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Grandmaternal effects in preindustrial Lapland

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The grandmother hypothesis proposes that the prolonged post-reproductive lifespan of women has evolved because grandmothers have been able to increase their own inclusive fitness by promoting the lifetime reproductive success of their adult children. Although several studies have provided support for the grandmother hypothesis, there is a lack of studies concerning the association between the female post-reproductive longevity and the number of adult grandchildren, that is, the association between a woman's post-reproductive lifespan and the lifetime reproductive success of her adult children. Here, I used multigenerational demographic data collected from preindustrial Lapland to investigate 1. whether the lifespan of post-reproductive women was associated with the number of adult grandchildren, 2. whether having a living grandmother affected the survival of her grandchildren, and 3. whether the geographical proximity of the grandmother affected the survival of the grandchildren. I found that the lifespan of post-reproductive women was associated with the number of adult grandchildren: the women gained ten percent more adult grandchildren for every ten years of their post-reproductive lifespan. Moreover, having a living maternal grandmother decreased the grandchildren's mortality risk from the age of three onwards, and having a living paternal grandmother decreased the grandchildren's mortality risk from the age of four onwards. The geographical proximity of the maternal grandmother was not associated with the mortality risk of the grandchildren. Altogether, these results provide support for the hypothesis that the prolonged post-reproductive lifespan of women has evolved because grandmothers have promoted the lifetime reproductive success of their adult children and simultaneously their own inclusive fitness.

Key words: Female post-reproductive lifespan, grandmother hypothesis, lifetime reproductive success, mortality, geographical distance

Contents

1. INTRODUCTION

Human life history differs from that of other mammals in several ways, but one long-standing puzzle is the prolonged post-reproductive lifespan of women (Hawkes & Blurton Jones 2005). Our lifespan is longer than that of any other terrestrial mammal, but women stop being able to reproduce in the middle of it (Pavelka & Fedigan 1991; Hawkes 2003). Most animals retain fertility close to their death (Ellis et al. 2018). In humans, however, women can live decades after menopause (Pavelka & Fedigan 1991; Hawkes 2003). This peculiarity in our life history also distinguishes us from our closest relatives, chimpanzees, in which only a small proportion of individuals are post-reproductive (Hill et al. 2001; Gurven & Kaplan 2007; Alberts et al. 2013). In both humans and chimpanzees, the fertility of females decreases to nearly zero around the age of 45 years (Gage 1998; Nishida et al. 2003; Thompson et al. 2007). In chimpanzees, however, the maximum post-reproductive lifespan is only a few years (Hill et al. 2001; Gurven & Kaplan 2007; Alberts et al. 2013). In humans, on the other hand, a third or more of women in any population are post-reproductive, and this also applies to modern hunter-gatherers and historical populations living in natural fertility and mortality conditions (Hawkes & Blurton Jones 2005; Gurven & Kaplan 2007). For instance, in several hunter-gatherer populations, even when the life expectancy at birth is less than 40 years, 63-77% of girls who survive to maturity will also reach post-reproductive age (Blurton Jones et al. 2002; Hawkes & Blurton Jones 2005; Hawkes & Smith 2010). Traditionally, the prolonged post-reproductive lifespan of women has been considered an evolutionary paradox because it has been thought that individuals should reproduce until they die to maximize the number of offspring in the future generations (Williams 1957; Hamilton 1966; Croft et al. 2015).

The peculiarities of human life history have been proposed to be related to us being cooperative breeders (Hrdy 2005). That means it is typical for us that not only the mother but several individuals, called allomothers, are participating in childcare (Mace & Sear 2005; Hrdy 2005, 2007; Isler & van Schaik 2012). In other great apes, only mothers are usually responsible for childrearing (Mace & Sear 2005). The cooperative breeding theory underlines that human children are especially dependent on food, care, and protection provided by adults, much longer than the offspring of other mammals (Hrdy 2005, 2007). However, human babies are weaned earlier than the offspring of most other great apes, much earlier than children can feed independently (Hawkes et al. 1998; Kennedy 2005). Moreover, humans have shorter interbirth intervals than many other great apes (Galdikas

& Wood 1990; Kaplan et al. 2000; Isler & van Schaik 2012). As a result, in a family, there can be many children at different stages of dependency at the same time, leading to an increased need for additional help in taking care of the children. According to the theory, this need for help would not have evolved if the help provided by the allomothers had not been likely in our evolutionary past (Hrdy 2001; Hawkes & Blurton Jones 2005). Allomothers are often close relatives who can increase their own inclusive fitness by helping to take care of the children of their close relatives, as predicted by kin selection theory (Hamilton, 1964a, 1964b). In most cooperatively breeding species, the helpers are pre-reproductive individuals who postpone their own reproduction and help their parents to breed (Emlen 1995). In humans, however, particularly important helpers seem to be the post-reproductive grandmothers, as suggested by the grandmother hypothesis (Hawkes et al. 1998).

The grandmother hypothesis proposes that natural selection could have favored prolonged postmenopausal lifespan during human evolution because grandmothers, the special class of allomothers, have been able to promote the transmission of their genes to subsequent generations by helping their adult children to reproduce (Hawkes et al. 1998). As a result, the long-lived women have had more grand-offspring and their genes have become more common in the population. This way, the grandmothers have been able to increase their own inclusive fitness while increasing the reproductive success of their adult children (Hawkes et al. 1998). There are numerous ways in which grandmothers can help the family. They can, for instance, help with direct childcare, protect grandchildren from injuries, help with domestic tasks, give advice and support to the family, and improve their grandchildren's nutritional status (Hawkes et al. 1997; Sear et al. 2000; Gibson & Mace 2005; Tanskanen & Danielsbacka 2019). If this kind of helping through grandmotherhood has led to the evolution of post-reproductive longevity, as suggested by the hypothesis, this longevity is a fitness enhancing trait and not an evolutionary paradox (Hawkes et al. 1998; Lahdenperä et al. 2004).

According to the grandmother hypothesis, a grandmother can promote her inclusive fitness in two ways: by promoting the reproduction of her adult children (more grandchildren are born) and by promoting the survival of her grandchildren into adulthood (Hawkes et al. 1998; Chapman et al. 2021). Together, these components form the lifetime reproductive success of a grandmother's adult children. Many studies in traditional and historical populations living in natural mortality and fertility conditions have found positive associations between the presence of a grandmother and fertility of her children or survival of her grandchildren (Sear and Mace 2008; Sear and Coall 2011; Tanskanen & Danielsbacka 2019). However, few studies have investigated the association between the post-reproductive lifespan and the inclusive fitness of a woman in terms of the number of grandchildren born or survived into adulthood. In the first study to investigate this question, researchers found that in pre-industrial Finland and Canada, a woman had an average of two more grandchildren born for every ten years she lived after the age of 50 (Lahdenperä et al. 2004). Engelhardt et al. (2019) found the same association with French settlers in preindustrial Canada; grandmothers had two additional grandchildren born for every ten years of their post-reproductive lifespan. However, there is a lack of studies concerning the effect of the female post-reproductive longevity on the number of grandchildren who have survived to maturity, that is, the effect of a woman's post-reproductive lifespan on the lifetime reproductive success of her adult children.

In many previous studies the survival status of a grandmother (dead or alive) has been used to describe the availability of her help. However, there are problems with using only the survival status as a predictor of grandmaternal help as the survival status does not tell where the grandmother has lived and whether there has been actual contact between the grandmother and her grandchildren (Snopkowski & Sear 2016). To solve this problem, some researchers have used geographical proximity between a grandmother and her grandchildren, usually whether the grandmother lives in the same village or parish as her grandchildren or elsewhere, as grandmothers are predicted to have been more likely to help if they have lived close to the family (Voland & Beise 2002; Lahdenperä et al. 2004; Johow & Voland 2012; Chapman et al. 2021; Havlíček et al. 2021). The geographical proximity of the grandmother has likely been particularly important factor in historical times when transport has not been as efficient as today. Still, not much is known about how close to the family a grandmother needs to live in order to have a positive influence on her grandchildren. In one study, however, researchers measured the actual geographical distance between a mother and a grandmother in preindustrial Canada, and their results showed that when the distance increased, the number of grandchildren born was lower, the lifetime reproductive success of the mother was decreased, and the age at first birth was increased (Engelhardt et al. 2019). Still, more studies are needed to find out whether and how the geographical proximity of the grandmother is associated with the survival probability of the grandchildren.

Grandmaternal effects are known to vary depending on the context (Coall and Hertwig 2010). In addition to geographical proximity, there are other factors that can modulate the influence a grandmother has on her grandchildren. For example, grandmaternal effects can depend on the age and sex of the grandchild and the lineage (maternal vs. paternal) of the grandmother. Positive grandmaternal effects are often reported to have begun after the grandchild is no longer breastfed (Beise & Voland 2002; Sear et al. 2002; Voland & Beise 2002; Lahdenperä et al. 2004; Beise 2005; Chapman et al. 2019, 2021). The survival of infants, in contrast, is primarily affected by breastfeeding rather than additional help in childcare. For instance, in the studies investigating grandmaternal effects in preindustrial Finland, the presence of a grandmother has been positively associated with the survival of her grandchildren after the age of 2 years but not before (Lahdenperä et al. 2004; Chapman et al. 2021). According to some studies, grandmaternal effects may also differ depending on the sex of the grandchild (Jamison et al. 2002; Fox et al. 2009; Chapman et al. 2018). Moreover, the lineage of the grandmother is likely to modulate grandmaternal effects as there is a growing number of studies suggesting that maternal grandmother is the most important helper in terms of survival of her grandchildren (Sear & Mace 2008; Daly & Perry 2017; Perry & Daly 2017; Tanskanen & Danielsbacka 2019). Furthermore, the source of livelihood of the family is likely an important factor which can affect, for example, the overall mortality levels of children, birth rates, or availability of childcare assistance. However, there is a lack of studies investigating whether a grandmother's survival status is differently associated with the survival of her grandchildren depending on the source of livelihood of the family.

In this study, I will use multigenerational demographic data collected from Lutheran church registers of northern Finland between years 1640–1920 to investigate key questions related to the grandmother hypothesis. First, I will investigate whether the lifespan of the post-reproductive women was associated with the number of grandchildren surviving to adulthood. Second, I will study whether having a living grandmother affected the survival probability of the grandchildren, and third, whether the geographical proximity of the grandmother played a role in the survival of the grandchildren. Moreover, I will investigate whether the possible grandmaternal effects depend on the age and sex of the grandchild and whether there are differences in grandmaternal effects based on how nomadic life the family has lived, i.e., the source of livelihood of the family. As a large proportion of the population in this study were Sami who breastfed their children comparatively long (1.5–3 years), the weaning age has likely been higher than in preindustrial southern Finland (Itkonen 1948). Hence, the association between a grandmother's survival status and the mortality risk of her grandchildren is expected to begin later than in the studies concerning southern preindustrial Finland. Furthermore, the nomadic families lived and traveled in family groups which often included grandparents (Itkonen 1948), and grandmothers and their grandchildren have likely spent a lot of time together. Hence, the positive effects of the grandmother could be particularly strong in the nomadic families.

2. DATA AND METHODS

2.1. Study population and demographic data

This study is based on multigenerational demographic data collected from historical parish records kept by the Lutheran church in three parishes of northern Finland (Enontekiö, Inari and Utsjoki). In Finland, under the Swedish Church Law, the Lutheran Church was legally required to maintain population registers since the late 17th century, and by the mid-18th century, these records were being collected for the whole country (Gille 1949). These church records contain all births, marriages, and deaths for each parish.

The study population consists of indigenous Sami and sympatric Finnish settlers. During the study period (individuals were born between the years 1639–1920) the Sami living in the study parishes depended mainly on hunting, fishing, gathering, and nomadic reindeer herding (Itkonen 1948). The Sami of Utjoski were semi-nomadic fishers and reindeer herders. The Sami of Inari were semi-nomadic or sedentary and depended mainly on hunting and fishing for their livelihood while the Sami of Enontekiö were nomadic reindeer herders who followed the seasonal migrations of their herd and lived in temporary dwellings (Itkonen 1948). The Finns were sedentary farmers who practiced animal husbandry and small-scale agriculture. Both Sami and Finns experienced natural fertility and mortality due to absence of modern birth control methods or medical care (Itkonen 1948).

I got the demographic data (collected from the church registers and digitalized) from one of my supervisors. This dataset contains records from 12,675 individuals born between 1639 and 1920. Among them, I connected the information about each individual grandchild (F2) to that of their parents (F1) and grandmothers (F0) using ID-codes recorded in the digitalized version of the data. For 8396 individuals, at least one of the grandmothers could be found. Maternal grandmothers were found for 5533 individuals and paternal grandmothers for 7401 individuals. Both grandmothers were found for 4538 individuals.

2.2. Statistical analyses

2.2.1. Lifespan of the post-reproductive women and the number of adult grandchildren

In order to study the association between the lifespan of post-reproductive women and the number of surviving grandchildren, all women in the data who lived at least to the age of 50 and had at least one adult child, were included in the analysis. For each woman, the number of grandchildren that survived to the age of 15 years was calculated. Further, to study whether the lifespan of post-reproductive women was differently associated with the number of adult grandchildren depending on a woman's degree of pastoralism, those women whose degree of pastoralism was unknown were excluded from the analysis (58 women). Thus, the total sample size in the analysis was 877 women. 50 years was the age in which 99% of women had stopped reproducing in the population, based on their age at last reproduction, and a similar cut-off (99% age) has been used in the studies investigating the association between the female post-reproductive lifespan and the number of grandchildren born (Engelhardt et al. 2019).

Generalized linear mixed model with a negative binomial error distribution and log link function was fitted to investigate the association between the lifespan of post-reproductive women and the number of adult grandchildren. Fit statistics showed that negative binomial error distribution was more suitable for the model than Poisson distribution.

The response variable was the number of grandchildren who had survived to the age of 15, and the main explanatory variable was the lifespan of the post-reproductive women. The other explanatory variables were a woman's parish, degree of pastoralism (nomadic, semi-nomadic or sedentary), wealth (1–3, where a higher number means greater wealth), and birth year (modeled as a nonlinear B-spline effect of the birth year). I also investigated whether the lifespan of the post-reproductive women was differently associated with the number of adult grandchildren depending on a woman's degree of pastoralism, tested as an interaction term between the lifespan of post-reproductive women and the degree of pastoralism. All variables used in the analysis are shown in the table (Table 1).

Table 1. Variables used in the generalized linear mixed model of the effect of the lifespan of post-reproductive women on the number of adult grandchildren

Variable	Type	Description	Scale
The number of adult grandchildren	Response	Count	0–83
Lifespan of post-reproductive women	Fixed	Continuous	Lifespan in years, 50–100
Woman's wealth	Fixed	Continuous	1–3, where a higher number means greater wealth
Degree of pastoralism, i.e., how nomadic lifestyle the family had	Fixed	Categorical, 3-level factor	yes (2) intermediate (1), no (0)
Parish	Fixed	Categorical, 3-level factor	Enontekiö, Inari, Utsjoki
Woman's birth year		B-spline	1641–1887

2.2.2. Presence of the grandmother and mortality of her grandchildren

For 5533 grandchildren, their maternal grandmothers were known. 52 of the grandchildren were excluded from the analysis as there was no birth year marked for them in the records. Further, the grandchildren whose sex and the degree of pastoralism of their family were not known were excluded (323 grandchildren). Thus, the sample size in the maternal grandmother model was 5133 grandchildren.

For 7401 grandchildren, their paternal grandmothers were known. 90 of the grandchildren were excluded from the analysis as there was no birth year marked for them in the records. Further, the grandchildren whose sex and the degree of pastoralism of their family were not known were also excluded (522 grandchildren). Thus, the sample size in the paternal grandmother model was 6789 grandchildren.

For 2745 grandchildren in the maternal grandmother dataset and 3594 grandchildren in the paternal grandmother dataset, the death year was unknown. Death entry can be missing, for instance, because of under-registration, missing/destroyed original registers, the person moving out of the area, or the death occurring after the end of the observation period. These grandchildren with a missing death year were considered to have survived and were censored at the age of 18 years as has been done in several previous studies (Beise 2005). While this may underestimate the level of mortality, it has been argued that the error is smaller than if these children were left out, which could substantially overestimate mortality (Beise 2005). Moreover, it has been proposed that a death of a child would most likely have been recorded, and it is likely that at least a considerable number of individuals with missing death information are adults who have, for instance, moved out of the area covered by the registers or survived beyond the observation period (Beise 2005).

I used discrete time-event model with a binomial error distribution and logit link function to investigate whether the survival status (dead or alive) of the grandmother was associated with the mortality risk of her grandchild each year from birth to the age of 15 years. With time-event model, it is possible to study the influence of time-dependent variables, such as the survival status of a grandmother, on a grandchild's probability of dying each year, for example, from birth to adulthood (Allison, 1982).

The response variable was whether a child survived in each age or died. The main explanatory variable was the time-dependent survival status of the grandmother at each age. I also investigated whether the grandmother's survival status was differently associated with the mortality risk of the grandchildren in different ages, tested as an interaction between the age of the grandchild and the survival status of the grandmother. The other explanatory variables were the age and sex of the grandchild, parish, wealth, and the degree of pastoralism of the family, age of the mother when the child was born, and the time-dependent survival status of the mother as fixed factors. Additionally, I investigated whether the grandmother's survival status was differently associated with the mortality of the grandchildren depending on the degree of pastoralism of the family (tested as an interaction term between variables "degree of pastoralism" and "survival status of the grandmother") or according to the sex of the grandchild (tested as an interaction term between variables "grandchild's sex" and "survival status of the grandmother"). Initially I also intended to test whether the grandmother's survival status was differently associated with the mortality risk of the grandchildren depending on the wealth (either as continuous or categorical variable) of the family, but there was little variation in wealth between the families. Most families (78% of the grandchildren) in the data represented the average wealth group ‘2’, and, thus, the sample sizes for the wealth classes ‘rich’ and ‘poor’ would have been considerably smaller than the sample size in the wealth class ‘average’.

Analyses were performed separately for maternal and paternal grandmothers as the sample size would have decreased substantially if only those grandchildren were included whose both grandmothers and their survival information were known (n=3044 if both grandmothers were included vs n=5133 in the maternal grandmother model and n=6789 in the paternal grandmother model). In the maternal grandmother model, the mother’s identity nested within maternal grandmother’s identity was set as a random factor to take into account the possible shared family effects between siblings and cousins. In the paternal grandmother model, the father’s identity nested within paternal grandmother’s identity was fitted as a random factor. All variables used in the analyses are shown in the table (Table 2.).

Table 2. Variables used in all time-event models: the effect of the survival status or geographical proximity of the grandmother on the mortality risk of her grandchildren

Variable	Type	Description	Scale
Grandchild’s mortality	Response	Binary	dead (0) or alive (1)
Grandchild’s age	Fixed	Continuous	age in years, 0–15
Survival status of the grandmother	Fixed, time-varying	Binary	dead (0) or alive (1)
Survival status of the mother	Fixed, time-varying	Binary	dead (0) or alive (1)
Maternal age at birth	Fixed	Continuous	age in years, 13–58
Grandchild’s sex	Fixed	Categorical, 2-level factor	male (1), female (2)

Variable	Type	Description	Scale
Wealth of the family	Fixed	Continuous	1–3, where a higher number means greater wealth
Degree of pastoralism, i.e., how nomadic lifestyle the family had	Fixed	Categorical, 3-level factor	yes (2), intermediate (1), no (0)
Parish		Categorical, 3-level factor	Enontekiö, Inari, Utsjoki
Grandchild's birth cohort	Fixed	Categorical	1: 1700–1740; 2: 1750–1790; 3: 1800–1840; 4: 1850–1890; 5: 1900–1920
Mother ID	Random		
Father ID	Random		
Maternal grandmother ID	Random		
Paternal grandmother ID	Random		

2.2.3. Geographical proximity of the grandmother and mortality of her grandchildren

The geographical proximity between a grandmother and her grandchild was measured using the distance (in kilometers) between the birth village of a grandchild and the last known village of the grandmother. If both the grandmother and her grandchild were living in the same village, their geographical distance was marked as zero. For nomadic families, the proximity of the grandmother was measured using winter villages, i.e., the village where a nomadic family lived during winters. The geographical proximity of the maternal grandmother was determined for 3325 grandchildren, and the proximity of the paternal grandmother was determined for 4401 grandchildren. The distances were measured using the MapSite of National Land Survey of Finland (Maanmittauslaitos 2022) and distance counters in internet. For instance, in Avståndskalkylator (Distance.to 2022) it was possible to measure the distances between historical Finnish villages, not all of which could be found in the map of National Land Survey of Finland, as well as those villages that belong to Sweden. Because many villages in the dataset were historical villages, I also used historical maps found in the literature (Itkonen 1948; Enbuske 2008).

In the geographical proximity model, only living grandmothers were included because only grandmothers who are alive can provide help. Further, only grandchildren whose birth year, sex, and degree of pastoralism were known were included. Thus, the sample size was 1823 grandchildren in the maternal grandmother dataset and 2023 grandchildren in the paternal grandmother dataset. However, 78% of the grandchildren lived in the same village as their paternal grandmother, and only a few of the grandchildren not living in the same village as their paternal grandmother died during the observation period. Therefore, I was able to perform the distance analysis only for maternal grandmothers.

Discrete time-event model with a binomial error distribution and logit link function was conducted to examine whether the geographical distance between a grandmother and her grandchild was associated with the probability that a grandchild would die in each age, from birth to the age of 15 years. The response variable was the survival status of a grandchild (dead or alive). The main explanatory variable was the geographical proximity of the grandmother, as a continuous, linear variable. Other variables were the same as in the time-event analyses described in the section 2.2.2. I also investigated whether the geographical proximity of the grandmother was differently associated with the mortality risk of the grandchildren depending on the age or sex of the grandchild or the degree of pastoralism of the family (age/sex/pastoralism-interactions with geographical proximity of the grandmother).

All the models were run with the Glimmix Procedure in SAS software (Enterprise Guide 7.1). The level of significance was set at P-value <0.05. In the final models, all main terms and significant interactions were included.

3. RESULTS

3.1. Lifespan of the post-reproductive women and the number of adult grandchildren

The post-reproductive women (N=877) who had at least one adult child, lived an average of 73.28 years (range: 50–100 years, SD: 10.66). These women had an average of 6.12 children (range: 1–15, SD: 2.76) and 10.69 grandchildren (range: 0–108, SD: 11.49), from which an average of 8.47 grandchildren survived to adulthood (range: 0–83, SD: 9.09). 29% of the women were nomadic, 33% were semi-nomadic, and 38% were sedentary. 46% of the women lived in Enontekiö, 38% lived in Inari, and 16% lived in Utsjoki. 10% of the women were born in the 17th century, 51% in the 18th century, and 39% in the 19th century. The average wealth of the women was 1.98 (range: 1–3, where a higher number means greater wealth, SD: 0.38).

There was a positive association between the lifespan of the post-reproductive women and the number of grandchildren that survived to the age of 15 years (Est=0.012, $F_{1,864}$=8.70, p=0. 0033) (Table 3). The women had, on average, 10 percent more adult grandchildren for every ten years of their post-reproductive lifespan (Rate Ratio/1 year = 1.012 ± SE 0.0040) (Figure 1). The number of adult grandchildren was also associated with a woman's birth year (modeled as a nonlinear B-spline effect of the birth year), and a woman's parish: women from Inari had more adult grandchildren than women from the other study parishes (Table 3). Moreover, the number of adult grandchildren was associated with a woman's degree of pastoralism; sedentary women had more adult grandchildren than nomadic women (Table 3). The interaction between a woman's degree of pastoralism and the length of her lifespan was not significant, that is, the lifespan of post-reproductive women was not differently associated with the number of adult grandchildren depending on the woman's degree of pastoralism (Table 3).

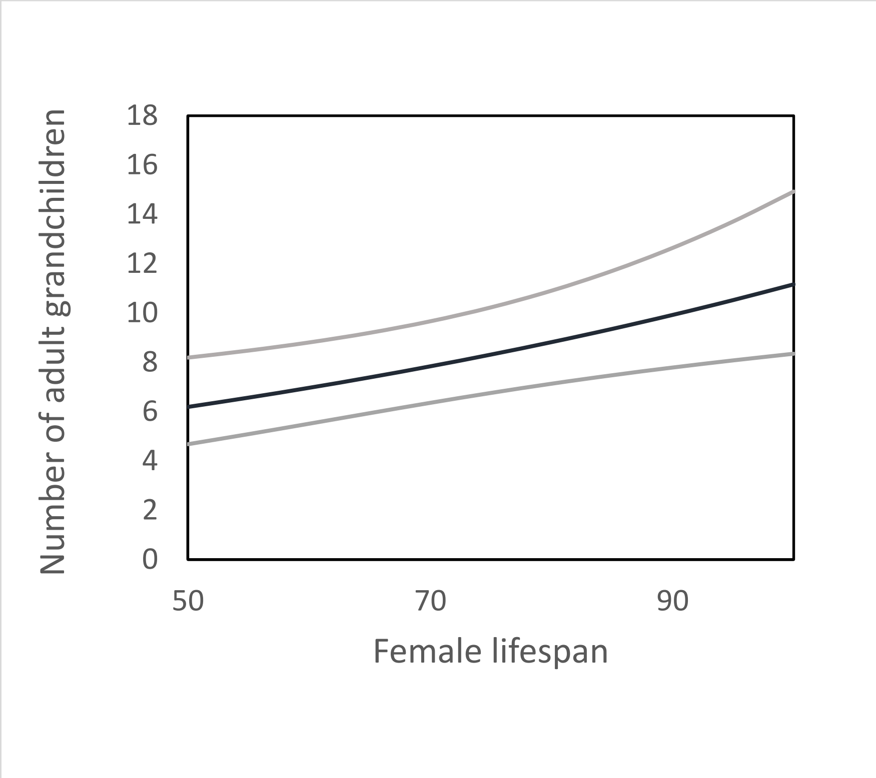

Figure 1. The lifespan of post-reproductive women and the number of adult grandchildren. The number of adult grandchildren was calculated as the number of grandchildren surviving to the age of 15 years. The figure shows model-derived prediction line with 95% confidence interval. The prediction line was drawn for women who were born in 1779, had wealth of 1.98, lived in Enontekiö, and were sedentary (the highest proportion for categorical variables and the average for continuous variables). N=877 women.

Table 3. **Generalized linear mixed model of the effect of the lifespan of post-reproductive women on the number of adult grandchildren in preindustrial northern Finland (n=877 women**). Terms included in the final model are shown above the dashed line.

Term	Category	Estimate ± SE	$F_{numdf, dendf}$	P-value
Intercept		-119.83 ± 20.43		
Lifespan of post-reproductive women		0.012 ± 0.0040	$8.70_{1, 864}$	0.0033
Woman's wealth		0.21 ± 0.13	$2.63_{1, 864}$	0.11
Degree of pastoralism			$11.11_{2, 864}$	<.0001
	sedentary	0.58 ± 0.13		

Term	Category	Estimate ± SE	$F_{numdf, dendf}$	P-value
	semi-no-madic	0.19 ± 0.15		
	nomadic	0		
Parish			$14.08_{2, 864}$	<.0001
	Enontekiö	0		
	Inari	0.61 ± 0.13		
	Utsjoki	0.064 ± 0.14		
Woman's birth year (B-spline)			$27.44_{6, 864}$	<.0001
Degree of pastoral-ism*lifespan of post-reproductive women			$0.33_{2, 862}$	0. 72
	sedentary	0.0032 ± 0.0097		
	semi-no-madic	0.0082 ± 0.010		
	nomadic	0		

The association between the lifespan of post-reproductive women and the number of adult grandchildren remained statistically significant also after controlling for the number of a woman's own children (Est=0.0090, $F_{1,863}$=5.68, p=0.017).

There was one woman in the data who had 83 adult grandchildren. She had 13 children of her own, ten of which had large families (8-14 children). The lifespan of post-reproductive women was positively associated with the number of adult grandchildren regardless of whether this woman was included in the analysis (Est=0.012, $F_{1,864}$=8.70, p=0. 0033) or not (Est=0.011, $F_{1,863}$=7.86, p=0.0052).

3.2. Presence of the grandmother and mortality of her grandchildren

Altogether, 16% of the grandchildren died before the age of 5 years, and 19% of the grandchildren died before the age of 15 years.

3.2.1. Maternal grandmother model

66% of those grandchildren whose maternal grandmother's identity and survival status were known had their maternal grandmother alive at birth. 24.6% of these grandchildren were nomadic, 29.8% were semi-nomadic, and 45.6% were sedentary. 40.7% of the grandchildren lived in Enontekiö, 45.6% lived in Inari, and 13.7% lived in Utsjoki. 27% of the grandchildren were born in the 18th century, 62% in the 19th century, and 11% in the 20th century. The average wealth of the families was 1.98 (range: 1–3, SD: 0.32). The average maternal age when the child was born was 32.36 years (range: 13–55, SD: 6.58). Among those grandchildren whose mother's survival status was known, 95% had their mother alive when they were 5 years old and 85% had their mother alive when they were 15 years old.

Overall, the mortality risk of the grandchildren decreased with age but there was a significant interaction between the age of a grandchild and the survival status of the maternal grandmother (Est=0.14, $F_{1,37540}$=18.37, $p<0.0001$) (Table 4). This means that the survival status of the maternal grandmother was differently associated with the mortality risk of the grandchildren in different ages (Figure 2). Before the age of 3 years, the mortality risk of a grandchild was not significantly associated with the survival status of the maternal grandmother (Table 5). From the age of 3 years, the grandchildren who had a living maternal grandmother had lower mortality risk than those grandchildren whose maternal grandmother was dead (Table 5). Age-specific odds-ratios for grandchildren's mortality risk if the maternal grandmother was dead versus if the maternal grandmother was alive are shown in Table 5. For instance, at the age of 5 years, grandchildren had over 64% higher odds of dying that year if their maternal grandmother was dead compared to if she was alive.

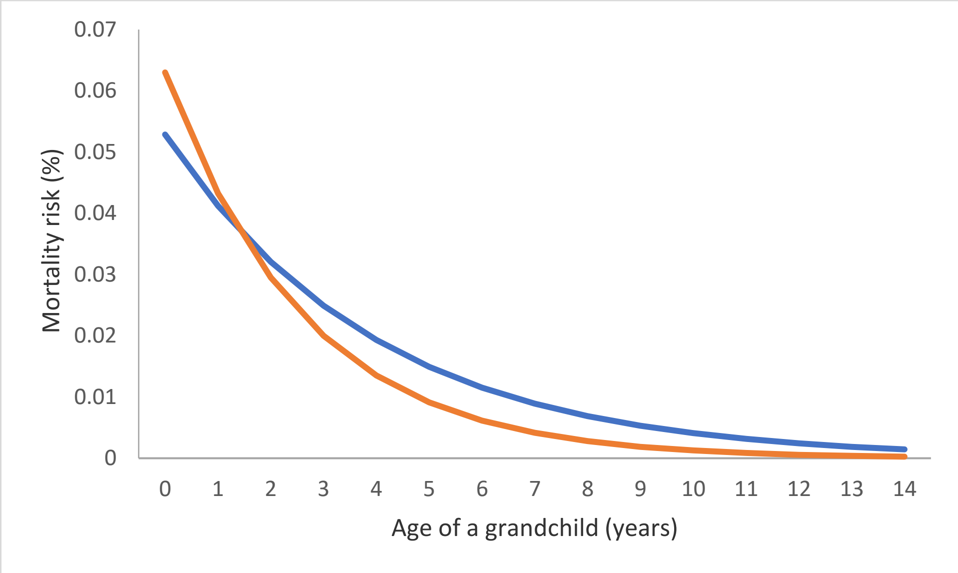

Figure 2. Grandchild's probability of dying in each age when the maternal grandmother was alive (orange) versus when the maternal grandmother was dead (blue). The figure shows model-derived prediction lines. Predictions were drawn for grandchildren who were born in the cohort 4 (between 1850–1890), were female, had a mother who was 32 years old when the child was born, had wealth of 1.98, lived in Inari, and were sedentary (the highest proportion for categorical variables and the average for continuous variables). N=5133 grandchildren.

Moreover, there was a non-significant trend showing that the survival status of the maternal grandmother could have been differently associated with the survival of her grandchildren depending on the degree of pastoralism of the family ($F_{2,1951}$=2.27, p=0.10) (Table 4). In nomadic families, having a living maternal grandmother may have had a particularly positive effect in reducing the mortality of the grandchildren (Table 4). In sedentary families, the survival status of the maternal grandmother may also have been positively associated with improved survival of the grandchildren whereas in semi-nomadic families, there may have been no difference in the mortality of the grandchildren depending on whether the maternal grandmother was alive or not (Appendix 1).

The interaction between the sex of a grandchild and the survival status of the maternal grandmother was not statistically significant. That is, the survival status of the maternal grandmother was similarly associated with mortality of boys and girls (Table 4).

Grandchild's mortality was also associated with the survival status of the mother, maternal age at birth, a grandchild's birth cohort, and the degree of pastoralism of the family. Mortality risk was lower when the mother was alive and when she was young. Mortality of the grandchildren was higher in nomadic families than in semi-nomadic or sedentary families. Grandchildren's mortality was not associated with wealth or parish of the family. Mother's identity nested within maternal grandmother's identity significantly explained variance in grandchild mortality (Table 4).

Table 4. Discrete time-event model of the effect of the maternal grandmother's survival status on the death risk of a grandchild from birth to the age of 15 years (0–14.99) in preindustrial northern Finland (n=5133 grandchildren). Positive estimates reflect increasing death risk. Fixed terms included in the final model are shown above the dashed line. In addition, mother ID nested within maternal grandmother ID was set as a random term.

Fixed Effects	Category	Estimate ± SE	$F_{numdf,\ dendf}$	P-value
Intercept		-2.59 ± 0.59		
Survival status of the maternal grandmother			$1.95_{1,2527}$	0.16
	dead	-0.19 ± 0.13		
	alive	0		
Grandchild's age		-0.40 ± 0.026	$412.82_{1,37540}$	<.0001
Grandchild's sex			$2.22_{1,37166}$	0.14
	female	0		
	male	0.13 ± 0.087		
Survival status of the mother			$4.02_{1,7498}$	0. 045
	dead	0.42 ± 0.21		
	alive	0		
Maternal age at birth		0.015 ± 0.0071	$4.33_{1,7474}$	0.037
Wealth of the family		-0.099 ± 0.19	$0.27_{1,543.9}$	0.60
Degree of pastoralism			$10.47_{2,518.9}$	<.0001
	nomadic	0		

	semi-no-madic	-0.79 ± 0.20		
	sedentary	-0.67 ± 0.16		
Parish			$1.58_{2,494.3}$	0.21
	Enontekiö	0.22 ± 0.21		
	Inari	-0.053 ± 0.19		
	Utsjoki	0		
Grandchild's birth co-hort			$5.77_{4,1178}$	0.0001
	1700–1740	-0.56 ± 0.41		
	1750–1790	-0.10 ± 0.26		
	1800–1840	-0.34 ± 0.25		
	1850–1890	0.33 ± 0.21		
	1900–1920	0		
Grandchild's age*sur-vival status of the ma-ternal grandmother		0.14 ± 0.032	$18.37_{1,37540}$	<.0001
Degree of pastoral-ism*survival status of the maternal grand-mother			$2.27_{2,1951}$	0.10
	nomadic	0		
	semi-no-madic	-0.54 ± 0.26		
	sedentary	-0.16 ± 0.23		
Grandchild's sex*sur-vival status of the ma-ternal grandmother			$0.68_{1,37539}$	0.41
	male	0.14 ± 0.17		
	female	0		
Random Effects		Estimate ± SE	ChiSq	Pr > ChiSq

Mother ID nested within maternal grand-mother ID		0.43 ± 0.080	61.68	<.0001

Table 5. Odds-ratios (OR) for grandchild's age-specific mortality risk if the maternal grandmother was dead versus if the maternal grandmother was alive (reference). ORs higher than 1.0 indicates higher mortality risk.

Total number of deaths in each age	Grandchild's age	Estimate (OR)	95% Confidence Limits
567/5133	0	0.83	0.64; 1.078
99/4566	1	0.95	0.76; 1.20
74/4467	2	1.091	0.88; 1.36
53/4393	3	1.25	1.004; 1.56
39/4340	4	1.43	1.13; 1.82
32/4301	5	1.64	1.25; 2.16
35/4269	6	1.88	1.38; 2.58
16/4234	7	2.16	1.51; 3.10
22/4218	8	2.48	1.64; 3.75
17/4196	9	2.84	1.78; 4.53
18/4179	10	3.26	1.93; 5.50
18/4161	11	3.73	2.086; 6.68
13/4143	12	4.28	2.26; 8.11
10/4130	13	4.90	2.44; 9.87
15/4120	14	5.62	2.63; 12.010

3.2.2. Paternal grandmother model

55% of those grandchildren whose paternal grandmother's identity and survival status was known had their paternal grandmother alive at birth. 28.15% of these grandchildren were nomadic, 27.43% were semi-nomadic, and 44.42% were sedentary. 47.75% of the grandchildren lived in Enontekiö, 37.59% lived in Inari, and 14.66% lived in Utsjoki. 33% of the grandchildren were born in the 18th century, 59% in the 19th century, and 8% in the 20th century. The average wealth of the families was 2.00 (range: 1–3, SD: 0.31).

The average maternal age when the child was born was 32.60 years (range: 13–58, SD: 6.68). Among those grandchildren whose mother's survival status was known, 94% had their mother alive when they were 5 years old and 84% had their mother alive when they were 15 years old.

As with maternal grandmothers, there was a significant interaction between the age of a grandchild and the survival status of the paternal grandmother (Est=0.063, $F_{1,50810}$=5.19, p=0.023) (Table 6). That is, the survival status of the paternal grandmother was differently associated with the mortality of the grandchildren in different ages (Figure 3). Before the age of four years, the mortality risk of a grandchild was not significantly associated with the survival status of the paternal grandmother (Table 7). From the age of 4 years, the grandchildren who had a living paternal grandmother had lower mortality risk than those grandchildren whose paternal grandmother was dead (Table 7). Age-specific odds-ratios for grandchildren's mortality risk if the paternal grandmother was dead versus if the paternal grandmother was alive are shown in Table 7. For instance, at the age of 5 years, the grandchildren whose paternal grandmother was dead had 31% higher odds of dying that year than the grandchildren whose paternal grandmother was alive.

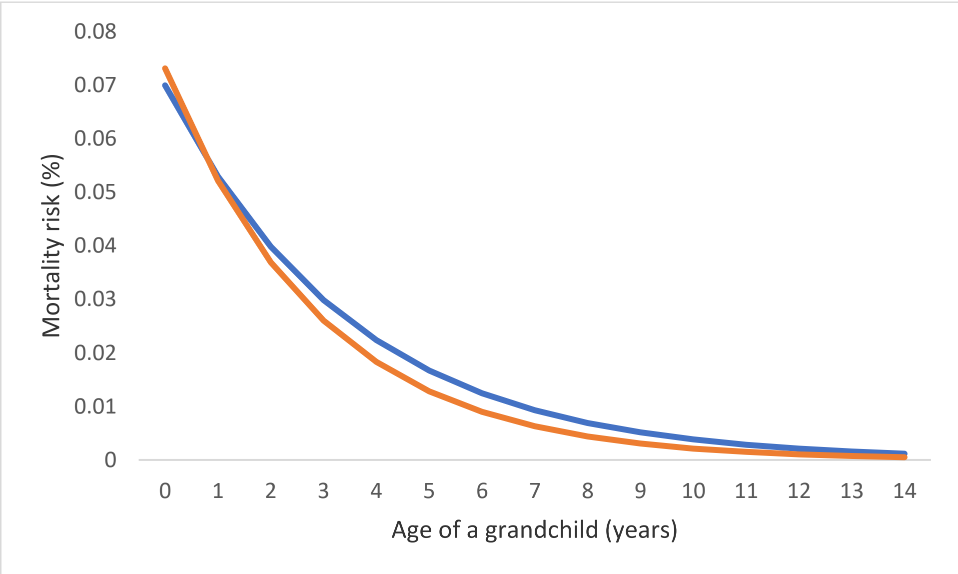

Figure 3. Grandchild's probability of dying in each age when the paternal grandmother was alive (orange) versus when the paternal grandmother was dead (blue). The figure shows model-derived prediction lines. Predictions were drawn for grandchildren who were born in the cohort 4 (between 1850–1890), were female, had a mother who was 32 years old when the child was born, had wealth of 2.0, lived in Enontekiö, and

were sedentary (the highest proportion for categorical variables and the average for continuous variables). N=6789 grandchildren.

The interaction between the sex of the grandchild and the survival status of the paternal grandmother was not statistically significant. That is, the survival status of the paternal grandmother was similarly associated with mortality of boys and girls (Table 6). In addition, the interaction between the degree of pastoralism of the family and the survival status of the paternal grandmother was not statistically significant. That is, the survival status of the paternal grandmother was similarly associated with mortality of the grandchildren regardless of the degree of pastoralism of the family (Table 6).

Grandchild's mortality was also associated with the sex of the grandchild, the survival status of the mother, the birth cohort of the grandchild, and the degree of pastoralism of the family (Table 6). Mortality of boys was higher than mortality of girls, the mortality risk was lower when the mother was alive, and mortality was higher in nomadic grandchildren than in semi-nomadic or sedentary grandchildren. Grandchildren's mortality was not associated with wealth of the family (Table 6). Father's identity nested within paternal grandmother's identity significantly explained variance in grandchild mortality (Table 6).

Table 6. Discrete time-event model of the effect of the paternal grandmother's survival status on the death risk of a grandchild from birth to the age of 15 years (0–14.99) in preindustrial northern Finland (n=6789 grandchildren). Positive estimates reflect increasing death risk. Fixed terms included in the final model are shown above the dashed line. In addition, father ID nested within paternal grandmother ID was set as a random term.

Fixed Effects	Category	Estimate ± SE	$F_{numdf, dendf}$	P-value
Intercept		-2.23 ± 0.48		
Survival status of the paternal grandmother			$0.21_{1,3308}$	0.65
	dead	-0.048 ± 0.10		
	alive	0		
Grandchild's age		-0.36 ± 0.023	$545.87_{1,50810}$	<.0001
Grandchild's sex			$3.84_{1,32976}$	0.050
	female	0		

	male	0.14 ± 0.074		
Survival status of the mother			$9.02_{1,8401}$	0.0027
	dead	0.51 ± 0.17		
	alive	0		
Maternal age at birth		0.0085 ± 0.0058	$2.18_{1,7308}$	0.14
Wealth of the family		-0.11 ± 0.15	$0.58_{1,783.9}$	0.45
Degree of pastoralism			$16.11_{2,694.5}$	<.0001
	nomadic	0		
	semi-nomadic	-0.68 ± 0.15		
	sedentary	-0.62 ± 0.12		
Parish			$2.19_{2,687.3}$	0.11
	Enontekiö	0.23 ± 0.15		
	Inari	-0.0044 ± 0.15		
	Utsjoki	0		
Grandchild's birth cohort			$7.69_{4,1356}$	<.0001
	1700–1740	-0.74 ± 0.30		
	1750–1790	-0.45 ± 0.22		
	1800–1840	-0.53 ± 0.22		
	1850–1890	0.028 ± 0.20		
	1900–1920	0		
Grandchild's age*survival status of the paternal grandmother		0.063 ± 0.028	$5.19_{1,50810}$	0.023
Grandchild's sex*survival status of the paternal grandmother			$0.63_{1,50809}$	0.43
	male	-0.12 ± 0.15		
	female	0		

Degree of pastoralism*survival status of the paternal grandmother			$0.55_{2,2093}$	0.58
	nomadic	0		
	semi-nomadic	-0.22 ± 0.21		
	sedentary	-0.074 ± 0.18		
Random Effects		Estimate ± SE	ChiSq	Pr > ChiSq
Father ID nested within paternal grandmother ID		0.21 ± 0.055	24.06	<.0001

Table 7. Odds-ratios (OR) for grandchild's age-specific mortality risk if the paternal grandmother was dead versus if the paternal grandmother was alive (reference). ORs higher than 1.0 indicates higher mortality risk.

Total number of deaths in each age	Grandchild's age	Estimate (OR)	95% Confidence Limits
730/6789	0	0.95	0.78; 1.17
134/6059	1	1.02	0.85; 1.21
98/5925	2	1.08	0.92; 1.28
62/5827	3	1.15	0.97; 1.37
58/5765	4	1.23	1.016; 1.48
36/5707	5	1.31	1.048; 1.63
39/5671	6	1.39	1.073; 1.81
26/5632	7	1.48	1.093; 2.013
31/5606	8	1.58	1.11; 2.25
23/5575	9	1.68	1.13; 2.51
30/5552	10	1.79	1.14; 2.82
21/5522	11	1.91	1.16; 3.16
16/5501	12	2.035	1.17; 3.54
20/5485	13	2.17	1.18; 3.97

Total number of deaths in each age	Grandchild's age	Estimate (OR)	95% Confidence Limits
16/5465	14	2.31	1.20; 4.46

3.3. Geographical proximity of the grandmother and mortality of her grandchildren

3.3.1. Where did the grandmothers live?

53% of the grandchildren (967/1823) lived in the same village as their maternal grandmother. Hence, the proximity of the maternal grandmother was marked as zero for these grandchildren. Almost all grandchildren lived in the same parish as their maternal grandmother: only 5 grandchildren of a single maternal grandmother lived in a different parish than their maternal grandmother. The average distance between a grandchild and the maternal grandmother was 18.14km (range: 0–98, SD: 24.39). The average distance of the maternal grandmother was 14.88km (range: 0–98, SD: 20.18) in the sedentary families, 15.57km (range: 0–89, SD: 25.33) in the semi-nomadic families, and 27.08km (range: 0–98, SD: 30.22) in the nomadic families. Distribution of maternal grandmother–grandchild pairs by the maternal grandmother's distance are shown in the figure (Figure 4).

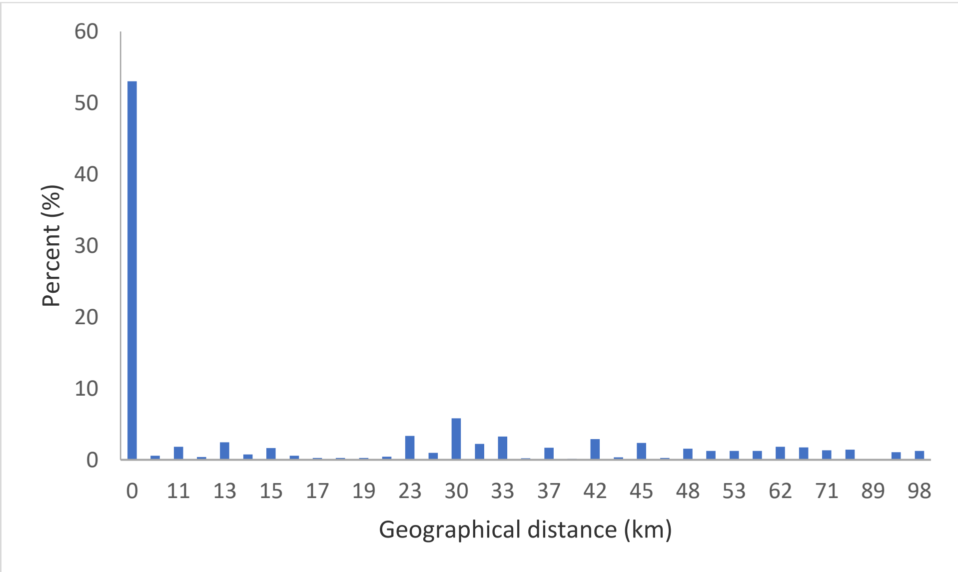

Figure 4. Percentages of maternal grandmother–grandchild pairs by geographical proximity of the maternal grandmother (n=1823 pairs)

68% of the grandchildren (1367/2023) lived in the same village as their paternal grandmother. Hence, the proximity of the paternal grandmother was marked as zero for these grandchildren. Almost all grandchildren lived in the same parish as their paternal grandmother: only 14 grandchildren from two different grandmothers lived in a different parish than their paternal grandmother. The average distance between a grandchild and the paternal grandmother was 12.77km (range: 0-112, SD: 22.03). The average distance of the paternal grandmother was 13.46km (range: 0–112, SD: 22.43) in the sedentary families, 11.64km (range: 0–77, SD: 23.17) in the semi-nomadic families, and 11.74km (range: 0–98, SD: 20.56) in the nomadic families. Distributions of paternal grandmother–grandchild pairs by the paternal grandmother's distance are shown in the figure (Figure 5).

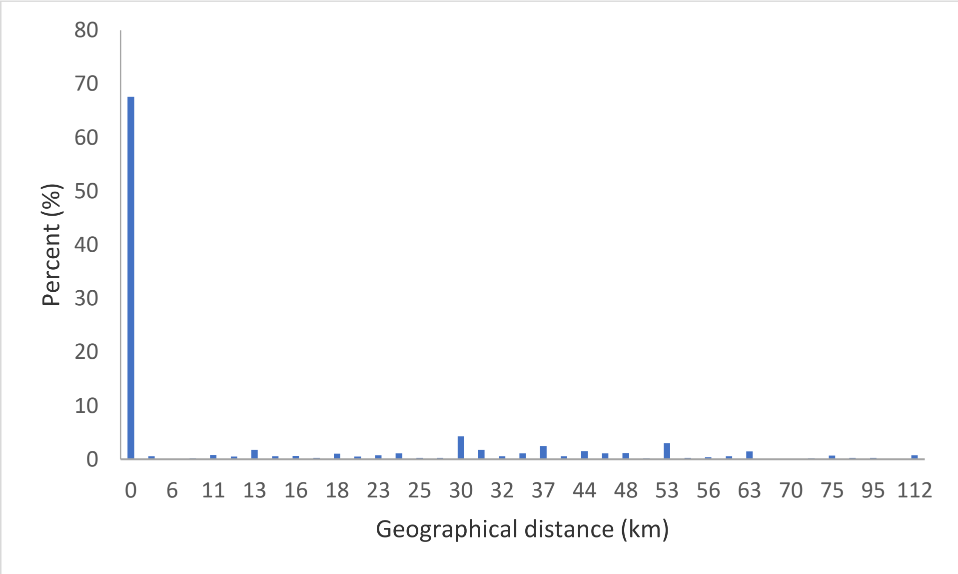

Figure 5. Percentages of paternal grandmother–grandchild pairs by geographical proximity of the paternal grandmother (n=2023 pairs)

3.3.2. Geographical proximity of the maternal grandmother and mortality of her grandchildren

The geographical proximity of the maternal grandmother was not associated with the grandchildren's mortality (Est=0.0019, $F_{1,219.4}$=0.30, p=0.58) (Table 8). Moreover, none of the interactions in the model were statistically significant. This means that the geographical proximity of the maternal grandmother was not differently associated with the mortality risk of the grandchildren depending on the age or sex of the grandchild or the degree of pastoralism of the grandchild's family (Table 8). Neither was grandchildren's mortality associated with grandchild's sex, birth cohort, parish, the survival status of the mother, or wealth of the family (Table 8). Grandchildren's mortality was associated with grandchild's age, and the degree of pastoralism of the family, and there was a close to significant association between grandchildren's mortality and maternal age at birth (Table 8). Mother's identity nested within maternal grandmother's identity significantly explained variance in grandchild mortality (Table 8).

Table 8. Discrete time-event model of the effect of geographical proximity of the maternal grandmother on the death risk of a grandchild from birth to the age of 15 years (0-14.99) in preindustrial northern Finland (n=1823 grandchildren). Positive estimates reflect increasing death risk. Fixed terms included in the final model are shown above the dashed line. In addition, mother ID nested within maternal grandmother ID was set as a random term.

Fixed Effects	Category	Estimate ± SE	$F_{numdf, dendf}$	P-value
Intercept		-3.66 ± 0.89		
Geographical proximity of the maternal grandmother		0.0019 ± 0.0034	$0.30_{1,219.4}$	0.58
Grandchild's age		-0.40 ± 0.030	$172.58_{1,12969}$	<.0001
Grandchild's sex			$0.12_{1,12969}$	0.72
	female	0		
	male	0.047 ± 0.13		
Survival status of the mother			$0.10_{1,3988}$	0.75
	dead	0.14 ± 0.45		
	alive	0		
Maternal age at birth		0.019 ± 0.011	$3.17_{1,3960}$	0.08
Wealth of the family		0.27 ± 0.30	$0.78_{1,178.3}$	0.38
Degree of pastoralism			$3.25_{2,255.9}$	0.04
	nomadic	0		
	semi-nomadic	-0.43 ± 0.34		
	sedentary	-0.58 ± 0.23		

Parish			$0.09_{2,263.8}$	0.9105
	Enontekiö	0.14 ± 0.38		
	Inari	0.15 ± 0.35		
	Utsjoki			
Grandchild's birth cohort			$1.02_{4,472.6}$	0.40
	1700–1740	-0.54 ± 0.63		
	1750–1790	0.012 ± 0.41		
	1800–1840	0.0042 ± 0.39		
	1850–1890	0.35 ± 0.33		
	1900–1920	0		
Grandchild's age*geographical proximity of the maternal grandmother		0.0014 ± 0.0012	$1.43_{1,12968}$	0.23
Grandchild's sex*geographical proximity of the maternal grandmother			$0.64_{1,12968}$	0.43
	male	-0.0045 ± 0.0057		
	female	0		
Degree of pastoralism*geographical proximity of the maternal grandmother			$0.02_{2,258.7}$	0.98
	nomadic	0		
	semi-nomadic	0.0023 ± 0.013		
	sedentary	0.0010 ± 0.0077		
Random Effects		Estimate ± SE	ChiSq	Pr > ChiSq
Mother ID nested within maternal grandmother ID		0.34 ± 0.12	14.78	<.0001

4. DISCUSSION

In this study, I used multigenerational demographic data collected from church registers of northern Finland between years 1640–1920 to investigate several key questions related to the grandmother hypothesis. To my knowledge, this was the first study to investigate the predictions of the grandmother hypothesis in Sami.

4.1. Lifespan of the post-reproductive women and the number of adult grandchildren

According to the grandmother hypothesis, the prolonged post-reproductive lifespan of women has evolved because grandmothers have been able to increase their own inclusive fitness by promoting the lifetime reproductive success of their adult children (Hawkes et al. 1998). To my knowledge, the current study was the first study to investigate the association between the lifespan of post-reproductive women and the number of grandchildren surviving to adulthood, that is, the association between the lifespan of a post-reproductive woman and the lifetime reproductive success of her adult children.

The lifespan of the post-reproductive women was positively associated with the number of grandchildren who survived to the age of 15 years. The women gained, on average, ten percent more adult grandchildren for every ten years of their post-reproductive lifespan. This association was similar in nomadic, semi-nomadic, and sedentary women. According to the results of this analysis, the post-reproductive women in historical Lapland could have been able to promote the lifetime reproductive success of their adult children and simultaneously their own inclusive fitness while living long after ceasing their own reproduction.

There is a growing number of studies concerning the effects of a living mother/mother-in-law on the reproductive success of her daughter/daughter-in-law (Sear & Coall 2011; Tanskanen & Danielsbacka, 2019). However, reproductive success has often been measured using, for instance, interbirth intervals or the age at first birth (Sear & Coall 2011). Additionally, the association between the survival status or geographical proximity of the grandmother and the lifetime reproductive success of her adult children has been studied (Lahdenperä et al. 2004; Engelhardt et al. 2019). For instance, it was found in the study concerning 18th and 19th century Finnish population that the presence of a post-reproductive grandmother was associated with greater lifetime reproductive success of her adult children (Lahdenperä et al. 2004). The same study was also the first to investigate the association between the female post-reproductive lifespan and the number of grandchildren born. However, before this study, there has been a lack of studies concerning the association between the lifespan of a post-reproductive woman and the lifetime reproductive success of her adult children.

One limiting factor in my analysis is that some women likely have moved out of the area, to Norway for example, and started a family in the new area. Thus, the children of such women are not recorded in the church registers of Enontekiö, Inari, or Utsjoki. In consequence, the total number of children and grandchildren for these women may be higher than what has been recorded in the demographic data. Another source of error is that I did not exclude women born at the end of the observation period (except that a woman had to survive at least to the age of 50), and thus, not all of the grandchildren of these women have been born before the end of the observation period.

Furthermore, as often in studies of human life history evolution, this study is based on correlational data, and therefore the interpretation of causality is problematic. Moreover, there is a possibility that both the dependent and the independent variable are affected by some shared factor, for example shared genes or better environment, between the grandmother and her grandchildren. I have, however, controlled for possible confounding factors, for example wealth of the family, to reduce this risk. Furthermore, in time-event analyses, I have used mother's/father's identity nested within grandmother's identity to take into account possible shared family effects between siblings and cousins.

4.2. Presence of the grandmother and mortality of her grandchildren

The survival status of the grandmother was differently associated with the mortality risk of her grandchildren depending on the age of a grandchild. Before the age of three years, mortality of the grandchildren did not differ depending on the survival status of the maternal grandmother. From the age of three years, however, the grandchildren who had a living maternal grandmother had lower risk of dying that year than the grandchildren whose maternal grandmother was dead. The association between the survival status of the maternal grandmother and survival of her grandchildren was similar in girls and boys. In the paternal grandmother model, it was from the age of four years, the grandchildren who had a living paternal grandmother had lower mortality risk than the grandchildren whose paternal grandmother was dead. As with maternal grandmothers, this association was similar in girls and boys. Additionally, the association between the survival status of the paternal grandmother and survival of her grandchildren was similar in nomadic, semi-nomadic, and sedentary families.

The results are consistent with the previous studies and theories concerning maternal grandmothers: the positive effects of the maternal grandmother are often reported to have begun when the child is a toddler and no longer breastfed by the mother (Sear & Mace 2008). There is great variation between studies in terms of the particular age in which the positive grandmaternal effects have been observed. However, in several studies concerning different populations, both historical populations and contemporary hunter-gatherers, the positive effects of the maternal grandmother have begun at the age of weaning, which varies between populations (Beise & Voland 2002; Sear et al. 2002; Beise 2005; Voland & Beise 2002). It has been suggested that the maternal grandmother has been particularly important for the survival of her grandchildren during and after the weaning age, which can be dangerous time, when the child is no longer solely dependent on the mother who, in turn, may already have a new child to breastfeed (Beise 2005; Sear & Mace 2008).

In this study, the association between the survival status of the maternal grandmother and the survival of her grandchildren began one year later than what has been reported in the studies concerning historical southern Finland (Lahdenperä et al. 2004; Chapman et al. 2019, 2021). This was in line with my expectations because a large proportion of the population in this study were Sami who usually breastfed their children comparatively long (1.5–3 years) (Itkonen 1948). Thus, the weaning age in this population has likely been higher than in southern Finland.

The survival status of the maternal grandmother could have been differently associated with the survival of her grandchildren depending on the degree of pastoralism of the grandchild's family. In nomadic families, having a living maternal grandmother may have had a particularly positive effect in reducing the mortality of the grandchildren. This was in line with my expectations as nomadic families lived and traveled in family groups which often included grandparents (Itkonen 1948), and grandmothers and grandchildren have likely spent a lot of time together. On the one hand, based on the analyses of the data used in this study, the mortality of children was higher in nomadic families than in semi-nomadic or sedentary families. This is concordant with the previous literature on the topic (Itkonen 1948). It has been discussed that the nomadic lifestyle with temporary dwellings was more dangerous than sedentary lifestyle with permanent houses (Itkonen 1948). For instance, colds and various accidents were more common in nomadic reindeer herders than in semi-nomadic or sedentary families (Itkonen 1948). It is possible that nomadic maternal grandmothers have reduced their grandchildren's mortality risk by looking after them and preventing accidents. On the other hand, it is possible that the positive effects of the maternal grandmother on the survival of her grandchildren are better seen in the nomadic families because there was more variation in the survival of children (i.e., higher level of mortality) in nomadic families compared to semi-nomadic or sedentary families. To my knowledge, the current study was the first study to investigate whether a grandmother's survival status has been differently associated with the survival of her grandchildren depending on the source of livelihood of the family.

Interestingly, also the survival status of the paternal grandmother was positively associated with the survival of her grandchildren, and the effect started when the grandchild was four years old. While maternal grandmother has often been reported to have decreased the mortality risk of her grandchildren, results for paternal grandmothers are more mixed (Sear & Mace, 2008). Sometimes paternal grandmother has reduced her grandchildren's mortality, sometimes there has been no association between the survival status of the paternal grandmother and the survival of her grandchildren, and sometimes paternal grandmother has even had a negative effect on the survival of her grandchildren (Sear & Mace, 2008). Moreover, when there has been an association between the presence of the paternal grandmother and the survival of her grandchildren, this association has started at different age than in case of maternal grandmothers, being strongest within the first year of a child's life (Beise & Voland 2002; Voland & Beise 2002; Beise 2005). In consequence, it has been hypothesized that maternal and paternal grandmothers affect grandchildren's mortality in different methods. Maternal grandmothers are considered to help with childcare and protect grandchildren, particularly during the weaning age, whereas paternal grandmothers are thought to affect more the conditions of the mother during pregnancy, which, in turn, may affect the survival probability of a child, either positively or negatively (Beise & Voland 2002; Sear & Mace 2008). However, it is possible that the negative association between the presence of the paternal grandmother and the survival of her grandchildren in the previous studies has been affected by paternal grandmothers being older than maternal grandmothers as the age of marriage has traditionally been higher for men than for women. The age of the grandmother has recently been shown to influence the association between the presence of the grandmother and the survival of her grandchildren (Chapman et al. 2019). In the first study to investigate this question, it was shown that when the grandmother was over 75 years old, there was no effect of the maternal grandmother and there was even a detrimental effect of the paternal grandmother on a grandchild's survival probability before the age of 2 years (Chapman et al. 2019). It has been suggested that the old grandmothers with weakened health become net-consumers rather than net-producers; they need more help and resources from their families and have reduced ability to invest in their grandchildren (Strassmann 2011; Chapman et al. 2019). In the current study, however, the survival status of the paternal grandmother was associated with lower death risk of the grandchildren from the age of four onwards. This suggest that in historical Lapland, also paternal grandmothers may have been able to promote the survival of their grandchildren after the weaning age. In order to compare the effects of maternal and paternal grandmothers in this population, however, both grandmothers should be included in the same model. In future studies, it would be interesting to investigate whether the survival status of the grandmother affects the association between the survival status of the other grandmother and the survival of the grandchildren in this population as well as whether the age of the grandmother is associated with the mortality risk of her grandchildren.

4.3. Geographical proximity of the grandmother and mortality of her grandchildren

As the survival status does not give information about where the grandmother has lived and whether she has been able to help the family, I investigated whether the grandmother's geographical proximity was associated with the survival of the grandchildren. To my knowledge, this was one of the first studies to investigate whether the grandmother's geographical proximity in kilometers is associated with the survival probability of her grandchildren.

Altogether, all grandmothers lived close to their grandchildren. 53% of the grandchildren were living in the same village as their maternal grandmother, and 78% of the grandchildren were living in the same village as their paternal grandmother. Additionally, only one maternal grandmother and two paternal grandmothers were living in a different parish than their grandchildren. Hence, it is possible that all grandmothers have lived close enough to be able to help the family.

The geographical proximity of the maternal grandmother was not associated with the grandchildren's mortality. Moreover, the geographical proximity of the maternal grandmother was not differently associated with the grandchildren's mortality depending on the age or sex of the grandchild or the degree of pastoralism of the family. The results could mean that a living maternal grandmother was always beneficial for the survival of her grandchildren regardless of where the grandmother has lived or, more likely, that the sample size of the grandmothers who have lived far from their grandchildren was so small that it did not allow detecting small differences statistically.

It should be noted that in the previous studies, the differences in grandmaternal effects have usually occurred on the parish level. That is, the grandmothers who have lived in the same parish as their grandchildren have had stronger positive effect on the survival of their grandchildren than the grandmothers who have lived in a different parish (Beise & Voland 2002; Lahdenperä et al. 2004). It is also noteworthy that the geographical distance likely has not had the same significance for all families. Nomadic families were used to traveling longer distances than sedentary families (Itkonen 1948). Based on this, one would predict that in sedentary families, the geographical proximity of the grandmother would have a stronger effect on the survival of her grandchildren than in nomadic families. However, the geographical proximity of the maternal grandmother was not differently associated with the mortality risk of the grandchildren depending on how nomadic lifestyle the family had. This further supports the idea that all grandmothers have lived close enough to be able to help the family. Moreover, sedentary and semi-nomadic maternal grandmothers lived closer to their grandchildren than nomadic maternal grandmothers in this population.

One limiting factor in my analysis is that the geographical proximity of the grandmother was measured between the birth village of a grandchild and the last known village of the grandmother. However, there was no information about the precise area in the village where the grandchild or the grandmother have lived. Thus, one source of error is that in some cases, people living in the neighboring villages have, in reality, lived closer together than people living in the same village. Another factor to be noted is that the sample size was considerably smaller than in the previous time-event models because only living grandmothers were included, and grandchild's and grandmother's home villages had to be known. The limiting factor for the analysis is, however, the number of events, i.e., the number of deaths, at different ages of the grandchildren and for different distances of the grandmother. The low number of deaths, particularly among the grandchildren of paternal grandmothers who have lived in a different village than their grandchildren, was the reason I performed the distance analysis only for maternal grandmothers. Overall, the low mortality of children in this population is interesting considering the fact that in preindustrial times, the mortality of children was usually high. It should be noted that the true level of mortality cannot be determined due to the large number of missing death entries which is a common problem with historical, demographic datasets. However, it has been reported before that in preindustrial Lapland, the mortality of infants and children has been lower than elsewhere in Finland at the same time (Enbuske, 2008).

Taken together, the results of this study show that the post-reproductive women of historical Lapland have been able to increase the lifetime reproductive success of their adult children while living long after ceasing their own reproduction: there have been more grandchildren surviving to adulthood when the grandmother has lived years after the age of 50. Moreover, the living maternal and paternal grandmothers likely have been able to reduce their grandchildren's mortality risk after the weaning age which is a critical time for survival of children. The geographical proximity of the maternal grandmother was not associated with the mortality risk of the grandchildren, and it is likely that all grandmothers have lived close enough to be able to help the family. The results of this study provide support for the hypothesis that the prolonged post-reproductive lifespan of women has evolved because grandmothers have been able to promote the lifetime reproductive success of their adult children, and thus, their own inclusive fitness.

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7. APPENDICES

Appendix 1. Presence of the maternal grandmother and mortality of her grandchildren in nomadic, semi-nomadic, and sedentary families

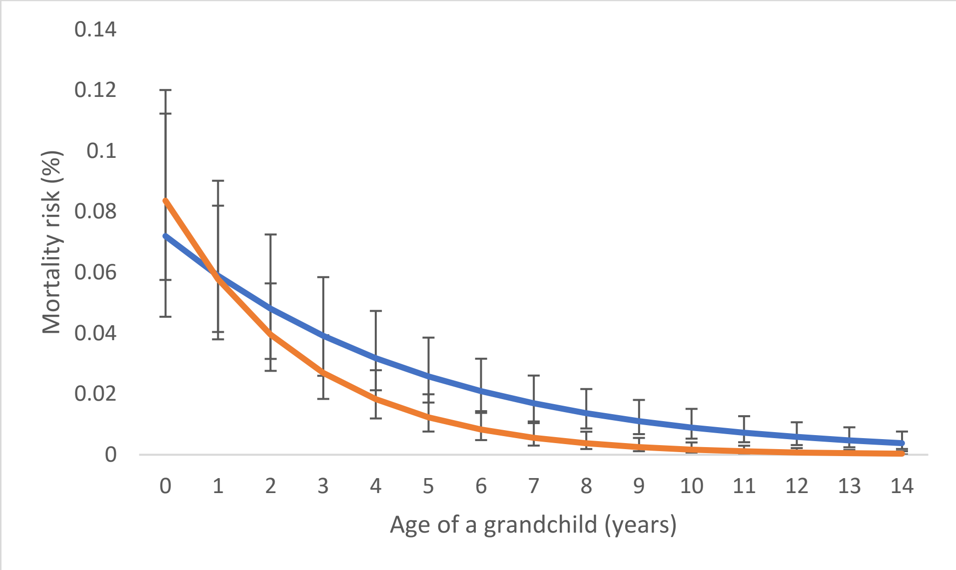

Figure 6. Nomadic grandchild's probability of dying in each age when the maternal grandmother was alive (orange) versus when the maternal grandmother was dead (blue). The figure shows model-derived prediction lines with 95% confidence intervals. Predictions were drawn for grandchildren who were born in the cohort 2 (between 1750–1790), were female, had a mother who was 32 years old when the child was born, had wealth of 2.12, and lived in Enontekiö (the highest proportion for categorical variables and the average for continuous variables).

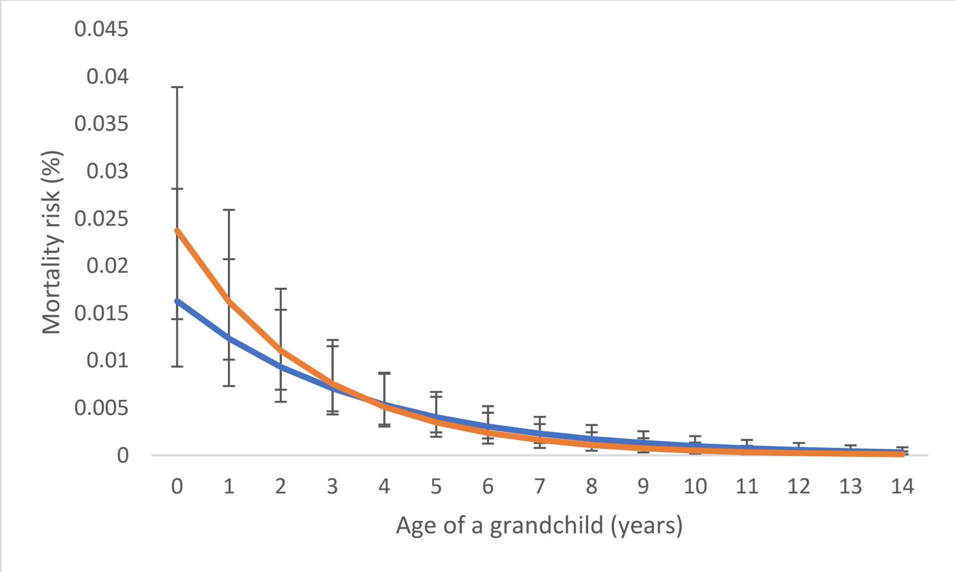

Figure 7. Semi-nomadic grandchild's probability of dying in each age when the maternal grandmother was alive (orange) versus when the maternal grandmother was dead (blue). The figure shows model-derived prediction lines with 95% confidence intervals. Predictions were drawn for grandchildren who were born in the cohort 3 (between 1800–1840), were female, had a mother who was 33 years old when the child was born, had wealth of 1.80, and lived in Inari (the highest proportion for categorical variables and the average for continuous variables).

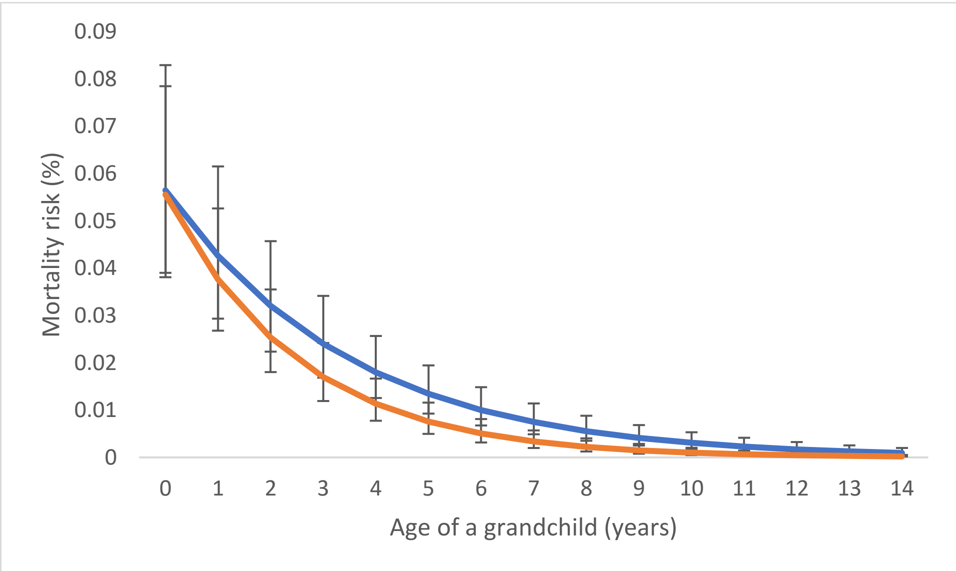

Figure 8. Sedentary grandchild's probability of dying in each age when the maternal grandmother was alive (orange) versus when the maternal grandmother was dead (blue). The figure shows model-derived prediction lines with 95% confidence intervals. Predictions were drawn for grandchildren who were born in the cohort 4 (between 1850–1890), were female, had a mother who was 32 years old when the child was born, had

wealth of 2.03, and lived in Inari (the highest proportion for categorical variables and the average for continuous variables).