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Evolutionary demography of agricultural expansion in preindustrial northern Finland

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A shift from nomadic foraging to sedentary agriculture was a major turning point in human evolutionary history, increasing our population size and eventually leading to the development of modern societies. We however lack understanding of the changes in life histories that contributed to the increased population growth rate of agriculturalists, because comparable individual-based reproductive records of sympatric populations of agriculturalists and foragers are rarely found. Here, we compared key life-history traits and population growth rate using comprehensive data from the seventieth to nineteenth century Northern Finland: indigenous Sami were nomadic hunter-fishers and reindeer herders, whereas sympatric agricultural Finns relied predominantly on animal husbandry. We found that agriculture-based families had higher lifetime fecundity, faster birth spacing and lower maternal mortality. Furthermore, agricultural Finns had 6.2% higher annual population growth rate than traditional Sami, which was accounted by differences between the subsistence modes in age-specific fecundity but not in mortality. Our results provide, to our knowledge, the most detailed demonstration yet of the demographic changes and evolutionary benefits that resulted from agricultural revolution.

1. Introduction

Major shifts in human speciation and evolution are suggested to have taken place during the Pleistocene (approx. 1.8 million to 12 000 years ago), a time period when humans were nomadic foragers practicing hunting and gathering [1]. After a rather rapid and recent development of agriculture (i.e. domestication of animals and plants) approximately 11–12 000 years ago (kya), larger permanent population settlements and higher population densities and growth rates emerged, but also presumably a decline in health and survival [2,3]. A common explanation for the increased, and perhaps less crash-prone [4,5], population growth since the invention of agriculture has been that the higher food production and better storage of resources, accompanied with sedentarism and dietary transition to a carbohydrate diet, led to higher a birth rate of agriculturalists (reviewed in [6–9]). The relative importance of fecundity versus mortality changes for population growth is however currently under debate [7,10–12], and surprisingly little is still known of the agriculture-related demographic changes that mediated the higher Darwinian fitness of agriculturalists compared with foragers.

To better understand how the transition from foraging to agriculture shaped human demography, one needs to compare the life histories of sympatric populations practising these different modes of subsistence using individual-based records [8]. The data required for such comparisons have been difficult to compile, and previous studies on agriculture-related influences on reproduction and

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mortality have mainly been based on cross-cultural comparisons [6] and archaeological and palaeodemographic data that have their own inherent caveats [7,8]. Most importantly, data on individual-level fitness components, i.e. lifetime reproductive scheduling and success, have been largely lacking [13]. An additional complication has been that in some areas where foragers and agriculturalists live in sympatry, they have already been influenced by modern lifestyles [6,14], making the conclusions based on these data problematic. Only few studies have thus focused on individual-level records and investigated variation in underlying life-history traits that are assumed to be related to differential overall reproductive rates and evolutionary success of agriculturalists. Kramer & Greaves [15] studied 73 contemporary Pume mothers, an ethnic group of Native South Americans, by calculating their total fertility rates, infant mortality and birth intervals. These women consist of two groups: the savannah Pume are foragers migrating during dry and wet seasons, and experience nutritional stress especially during the wet season, whereas the horticulturalist river Pume inhabit permanent villages all year round and have better nourishment compared with savannah Pume. In line with the expectations, Kramer & Greaves [15] found that river Pume have shorter interbirth intervals, better infant survival, higher parity and more surviving children than the savannah Pume. While demonstration of differences in such life-history traits is valuable, they are not necessarily informative in contrasting the expected population growth rates of people adhering to different livelihoods. This is because population growth rate is an integrated measure of performance of a set of individuals regarding multiple life-history traits, which may show trade-offs [16]. In particular, population growth rates are typically considered to be rate-sensitive, where early-life reproduction and survival contribute disproportionally more to growth rates than late-life performance. Hence, studies using larger samples and measuring the population growth rates of the competing subsistence modes are needed to properly understand the demographic changes during agricultural expansion.

We compared the evolutionary demography of indigenous Sami to sympatric settled agricultural Finns in Northern Finland between the seventeenth and nineteenth centuries. During the study period, the main subsistence mode differed between these monogamous Sami and Finns, the Sami practising predominantly hunting, fishing and gathering and, to a lesser extent, nomadic reindeer herding, whereas the Finns were almost exclusively agriculturalists, relying on animal husbandry (pastoral farming or dairy farming) [17,18]. We examined: (i) whether key life-history traits differed between families practising traditional livelihoods and agriculture, and (ii) by using matrix population models of whether population growth rates differed between these two livelihoods using data from 2938 families. We expect that agricultural families had higher reproductive success, perhaps, irrespective of their higher parental mortality, which should eventually be manifested as a faster population growth rate.

Our dataset has novel assets for addressing these aims. First and most importantly, in addition to information on livelihood, our data include information on the ethnic background of families. This is important, because cultural practices may influence life-history strategies and genetically Sami and Finns are two distinct groups [19]. Second, our study period predates the demographic transition (i.e. gradual shift to lower birth and death rates) in Finland and the introduction of modern medical care or birth control methods among either of the groups. This study is also, to our knowledge, the first to contrast the relative age-specific fecundity and mortality contributions to population growth rates and, thus, first to answer the question of the relative importance of reproduction versus mortality changes for agricultural population expansion [7].

2. Material and methods

(a) Demographic data

Our data on the historical Sami and Finns were extracted from historical parish registers kept by the Lutheran church [20], consisting of Utsjoki, Inari, Enontekiö and Sodankylä parishes that situate in Northern Finland. These registers consist of continuous baptism, burial and marital records of the parishes. The ethnicity of the inhabitants, based on nomenclature, was determined from the parish records by a professional historian (M. Enbuske). The origin of Sami is not yet fully understood, but they probably inhabited Finland in few numbers since the last glacial epoch (ending in Finland around 10 000 years ago) before the ancestors of Finns came mainly from Estonia approximately 2000 years ago [19].

The expansion of Finns to Northern Finland was supported by the legislations from the Swedish crown [18]. The first Finnish settlers arrived at Sodankylä and Enontekiö parishes during the middle of the seventeenth century [18]. In Enontekiö, they had almost entirely populated the parish towards the end of the nineteenth century, mainly because of the closing of Swedish and Norwegian borders in 1809 and 1852, respectively, which excluded many reindeer herding Sami of Enontekiö and Utsjoki parishes from Finnish church registers [18]. In Inari parish, the first Finnish settlers arrived approximately a century later, but in low numbers, and their population did not start to increase until the middle of nineteenth century [17,18]. The inhabitants of Utsjoki parish were exclusively Sami until the end of the nineteenth century [18]. Marriages between Sami and Finns consisted of just a few percentage of all marriages [18]. The population size of settled Finns was almost solely owing to intrinsic increase, because immigration from Southern parts of the country was negligible until the end of the nineteenth century [18].

Until the middle of the eighteenth century, all the Sami living in our study parishes were nomadic foragers, practising mainly hunting and fishing and small-scale gathering. During the study period, the Sami started to diverge in their chief source of livelihood, except in Inari parish where the Sami remained as hunters and fishers. The Sami of Enontekiö parish started to practise nomadic reindeer herding [17,18]. In Utsjoki parish, some Sami families started to practise nomadic reindeer herding (approx. 40% at the beginning of the nineteenth century although their numbers dropped dramatically after the closing of Norwegian border in 1852), whereas others continued to practise their main livelihood, fishing [17,18]. The hunter-fisher Sami of Utsjoki and Inari parish were naturally less mobile compared with reindeer herding Sami who lived in temporary tents and followed the seasonal migrations of their reindeer [17]. By contrast, the settled Finns were sedentary agriculturalists, practising mainly animal husbandry (or pastoral/dairy farming) by raising cattle and sheep and small-scale unsophisticated farming (mainly barley and also potatoes towards the end of the nineteenth century) [17,18]. Environmental conditions were harsh and unfavourable for crop cultivation owing to low average annual mean temperature and short growth season [17].

Note that classifying the reindeer herding Sami as traditional foragers may be problematic, because their lifestyle resembled that of pastoralists, which are considered as agriculturalists

Table 1. Descriptive statistics of the variables studied between the Sami and Finns of Northern Finland, divided by the main livelihood of the families.

	Sami				Finns			
	traditional		agricultural		traditional		agricultural	
trait	*n*	mean (s.d.)	*n*	mean (s.d.)	*n*	mean (s.d.)	*n*	mean (s.d.)
number of offspring born	1366	3.82 (2.8)	613	4.04 (2.8)	62	3.58 (2.6)	870	4.07 (3.3)
% of offspring surviving	1163	77.0 (27.9)	549	82.7 (25.3)	52	75.9 (27.8)	723	82.0 (25.1)
mother's age at first reproduction	881	27.1 (5.9)	510	27.0 (5.5)	45	27.2 (4.7)	632	26.0 (5.6)
mother's age at last reproduction	881	38.1 (6.9)	510	36.7 (7.0)	45	37.0 (6.4)	632	36.2 (7.6)
mean interbirth interval	881	2.11 (1.1)	510	1.83 (1.1)	45	1.95 (0.8)	632	1.71 (1.0)
maternal lifespan[a]	933	70 (68, 72)	522	65 (59, 69)	48	60 (45, 64)	648	67 (63, 69)
paternal lifespan[a]	994	67 (66, 68)	547	71 (69, 73)	51	67 (58, 70)	661	69 (65, 72)

[a] The value given is median survival time (95% CIs) estimated by the Kaplan–Meier method accounting for right-censoring.

[21]. The key difference between reindeer herding Sami and pastoralists in favour of Sami herding being a forager strategy (as considered in [21]) is that their reindeers were semi-wild as Sami did not control the foraging behaviour or reproduction of their herds [18]. Moreover, current anthropological literature acknowledges that traditional strict distinction between prehistoric foraging and farming is too simplistic and fails to recognize the probable wide spectrum of livelihoods that existed between the ends of the forager–farming continuum [21].

Our study included individuals who were born between the years 1641 and 1884, a total of 3054 families. For these families, we recorded several life-history traits that have previously been shown to be important fitness components in these populations [20]: a mother's ages at first and last reproduction and her mean interbirth interval, lifetime fecundity, offspring survival to adulthood (18 years old) and parental lifespans (table 1). In order to control for temporal and spatial variation, birth cohort (before 1740, 1740–1790, later than 1790) based on the women's birth year and study parish was recorded. Because birth year was missing for some women, our final sample size was 2938.

(b) Statistical analysis

(i) Comparison of life histories

Structural equation modelling (SEM) [22] was used to estimate the differences in the life-history traits recorded between the livelihoods, ethnicity and their interaction, controlling for temporal and spatial variation. The independent variables were effect coded, meaning that comparisons were made against the overall mean of the trait(s). This makes the simultaneous interpretation of the now orthogonal main terms and their interaction more straightforward (note that dummy coding produces essentially the same results for these data). All response variables were treated as continuous, except maternal and paternal lifespan that were treated as continuous-time survival variables with right-censoring (age at last reproduction was used as event time in the cases of missing data on age at death), estimated by Cox regressions [23]. Prior to the SEM analysis, the assumption of proportional hazards was tested by performing Cox regression models for both maternal and paternal lifespan by including time-dependent effects of subsistence mode and ethnicity into the models [24] using SAS statistical package version 9.4 (SAS Institute Institute, Cary, NC, 2002–2013). No evidence for the non-proportional influence of livelihood and ethnicity was found for maternal ($\chi^2_2 = 2.77$, $p = 0.25$) and paternal lifespan ($\chi^2_2 = 0.29$, $p = 0.87$). All the residual errors of dependent variables were allowed to correlate, because the traits were measured from the same families. Because the error term is not defined for Cox equations by default, they were estimated by constructing random latent factors for which the loading of a survival outcome and factor variance were fixed at unity and a factor mean was fixed to zero. The loadings of other dependent variables on those factors represent residual covariances between the survival outcomes and dependent variables. Owing to the inclusion of time-to-event outcomes, no commonly used test statistics and fit indexes were available to examine the overall fit of the model to the data as means, variances and covariances are not sufficient for model estimation in this case. SEM was estimated with a robust maximum-likelihood estimator that is insensitive to non-normal outcomes using MPlus version 7.11 [25]. Missing data on dependent variables were handled using full information maximum-likelihood estimation that assumes data are missing at random.

(ii) Comparison of population growth rates using life table response experiment

The information on reproduction and survival contained in a life table allows calculating the projected population growth rate λ following standard matrix modelling (Leslie matrix, [25]). Based on Leslie matrices specific to each ethnicity and livelihood (i.e. 2×2 factorial design), a linear additive function was constructed to detail how the levels of these factors affect λ; a so-called life table response experiment (LTRE) [26]. An LTRE first considers how the factorial levels and their interaction affect age-specific reproduction and survival, when compared with the λ of a matrix which is the arithmetic mean of, in our case, four Leslie matrices (2×2 factorial design of factors ethnicity and livelihood). In a second step, the so-called contributions of the differences in age-specific fecundity and survival across factorial levels to a change in λ are calculated [26]. Because λ is a rate-sensitive measure of fitness, large differences in fecundity or mortality across factorial levels do not necessarily make large contributions to a change in λ. In particular, in a growing population, reproduction and survival contribute more to population growth rate at early ages then at late age. For ease of interpretation, we here recalculated all contributions to a change in λ as

Table 2. Results of SEM comparing the life-history traits between families of different livelihoods, ethnicity and their interaction. (Parameter estimates for birth cohort and study parish as well as residual covariances among traits have been omitted for simplicity. Note that parameters of parental lifespan are on a log scale).

	β	s.e.	*z*-value	*p*-value
total number of offspring				
livelihood	0.265	0.100	2.658	0.008
ethnicity	−0.048	0.096	−0.503	0.615
livelihood × ethnicity	−0.020	0.096	−0.210	0.833
offspring survival to adulthood				
livelihood	0.450	1.120	0.399	0.690
ethnicity	0.860	1.250	0.686	0.493
livelihood × ethnicity	−0.200	0.590	−0.344	0.731
maternal interbirth interval				
livelihood	−0.110	0.037	−2.971	0.003
ethnicity	−0.029	0.036	−0.813	0.416
livelihood × ethnicity	−0.070	0.037	−1.925	0.054
maternal age at first reproduction				
livelihood	−0.150	0.210	−0.699	0.484
ethnicity	0.100	0.210	0.461	0.645
livelihood × ethnicity	−0.220	0.210	−1.058	0.290
maternal age at last reproduction				
livelihood	−0.130	0.270	−0.464	0.643
ethnicity	−0.070	0.270	−0.252	0.801
livelihood × ethnicity	−0.480	0.270	−1.776	0.076
maternal lifespan				
livelihood	−0.333	0.147	−2.261	0.024
ethnicity	0.193	0.110	1.754	0.079
livelihood × ethnicity	−0.124	0.135	−0.921	0.357
paternal lifespan				
livelihood	−0.023	0.087	−0.259	0.796
ethnicity	−0.119	0.113	−1.049	0.294
livelihood × ethnicity	0.133	0.094	1.405	0.160

contrasts to the contributions made by the corresponding matrix elements in the Leslie matrix for traditional Sami (see the electronic supplementary material).

Contributions to a change in λ owing to fecundity and survival differences were reported separately, either grouped over all age classes or grouped in age classes of 10 years. However, we do not report the contributions of age classes above 60 to population growth rate separately because these were negligible.

The life table specific to each ethnicity and livelihood was constructed on the basis of a variable number of individuals. We took the demographic uncertainty inherent to these differences in ‘cohort size’ forward into the LTRE by Monte Carlo simulations. In each of 1000 simulation rounds, we assumed the number of female offspring to be equal to the number of individuals belonging to each combination of ethnicity and livelihood on which the life table was based. In each simulation round, simulated life tables were constructed for each combination of ethnicity and livelihood by making random draws for the number of women surviving for age x to age $x+1$ from a binomial distribution, assuming that expected age-specific survival followed the estimated life table specific to each ethnicity and livelihood. Similarly, age-specific demographic fecundity was simulated based on estimated age-specific fecundity and the twinning rate observed for each ethnicity and livelihood. An LTRE was performed on each of these simulated life tables. We used a density kernel to estimate the mode and 95% credible interval (CRI) of all LTRE contrasts. The entire LTRE procedure was conducted in R [27]. Details and R scripts are provided in the electronic supplementary material.

3. Results

(a) Comparison of life histories

We found considerable differences between the livelihoods in a number of life-history traits. Agricultural lifestyle significantly increased the total number of offspring born to a family by 0.27 children (95% confidence intervals (CIs) = 0.07, 0.46) from population mean, with the average number (s.d.) of offspring born to families practising traditional

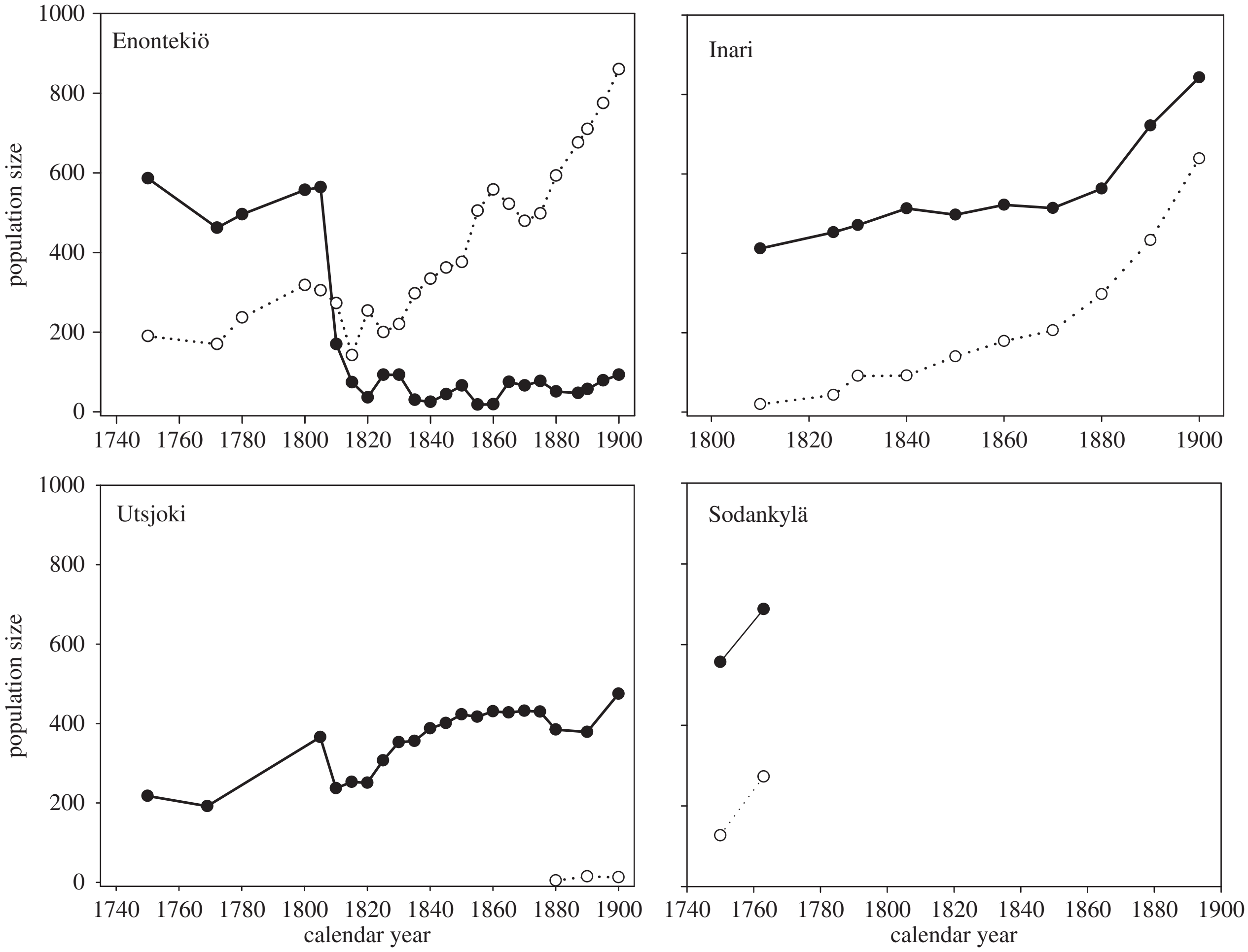

Figure 1. Temporal variation of population size among Finns (open circles) and Sami (filled circles) in study parishes (data from Statistics Finland). For comparison, it is estimated that in the year 1750 there was a total of 2022 inhabitants in Finnish Lapland, whereas the corresponding numbers in the years 1850 and 1900 were 4437 and 10357, respectively [18]. Note that the population decline of Sami of Enontekiö was due to the closing of the Swedish border in 1809 that excluded many nomadic Sami families from Finnish church registers and in Sodankylä, the determination of ethnicity from national statistic becomes unavailable at the end of the nineteenth century.

livelihoods equating to 3.8 (2.8) and to families practising agriculture 4.1 (3.1; table 2). Both types of families raised a similar percentage of these offspring to adulthood compared with population mean with families practising agriculture raising 82.3% (25.2) of the born offspring into adulthood and families practising traditional livelihoods 76.9% (27.9; table 2). The larger family size of agricultural lifestyle was partly achieved by this lifestyle being associated with shorter birth-intervals: the mean interbirth interval for women in agricultural families was 1.8 (1.0) years, whereas women in traditional livelihoods had another birth on average every 2.1 (1.1) years. Compared with population mean, the mean interbirth interval of agricultural women was reduced by 0.11 (95% CI = −0.18, −0.04) years. The influence of livelihood on maternal interbirth intervals tended to also be moderated by ethnicity (table 2), with maternal mean interbirth interval being further reduced by 0.07 (95% CIs = −0.14, 0.00) years among agricultural Finns. Women in agricultural families also experienced a 72% (95% CI = 0.51, 0.92) lower hazard of death than other women in the population. Maternal age at first and last reproduction and paternal mortality did not vary between livelihoods, and ethnicity did not independently influence any of the traits studied (table 2).

When we excluded the Enontekiö Sami from the analyses ($n = 730$), who were nomadic reindeer herders during the study period (see Material and methods), we obtain largely the same results (see the electronic supplementary material, table S1).

(b) Comparison of population growth rates

The population of Finnish Lapland in general increased during the study period owing to high fertility and, most importantly, low mortality which was due to absence of severe disease epidemics compared with the rest of Finland [18]. The increasing trend in population size is also seen in our study parishes (figure 1).

The LRTE showed that the population growth rates (95% credible intervals (CRI)) for traditional Sami and Finns were 1.0343 (1.0331, 1.0357) and 1.0337 (1.0259, 1.0383), respectively. Agricultural livelihood among both ethnic groups was associated with somewhat higher population growth rate: the population growth rate for agricultural Sami was 1.0367 (1.0347, 1.0384), whereas for agricultural Finns, it was 1.0407 (1.0350, 1.0448). That is, agricultural Finns had 6.2% higher annual population growth rate than traditional Sami. Over 100 years, this means that the projected population size of agricultural Finns exceeded that of forager Sami by 86%.

When partitioning out the contributions of age-specific fecundity to the population growth rate of agricultural versus traditional livelihoods, we found that having an agricultural

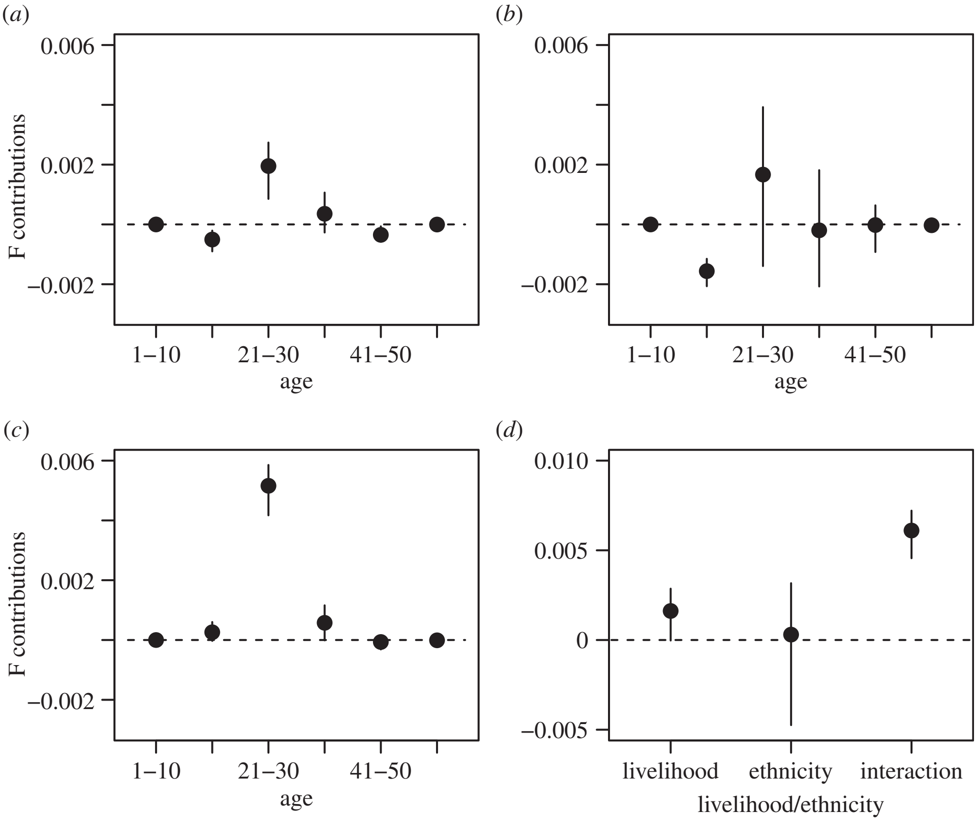

Figure 2. Contrast contributions to population growth rate caused by fecundity (F) and their 95% CRI. Values are contrasts to the contribution of corresponding elements in the population projection matrix for traditional Sami caused by the factors livelihood ((*a*), contrasting agricultural versus traditional livelihoods), ethnicity ((*b*), contrasting Finns against Sami people) and their interaction ((*c*), contrasting agricultural Finns against traditional Sami). (*a*–*c*) show the age-specific contributions for ages 1–60 grouped in age classes of ten years. (*d*) sums up all the age-specific contributions (ages 1–100).

livelihood makes a positive fecundity contribution to population growth rate during ages 21–30, and particularly among agricultural Finns, when reproductive rates in general were also highest, whereas there were little differences between the livelihoods at other ages (figure 2*a*,*c*). Some differences in age-specific fecundity were also explained by the ethnic background: Finns had a significantly lower fecundity contribution compared with Sami at the very early age-class (ages 11–20), but the differences at other ages were small when considering ethnicity alone (figure 2*b*). Summing up over all age-classes, there was some evidence that fecundity benefits associated with an agricultural livelihood increase population growth, although the lower CRI does narrowly include zero (figure 2*d*). Furthermore, the significant interaction between ethnicity and livelihood provided strong evidence that being an agricultural Finn increases population growth rate (figure 2*d*), because of higher fecundity at prime reproductive ages (21–30), making a strong contribution to population growth rate. The corresponding contrasts for survival contributions showed that neither ethnicity nor livelihood makes independent contributions to population growth (figure 3).

Excluding the Enontekiö Sami from life tables does not qualitatively change our conclusions (see the electronic supplementary material, figures S1–S2).

4. Discussion

Despite the long cross-disciplinary interest in understanding transitions from foraging to agriculture, we still lack knowledge of how these two livelihoods affected the demographic variation in sympatric populations. Our data from historical Northern Finland provide novel insights into this question by showing that agricultural families depending mainly on animal husbandry (mainly Finns) had higher fecundity, faster birth spacing and lower maternal mortality compared with the rest of the population. As a result, the annual estimated population growth rate of agricultural Finns was 6.2% higher compared with traditional Sami. Disregarding the reindeer herding Sami of Enontekiö parish that had a lifestyle close to agricultural pastoralists did not change these conclusions.

Our study extends the current knowledge based on cross-cultural comparisons [6] and archaeological and palaeodemographic data [7,8]. No earlier study has been able to compare sympatric but virtually non-mixing populations of agriculturalists and foragers using complete individual-level life histories and who have similar access (or no access) to healthcare, and investigated how the differences in fecundity and mortality translate to population growth rate. Along with a larger geographical population trend, both the Finns and Sami showed population growth during the study period, but the population of agricultural Finns grew fastest and significantly exceeded that of the traditional Sami foragers. The faster population growth rate of agricultural Finns was largely intrinsic in nature, because the immigration from the Southern parts of the country was negligible at the time [18].

The relative importance of fecundity versus mortality changes contributing to high population growth following the agricultural expansion has been under debate for decades [7,10–12]. Here, to the best of our knowledge, for the first time, we contrasted the relative influences of age-specific fecundity and mortality on differences in population growth rates

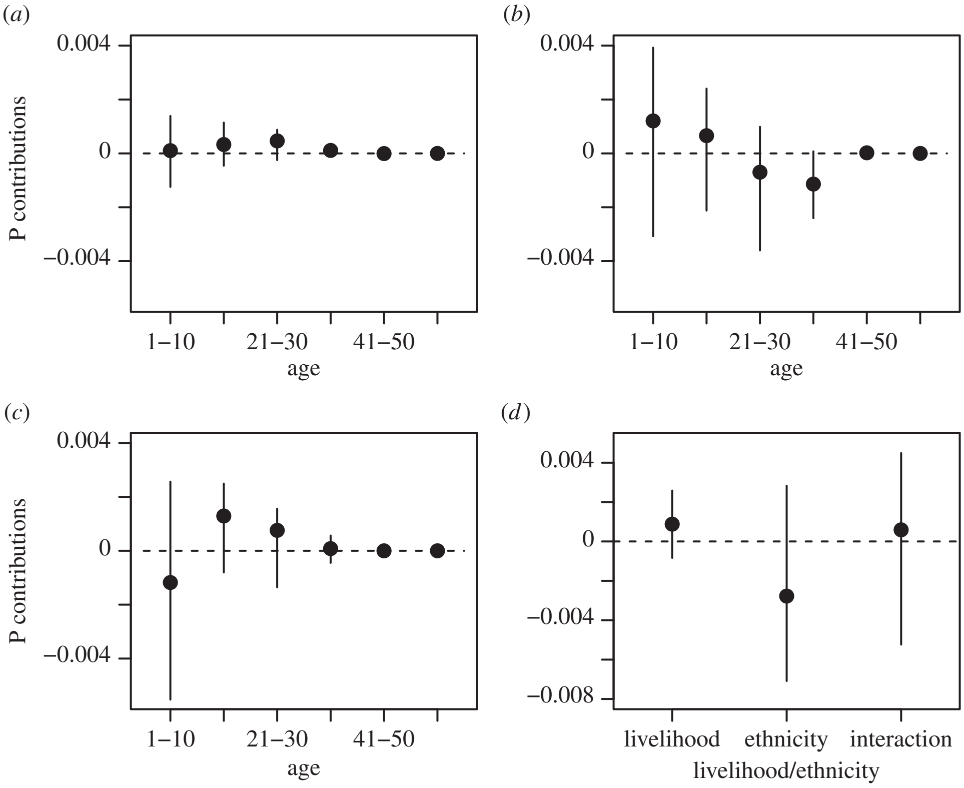

Figure 3. Contributions to population growth rate caused by survival (P) and their 95% CRI. Contributions here denote contrasts to the contribution of corresponding elements in the population projection matrix for traditional Sami due to livelihood ((*a*), contrasting agricultural versus traditional livelihoods) to ethnicity ((*b*), contrasting Finns against Sami people) and their interaction ((*c*), contrasting agricultural Finns against traditional Sami). (*a*–*c*) show the age-specific contributions for ages 1–60 grouped in age classes of 10 years. (*d*) sums up all the age-specific contributions.

between foragers and agriculturalist. Our results show that in historical Northern Finland the higher population growth rate of agriculturalists over foragers was owing to differences in fecundity contributions and not mortality contributions. More specifically, the stronger fecundity component of population growth rate that was seen especially in agricultural Finns was owing to their higher fecundity contribution during the primary reproductive ages, i.e. the ages of 21–30 years. This is in accord to a previous study among partly the same populations (but without making a distinction between Sami and Finns or agriculturalist and foragers) using individual finite rate of increase (λ_{ind}) as a fitness measure [28], which is however not directly comparable to population-level λ.

In contrast to the common beliefs of adverse survival and health consequences following agricultural transition, we found that adult-age mortality of mothers in agricultural families was lower than expected, whereas male mortality seemed unrelated to subsistence mode. Moreover, we found no livelihood-based difference in mortality prior to adulthood. The commonly made argument of higher mortality accompanying transition to agriculture is based on the indirectly inferred and error-prone archaeological and palaeodemographic data [7], although not all such studies have found mortality-differences between agriculturalists and foragers [29]. Our study thus stands out by being, to our knowledge, the first to directly contrast the lifelong mortality differences between foragers and agriculturalists.

Cross-cultural comparisons have suggested that intensive farmers, not horticulturalist, enjoy higher reproductive success compared with foragers [6,13]. Our results do not seem to support this conclusion, because in preindustrial Northern Finland where environmental conditions were unfavourable for intensive farming, agricultural lifestyle based on animal husbandry was sufficient to increase the fecundity of agriculturalist above sympatric foragers. The higher fecundity of agriculturalists compared with foragers has been suggested to relate to sedentary lifestyle and to shift to a carbohydrate diet [6–9]. Although forager Sami were clearly more mobile than agricultural Finns, sedentary lifestyle has been suspected not to fully explain fecundity differences among foragers and agriculturalists globally [4]. As the agricultural Finns in Northern Finland relied on dairy products instead of intensive farming, their diet did not markedly differ from that of forager Sami. Therefore, dietary differences provide an unlikely explanation for the differences observed in foragers and agriculturalists in preindustrial Northern Finland.

Transition to agriculture may also have facilitated earlier weaning and shorter birth intervals [30,31]. In line with this, agricultural Finns showed shorter birth spacing than forager Sami. In their cross-cultural study, Sellen & Smay [32], however, found that subsistence mode was not strongly associated with breastfeeding and weaning practices. The Sami started to introduce solid foods to infants at the age of six months but continued breastfeeding until they were 1.5–2 years old or older [17]. By contrast, infants of agricultural Finns were generally fed by cows milk [33,34]. Moreover, energetic stress may have suppressed female reproductive function more among foraging Sami women owing to their higher energy expenditure through, for example, work load, breastfeeding and mobility [6,35,36]. Therefore, the different nursing (mainly lactation) customs between Sami and Finns may have been proximate mechanisms responsible for the differences in interbirth intervals and fecundity found here.

Although our findings generally support the currently favoured demographic diffusion model of agricultural expansion over a cultural diffusion model [37], cultural transmission of traits or knowledge (e.g. agricultural technologies) could also partly explain the demographic changes accompanied by agricultural revolution [38,39]. This might provide the answer for why subsistence mode directly did not have a strong influence on population growth rate, but only among families of Finnish ethnicity. In other words, the settled Finns were already familiar with agricultural practices when arriving in Northern Finland, whereas the indigenous Sami had no prior experience of such practices.

Nevertheless, because the sympatric Sami and Finns were genetically distinct groups [19] and because several human life-history traits have been shown to be partly genetically determined in preindustrial European agricultural populations [40,41], we cannot overlook the possibility that the demographic differences found may have partly resulted from the genetic differences between the groups. Although separating the genetic influences from cultural ones by accounting for ethnicity is not possible, we found no indication that such influences would have directly explained the demographic variation in this population.

Our study provides, to our knowledge, the most comprehensive and detailed evidence yet of the demographic changes accompanied with agricultural way of life and how these changes translated to higher population growth rate over sympatric foragers in preindustrial era. As already evident in this population, agricultural lifestyle of animal husbandry started to take over the traditional Sami livelihoods: 32% of Sami families in these data adopted more of an agricultural way of life during the study period. This adoption of livelihoods was not however totally asymmetrical, because at the end of the nineteenth century 6.5% of Finns had adopted reindeer herding as their secondary livelihood [18]. How these results compare with the origin of agriculture during Neolithic or agricultural expansions in other areas during prehistory remain currently unknown because, for example, similar individual-based datasets between different sympatric subsistence modes over time are rare.

Data accessibility. Access to the data analysed in this study may be requested by contacting S.H. (sayrhe@utu.fi).

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References

1. Hrdy SB. 2000 *Mother nature: maternal instincts and how they shape the human species*. London, UK: Vintage.
2. Lewin R, Foley R. 2004 *Principles of human evolution*. Malden, MA: Blackwell Science Ltd.
3. Gupta AK. 2004 Origin of agriculture and domestication of plants and animals linked to early Holocene climate amelioration. *Curr. Sci.* **87**, 54–59.
4. Boone JL. 2002 Subsistence strategies and early human population history: an evolutionary ecological perspective. *World Arch.* **34**, 6–25. (doi:10.1080/00438240220134232)
5. Tallavaara M, Seppä H. 2011 Did the mid-Holocene environmental changes cause the boom and bust of hunter–gatherer population size in eastern Fennoscandia. *The Holocene* **22**, 215–225. (doi:10.1177/0959683611414937)
6. Bentley GR, Paine RR, Boldsen JL. 2001 Fertility changes with the prehistoric transition to agriculture. In *Reproductive ecology and human evolution* (ed. PT Ellison), pp. 203–231. New York, NY: Aldine de Gruyter.
7. Gage TB, deWitte S. 2009 What do we know about the agricultural demographic transition? *Curr. Anthropol.* **50**, 649–655. (doi:10.1086/605017)
8. Bocquet-Appel J-P. 2011 The agricultural demographic transition during and after the agriculture inventions. *Curr. Anthropol.* **52**, S497–S510. (doi:10.1086/659243)
9. Volk AA, Atkinson JA. 2013 Infant and child death in the human environment of evolutionary adaptation. *Evol. Hum. Behav.* **34**, 182–192. (doi:10.1016/j.evolhumbehav.2012.11.007)
10. Pennington RL. 1996 Causes of early human population growth. *Am. J. Phys. Anthropol.* **99**, 259–274. (doi:10.1002/(SICI)1096-8644(199602)99:2<259::AID-AJPA4>3.0.CO;2-U)
11. Sellen DW, Mace R. 1999 A phylogenetic analysis of the relationship between sub-adult mortality and mode of subsistence. *J. Biosoc. Sci.* **31**, 1–16. (doi:10.1017/S0021932099000012)
12. Kramer KL, Boone JL. 2002 Why intensive agriculturalists have higher fertility: a household energy budget approach. *Curr. Anthropol.* **43**, 511–517. (doi:10.1086/340239)
13. Bentley GR, Jasienska G, Goldberg T. 1993 Is the fertility of agriculturalists higher than that of nonagriculturalists? *Curr. Anthropol.* **34**, 778–785. (doi:10.1086/204223)
14. Marlowe FW. 2005 Hunter–gatherers and human evolution. *Evol. Anthropol.* **14**, 54–67. (doi:10.1002/evan.20046)
15. Kramer KL, Greaves RD. 2007 Changing patterns of infant mortality and maternal fertility among Pumé foragers and horticulturalist. *Am. Anthropol.* **109**, 713–726. (doi:10.1525/aa.2007.109.4.713)
16. Stearns SC. 1992 *The evolution of life-histories*. Oxford, UK: Oxford University Press.
17. Itkonen T. 1948 *Suomen Lappalaiset*, vol. 2. Porvoo, Sweden: WSOY.
18. Enbuske M. 2008 *Vanhan Lapin valtamailla: asutus ja maankäyttö Kemin Lapin ja Enontekiön alueella 1500-luvulta 1900-luvun alkuun*. Helsinki, Finland: Suomen Kirjallisuuden Seura.
19. Norio R. 2000 *Suomineidon geenit*. Keuruu, Finland: Otava.
20. Helle S, Lummaa V, Jokela J. 2005 Are reproductive and somatic senescence coupled in humans? Late, but not early, reproduction correlated with longevity in historical Sami women. *Proc. R. Soc. B* **272**, 29–37. (doi:10.1098/rspb.2004.2944)
21. Barker G. 2006 *The agricultural revolution in prehistory. Why did foragers become farmers?* New York, NY: Oxford University Press Inc.
22. Green SB, Thompson MS. 2012 A flexible structural equation modeling approach for analyzing means. In *Handbook of structural equation modeling* (ed. RH Hoyle), pp. 393–416. New York, NY: The Guilford Press.
23. Cox DR. 1972 Regression models and life tables. *J. R. Stat. Soc.* **B34**, 187–220.
24. Allison PD. 2010 *Survival analysis using SAS: a practical guide*, 2nd edn. Cary, NC: SAS Institute Inc.
25. Muthén LK, Muthén BO. 1998–2012 Mplus user's guide, 7th edn. Los Angeles, CA: Muthén & Muthén.
26. Caswell H. 2001 *Matrix population models. Construction, analysis and interpretation*, 2nd edn. Sunderland, MA: Sinauer Associates, Inc.
27. R Core Team. 2012 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
28. Käär P, Jokela J. 1998 Natural selection on age-specific fertilities in human females: comparison of individual-level fitness measures. *Proc. R. Soc. Lond. B* **265**, 2415–2420. (doi:10.1098/rspb.1998.0592)
29. Gage TB. 2000 Demography. In *Human biology: an evolutionary and biocultural approach* (eds S Stinson, B Bogin, R Huss-Ashmore, D O'Rourke), pp. 507–552. New York, NY: John Wiley and Sons.
30. Buikstra J, Konigsberg L, Bullington J. 1986 Fertility and the development of agriculture in the prehistoric Midwest. *Am. Antiquity* **51**, 528–546. (doi:10.2307/281750)

31. Larsen CS. 1995 Biological changes in human populations with agriculture. *Ann. Rev. Anthropol.* **24**, 185–213. (doi:10.1146/annurev.an.24.100195.001153)
32. Sellen DW, Smay D. 2001 Relationship between subsistence and age at weaning in 'preindustrial' societies. *Hum. Nat.* **12**, 47–87. (doi:10.1007/s12110-001-1013-y)
33. Moring B. 1998 Motherhood, milk, and money: infant mortality in pre-industrial Finland. *Social His. Med.* **11**, 177–196. (doi:10.1093/shm/11.2.177)
34. Thorvaldsen G. 2008 Was there a European breastfeeding pattern? *Hist. Famil.* **13**, 283–295. (doi:10.1016/j.hisfam.2008.08.001)
35. Jasienska G. 2001 Why energy expenditure causes reproductive suppression in women. In *Reproductive ecology and human evolution* (ed. PT Ellison), pp. 59–84. New York, NY: Aldine de Gruyter.
36. Larsen CS. 2005 The agricultural revolution as environmental catastrophe: implications for health and lifestyle in the Holocene. *Quater. Int.* **150**, 12–20. (doi:10.1016/j.quaint.2006.01.004)
37. Gignoux CR, Henn BM, Mountain JL. 2011 Rapid, global demographic expansions after the origins of agriculture. *Proc. Natl Acad. Sci. USA* **108**, 6044–6049. (doi:10.1073/pnas.0914274108)
38. Borgerhoff Mulder M, Nunn CL, Towner MR. 2006 Cultural macroevolution and the transmission of traits. *Evol. Anthropol.* **15**, 52–64. (doi:10.1002/evan.20088)
39. Fogarty L, Creanza N, Feldman MW. 2013 The role of cultural transmission in human demographic change: an age-structured model. *Theor. Popul. Biol.* **88**, 68–77. (doi:10.1016/j.tpb.2013.06.006)
40. Pettay JE, Kruuk LEB, Jokela J, Lummaa V. 2005 Heritability and genetic constraints of life-history trait evolution in pre-industrial humans. *Proc. Natl Acad. Sci. USA* **102**, 2838–2843. (doi:10.1073/pnas.0406709102)
41. Gögele M, Pattaro C, Fuchsberger C, Minelli C, Pramstaller PP, Wjst M. 2011 Heritability analysis of life span in a semi-isolated population followed across four centuries reveals the presence of pleiotropy between life span and reproduction. *J. Gerontol. A. Biol. Sci. Med. Sci.* **66A**, 26–37. (doi:10.1093/gerona/glq163)