelians both before and after the war. The circles indicate the mean values, the thick lines represent the 50% HDI and the thin lines indicate the 95% HDI. The solid vertical line (odds ratio = 1) indicates that the predictor has no effect on the outcome.

intermarrying if their husband is from a higher social class and a 70% (95% HDI: 66–74%) chance if he is from a lower social class (Fig. 2, left panel). Although both before and after the war some degree of hypergamy was achieved by evacuees who intermarried regardless of whether they returned to Karelia, after the war, marrying up strongly predicts intermarriage for evacuees who remain in western Finland (see Supplementary Table 4). For example, a male evacuee who remains in western Finland and marries up after the war has a 63% (95% HDI: 58–67%) chance of marrying into the host population, whereas if this same individual returns to Karelia, their predicted probability of marrying up and into the host population falls to 49% (95% HDI: 45–53%). Thus, evacuees who remain in western Finland are not only more likely to marry into the host population after the war (P1b) but they are also more likely to marry up when they do (P1c). Finally there were some basic sex differences between the probability of males and females intermarrying and returning to Karelia (see Supplementary Table 8).

There was no evidence in any of the models that evacuees born in towns with larger populations will be more likely to intermarry either before or after the war (P1d) (see Supplementary Tables 1–4). Finally, there was some evidence for P1e that more-educated individuals tended to marry resident Finns, although the pattern is slightly weaker for those married after the war. Before the war, an uneducated Karelian has a 24% (95% HDI: 22–25%) predicted probability of intermarriage, which increases to 30% for an educated Karelian (95% HDI: 27–32%). After the war, an uneducated Karelian has a 61% (95% HDI: 58–64%) predicted probability of marrying a resident Finn versus 68% (95% HDI: 64–72%) for an educated evacuee (see Fig. 2a and Supplementary Table 1).

We found mixed support for the prediction (P2a) that evacuees who marry fellow Karelians will have more children. If they were married before the war, they do have more children, but this is not true for those who marry after the war. In particular, our model predicts that, before the war, an 'average' Karelian who marries another Karelian will have 0.23 more children—2.93 (95% HDI: 2.83–3.01) children if they marry a fellow Karelian versus 2.70 (95% HDI: 2.61–2.80) children if they marry someone from western Finland. However, after the war, the model predicts that marrying a fellow evacuee results in 0.15 fewer children on average: 2.27 (95% HDI: 2.14–2.33) children for Karelians who marry other Karelians versus 2.42 (95% HDI: 2.32–2.50) children for Karelians who marry someone from the host population (see Fig. 4 and Supplementary Table 2). There are also differences between the mean age at marriage and age at first birth between evacuees who marry into the host population and those who marry fellow Karelians. Before the war, both male and female evacuees who intermarry marry later, have their first child later than evacuees who marry other Karelians. The opposite pattern is seen for evacuees who marry after the war (see Supplementary Table 8). Finally, cohort fertility estimates for non-Karelian Finns and Karelians born between 1890 and 1940 suggest that non-Karelian Finns have the same or slightly higher fertility rates as Karelians (see Supplementary Table 9).

We also found mixed support for the prediction (P2b) that evacuees who return to Karelia will have more offspring. An 'average'

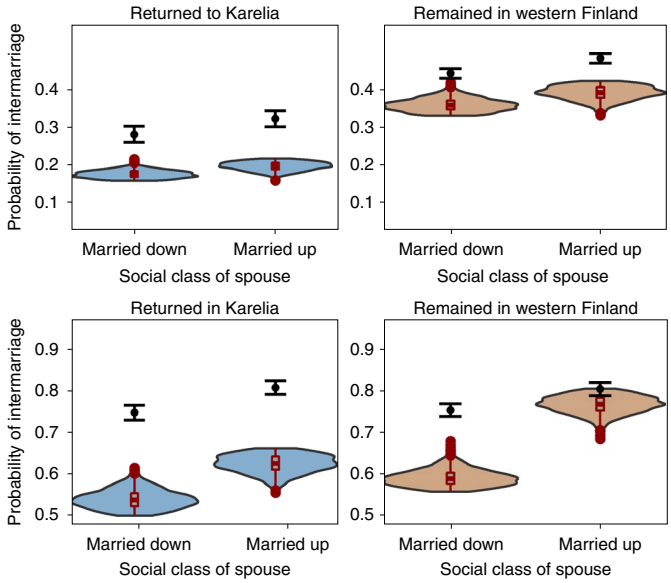

Fig. 3 | Intermarriage is positively associated with marrying up both before and after the war. Posterior distribution predictions are generated from the full model shown in the top panel of Supplementary Table 1 ($n = 26{,}757$). Before the war (top panels), Karelians who intermarry are both more likely to marry up (*x* axis: the right side is higher than the left; see also Supplementary Table 2, top panel: hypergamy, mean: 0.10, 95% CI: 0.06–0.16) and more likely to remain in western Finland during the war (in the right panel, the brown plots are higher than the blue plots in the left panel; see also Supplementary Table 2, top panel: returned to Karelia, mean: 0.57, 95% CI: −0.71 to −0.45). After the war (bottom panels), the same pattern is evident. Evacuees who intermarry are also more likely to marry up (*x* axis: married up is higher than married down; see also Supplementary Table 2, third panel: hypergamy, mean: 0.09, 95% CI: 0.00–0.17) and this is particularly true for those who remained in western Finland during the war (married up category on the lower right panel (brown) is higher than married up posterior (blue) on the lower left panel; see also Supplementary Table 2, third panel: returned to Karelia, mean: 0.20, 95% CI: −0.04 to 0.44). In other words, both before and after the war, the probability of marrying down is higher for evacuees who married fellow Karelians and for evacuees who returned to Karelia, whereas the probability of marrying up is higher for individuals who remain in western Finland throughout the war and married a western Finn (see Supplementary Tables 1 and 2 for full models and Supplementary Tables 5 and 7 for observed data sample sizes and percentages). Model predictions (posterior distributions) are less pronounced than differences in the raw data (error bars) before and after the war because the posterior predictions account for all of the additional variables and interactions entered into the model. The posterior distribution plots (filled in) include the model predicted 95% HDIs with the lower and upper hinges of the box plots corresponding to the first and third quartiles. Points with error bars are the observed value means and s.e., respectively.

evacuee who marries before the war and returns is predicted to have 2.85 (95% HDI: 2.76–2.94) children if he or she returns and 2.85 (95% HDI: 2.75–2.94) children if he or she remains. However, for those who married after the war, the model predicts that evacuees who return will have 0.20 more children than those who remain—2.35 (95% HDI: 2.26–2.45) children for evacuees who return versus 2.19 (95% HDI: 2.10–2.27) children for evacuees who remain (see Figs. 2b and 4 and Supplementary Tables 1, 2 and 4). Although, there was an interaction between intermarriage and returning for evacuees who were married after the war. Evacuees who married after 1945 and returned to Karelia had higher reproductive outcomes if they married into the host population: 2.52 (95% HDI: 2.41–2.61) for evacuees who married someone from western Finland versus 2.27 (95% HDI: 2.17–2.37) for evacuees who married fellow Karelians (Fig. 4, bottom left panel). But this effect was even stronger for evacuees who remained in western Finland throughout the war: 2.36 (95% HDI: 2.29–2.44) for evacuees who married someone from western Finland versus 2.02 (95% HDI: 1.95–2.11) for evacuees who married fellow Karelians (Fig. 4, bottom right panel).

Posterior distribution means and HDIs displaying the relative effect—the proportional change in an outcome induced by a single predictor—for models predicting (1) the probability of intermarriage and (2) reproductive outcomes for all predictors that do not overlap with zero are shown in Fig. 2 for all evacuees. For model results separated by those who were married before and after the war, see Supplementary Figs. 1 and 2. For parameter estimates and 95% HDIs for all predictors entered into all models, see Supplementary Tables 1–4. Results of the models run on the full sample of evacuees are shown in Supplementary Table 1, results delimited by whether evacuees were married before or after the war are shown in Supplementary Table 2, results of models separating evacuees into those who returned to Karelia and those who remained in western Finland are shown in Supplementary Table 3 and all combinations of these groups (that is, married before the war and returned, married before the war and remained, married after the war and returned, and married after the war and remained) are shown in Supplementary Table 4.

Summary statistics and frequencies are shown in the Supplementary Information: Description of Data and Supplementary Tables 5–9. Variables that were not entered into the models are discussed in the Supplementary Information: Variables Dropped from Models. The mean age of the individuals that we used in our models was 31 years when the war began (for the evacuee age distribution, see Supplementary Fig. 5).

The results of our analysis point to the importance of considering trade-offs between the social and reproductive benefits generated by maintaining within-group bonds and social networks and the economic benefits that may be gained through integration and what are likely to be weaker bridging social ties. Understanding the conditions that facilitate the integration of displaced populations into host societies has received considerable attention, and much of this research has focused on attempting to explain the causes of conflict between immigrant and host communities while exploring policies that are expected to build social capital. However, a fundamental concern of this effort is the need to understand the costs and benefits of bonding and bridging social networks. Our analysis indicates that bonding social networks enhance reproductive outcomes and that bridging social networks offer opportunities to improve social and economic outcomes.

Overall, these results suggest that integration involves a trade-off between reproduction and status. For all evacuees, remaining in western Finland; getting an education, working in technical professions, offices and non-agricultural occupations; and hypergamy (that is marrying someone from a higher social class) all predict an increased probability of marrying someone from western Finland. However, many of these same factors that predict social integration also predict lower reproductive outcomes (see Supplementary Table 1), and these trade-offs change in important ways in both the pre-war and the post-war environments (Supplementary Table 2) and between evacuees who return to Karelia and evacuees who remain in western Finland (Supplementary Table 3). Younger evacuees, for example, are more likely to marry into the host population after the war ends, whereas evacuees who return to Karelia are less likely to intermarry both before and after the war. Although education is positively associated with the probability of marrying someone from western Finland before the war, it does not predict marrying into the host population after the war (Supplementary Table 2). Perhaps this is because education, which is often seen to

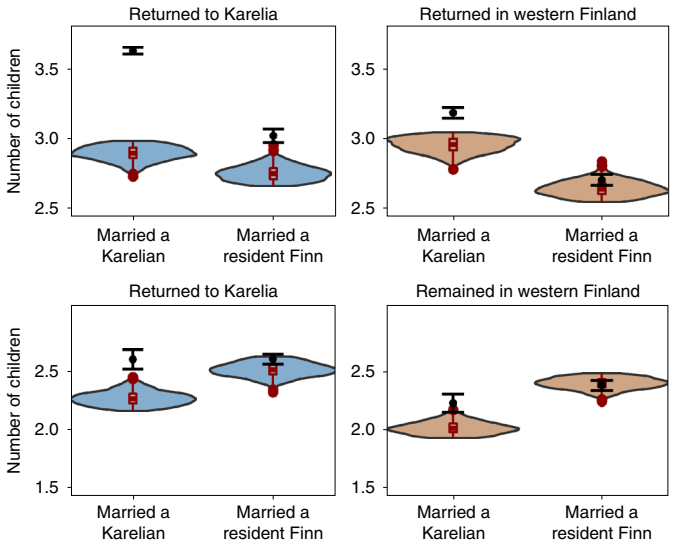

Fig. 4 | Reproductive costs of intermarriage are only evident before the war. Posterior distribution predictions are generated from the full model shown in the bottom panel of Supplementary Table 1 ($n = 26{,}757$). Before the war (top panels), evacuees who marry other Karelians have more children (see Supplementary Table 2, second panel: intermarriage, mean: −0.11, 95% CI: −0.13 to −0.08) and there are no differences between evacuees who return and evacuees who remain (see Supplementary Table 2, second panel: returned to Karelia, mean: −0.14, 95% CI: −0.18 to 0.10). After the war (bottom panels), evacuees who returned to Karelia have more children than those who remain in western Finland (errors bars and posterior distributions in the bottom left panel are higher than the bottom right panel) and marrying a resident Finn is positively associated with higher fertility (see model results for each panel in Supplementary Tables 2–4). This is particularly true for evacuees who remain in western Finland (bottom right panel; see also Supplementary Table 4: intermarriage, mean: 0.22, 95% CI: 0.09–0.33) (see Supplementary Table 1 for full models and Supplementary Table 5 for observed data means). Model predictions (posterior distributions) can be less pronounced than differences in the raw data (error bars) because the posterior predictions account for all of the additional variables and interactions entered into the model. The posterior distribution plots include the model predicted 95% HDIs with the lower and upper hinges of the box plots corresponding to the first and third quartiles. Points with error bars are the observed value means and s.e., respectively.

produce stronger bridging ties between individuals[44], plays a more important role in integration when families and extended families are geographically separated, which was probably more often the case before the war. Intermarriage, meanwhile, is positively associated with hypergamy for evacuees who marry both before and after the war (Figs. 2a and 3 and Supplementary Table 2), whereas returning to Karelia negatively predicts the probability of intermarriage for all evacuees. Regardless of when they were married, evacuees who remain in western Finland are not only more likely to marry people from western Finland but they are also more likely to marry up when they do. Although this is hardly surprising for evacuees who marry before the war (for example, they have a Karelian spouse and are likely to have stronger ties to Karelia), it is interesting that unmarried individuals who remain in western Finland throughout the war are more likely to marry someone from a higher social class if they marry into the host population. This suggests that there may be a dual benefit associated with more rapid assimilation (that is, remaining and intermarrying) after the war. However, it is important to note that socioeconomic status is not the only thing being traded in marriage markets and that preferences for marrying within one's own group and class often differs between social classes and occupations. A study from 1990s Sweden, for example, showed that age was the best predictor of intermarriages between native-born Swedes and immigrants[45], and both lower classes and non-farmers were shown to be the most likely to marry outside their own socioeconomic class in modern-day Finland[46].

Karelians who marry western Finns before the war have fewer children than those who marry other Karelians, whereas evacuees who marry western Finns after the war have more children, particularly if they remained in western Finland throughout the war (see Figs. 2a and 4). To make sense of this result, it is useful to consider the differences between the pre-war and post-war environments. Before the war, Karelians were the major ethnic group living in Karelia. Thus, if you married a non-Karelian before the war, you and your non-Karelian spouse are likely to be both geographically and culturally separated from many of the tight in-group social networks (for example, family members and friends) that build bonding social capital. However, after 1945, Karelians are a minority group living in a new place in western Finland. In this situation, having a non-Karelian spouse may not be as detrimental to the maintenance of tight within-group social networks. In fact, having a spouse from western Finland may actually be a benefit as you are able to form tight social bonds with individuals and family members who are now your neighbours. The higher fertility outcomes among evacuees who remain in western Finland throughout the war further support this interpretation and suggest that when the Karelians who remain also end up marrying into the host population, they may be better able to develop new social connections. This indicates that rapid assimilation by a minority group when they are young enough (P1a) may help to mitigate the reproductive declines more generally associated with integration. Thus, although these results fit within the framework of a growing body of research showing that intergroup marriages can reduce fertility[29], the pre-war and post-war fertility differences for Karelians who intermarry suggest that these outcomes also depend on the degree of geographical and cultural assimilation of the migrant population. Conversely, evacuees who marry resident Finns after the war also marry earlier and have their first child at a younger age than evacuees who marry other Karelians, opposite to the pattern that we see before the war (Supplementary Table 8). This suggests that it may simply be harder to find a Karelian spouse after the war when Karelians are now in the minority. It should be noted that, although these data include individuals who did not report having any children, they are representative of a demographically unstable population and do not include individuals who were never married. Thus, we must be careful not to infer evolutionary fitness from these results. However, it should also be noted that these discordant reproductive outcomes are unlikely to be driven by differences in fertility rates between Karelians and western Finns because data over this period indicate that non-Karelian Finns have the same or slightly higher fertility rates as Karelians (Supplementary Table 9).

We found no evidence to support Allport's contact hypothesis[13] that larger, more diverse communities, which encourage more frequent interactions between different groups of people, will promote integration. None of the models showed any relationship between the population of one's birthplace and either the probability of intermarrying or reproductive outcomes. However, it is important to recognize that these data may not offer the best test of the contact hypothesis. There are many reasons that migrants may decide to intermarry and remain in the host community (for example, employment, social services, where you were placed and what you left behind) that are unrelated to the tolerance and openness of the host population. In addition, the dramatic decline in class differences following the war, the government intervention and the high post-war intermarriage rate (75%) offers some limited support for Allport's contention that a precondition of successful integration is

equal status between groups. Nevertheless, the population of the towns in which Karelians were born does not seem to have an effect on the probability of intermarriage or reproduction.

The conditions that affect the reproduction and integration of the Karelian evacuees can be understood within the framework of evolutionary theory. The ecological constraints placed on refugees, including war and an evacuation, can have predictable effects on their behaviour, such as who they marry, whether they return to their place of birth given the opportunity and when they start reproducing, all of which can affect social capital. Human groups are organized around marriage, kinship and reciprocity[47] and there is good evidence for parochial altruism—the tendency to direct altruism preferentially towards one's own group and eschew interactions with outsiders[28]. If natural selection has favoured this type of tribalism (that is, preferential interactions with in-group members and hostility towards outgroups), then humans may be predisposed towards sanctioning individuals who develop bridging social ties and attempt to integrate. An analysis of the reproductive consequences of marriages in a tribal society in the Amazon shows that parents and brothers have higher lifetime reproductive success when their respective children and sisters marry more closely related individuals, supporting this interpretation[47]. Thus, the increased fertility associated with marrying within one's own cultural group and returning to Karelia in the population studied here can be viewed as the result of adaptations favouring parochialism and bonding social networks[28]. At the same time, bridging social networks and community integration have been cited as two of the most important factors predicting intergenerational upward social mobility in the United States[48], and a study of economic outcomes from the Karelian evacuation showed that the incomes of male evacuees increased compared to Finnish men who were not displaced[49]. Parochialism may therefore have social and economic costs that may include missed opportunities to marry into a higher social class. Nevertheless, some groups may be able to successfully gain the economic benefits of integration without experiencing the costs of reduced fertility, and it is interesting to note that, in our study, farmers who owned larger plots of land were both more likely to intermarry and had higher fertility after the war. Overall, however, in an increasingly global economy, the benefits of bonding social capital, including increased security, solidarity, within-group trust and mutual aid, may be offset by restricted freedom of movement, reduced economic opportunities and less integration.

Our results indicate that many of the same variables affect reproduction and integration oppositely. Intermarriage rates between migrant and host populations are a commonly used metric to assess social integration[50] and intermarriage is commonly viewed by immigrants as the final step in the process of integration[51]. Thus, intermarriage provides strong but indirect evidence that boundaries between groups have weakened and that migrants who intermarry are being exposed to natives by living in the same neighbourhoods, attending the same schools and sharing the same socioeconomic status[52]. However, another commonly used marker of social integration is the length of time spent in the host community[52], whereas returning to one's natal community is frequently used to assess bonding social capital. Although the ability to return home shortly after a forced migration is rarely available for refugees from war, this opportunity is common for refugees from natural disasters. An analysis of evacuees from hurricane Katrina in the United States, for example, found that tighter social networks among Vietnamese Americans resulted in them returning at much higher rates than African Americans[53]. Other studies have suggested that this was also the case for the Katrina diaspora more generally and that the size of social networks among family and friends predicted the probability of individuals returning to New Orleans[54]. However, even when refugees have the opportunity to return home, not all of them do and they are rarely displaced a second time, so the Karelian evacuees allow us to compare the life outcomes of individuals all living in the same place at the same time.

Although we are using intermarriage and the probability of reverse migration to measure the level of social integration of an individual, these variables are likely to be both a cause and an effect of integration and neither variable is exogenous to the model. In other words, individuals who have more bridging social connections are more likely to intermarry and remain in the host society, whereas those with more bonding social connections are more likely to marry within their own group and return to their natal communities, which only serves to further strengthen their respective bridging and bonding social networks[24]. It is also important to note that, although we have used intermarriage as a proxy to measure integration and used the social class (that is, occupation) of one's spouse to measure economic and social success, any broader interpretation of these results depends in large part on how these key concepts are defined.

The evacuations from Karelia were part of the largest mass exodus in history during World War II, in which an estimated 60 million people were forcibly displaced[55]. Our analyses suggest that many of these evacuees faced a trade-off between the economic benefits of integration and fertility benefits associated with maintaining strong ties within the Karelian diaspora. These findings are of general interest across academic disciplines and have substantial implications for public policy. Europe is currently facing the largest influx of refugees since World War II, and the European Union has identified a list of basic principles to help immigrants integrate, including finding employment and trying to increase the frequency of interactions between immigrants and natives[56]. In Germany, fewer than 15% of first-time asylum applicants had gone to University and reports suggest that less-educated immigrants struggle disproportionately[57]. Overall, however, our results indicate that evacuees who intermarry and remain in the host society gain socioeconomic benefits but suffer reduced fertility, which suggests that integration involves trade-offs between within-group 'bonding' social networks and between-group 'bridging' networks.

Methods

All methods and statistical analyses were pre-registered on 30 November 2017, which was before our accessing of these data. The predictor variables, outcome variables, model selection criteria and proposed analyses outlined below are nearly identical to those identified in the Open Science Framework pre-registration[58]. All discrepancies and their rationale are identified in the Supplementary Information: Pre-registration. All R codes used to select and transform the data, run the models and construct the figures can be found on this GitHub repository: https://github.com/robertlynch66/NHB_ms_revisions or in the Supplementary Software section.

Data. Structured interviews of Karelian evacuees were published in a four volume set called 'Siirtokarjalaisten tie'[59]. The project was part of an effort to record the lives of the Karelian migrants. Over 300 individuals were trained to conduct these interviews, which took place between 1968 and 1970, and an effort was made to locate all people who were evacuated from Karelia during the war. Each entry in the published books lists the name, sex, date of birth, birthplace, occupation, year of marriage, reproductive records (name, sex and date of birth of all children), membership in various organizations and the years and names of all the places they had lived from birth until the time they were interviewed. If they were married, the name, date of birth, birthplace and occupation of their spouse are also listed. These books were scanned and software was developed (Kaira Core and Natural Language Processing (NLP) software designed for use with the Finnish language) to digitize and extract the records (see Loehr et al.[60] for a detailed description of data extraction methods and the MiKARELIA database). We extracted their name, sex, year of birth, occupation, spouse, spouse's occupation, the names of all the places they had lived and the years they moved, their year of marriage and their number of children. Overall, there are data on approximately 250,000 individuals, including children and spouses. Here, we focus on a subset ($n = 26{,}757$) of individuals who were born in Karelia, lived in Karelia immediately prior to the Soviet Union invasion in 1939, were between 14 and 70 years of age when the first evacuation occurred (so that they were sexually mature when the war began) and for whom we had complete data regarding their sex, year of birth, birthplace, occupation, education, number of children, movements, wedding year, spouse's occupation and spouse's birthplace. The most limiting factor was wedding year, which was missing for 51% of the sample. No statistical methods were used to

pre-determine sample sizes, but our sample sizes are comparable to those used by Kulu et al.[29] and larger than those reported in other previous publications[49] (see Supplementary Information: Missing Data and Selection Bias).

Outcome variables. (1) A dummy variable measuring whether an individual intermarried was created to measure social integration and (2) the number of offspring produced before the evacuees were interviewed in 1970 was used to measure lifetime reproductive success.

Predictor variables. In all models were sex (1 = male), age (in years), logged population of birthplace, hypergamy— categorical ordinal rankings for individuals who married someone of lower (−1), same (0) or higher social class (1), dummy variables for the following 7 occupations: technical professionals, office workers, business, agricultural, transportation, factory workers and the service industry, a dummy variable indicating whether a particular occupation required an education (1 = yes), a dummy variable indicating whether they were married after 1945 (1 = yes) and a dummy variable indicating whether they returned to Karelia during the war (1 = yes). Place of birth was entered as a random effect in all models. For all models predicting reproductive outcomes, intermarriage (married a Karelian or married a resident Finn) was added as a covariate. Populations of towns located in Finland were obtained from the 1950 census Statistics Finland, which lists the number of individuals who were born in each location in Finland at the time they were censused in 1950 (ref. [61])— the closest census to the Soviet Union invasion—and the populations of Karelian towns were obtained by conducting searches for the old town names, most of which have their own Wikipedia page, and entering the population estimate for the town immediately prior to the Soviet Union invasion. Social class, which was used to determine hypergamy, was organized into seven ordered groups as defined by Waris et al. for 1940 Finland[62]. There were 1,580 distinct occupations listed and they were organized into seven categories as defined by the 1950 Finnish census (for details regarding the coding of both social class and occupation, see Supplementary Information: Social status and Occupations). We also flagged individuals if either they or their spouse were members of a Karelian society called 'Karjalaseura', which was founded in 1940 as a way to connect with other evacuees and aims to promote and preserve Karelian culture.

Data normalization. The populations of birthplaces were natural log transformed and scaled to values between 0 and 1, with higher values representing larger populations. Age was calibrated from birth year to reflect an evacuees age in years at the time of the evacuation.

Statistical analysis. We used Bayesian inference for all statistical analyses. In a Bayesian framework, each model conditions data on prior probability distributions and uses Monte Carlo sampling methods to generate posterior distributions for the parameters. The priors are the initial probabilities for each possible value of each parameter. This type of analysis allows us to compare posterior distributions across occupational categories, sexes, age groups, marriage types and migration profiles without relying on specific post-hoc tests[63] and obviates the need to adjust for multiple comparisons[64]. We are also better able to visualize and interpret differences between parameter estimates relative to a specific value by reporting and displaying the entire posterior distribution for each predictor and showing the HDIs that reveal the most credible values for each parameter estimate. Here, we assume that 95% HDIs, which do not include zero, are evidence that the parameter value is credibly different from the baseline.

To analyse which factors predict the probability of an evacuee intermarrying and which predict reproductive outcomes, we ran models on the full sample of evacuees for which we had complete data (see above) ($n = 26{,}757$) and included interactions between sex and age and both returned to Karelia and married after 1945. We also entered an interaction between married after the war and hypergamy for the intermarriage model only. For the reproductive outcomes models, we also included additional interactions between intermarriage and sex, hypergamy, married after the war and returned to Karelia (see Supplementary Information: Model Selection and Interactions, and Supplementary Table 10). These interactions were included because we were primarily interested in analysing differences between evacuees who returned to Karelia and those who did not, while also understanding that the environment and mating market were very different before the war when Karelians were all living together and after the war when they were all living in their host cities or towns (see pre-registration: https://osf.io/dvkfz/). Because there were many significant interactions between the two key dummy variables 'married after 1945' and 'returned to Karelia' (see Fig. 2 and Supplementary Table 1) and because these variables were central to our hypotheses and all of our models, we further subdivided the data into the following groups—evacuees who married before the war ended in 1945, evacuees who married after the war ended, evacuees who returned to Karelia during the war and evacuees who remained in western Finland throughout the war—and ran models on all combinations of these groupings (see Supplementary Tables 1–4 and Supplementary Figs. 1 and 2). For more details on model validity, posterior predictive checks and detailed model specifications, see Supplementary Information: Model Validity, Effects and Specifications.

Factors affecting the probability of intermarriage. A Bayesian generalized linear mixed-effects model logistic regression was designed to assess which factors predict the probability of intermarriage (that is, marrying someone from western Finland) (Supplementary Fig. 1 and Supplementary Table 1, top panel). These data were subdivided between evacuees who married before and after the war (Figs. 2a and 3 and Supplementary Table 2) to test the following predictions about how these factors differentially affect who evacuees marry before the war when they are living in Karelia and who they marry after the war ends when they are living in western Finland: both before and after the war (P1a) younger evacuees, (P1b) evacuees who returned to Karelia during the war, (P1d) evacuees who were born in places with larger populations and (P1e) more-educated evacuees will be more likely to intermarry, and after the war (P1c), evacuees who marry into the host population will be more likely to marry someone from a higher social class.

Factors affecting reproductive outcomes. A Bayesian generalized linear mixed-effects model Poisson regression was designed to assess reproductive outcomes and to test the following predictions: (P2a) evacuees who marry other Karelians and (P2b) evacuees who return to Karelia between 1941 and 1944 will have more children across all birth cohorts, occupations, sexes and social classes (Supplementary Fig. 2 and Supplementary Table 1, bottom panel). Although these predictions were made for evacuees regardless of when they were married, we also subdivided the data into evacuees who married before the war and those who married after the war to determine whether these differences are affected by the significant differences between pre-war and post-war environments (Figs. 2b and 4 and Supplementary Table 2). Because some weight was assigned to two different models used to predict reproductive outcomes (see Supplementary Information: Model Selection and Interactions, and Supplementary Table 10), all predictions in the results section and predictions used to construct Fig. 4 use the 'ensemble' function in the 'rethinking' package in R to weigh predictions by their respective model weights.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Code availability

The code used to produce these models, generate all results and produce all of the figures and tables in this paper and the Supplementary Information is available on GitHub, https://github.com/robertlynch66/Migrations-revisions-NHB, and is also included in Supplementary Software.

Data availability

The data that were used to generate these results and that support the findings of this study are available on GitHub: https://github.com/robertlynch66/Migrations-revisions-NHB.

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Author contributions

R.L. wrote the first draft of the manuscript, conducted the statistical analysis and created the figures and tables. K.P. and K.M. helped design the statistical models. J.L. and V.L. planned the study and oversaw data collection. All authors helped to write and edit the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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☒	☐ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated
☐	☒ Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	Structured interviews of Karelian evacuees were published in a four volume set called 'Siirtokarjalaisten tie'(Anon. 1970-1971). The project was part of an effort to record the lives of the Karelian migrants. Over 300 individuals were trained to conduct these interviews which took place between 1968 and 1970 and an effort was made to locate all people who were evacuated from Karelia during the war. Each entry in the published books lists the name, sex, date of birth, birthplace, occupation, year of marriage, reproductive records (name, sex, and date of birth of all children), membership in various organizations and the years and names of all places where they have lived from birth until the time they were interviewed. If they were married, the name, date of birth, birthplace and occupation of their spouse are also listed. These books were scanned and software was developed (Kaira Core and Natural Language Processing (NLP) software designed for use with the Finnish language) to digitize and extract the records (see Loehr et al (2017) for a detailed description of data extraction methods and the MiKARELIA database). We extracted the name, sex, year of birth, occupation, spouse, spouse's occupation, the names of all places they had lived and the years they moved, their year of marriage and their number of children. Overall there are data on approximately 250,000 individuals, including children and spouses, but here we focus on a subset of 26,757 individuals who were personally interviewed for this project, were born in Karelia, lived in Karelia immediately prior to the Soviet invasion in 1939 and for whom data was complete for all variables of interest.
Data analysis	These data were analyzed using the rethinking package in R version 3.5.1. We used Bayesian inference for all statistical analyses. In a Bayesian framework, each model conditions data on prior probability distributions and uses Monte-Carlo methods to generate posterior distributions for the parameters. The priors are the initial probabilities for each possible value of each parameter. This type of analysis allows us to compare posterior distributions across occupational categories, sexes, age classes, marriage types and migration profiles

without relying on specific post-hoc tests(McElreath 2015) while obviating the need to adjust for multiple comparisons(Gelman, Hill, and Yajima 2012). We are also better able to visualize and interpret differences between parameter estimates relative to a specific value by reporting and displaying the entire posterior distribution for each predictor and showing the highest density intervals (HDI) to reveal the most credible values for each parameter estimate. Here we assume that 95% highest density intervals which do not include zero are evidence that the parameter value is credibly different from the baseline. The R code for all analyses can be found in Supplementary Materials section 'R Code for all Models'.

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Data

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

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- A list of figures that have associated raw data
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The data that supports the findings of this study and code for all the models used to generate these results and produce the figures are available on Github: https://github.com/robertlynch66/NHB_ms_revisions.

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Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This is an observational study which provides a quasi natural experiment on some of the factors which influence the reproduction and integration of a population of evacuees during World war II.
Research sample	Structured interviews of Karelian evacuees were published in a four volume set called 'Siirtokarjalaisten tie'(Anon. 1970-1971). The project was part of an effort to record the lives of the Karelian migrants. Over 300 individuals were trained to conduct these interviews which took place between 1968 and 1970 and an effort was made to locate all people who were evacuated from Karelia during the war. Each entry in the published books lists the name, sex, date of birth, birthplace, occupation, year of marriage, reproductive records (name, sex, and date of birth of all children), membership in various organizations and the years and names of all places where they have lived from birth until the time they were interviewed. If they were married, the name, date of birth, birthplace and occupation of their spouse are also listed. These books were scanned and software was developed (Kaira Core and Natural Language Processing (NLP) software designed for use with the Finnish language) to digitize and extract the records (see Loehr et al (2017) for a detailed description of data extraction methods and the MiKARELIA database). We extracted the name, sex, year of birth, occupation, spouse, spouse's occupation, the names of all places they had lived and the years they moved, their year of marriage and their number of children. Overall there are data on approximately 250,000 individuals, including children and spouses, but here we focus on a subset of 26,757 individuals who were personally interviewed for this project, were born in Karelia, lived in Karelia immediately prior to the Soviet invasion in 1939 and for whom data was complete for all variables of interest.
Sampling strategy	This is a population based database and an attempt was made to interview all evacuees who were still alive in 1970. However, because some evacuees were no longer alive in 1970 some of the older evacuees are missing from our sample. Also the sample used was based on individuals for whom complete data was available (e.g sex, age, occupation, spouse, spouses occupation, birth place, spouses birth place, all the places where they lived, moved, and all their children).
Data collection	Each entry in the published books lists the name, sex, date of birth, birthplace, occupation, year of marriage, reproductive records (name, sex, and date of birth of all children), membership in various organizations and the years and names of all places where they have lived from birth until the time they were interviewed. If they were married, the name, date of birth, birthplace and occupation of their spouse are also listed. These books were scanned and software was developed (Kaira Core and Natural Language Processing (NLP) software designed for use with the Finnish language) to digitize and extract the records (see Loehr et al (2017) for a detailed description of data extraction methods and the MiKARELIA database). We extracted the name, sex, year of birth, occupation, spouse, spouse's occupation, the names of all places they had lived and the years they moved, their year of marriage and their number of children.
Timing	Interviews were conducted between 1968 and 1970
Data exclusions	Individuals with missing information on any of the variables of interest -- sex, age, occupation, spouse, spouses occupation, birth place, spouses birth place, all the places where they lived, moved, and all their children-- were excluded from these analyses.

Non-participation	NA
Randomization	Four groups and their combinations were delimited for these analyses in a quasi experimental design. These groups are evacuees who 1) returned to Karelia, 2) those who remained in western Finland, 3) those who were married before the war ended, and 4) those who were married after the war ended.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging