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Food and fitness: associations between crop yields and life-history traits in a longitudinally monitored pre-industrial human population

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Severe food shortage is associated with increased mortality and reduced reproductive success in contemporary and historical human populations. Studies of wild animal populations have shown that subtle variation in environmental conditions can influence patterns of mortality, fecundity and natural selection, but the fitness implications of such subtle variation on human populations are unclear. Here, we use longitudinal data on local grain production, births, marriages and mortality so as to assess the impact of crop yield variation on individual age-specific mortality and fecundity in two pre-industrial Finnish populations. Although crop yields and fitness traits showed profound year-to-year variation across the 70-year study period, associations between crop yields and mortality or fecundity were generally weak. However, post-reproductive individuals of both sexes, and individuals of lower socio-economic status experienced higher mortality when crop yields were low. This is the first longitudinal, individual-based study of the associations between environmental variation and fitness traits in pre-industrial humans, which emphasizes the importance of a portfolio of mechanisms for coping with low food availability in such populations. The results are consistent with evolutionary ecological predictions that natural selection for resilience to food shortage is likely to weaken with age and be most severe on those with the fewest resources.

Keywords: human life history; environmental variation; survival rates; nutrition; age-by-environment interactions

1. INTRODUCTION

Estimates suggest that over 70 million people died during famines in the twentieth century [1], and crop failures were also a major source of mortality in historical populations. For example, the 1846–1851 Irish famine resulted in approximately 860 000 deaths [2], and the 1696–1697 Finnish famine reduced the population by around one-third [3]. Food shortage may also negatively affect reproduction, with birth rates decreasing and stillborn rates increasing during famine [4]. The strength of such effects may vary within populations, with larger effects often observed in individuals of low socio-economic status [5,6] and in the youngest and oldest individuals [7,8].

The majority of studies on associations between food availability and human health or fitness have focused on prolonged or acute malnutrition, despite the relative infrequency of such events in human history, with most of the variation in food availability corresponding to small-scale

seasonal or annual fluctuations [4]. Seasonal variation is known to be important and has been shown to correspond to variation in mortality [9] and birth weights [10] across the year, although it is more predictable than the entirely unpredictable annual variation [11] that we investigate here. Little is known about the effects of small-scale variation in food availability on fitness, despite its importance for understanding the role of environmental variation in shaping human life-history traits. Environmental variation profoundly influences patterns of mortality, reproduction and natural selection in wild animal populations [12], but few individual-level investigations of humans exist. This may stem from the challenge of quantifying variation in food availability in pre-industrial populations, a number of correlates of which have been employed. These include climatic conditions that have been reconstructed from historical data on climate proxies [13] and may affect harvest success, but such large-scale measures are unlikely to accurately reflect local conditions, which vary considerably across space [14]. Grain prices are another estimate of food availability and have been linked with mortality rates, but are often measured at the national level. A series of studies of associations between demography and variation

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in grain prices in Europe by Galloway and others have shown that increased grain prices can be associated with increased mortality [5,7,15] and reduced fecundity [6]. However, other studies have reported only weak correlations [16,17], emphasizing that they may not reflect local conditions. Here, we use 'grain figures', the amount of crop grain harvested relative to the amount sown, which varies across small spatial scales and is uncorrelated with population size and the amount of land farmed [18]. That grain yield reflects variation in food availability is suggested by the correspondence between low grain yields and reported famine [19], and that birth year grain figures are associated with the probability of marriage, reproduction and offspring survival [20]. Nevertheless, to our knowledge, associations between such small-scale variation in food availability and immediate mortality and fecundity are yet to be studied in any population.

We investigated effects of annual grain figures on mortality and fecundity in a pre-industrial, natural fertility Finnish population. In these populations, considerable between-individual variation in these vital rates induced a substantial opportunity for selection to operate on heritable traits related to fitness [21]. Population registers for the entire population have been maintained in Finland since 1750, allowing tracking of individuals from birth and providing accurate information on age-specific mortality and reproduction. A long time series (a total of 100 589 person-years) provides a rare opportunity to investigate longitudinal individual-level associations between food availability and mortality, within a large range of environmental conditions rather than focusing on extremes. Firstly, we investigated associations between annual crop yields and individual mortality across the lifespan of 5606 individuals. Secondly, we tested whether these associations varied with age or social class, because fitness is influenced by interactions between age and environmental conditions in wild animal populations, and social class predicts several measures of fitness in this population [22]. Thirdly, we investigated the effects of annual grain figures on variation in female annual reproductive success (ARS). We predicted that lower grain figures would be associated with higher mortality and lower fecundity. We also predicted that the positive association between grain figures and measures of annual fitness will be the strongest in the youngest and oldest individuals, and in those of low socio-economic status.

2. MATERIAL AND METHODS

(a) Study populations

We analysed associations between grain figures and individual mortality and fecundity, using data collected from Finnish church records. Since the eighteenth century, the Lutheran church has recorded all births, marriages and deaths in Finland, allowing individuals to be followed from birth, through adulthood, to death [23]. We have used these sources to construct individual life histories for over 10 rural populations, known as 'parishes', for analysis of life-history variation [20]. Here, we used individuals from two of these parishes, Ikaalinen and Tyrvää, which are located within 50 km of areas for which grain yield data were available.

Infectious diseases were the major source of mortality in nineteenth-century Finland, and mortality in our populations was high, with 46 per cent of individuals dying

before age 15. The annual mortality rate of 25.3 per thousand corresponded well with an estimate of 25.9 for rural areas between 1816 and 1865 [24]. The populations were strictly monogamous, with divorce forbidden by the church and adultery punishable, suggesting that the non-paternity rate was low. Women generally married in their mid-twenties, around 97 per cent of children were born in wedlock and 99 per cent of women finished reproducing by age 45 [20].

All individuals included in the analysis of survival and fecundity had known mothers and were assigned a social class, based on their father's occupation (standardizing social class for individuals dying in childhood and those surviving to adulthood), because social class is related to key life-history traits in this population [22]. We classified individuals into three social classes based on occupations: the wealthy class included farm-owners and merchants; the middle class, craftsmen and tenant farmers; the poor, crofters and labourers [22].

(b) Crop yield data

Our populations were agricultural, depending largely on the cultivation of rye and barley [25,26]. Around 60 per cent of energy consumed by working people was contributed by rye, 20 per cent came from potatoes and barley [27], and this was supplemented by meat, fish and dairy from domesticated and wild sources [28]. Rye, ground to make bread, was of primary importance, whereas barley was used to brew beer and contributed significantly to nutrition [27]. Annual harvest success is estimated by grain figures, quantified as the amount of grain harvested as a multiple of the quantity sown ('yield' from herein), a measure that is unbiased by variation in the area cultivated, the intensity of planting and population size. Thus, although grain yields do not directly measure *per capita* food availability, this measure is relative to the success of other years and as such reflects between-year variation in harvest success. Grain figures collected across Finland are poorly spatially correlated in comparison with climate data, and many of the data series last only a couple of decades [18]. Therefore, we selected data to maximize the length of the study period and the proximity to our study populations. We used grain yield data collected during 1804–1874 from the Spåre family archive [29] from the estate of Valkila, located within 35 and 40 km of the centres of Ikaalinen and Tyrvää, respectively. Ideally, grain yield data would have been available at the centre of each parish, or from multiple sources, but no other such lengthy time series were available close to parishes with available life-history records. Grain yield data collected across such distances have a correlation of 0.65–0.80 [18], suggesting that Valkila data represent well the conditions at each of our study parishes. We assessed associations between individual mortality and fecundity in each year and variation in grain yields recorded in the previous year to account for immediate effects of grain yields on mortality and to avoid the interpretation that associations could be driven by mortality of workers leading to a poor harvest.

We also used spring temperature, reconstructed from phenological and climatic records [14], and North Atlantic Oscillation, an indicator of large-scale climatic conditions reconstructed from proxy data as measures of climatic conditions [30]. These data were used to test whether observed associations between grain yields and fitness were driven by climatic conditions, but because results were unchanged when these were included as covariates in the

models described below, we present results from simpler models without these measures.

(c) *Statistical analysis*

(i) *Age-specific mortality*

All individuals included in analysis of mortality were born in Ikaalinen or Tyrvää during 1722–1874, and were of known death dates if they died within this period, or were known to have survived to the end of the period. A total of 6.5 per cent of individuals migrated or disappeared from records during the study period, and were removed from the analysis. Individual life histories were divided so that each individual had a single record for each year of life. We analysed associations between the previous year's crop yield and individual mortality as a binomial trait (0 = survived to the end of the year; 1 = died). Individuals not born in the study parish were excluded, as were those who emigrated during the study period; those emigrating after 1875 were retained. Data were split according to parish and sex, resulting in four independent datasets: Ikaalinen males (34 643 records from 2026 individuals); Ikaalinen females (30 049 records; 1831 individuals); Tyrvää males (17 013 records; 873 individuals); Tyrvää females (18 884 records; 876 individuals). This approach forestalled the fitting of complex three-way interactions and improved model convergence, as well as allowing us to replicate and observe the generality of our findings.

We analysed associations between individual mortality and the previous year's grain yields with generalized linear mixed-effects models (GLMMs) using the package 'lme4' in R [31]. This method was chosen for several reasons: firstly, we considered individual survival across discrete time periods (year-to-year); secondly, we considered a variety of individual covariates that varied between years [32]; thirdly, we included random effects [33]. We included a random effect of individual identity to account for between-individual variation in survival probability, and random effects of year and maternal identity to account for non-independence of mortality of individuals recorded in the same year or from the same family.

We also accounted for a number of other variables that potentially affected mortality. We constructed a base model for each dataset with social class as a fixed factor with three levels as described above. Birth order is associated with inheritance of wealth, survival and reproductive success in these populations [34], and so was included as a fixed factor with two levels (firstborn versus subsequent). Similarly, twins have lower survival than singletons [35], and so we included birth status as a fixed factor (singletons versus twins). We also included age (the maxima in our four datasets were 89–96) as linear and quadratic covariates. We tested the significance of these variables by dropping terms sequentially from GLMMs of mortality and comparing them using Akaike's information criterion (AIC), only retaining terms that when dropped increased model AIC [36].

We then added terms for linear and quadratic grain yields to these base models, followed by interactions of increasing complexity. Interactions between grain yields and age tested the prediction that low yields would have the greatest effects on the mortality of the youngest and oldest individuals, and interactions between grain yields and social class tested the prediction that individuals of the lowest social class would be most adversely affected. We selected the model with the lowest AIC for each dataset, allowing us to critically compare

models with different parameters and different grains and select the most parsimonious model [36].

(ii) *Age-specific reproductive success*

We analysed age-specific reproductive success in females (born 1762–1854) only. We restricted analysis to the first marriages of women aged 16–45, because 97 per cent of children are born within wedlock, the majority of widowed females do not remarry and over 99 per cent of offspring are born between these ages [20]. The records for an individual female began at the onset of her first marriage (or the beginning of the crop data series, if she was married before then), and ended when she reached age 45, when she or her first spouse died or when the crop data ended, whichever occurred first.

We analysed associations between the previous year's grain yields and the probability of a female giving birth in the current year, or ARS, as a binomial trait (0 = female did not give birth; 1 = female produced at least one child; 1.55% were twin births and scored as singletons). Social class was assigned on the basis of father's occupation; all analyses were repeated with husband's occupation, but results were unaffected. We excluded infertile couples by including only women producing at least one offspring. We analysed 2934 records from 195 women in Ikaalinen and 2888 records from 202 women in Tyrvää.

The base binomial GLMMs included social class, twin status and birth order as above, as well as a factor for whether or not a female reproduced in the previous year, because breastfeeding reduces conception probability. We also included linear and quadratic terms of age at first and last reproduction to account for differences in ARS between females that started and finished reproduction at different ages [37]. We also included linear and quadratic terms for individual age, and all covariates were mean-centred to aid model convergence. The base model and best-supported crop model were determined by comparing model AIC values.

(iii) *Annual mean crop yields*

Both rye and barley represented an important component of the Finnish diet [27], but the rye harvest was more dependent on temperature and barley more sensitive to precipitation [25,26]. Planting multiple crops may have been a strategy for coping with climatic variation [38], and therefore the combination of the two grains may have had more important consequences for individuals than either crop separately. Therefore, we repeated all of the above analysis with the previous year's annual mean of rye and barley yields (i.e. (rye + barley)/2).

3. RESULTS

(a) *Crop yields and mortality*

Yields of both rye and barley varied considerably during the study period (figure 1). For each of the four datasets (males and females from each parish), we selected the best model describing variation in mortality from the same candidate set. In general, the best-supported models were consistent in the importance of the fixed effects controlled for. The parameter estimates for these variables are shown in the electronic supplementary material, tables S1 and S2.

In Ikaalinen males, the model with the highest support contained the interaction between age and barley

Table 1. Generalized linear mixed-effects models of mortality for Ikaalinen males and females were compared using Akaike's information criterion (AIC). Δ AIC values are reported relative to the model with the lowest value, highlighted in bold italics. The model for females highlighted in bold is a non-nested model with similar explanatory power (Δ AIC < 2) to the best-supported model. 'd.f.' reports the number of degrees of freedom. Descriptions of the terms in the final models are provided in the electronic supplementary material, table S1.

model	males			females		
	d.f.	AIC	Δ AIC	d.f.	AIC	Δ AIC
base	10	8459.38	15.33	9	7103.77	2.90
base + rye	11	8460.69	16.64	10	7105.71	4.84
base + barley	11	8461.38	17.33	10	7105.16	4.29
base + rye ²	12	8462.69	18.64	11	7106.87	6.00
base + barley ²	12	8461.04	16.99	11	7106.21	5.34
base + rye + barley	12	8462.69	18.64	11	7107.11	6.24
base + rye + barley + rye : barley	13	8464.19	20.14	12	7107.31	6.44
base + rye + age : rye	12	8461.61	17.56	11	7104.16	3.29
base + rye + social : rye	13	8464.19	20.14	12	7103.45	2.58
base + rye + age : rye + social : rye	14	8464.78	20.73	13	7100.87	0
base + barley + age : barley	12	8444.05	0	11	7102.09	1.22
base + barley + social : barley	13	8460.42	16.37	12	7108.27	7.40
base + barley + age : barley + social : barley	14	8445.79	1.74	13	7105.71	4.84

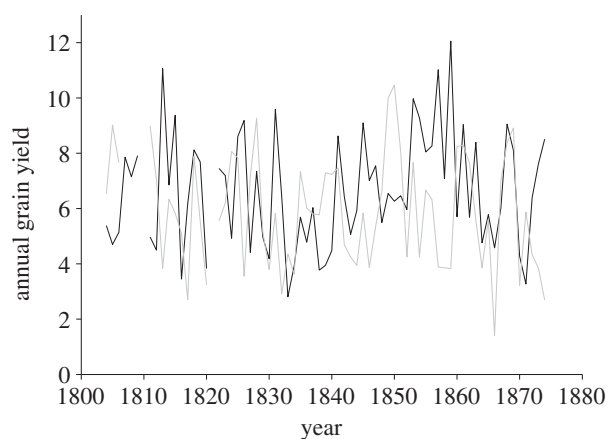


Figure 1. Annual variation in rye (black line) and barley (grey line) grain yields from Valkila, calculated as the amount of grain yielded as a multiple of the amount of grain sown. There is no temporal trend, and the dynamics of rye and barley are quite distinct.

yield (table 1), which suggested that barley yield had no influence on individual mortality until around age 60; from that point onwards, older individuals experienced higher mortality at lower crop yields (figure 2a). Two models explained mortality in Ikaalinen females almost equally well (table 1). The best-supported model contained significant interactions between age and rye yield, and social class and rye yield. The interaction with age suggested a negative influence of crops on mortality only in the oldest individuals (figure 2b), whereas the interaction with social class suggested no association between rye yield and mortality in wealthy and middle-class individuals, but a negative association between crop yields and mortality in the poorest individuals (figure 2c). A competing model included an interaction between age and barley yield, and received almost equivalent support (table 1 and figure 2d). Thus, two non-nested models explained the data almost equally well.

The best-supported model for Tyrvää males contained an interaction between age and barley yield (table 2), and suggested that barley yield had no influence on mortality until post-reproductive ages (figure 3a). The best-supported model for Tyrvää females contained interactions between rye yield and age, and rye yield and social class (table 2). However, the model containing only the interaction between rye yield and age explained the data almost as well, suggesting that the evidence for an interaction between social class and rye yield in Tyrvää females was weak. However, the interaction between rye yield and age improved model fit considerably (figure 3b).

(b) Crop yields and annual reproductive success

There was a considerable inter-annual variation in ARS: for instance, 21.94 per cent of women in Ikaalinen produced a child in 1873, but only 7.75 per cent did so in 1868; in Tyrvää, 26.05 per cent of women produced a child in 1870, but only 6.52 per cent of women reproduced in 1827.

The parameter estimates from the base models for ARS are shown in the electronic supplementary material, table S3. In Ikaalinen, none of the models including crop effects were better supported than the base model (table 3). The best-supported model for ARS in Tyrvää included an interaction between age and rye grain yield, but received only marginally better support than the base model (Δ AIC = 0.54). Hence, crop yields were only weakly associated with ARS.

(c) Annual mean crop yields

We repeated all of the above analyses, taking the mean of rye and barley yields to describe food availability in each year. The results reflected those using separate crops, because in all four datasets, higher mean crop yield was associated only with lower mortality in post-reproductive individuals (see the electronic supplementary material, tables S4 and S5, and figure S1). In agreement with the separate rye and barley models, there were no strong associations between crop yields and female ARS (see the electronic supplementary material, table S6).

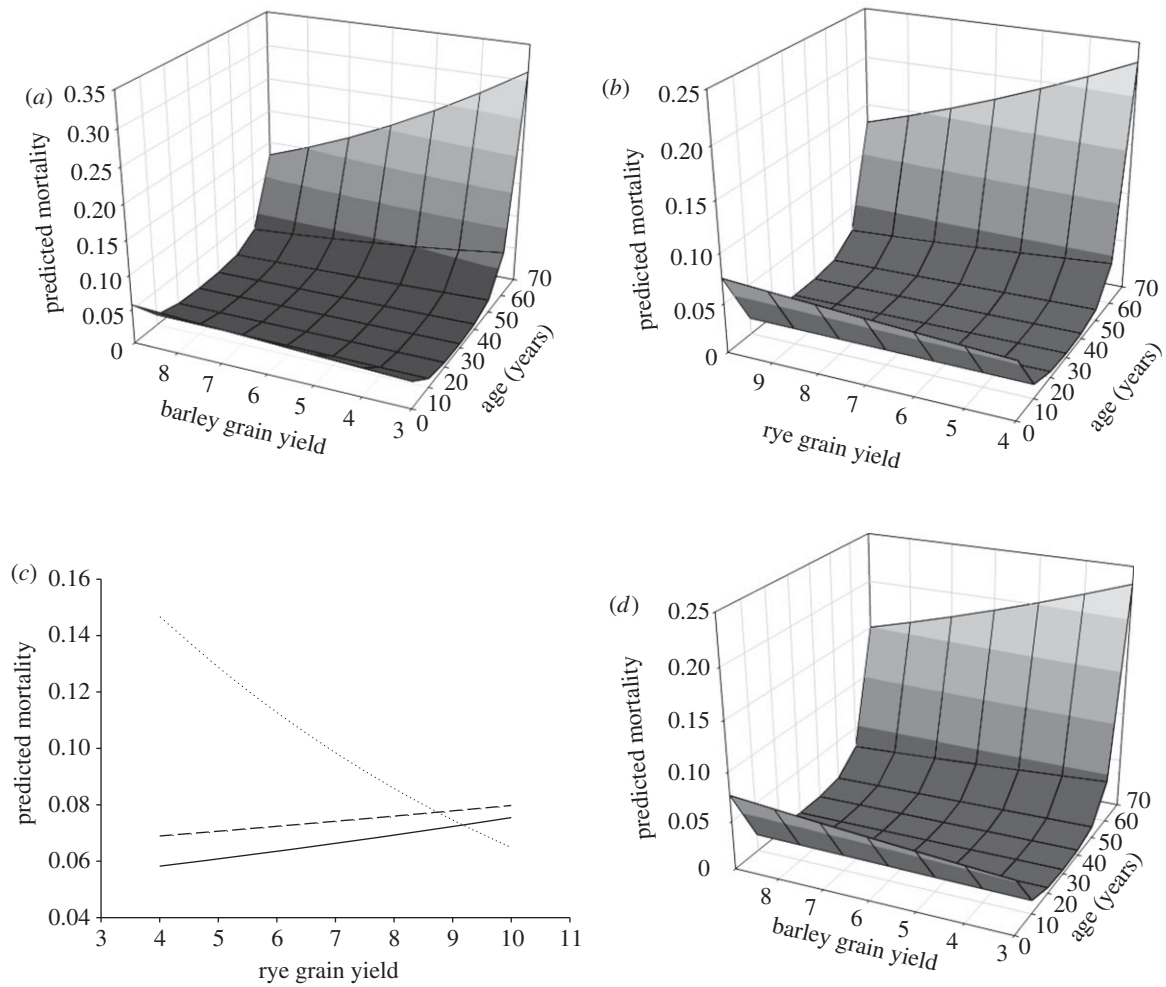


Figure 2. Generalized linear mixed-effects model predictions for the effects of crop yields on mortality in males and females in Ikaalinen. (a) The significant interaction between barley grain yield and age in the best-supported model for Ikaalinen males; the best-supported model of mortality for Ikaalinen females contained significant interactions between (b) rye yield and age and (c) rye yield and social class, where wealthy, solid line, middle, dashed line and poor, dotted line; (d) the second best-supported model of mortality in Ikaalinen females supported an interaction between age and barley grain yield.

Table 2. Generalized linear mixed-effects models of mortality for Tyrvää males and females. Δ AIC values are shown relative to the model with the lowest value, highlighted in *italics*; more parsimonious models with similar explanatory power (where Δ AIC < 2) are highlighted in **bold**. ‘d.f.’ indicates the number of degrees of freedom. Descriptions of the terms in the final models are provided in the electronic supplementary material, table S2.

model	males			females		
	d.f.	AIC	Δ AIC	d.f.	AIC	Δ AIC
base	9	3646.32	5.18	10	3743.04	5.83
base + rye	10	3646.72	5.58	11	3743.34	6.13
base + barley	10	3646.19	5.05	11	3743.05	5.84
base + rye ²	11	3648.46	7.32	12	3745.33	8.12
base + barley ²	11	3647.35	6.21	12	3743.46	6.25
base + rye + barley	11	3646.56	5.42	12	3743.29	6.08
base + rye + barley + rye : barley	12	3646.56	5.42	13	3742.61	5.40
base + rye + age : rye	11	3644.44	3.30	12	3737.59	0.38
base + rye + social : rye	12	3649.08	7.94	13	3743.51	6.30
base + rye + age : rye + social : rye	13	3646.24	5.10	<i>14</i>	<i>3737.21</i>	<i>0</i>
base + barley + age : barley	11	3641.14	0	12	3738.79	1.58
base + barley + social : barley	12	3648.97	7.83	13	3739.13	1.92
base + barley + age : barley + social : barley	13	3644.72	3.58	14	3739.02	1.81

4. DISCUSSION

We used detailed longitudinal data incorporating information on ageing and socio-economic status to study

the independent effects of variation in two important food sources on mortality and fecundity in pre-industrial human populations. This study represents, to our

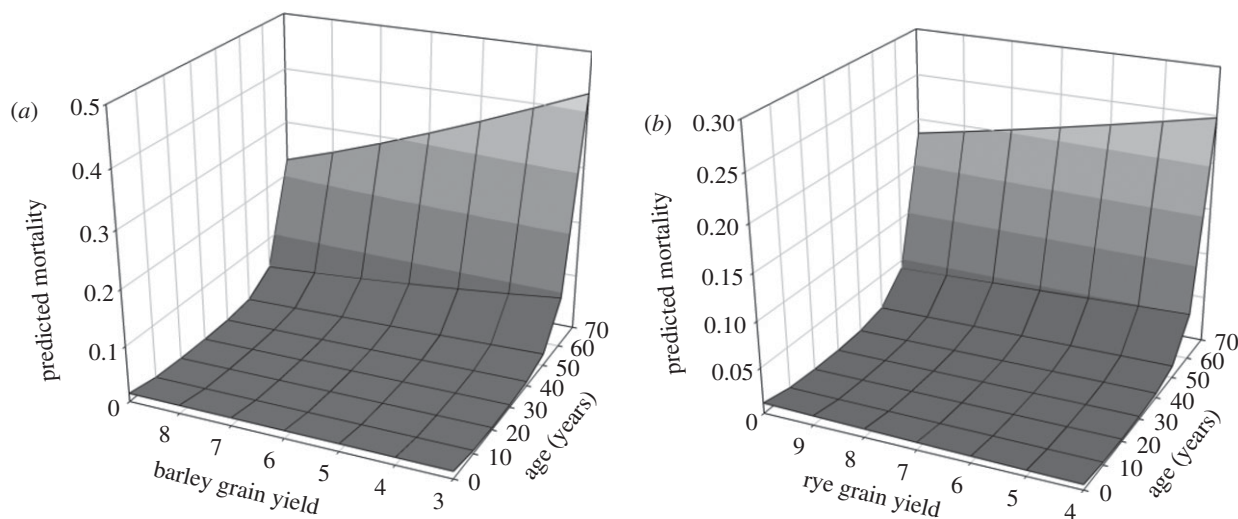


Figure 3. Generalized linear mixed-effects model predictions for effects of crop yield on mortality in Tyrvää males and females. There were significant interactions between crop yields and age in analysis of mortality in (a) Tyrvää males and (b) Tyrvää females, with increased mortality risk of post-reproductive individuals in years of low crop yields. Figures show predicted mortality from parameter estimates in the best-fitting GLMM models by model comparison in table 2.

Table 3. Generalized linear mixed-effects models of annual fecundity for females in Ikaalinen and Tyrvää. Δ AIC values are shown relative to the model with the lowest value, highlighted for each parish in italics; more parsimonious models with similar explanatory power (Δ AIC < 2) are highlighted in bold. 'd.f.' indicates the number of degrees of freedom. Descriptions of the terms in the final models are provided in the electronic supplementary material, table S6.

model	Ikaalinen			Tyrvää		
	d.f.	AIC	Δ AIC	d.f.	AIC	Δ AIC
base	7	2916.71	0	9	2592.22	0.54
base + rye	8	2918.37	1.66	10	2592.15	0.47
base + barley	8	2917.48	0.77	10	2594.19	2.51
base + rye ²	9	2920.32	3.61	11	2593.52	1.84
base + barley ²	9	2918.32	1.61	11	2595.58	3.90
base + rye + barley	9	2919.06	2.35	11	2594.10	2.42
base + rye + barley + rye : barley	10	2921.00	4.29	12	2596.04	4.36
base + rye + age : rye	9	2919.87	3.16	11	2591.68	0
base + barley + age : barley	9	2919.40	2.69	11	2594.79	3.11

knowledge, the first longitudinal, individual-based study of the associations between environmental variation and fitness traits from a pre-industrial population. As such, it complements previous work investigating the effects of famine on human populations, and provides a fuller picture of the extent to which environmental variation may shape human life-history traits. This study also complements previous studies of wild animal populations, which have shown that subtle environmental variation has important consequences for fitness, ageing and natural selection. We found that low crop yields were associated with increased mortality only in post-reproductive individuals and the poorest social class, and had little impact on female fecundity. Below, we discuss these findings in relation to historical, anthropological and evolutionary ecological literature, all of which illuminate our findings.

Although grain yields varied considerably, there was no association between food availability and mortality in the population as a whole. Variation in food availability can have a profound influence on mortality and population dynamics of wild animals [39], and high grain prices are

associated with higher mortality rates in human demographic and historical studies [5,7]. Our results are therefore perhaps against expectation, and suggest the importance of the portfolio of mechanisms developed by human populations for coping with food shortage, which have been widely discussed in the historical literature, but never in the context of individual-level mortality and fecundity [40–42]. Moreover, despite previous evidence for associations between grain prices and mortality rates [5,7], other works have shown only weak correlations [16,17]. The majority of mortality in the pre-industrial era was due to epidemics of smallpox, typhus, typhoid and influenza, and many studies have concluded that the dynamics of such diseases were largely independent of variation in harvest success or grain price [43–46], suggesting that other factors are more important in the spread of disease. However, individual nutrition is known to affect recovery from disease, and poor harvests have been associated with increased disease spread—for example, due to increased movement of people from rural to urban areas [44,47]. This may be unlikely in rural Finland, with its poor transport network, and

so it may be that only in years of catastrophic harvests were connections between nutrition, disease and mortality apparent. An additional explanation is that our populations are unusual and are uncommonly well-buffered against harvests. This is possible, but the consistency of the results across the populations, their location at the climatic limits of agriculture and their reliance on only two crops suggest that they are more, not less, likely to feel the adverse effects of poor harvests than other populations.

Food shortages have been a major selective pressure during human evolutionary history [8], through the majority of which our species have been hunter-gatherers (HGs). Ethnographic and simulation studies have shown that environmental variation may have a large impact on the dynamics of HG populations [48–50], but that such large-scale effects were somewhat dampened as agriculture spread [51,52]. This may translate to smaller scales, and our parish populations and individuals may not be expected to respond to environmental conditions as strongly as HG populations. In addition, selection for resilience to food shortage throughout human history has led to the development of an array of buffering mechanisms to reduce variance in nutrition, including sharing [53,54], exploiting a broader array of food sources [55] or following food resources across time and space [56], as exhibited by HG populations. Agricultural specialists also adopt a number of variance-reducing strategies such as trading, storage and diversification of crops, which are more developed at the geographic and climatic limits of agriculture [11]. This description applies to our Finnish populations, with their basic agricultural technology, unfavourable climate and rudimentary transport system [18,25,26]. Owing to the poorly developed transport network, migration was relatively rare and transport of large quantities of grain difficult, and famine-affected areas were often left to fend for themselves [57]. By excluding migrating individuals from our analyses, we have ensured that our findings are unaffected by biases created by the minority who migrated. Grain storage, a common strategy in agricultural populations [17], would have sustained populations through a poor year, though perhaps not several in succession [11]. Many agricultural systems planted multiple crop species to sustain themselves across the seasons and to maximize the chances of annual success [38,40], and in Finland, barley, potatoes, oats and wheat were cultivated alongside the predominant rye [18,27]. Finally, during poor years, populations may have relied more heavily on domesticated animals, game and wild foods. The analysis with separate rye and barley grains shows that mortality in post-reproductive individuals was affected by either rye (Ikaalinen and Tyrvää females) or barley (Ikaalinen males and females; Tyrvää males). The analysis with both grains combined showed that these patterns were replicated for total grain, suggesting that the total grain was a more important factor than either individual crop, emphasizing the importance of crop diversification. Annual rye and barley yields are uncorrelated (see the electronic supplementary material, figure S2), and hence despite large fluctuations, years where both crops failed would have been rare, making subsistence more secure [18].

Despite finding no general association between crop yields and mortality, our results were remarkably

consistent in predicting increased mortality among post-reproductive individuals in poor harvest years. The commonest causes of death in our post-reproductive individuals (excluding ‘old age’, 28% of deaths) were wasting, typhoid, pneumonia and oedema, which accounted for 50 per cent of deaths in this age group, and only 15 per cent in pre-reproductive individuals. Wasting and oedema are common signs of protein deficiency [28], and the relative prevalence of these in this age group may suggest an association with poor nutrition. Our findings have some precedent in population-level studies, such as a study showing that over 60s were more vulnerable to the immediate effects of grain prices on mortality in pre-industrial London [7]. Resilience to food shortage is likely to have been under natural selection throughout human evolution, spreading genes favouring such resilience [8]. Such effects are unlikely to persist into post-reproductive life owing to weakening natural selection with increasing age [58]. This suggests a potential evolutionary mechanism through which younger individuals could be more resilient to food shortage than post-reproductive individuals.

It is surprising that children were not adversely affected by low grain yields, because child mortality was extremely high. However, 58 per cent of child deaths were due to epidemic diseases (smallpox, influenza, shigellosis, yeast infection, whooping cough), the dynamics of which, as discussed above, may only be weakly associated with harvests and food prices. In addition, the quality and quantity of milk produced by mothers is largely unaffected by climate, work, infection and fasting [59,60]. Thus, even if mothers were undernourished, their offspring were unlikely to suffer direct effects of food shortages.

In Ikaalinen, females of the poorest social class were adversely affected by low rye yields, whereas individuals in the richer classes were not. This effect was predicted because landless individuals in northern Europe supplemented their diet, even during normal harvests, with unsuitable foods such as tree bark bread, straw, hay and even potentially toxic plants [28]. This could also explain the significant main effect of social class on mortality (see the electronic supplementary material, tables S1 and S2), though a number of factors could contribute to the higher mortality of the poor, including more stressful work, cramped living conditions facilitating disease transmission, lower access to healthcare and differences in child-rearing practices. Population-level studies have also shown that high grain prices had more adverse effects on survival [61] and birth rates [6] in poorer individuals than in the higher social classes. Our study suggests that this population-level pattern may also be evident at the individual level. However, an interaction between crops and social class was absent in males from both parishes and weak in Tyrvää females, and absent from analysis where both crops were combined, suggesting that in this population at least, even the poorest individuals suffered relatively small increases in mortality with variation in crop yield.

In contrast to post-reproductive mortality, annual fluctuations in crop yields were not strongly associated with variation in ARS in either of the study parishes. The explanations for mortality patterns are likely to apply to fecundity, and it is thought that while severe malnutrition may affect fertility, smaller-scale variation is less important

[62]. In addition, micronutrients are of great importance in fertility, and as such may have played a greater role in determining fecundity than macronutrients in populations experiencing largely adequate food supplies [62].

To conclude, we discovered weak but complex associations between grain yields and mortality in a pre-industrial human population. The majority of the population were resilient to variation in grain yields, but post-reproductive individuals and individuals of the poorest social class experienced elevated mortality in years of low yields. Associations between grain yields and female fecundity were weak. The results illustrate the effectiveness of a diverse portfolio of evolved strategies for coping with low food supplies, and are a rare example of the link between these and individual-level variation in mortality and fecundity. The results suggest that associations between food availability and mortality may have been restricted to very severe crop failures. Infectious disease epidemics, rather than food availability, have commonly been cited as the key determinant of mortality patterns in pre-industrial human populations [7,9,44,46,63]. Famines are often associated with direct causative agents of mortality, but this study suggests that small-scale fluctuations in food availability unaccompanied by disease outbreaks may be associated with mortality only in those that are already vulnerable.

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