The Effects of Early Childhood Stress on Mortality under Neolithization in the Levant
New Perspectives on Health Disparities in the Transition to Agriculture

Aaron J. Stutz, Fanny Bocquentin, Bérénice Chamel and Marie Anton
THE EFFECTS OF EARLY CHILDHOOD STRESS ON MORTALITY UNDER NEOLITHIZATION IN THE LEVANT: NEW PERSPECTIVES ON HEALTH DISPARITIES IN THE TRANSITION TO AGRICULTURE

A. J. STUTZ, F. BOCQUENTIN, B. CHAMEL AND M. ANTON

Abstract. This study investigates the causal relationships among early-life health conditions, mortality across the lifespan, and population growth during neolithization in the Levant. We analyze a comprehensive sample of 558 human skeletons, associated with mortuary features from 24 Levantine sites spanning the transition to agriculture, from the Early Natufian period to the Pre-Pottery Neolithic C (Southern Levant) and Pottery Neolithic periods (Northern Levant), mainly covering 13,000-6,000 BC. We find that early-life stress—as preserved in linear enamel hypoplasias (LEH) that we recorded in the study sample—not only increased dramatically in prevalence with the adoption of agriculture and village life. Early-life stress was also strongly associated with mortality in the juvenile, adolescent, and younger-adult life stages (ca. 5-29 years). This statistical link is independent of analysis of raw life-stage-at-death distributions, which may be heavily biased by ancient age or sex-skewed funerary recruitment practices. According to our results, biological well-being deteriorated with the adoption of agriculture and village life between ca. 9,000-6,000 BC. We find that the transition to agriculture raised risks for premature mortality across the Levant. We suggest that in the regional transition to agriculture, mortality and fertility rose together in a fragile dynamic, the balance of which may have shifted in the 7th millennium BC, as a rapid rise in early-life stress exposures reduced average well-being.

Résumé. Cette étude examine les relations de cause à effet entre l'état de santé des jeunes enfants, le taux de mortalité et la croissance de la population pendant la néolithisation du Levant. Nous analysons un échantillon de 558 individus découverts en contexte funéraire provenant de 24 sites qui couvrent la transition néolithique, du début du Natoufien au Néolithique précéramique (Levant sud)/début du Néolithique céramique (Levant nord), soit entre 13000 et 6000 cal. BC. Nous constatons que le stress biologique en début de vie, identifié à travers les hypoplasies linéaires de l’émail dentaire (LEH) que nous avons enregistré sur l’ensemble du corpus, a augmenté de façon spectaculaire en termes de fréquence avec l’adoption de l’agriculture et de la vie villageoise. Nous constatons également que ces marqueurs de stress préoces sont fortement liés à la mortalité des enfants, des adolescents et des jeunes adultes (environ 5-29 ans). Cette corrélation statistique est indépendante de l’analyse des distributions par âge au décès, qui peut être fortement biasée par le recrutement funéraire des défunts sur des critères liés à l’âge au décès et au sexe. Selon nos résultats, l’état de santé s’est détérioré avec l’adoption de l’agriculture et le développement de la vie communautaire entre 9000 et 6000 cal. BC. Nous constatons que la transition vers l’agriculture a entraîné une augmentation de la mortalité précoce dans tout le Levant. Nous suggérons que, lors de cette transition régionale vers l’agriculture, la mortalité et de la fertilité se sont développées en suivant une dynamique fragile, dont l’équilibre s’est rompu au VIIe millénaire av. J.-C. avec un développement fulgurant des stress biologiques en début de vie, et une réduction de l’état sanitaire général.

Keywords. Transition to agriculture, Levantine Epipaleolithic, Levantine Neolithic, Heterogeneity in frailty, Developmental origins of health and disease, Linear enamel hypoplasia, Paleodemography, Premature mortality

Mots-clés. Transition néolithique, Épipaléolithique levantin, Néolithique proche-oriental, variabilité de la fragilité, Origines Développementales de la Santé et des Maladies (DOHaD), hypoplasies linéaires de l’émail dentaire (LEH), Paléodémographie, mortalité précoce
INTRODUCTION

The Natufian archaeological culture (ca. 13,000-10,000 BC) traces the last Near Eastern hunter-gatherer societies who lacked farming neighbors (Bar-Yosef and Valla 2013). The succeeding Neolithic periods (Pre-Pottery Neolithic A-C [PPNA-C], ca. 10,000-6,400 BC, and Early Pottery Neolithic [Early PN], ca. 7,000-6,000 BC; table 1), though, did not begin with an abrupt shift to cultivation, domestication, food storage, and village life. Rather, early PPN horticulturalist-forager-hunters had neighbors who only hunted and gathered (Bar-Yosef and Meadow 1995). By ca. 7,000 BC—roughly at the onset of the PPNC period in the southern Levant and the Early PN period in the northern Levant—the wider region remained a mosaic of farmer-herders, hunter-gatherers, farmer-hunters, and specialized pastoralists (Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Arranz-Otaegui et al. 2016; Ibáñez et al. 2018; Munro et al. 2018). As in other world regions that underwent early, gradual agricultural transitions (Smith 2001; Zeder and Smith 2009; Bar-Yosef 2012), the Near Eastern “neolithization” process was intricate. The development of domestication and agriculture also came to involve diversified and expanded food storage within the context of durable, multi-room house compounds. The long-term shift to agriculture thus shaped early village life (Kuijt 2008; Belfer-Cohen and Goring-Morris 2011, 2014). Yet, more broadly, Near Eastern communities developed domestication and commensal relationships with diverse plants and animals, while also ecologically altering the landscape at wider geographic scales (Asouti and Kabukcu 2014; Asouti et al. 2015). As human demographic systems changed, cultural worlds also transformed with their constituent, larger-scale, more complex social networks (Price and Bar-Yosef 2010). From its late Upper Paleolithic underpinnings (Snir et al. 2015), Near Eastern agriculture emerged through a complex mosaic of biocultural and environmental changes (Smith and Horwitz 2007; Kuijt 2008; Goring-Morris and Belfer-Cohen 2011; Asouti 2013; Asouti and Fuller 2013; Riehl et al. 2015; Bocquentin in press). This study focuses on how shifts in human health fit in the wider, systemically complex transition. We investigate the following questions: how did the prevalence of early-life stress—which we measure via observations of linear enamel hypoplasias (LEH) in teeth from skeletons interred in Natufian and Neolithic sites—change with the development of Neolithic biocultural systems, and in turn, how did early-life health experiences affect regional patterns of survival and well-being at later life stages?

BACKGROUND

In substantial part, Near Eastern Neolithic research over the past two decades has highlighted the complicated biocultural and environmental interplay between local conditions and developments, on the one hand, and regional-scale connections—economic, ritual-religious, political, technological, and demographic—on the other (Asouti 2007; Goring-Morris and Belfer-Cohen 2011, 2014; Edwards 2016). Still, the long-standing, wider scholarly interest in the Near Eastern Neolithic period has found its focus on broad, hallmark biocultural evolutionary developments—not on the historical specificity of their origin. This is as much the case for understanding changes in economics, diet, health, demography, and variation in biological well-being, as it is for making sense of the community and cosmology-producing monuments, rituals and ritual offerings that constituted religious expression in early agricultural societies (Cauvin 2000; Guerrero et al. 2008; Pinhasi and Stock 2011; Bowles and Choi 2013; Winterhalder et al. 2015). In this article, we seek to reconcile these research trends, as we grapple with how neolithization’s complexity eventually gave rise to far-reaching transformations in human life and human conditions, as we investigate broad changes in health, demography and well-being.

This study relies on a comprehensive sample of 558 juvenile and adult skeletons from Natufian and Neolithic burial features (table 1), representing 24 archaeological sites across the Levant (fig. 1). Our focus is on life-stage-at-death-specific prevalence of LEH, which is a common, etiologically non-specific marker of physiological stress during dental crown formation (Goodman and Armelagos 1985; Goodman and Rose 1990; Lanphear 1990; Hillson and Bond 1997; Temple 2014, 2020). We investigate a question central to understanding the health of Natufian and early Neolithic people. How did community-level heterogeneity in exposure to early-life stress affect “downstream” mortality risks later in life? (Vaupel and Yashin 1985; Wood et al. 1992; Milner and Boldsen 2017) As domestication and agriculture became key components of Near Eastern biocultural systems, long-term changes in population variability in stress exposure would have had concomitant effects on heterogeneity in frailty. In turn, changes in the
Table 1 – *Observed numbers of individuals (total MNI) and individuals with observable teeth whose crowns form between one and five years of age (LEH study) from the Levantine burial sample in this study.*

<table>
<thead>
<tr>
<th>Period</th>
<th>Site</th>
<th>Region</th>
<th>Total MNI</th>
<th>LEH Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early Natufian 13,000-11,000 BC</td>
<td>Azraq 18</td>
<td>South</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>el-Wad</td>
<td>South</td>
<td>66</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>Erq el-Ahmar</td>
<td>South</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Hayonim Cave</td>
<td>South</td>
<td>21</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Kebara</td>
<td>South</td>
<td>77</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Mallaha</td>
<td>South</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Raqefet</td>
<td>South</td>
<td>31</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Wadi Hammeh 27</td>
<td>South</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Late/Final Natufian 11,000-10,000 BC</td>
<td>el-Wad</td>
<td>South</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Hayonim Cave</td>
<td>South</td>
<td>17</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Mallaha</td>
<td>South</td>
<td>70</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>Nahal Oren</td>
<td>South</td>
<td>32</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Shukbah</td>
<td>South</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Abu Hureyra</td>
<td>North</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Pre-Pottery Neolithic A 10,000-9,000 BC</td>
<td>Sheikh Hassan</td>
<td>North</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Dja`de el-Mughara</td>
<td>North</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Tell Mureybet</td>
<td>North</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Tell Qaramel</td>
<td>North</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Pre-Pottery Neolithic B 9,000-7,000 BC</td>
<td>Abu Ghosh</td>
<td>South</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Beisamun</td>
<td>South</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Motza</td>
<td>South</td>
<td>18</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Tel Roim West</td>
<td>South</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Abu Hureyra</td>
<td>North</td>
<td>94</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>Dja`de el-Mughara</td>
<td>North</td>
<td>63</td>
<td>47</td>
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<tr>
<td></td>
<td>Tell Aswad</td>
<td>North</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Tell Mureybet</td>
<td>North</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Pre-Pottery Neolithic C 7,000-6,400 BC</td>
<td>Abu Ghosh</td>
<td>South</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Ashkelon</td>
<td>South</td>
<td>26</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Atlit Yam</td>
<td>South</td>
<td>65</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>Beisamun</td>
<td>South</td>
<td>19</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Hagoshemrim</td>
<td>South</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Tel Roim West</td>
<td>South</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Abu Hureyra</td>
<td>North</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Early Pottery Neolithic 7,000-6,000 BC</td>
<td>Tell Ain el-Kerkh</td>
<td>North</td>
<td>56</td>
<td>46</td>
</tr>
</tbody>
</table>
distribution of frailty would have had cascading impacts on life-long health conditions, well-being and age-specific mortality risks (Cohen and Armelagos 1984; Bocquet-Appel 2002; Larsen 2006; Guerrero et al. 2008; Gage and DeWitte 2009; Goring-Morris and Belfer-Cohen 2011; Chamel 2014; Larsen et al. 2019). The analysis of statistical associations between early-life stress and life-stage-specific mortality can yield new insights into well-being and demography in the transition to agriculture.

Human biologists, economic historians, and bioarchaeologists, alike, have increasingly recognized the effects that early-life health experiences can have on later juvenile or adult health and survival outcomes. Theoretical modeling of life history strategies (Vaupel and Yashin 1985; Wood 1994, 1998) contributed critically to the initial identification of the osteological paradox, where seemingly hidden heterogeneity in stress and frailty can have surprising, differential effects on the associations between skeletal health and age-specific mortality outcomes (Wood et al. 1992). In addition, clinical, economic-historical, and bioarchaeological studies of heterogeneity in frailty have generated extensive evidence for the “developmental origins of health and disease” (DOHaD) framework for understanding how early-life stress—including fetal exposures—can have lasting downstream effects on morbidity in the face of infections, malnutrition and cardiovascular disease (Barker et al. 1990; Barker 2004; Boldsen 2007; Armelagos

**Fig. 1** – Natufian and Neolithic sites included in this study. See table 1 for details on time period/archaeological culture.

Building on foundational work on the associations between LEH and mortality in the prehistoric adoption of agriculture, we present a comprehensive effort to investigate the role of heterogeneity in frailty on changes in health and well-being in a long-term regional transition from hunting and gathering to agriculture (Goodman and Armelagos 1985; Armelagos et al. 2009). We emphasize that the DOHaD framework supports a major methodological advantage in bioarchaeology (Armelagos et al. 2009; Milner and Boldsen 2017; Temple 2019). Researchers have long recognized that direct paleodemographic analysis of archaeological age-at-death profiles entail profound theoretical difficulties. The reconstruction of life tables from age-at-death profiles typically requires uncertain assumptions about basic population rates (Bocquet-Appel and Masset 1977, 1982; Gage and DeWitte 2009). Methodological developments notwithstanding, age-at-death determinations themselves still have limited resolution and accuracy, at least for older adults (ca. ≥ 30-40 years; Milner and Boldsen 2012; Lanteri et al. 2018; Cabec et al. 2019; Naji in press). The theoretically modelled statistical inferences about measurable age-at-death patterns in a target burial assemblage depend strongly on the reference populations used to build the statistical models (Masset 1990; Konigsberg and Frankenberg 1992, 1994). In particular, the reference population sample’s age-specific variability in skeletal biology must be sufficiently comparable to that of the archaeological target population, so that inferences about skeletal aging patterns are accurate (Konigsberg and Frankenberg 2002; Usher 2002). Reference populations have been drawn from ethnographic studies, historical cemetery and anatomical collections, and diverse modern population records (Bocquet-Appel and Masset 1977; Gage and DeWitte 2009; Milner and Boldsen 2012). Moreover, an observed archaeological age-at-death distribution can be affected by cosmologically structured or socio-politically driven funerary recruitment practices, which can bias archaeological representation with respect to age and biological sex (e.g., Masset and Sellier 1990). This is a fundamental concern that Bocquentin has discussed at length for the Levantine Natufian context (Bocquentin 2003, 2007, 2014). As we focus on studying early-life stress and its effect on survival to subsequent life-stages—from later juvenile growth periods to adulthood past 30 years—we emphasize that this “DOHaD-derived” approach can shed light on changes in health, well-being and mortality in the transition to agriculture, while circumventing the pitfalls of looking directly at life-stage-at-death profiles (Milner and Boldsen 2017).

In this study we thus investigate how LEH-formation may have shifted in its statistical associations with survival to particular life-stages in Levantine communities, from the Natufian time-frame (ca. 13,000-10,000 BC) to the PPNC/Early PN timeframe (ca. 7,000-6,400 BC). The DOHaD framework generates clear theoretical predictions about how changes in stress-exposure affect age-specific risks of suffering inflammation or other stress responses, leading to skeletal traces such as LEH. Moreover, the DOHaD model emphasizes that early-life episodes of inflammation critically disrupt prenatal, neonate, infant, or early juvenile growth and development. Those experiencing early-life inflammation will likely remain frailest, raising risks for mortality in subsequent life stages (fig. 2). Thus, physiological stress-response in infancy or early juvenile growth stages is expected to be a significant risk factor for premature mortality in later juvenile, adolescent, early adult, and mature adult life stages.

According to the DOHaD model, other things being equal, when a community faces a significant decline in health conditions, the hazards for inflammation in the face of early-life stress will increase, and in turn, heterogeneity in frailty will also increase. Many individuals suffering early-life inflammation will develop greater frailty, raising their morbidity in the face of subsequent stress episodes. Such a pattern has been empirically documented in LEH occurrence in Late/Final Jomon Period hunter-gatherers in Japan (Temple 2014 and 2020). Even in healthy preindustrial populations, LEH prevalence should be highest among the most frail, who may survive childhood, but who then embody higher mortality risks, already in their adolescent and young-adult years (ca. 10-30 years). If population-level health were to decline, average frailty would increase in the population, but there might be greater heterogeneity among individuals. The result would not only involve higher life-stage-at-death-specific LEH
rates across the board; we would also observe a “leftward”—
that is, a younger—shift in the life-stage-at-death associated
with the peak rate of early-life stress exposure. Figure 2 illus-
trates an idealized ceteris paribus scenario of age-at-death
LEH prevalences for populations clearly differing in health
conditions. In analyzing the statistical associations between
LEH and life-stage-at-death in skeletal samples spanning the
Levantine transition to agriculture, we take a first look at how
the DOHaD framework may explain neolithization’s impact on
well-being and mortality over long-term and regional scales.

Fig. 2 – Theoretical distribution of linear enamel hypoplasia
prevalence, $P(\text{LEH}_{1-5})$, for tooth crowns forming between ages of one
and five years, across the span of mortality outcomes. The dotted line
represents a relatively healthy preindustrial population, with LEH
associated with lower rates of early-life inflammation, which are in
turn most often linked to elevated mortality in early adulthood. The
dashed line illustrates a relatively less healthy community—more
frequently exposed to infection or nutritional stress—with higher
rates of early childhood LEH, associated with a slightly reduced age
at peak risk for early mortality. The solid line shows a substantially
less healthy community, for which higher stress exposure (e.g.,
more frequent epidemics or nutritional stress) shift peak mortality
associated with early childhood LEH formation downward, into the
adolescent life stage.

MATERIALS AND METHODS

Our study draws on a comprehensive sample of 558 indi-
viduals recovered and documented as near-complete or partial
skeletons with at least partial dentitions. The individuals come
from mortuary features from 24 Natufian and Neolithic sites
(table 1). FB, BC and MA have identified a total of 790 individ-
uals (Bocquentin 2003, 2007; Lengyel et al. 2013; Chamel 2014;
Bocquentin and Garrard 2016; Bocquentin et al. in press), of
which 549 meet the following joint criteria: they have associated
or articulated permanent teeth whose crowns form prior to ca. 6
years; they could be aged to the broad categories 5-19 years
(juvenile) or $\geq$ 20 years (adult); and they were archaeologically
associated with a particular time period. These 549 individuals
were used in finer-grained analyses of change through time in
the association of LEH with life-stage-at-death. Nine additional
individuals with observable permanent teeth are from stratified
Natufian contexts, but they could not be assigned to Early versus
Late/Final periods (Belfer-Cohen 1991; Bocquentin 2003). With
these nine individuals included, we carried out analyses of
change through time, from the entire pooled Natufian hunt-
er-gatherer sample to subsequent Neolithic time periods. Thus,
558 individuals with at least one observable tooth were included
in our analyses.

We studied LEH prevalence in permanent teeth from indi-
viduals aged $\geq$ 5 years, in order to evaluate how LEH forming
in permanent tooth crowns in early childhood may associate
with mortality in particular life stages later in childhood and
adulthood. We focused on permanent incisors (I), canines (C),
first premolars (P1) and first molars (M1), whose crowns form
between 1 and roughly 5-6 years (Reid and Dean 2006; Reid
et al. 2008). When LEH is present, these permanent teeth
provide a record of early-childhood stress episodes that are
expected to increase frailty later in the juvenile or adult life
stages. With the study sample encompassing Levantine time
periods from the Early Natufian (ca. 13,000-11,000 BC) to the
PPNC/Early PN (combined northern and southern Levant, ca.
7,000-6,400 BC), we analyzed change over time in the associ-
ations between early-childhood biological well-being and
mortality, across the transition from hunting and gathering to
domestication, agriculture, expanded food storage, and village
settlement.

DETERMINING LIFE-STAGE AT DEATH

We consider the following life-stages at death, examining
individuals who survived early childhood (ca. $> 5$ years):
younger juveniles (5-9 years at death), adolescents (10-19 years
at death), younger adults (20-29 years at death), and older
adults ($> 30$ years at death). Here, we favored methodological
conservatism in order to reduce the risk of inaccurate age-at-
death determinations.

Age at death for immature skeletons ($\leq$ ca. 19 years) was
determined according to visual and radiographic observation
of tooth calcification, eruption, and wear. These subadult age
determinations were complemented by epiphyseal fusion data. Detailed methods are available in Bocquentin (Bocquentin 2003: 49-102). Those individuals aged 5-19 years were assigned to the broader “Juvenile” life-stage-at-death class. Where preservation permitted, we further subdivided them into younger juvenile (5-9 years) and adolescent (10-19 years) life-stage categories.

Among the skeletally mature individuals, life-stage at death was assigned to 20-29 year and ≥ 30-year categories—again, where possible—mainly based on clavicular fusion and age indicators from the pubic symphysis and the auricular surface of the ilium (Webb and Suchey 1985; Schmitt 2005), complemented by a discriminant analysis function approach to dental occlusal wear (Bocquentin 2003). Further methodological details are presented in Bocquentin (Bocquentin 2003). Due to incomplete preservation for many individuals, the sample of more precisely aged adults with observable teeth was substantially restricted. Nonetheless, out of 375 skeletally mature, adult individuals with observable teeth, 177 could be aged more precisely into the younger and older adult life-stage-at-death categories.

IDENTIFYING LINEAR ENAMEL HYPOPLASIA (LEH) PRESENCE VERSUS ABSENCE ON THE PERMANENT TEETH

The study included all permanent incisors (I1 and I2), canines (C), first premolars (P1) and first molars (M1) associated with the 558 partial and near-complete individual skeletons from the Levantine Natufian and Neolithic contexts (tables 1, 2). Each tooth (n = 5296) was examined visually with an 8× magnification lens. A tooth was coded as LEH-present if at least one linear enamel hypoplasia was present. Some teeth exhibited multiple LEHs and some exhibited both LEH and enamel pitting. In reducing the coding to LEH presence versus absence, we aimed to consider as broadly as possible those dental traces of early-life stress that we hypothesize to associate with earlier mortality.

We emphasize that only a very small number of coronal LEHs were observed on the upper dentition, that is, for the teeth on which we focused: permanent incisors, canines, P1’s, and M1’s. For the respective superior and inferior teeth, the height of all single LEHs (measured as height in mm above the dentine-enamel junction) was always less than the height of the most worn tooth in the sample. In cases where multiple LEHs formed, the height of the last-forming LEH was always less than the height of the most worn tooth in the sample. Thus, it is very unlikely that we have undercounted LEH presence on adult individuals with worn teeth.

STATISTICAL METHODOLOGY FOR ANALYZING ASSOCIATIONS BETWEEN LEH AND LIFE-STAGE-AT-DEATH

We carried out two successive statistical analyses of change in life-stage-at-death-specific LEH prevalence across the transition to agriculture. The first approach used the sample of 549 individuals, divided into juvenile (5-19 year) and adult (≥ 20 year) categories and separated into successive Early Natufian, Late/Final Natufian, PPNA, PPNB, and PPNC/Early PN periods. The time frames given for each period were based on published reviews of available radiocarbon dates (Goring-Morris and Belfer-Cohen 2011; Maher et al. 2011; Grosman 2013; Chamel 2014; Borrell et al. 2015; Edwards 2016). In table 1 we took a conservative approach in rounding beginning and end dates to the nearest half-millennium. The typologically Late Natufian sample from Raqefet Cave was assigned chronologically to the Early Natufian period, which spans the timeframe 13,000-11,000 BC (Barzilai et al. 2017). All other typologically Late or Final Natufian sites in our sample date to 11,000-10,000 BC (Grosman 2013). We recognized that the Natufian phenomenon is a Levantine archaeological culture. Yet, it is also largely definable as entirely coeval with the Late Epipaleolithic timeframe, consisting of an earlier and a later chronological horizon (Bar-Yosef and Belfer-Cohen 1989; Bar-Yosef 1998; Grosman 2013). There is limited chronological overlap between the Early and Late/Final Natufian archaeological cultures. Where 14C measurements suggest penecontemporaneous Early and Late Natufian-associated occupations—in the western Galilee and Mt. Carmel area—the overlap lasts up to several centuries (Henry et al. 1981; Weinstein-Evron et al. 2012; Caracuta et al. 2016; Barzilai et al. 2017). As the Late Natufian-associated occupation of Raqefet Cave is unique within our Late/Final Natufian sample, predating 11,000 BC, we emphasized its chronological position. Our analysis focused on change over time, not on variability among temporally overlapping archaeological cultures. In a future publication we will consider the complex chronology of the Early-Late Natufian archaeological transition in the southern Levant. Here, we relied on recent results concerning the Early-Late/Final Natufian temporal framework (Weinstein-Evron et al. 2012; Grosman 2013; Caracuta et al. 2016; Nishiaki et al. 2017; Barzilai et al. 2017; Richter et al. 2017). In our study of long-term chronological change, the Natufian period overall

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came into focus as a period with little clearly measureable overlap with the succeeding PPNA period (ca. 10,000-9,000 BC; Wicks et al. 2016). We further took into consideration the fact that the initial PN in the Northern Levant largely overlaps with the PPNC period in the Southern Levant. We combined these archaeological cultures into one temporal horizon, encompassing mainly ca. 7,000-6,000 BC (Chamel 2014; Edwards 2016; Borrell et al. 2019).

The aim of our first analysis was to consider gross differences in associations between early-life stress and mortality, here, distinguished as juvenile versus adult mortality, across the transition to agriculture. The study sample for this approach is summarized in table 2.

**Table 2 – Tooth counts\(^1\) and minimum number of individuals (MNI) in the analysis of LEH occurrence by more finely divided time-period and more broadly defined life-stage at death.**

<table>
<thead>
<tr>
<th>Period</th>
<th>Life-Stage at Death</th>
<th>Life-Stage at Death</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Juvenile</td>
<td>Adult</td>
</tr>
<tr>
<td>Early Natufian</td>
<td>563</td>
<td>912</td>
</tr>
<tr>
<td>MNI</td>
<td>53</td>
<td>98</td>
</tr>
<tr>
<td>Late/Final Natufian</td>
<td>211</td>
<td>737</td>
</tr>
<tr>
<td>MNI</td>
<td>24</td>
<td>76</td>
</tr>
<tr>
<td>PPNA</td>
<td>23</td>
<td>165</td>
</tr>
<tr>
<td>MNI</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>PPNB</td>
<td>357</td>
<td>751</td>
</tr>
<tr>
<td>MNI</td>
<td>43</td>
<td>108</td>
</tr>
<tr>
<td>PPNC/PN</td>
<td>393</td>
<td>712</td>
</tr>
<tr>
<td>MNI</td>
<td>51</td>
<td>76</td>
</tr>
</tbody>
</table>

The second approach used a smaller subsample (n = 347), including only those individuals for whom juveniles could be divided into younger juvenile (5-9 years) and adolescent (10-19 years) categories. We further sampled those adults who could be divided into younger (20-29 years) and older (≥ 30 years) groups. The study sample for this approach included the additional nine Natufian individuals whose stratigraphic position could not be clearly linked to Early or Late Natufian components at el-Wad and Hayonim Caves. Here, the Natufian sample was pooled as a single terminal Pleistocene hunter-gatherer cross-sectional sample. The highly fragmentary PPNA sample included too few adult skeletons that could be aged to the younger versus older categories. Thus, we excluded the PPNA period from the second analysis. Because our PPNA sample is only represented by sites in the Northern Levant—and because PPNA cultivation practices were highly variable, with domestication technologies barely developed or adopted (Willcox 2007, 2012; Asouti and Fuller 2012, 2013; Asouti et al. 2015; Arranz-Otaegui et al. 2016)—the second analysis could still focus on how early-life stress related to mortality across the more finely divided life history scheme, as we compared the association patterns before agriculture (all Natufian individuals, ca. 13,000-10,000 BC) with those after agricultural adoption (PPNB and PPNC/PN periods, respectively, encompassing ca. 9,000-6,000 BC). The second analysis sample is summarized in table 3.

**Table 3 – Tooth counts\(^2\) and minimum number of individuals (MNI) by broader time period and more detailed life-stage at death.**

<table>
<thead>
<tr>
<th>Period</th>
<th>Life-Stage at Death</th>
<th>Life-Stage at Death</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Younger Juvenile</td>
<td>Adolescent</td>
</tr>
<tr>
<td>PPNC/PN</td>
<td>216</td>
<td>177</td>
</tr>
<tr>
<td>MNI</td>
<td>35</td>
<td>16</td>
</tr>
</tbody>
</table>

**Monte Carlo Simulation of Independence between LEH and Life-Stage-at-Death**

In order to evaluate the statistical associations between LEH and mortality across age groups, we employed a nonparametric Monte Carlo simulation approach. The choice of statistical test was mainly driven by the highly variable preservation of dentitions among individuals. This was especially relevant for our statistical comparisons, because in general, different teeth exhibit significantly different liabilities to develop enamel hypoplasias (Goodman and Armelagos 1985; Goodman and Rose 1990; Lanphear 1990; Hillson et Bond 1997; Guatelli-Steinberg et al. 2004; Nelson 2018). As shown in figure 3, just over 20% of the total 5,296 teeth in the entire Levantine sample exhibit at least one LEH, but canines have a much higher LEH susceptibility than all other teeth, whereas M1’s relatively rarely

\(^1\) Refers to the permanent teeth studied, with relatively early-forming crowns: incisors, canines, P1 and M1.

\(^2\) Refers to the permanent teeth studied, with relatively early-forming crowns: incisors, canines, P1 and M1.
form LEH. A G-test of independence (Sokal and Rohlf 1995) between LEH formation and tooth yields a remarkably high G-statistic of 497, with an associated p-value essentially at zero. The G-statistic equals 2× the sum of log-likelihood values for observed-relative-to-expected counts in each cell of the 10 × 2 contingency table; \( p = 2.0 \times 10^{-101} \); n = 5,296 teeth; 10 upper and lower tooth types × LEH presence versus absence yields d.f. = 9. The teeth that happen to be preserved in association with a particular individual skeleton thus strongly affect the likelihood that at least one LEH will be observed. In our resampling-with-replacement procedure (see below), we thus randomly shuffled the observed dentitions across individuals, holding life-stage at death and time period constant. This Monte Carlo approach controlled for variability in taphonomic post-mortem loss of teeth, simulating independence of LEH, life-stage at death, and time period. A key aspect of this scenario is that LEH risk is simulated as constant over time and with respect to life-stage at death. We sought to evaluate the null hypothesis that the observed chronological variation in association between LEH and life-stage at death could have occurred randomly. We included individuals with complete as well as partial dentitions—even those with just one associated tooth. This allowed us to maximize the available number of teeth observed (table 2, 3).

**The Simulation Procedure: Repeated Random Resampling with Replacement**

In each of our two analyses (see above), we employed a random-resampling-with-replacement procedure, repeated 100,000 times. For each randomly resampled case, we tabulated the LEH relative frequency (number of teeth observed with LEH present/all teeth observed) in each age group and time period. We then calculated the test statistic: the sum of the squared deviations from the expected relative frequency, which was estimated from the total number of teeth with LEH in the study sample. The repeated resampling procedure generated a simulated random distribution of summed squared deviations from the expected LEH frequency. From this simulated distribution, we estimated the probability that the observed sum of squared deviations could have occurred by chance. We also recorded the probabilities that observed relative frequencies for LEH prevalence within life stages and time periods—that is to say, the observed values in the respective life-stage-at-death × time-period contingency tables in analyses 1 and 2—could have occurred by chance alone (Estabrook and Estabrook 1989; Estabrook 2011). Simulations for both statistical analyses described above were carried out with a custom macro in Excel VBA for Mac 2020.

**Procedures for ad hoc tests**

Where Monte Carlo simulation results raised questions about particular ad hoc 2 × 2 comparisons between life-stages at death and time periods, we employed the G-test of independence, which Sokal and Rohlf (1996) recommend over the Chi-square test.

**RESULTS**

Charting the presence versus absence of LEH on juveniles and adults across five successive time periods, table 4 summarizes the results of the first analysis, based on the sample of 549 individuals from the southern and northern Levant. In the transition to agriculture there was a long-term increase in LEH risk associated with juvenile and adult mortality, alike. With the available observed dentitions, the null expectation of constant LEH risk in both life stages and all time periods yields an estimated prevalence of 0.21. For the two life-stages at death in this analysis, observed in each of five time periods—yielding the 2 × 5 table (table 4)—the sum of squared deviations of observed LEH prevalence from the expected, constant level is 0.14. The Monte Carlo simulation with 100,000 iterations of resampling with replacement yields \( p = 0.03 \) that the observed
sum of squared deviations could be as high or higher by chance alone. There is an overall non-random interaction effect among LEH risk, life-stage at death, and time period.

Table 4 – Relative frequencies of teeth with linear enamel hypoplasia (LEH).

<table>
<thead>
<tr>
<th>P(LEH)</th>
<th>Juvenile (5-19 Years)</th>
<th>Adult (≥ 20 years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early Natufian</td>
<td>0.16</td>
<td>0.16 p = 0.03</td>
</tr>
<tr>
<td>13,000-11,000 BC</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late/Final Natufian</td>
<td>0.09 p = 0.01</td>
<td>0.13 p = 0.004</td>
</tr>
<tr>
<td>11,000-10,000 BC</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PPNA</td>
<td>0.35</td>
<td>0.11</td>
</tr>
<tr>
<td>10,000-9,000 BC</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PPNB</td>
<td>0.27 p = 0.009</td>
<td>0.15</td>
</tr>
<tr>
<td>9,000-7,000 BC</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PPNC/PN</td>
<td>0.46 p &lt; 1 × 10⁻³</td>
<td>0.35 p &lt; 1 × 10⁻¹</td>
</tr>
<tr>
<td>7,000-6,000 BC</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

This interaction effect is driven by the following significantly strong associations between higher or lower LEH risks, particular life-stage at death, and particular time period. First, Natufian hunter-gatherers interred in residential sites generally exhibit significantly low LEH risks, regardless of life-stage at death (table 4). Second, prior to the PPNC/PN time-frame—that is, before ca. 7,000 BC—adult mortality is associated with significantly low LEH prevalence, consistent with a key prediction of the DOHaD model. Reduced exposure to early-life stress is tied, in the maturation and aging process, to greater longevity. Third, LEH-risk shows a remarkable spike in association with juvenile and adult mortality, alike, in the PPNC/PN time period. Out of the 100,000 iterations of resampling with replacement, no randomized case yielded LEH risks as high as those observed for the PPNC/PN sample. Moreover, LEH prevalence is markedly higher for juvenile mortality than it is for adult mortality in the PPNC/PN period. This is consistent with one of the DOHaD model’s fundamental predictions, that increased early-life exposure to stress raises frailty, with a concomitant risk for earlier mortality (fig. 2). Among individuals dying in the juvenile life-stage, it was conspicuously more common to have experienced early childhood stress that led to LEH-formation. Figure 4 summarizes the results of this first analysis, illustrating the pattern of LEH risk with respect to the broad life-stage at death and the more finely detailed time-period.

Fig. 4 – The relative frequency of linear enamel hypoplasias in teeth, the crowns of which form mainly between ages one and five years, P(LEH_{1-5}), according to time period and life-stage at death—broken down simply into 5-19 years at death (juvenile) and ≥ 20 years at death (adult). The dotted line marks the estimated expected risk of LEH formation on teeth, under the null hypothesis that in all time periods, survival to all life-stages is associated with the same constant LEH risk.

The second analysis involves the more restricted sample of better-preserved individuals, whose life-stage at death could be assigned to the categories younger juvenile (5-9 years), adolescent (10-19 years), younger adult (20-29 years), and older adult (≥ 30 years; n = 347). As noted above, this sample also includes nine additional hunter-gatherers who could be assigned to a pooled Natufian subsample. Table 5 and figure 5 summarize this analysis, clarifying long-term biocultural evolutionary change in how early-life stress impacted survival rates later in life. Prior to 10,000 BC—that is, well before the establishment of widespread cultivation, intensified storage, and larger village settlements—Natufian hunter-gatherers generally appear relatively healthy, exposed to early-life stress significantly less frequently than later PPNB, PPNC and PN farmers (compare fig. 2 and 5). As shown in figure 5, LEH is rarely associated with Natufian younger juvenile mortality, but LEH prevalence rises in association with younger adult mortality, before declining significantly among those surviving to at least

3. The LEH presence relative frequency in each cell is based on counts of LEH presence and absence on the permanent incisors, canines, P1s and M1s associated with individuals belonging to the set of individuals with that cell’s life-stage at death and time period. The cells shaded in light grey exhibit statistically significantly low LEH risks, based on the Monte Carlo simulation with resampling with replacement. The dark grey cells exhibit statistically significant high LEH risks. The respective significant p-values are shown in the highlighted cells.
30 years. Overall Natufian LEH prevalence is relatively low: \( P(\text{LEH}_{\text{Natufian}}) = 0.17 \). In contrast, Neolithic agricultural populations—that is, PPNB, PPNC, and PN populations, ca. 9,000-6,000 BC—exhibit much higher LEH prevalence. Most strikingly, children born in PPNC/PN communities were exposed to early-life stress more frequently, regardless of how long they survived. The overall PPNC/PN frequency of LEH, \( P(\text{LEH}_{\text{PPNC/PN}}) = 0.43 \). However, this elevated rate of LEH-formation—and thus, the archaeologically visible rate of substantial early-life stress—appears mostly associated with mortality in the juvenile, adolescent, and younger-adult life stages. Those PPNC/PN individuals surviving to the “Older Adult” life-stage had somewhat lighter biological stress loads in early childhood, reflected in their life-stage-specific lower LEH frequencies (fig. 5). In the centuries after ca. 9,000 BP in the Levant, the peak LEH-mortality association shifts slightly, to an earlier life-stage—the adolescent stage. This result is strongly concordant with the predictions of the DOHaD model (fig. 2), suggesting that the long-term transition from Natufian hunting and gathering to Neolithic agriculture resulted in poorer early-life conditions, and that by the 7th millennium BC, this had led to increased mortality overall (cf. Paine and Boldsen 2002).4

Indeed, in the second analysis, the Monte Carlo simulation of constant LEH risk as a factor independent of life-stage survivorship and prehistoric time-period, reveals a statistically significant Natufian-Neolithic shift in association between LEH formation and life-stage at death. Among the cross-tabulated relative frequencies in each cell in the four life-stage-at-death × three time-period table (table 5), the observed sum of squared deviations, 0.27, is very unlikely to have been at least as high by chance alone \( (p = 0.001) \). As detailed in table 5, Natufian juvenile and older-adult mortality exhibit statistically significantly low rates of LEH-association, while PPNC/PN juvenile, adolescent, and younger adult mortality is statistically significantly associated with high LEH-risk.

### Table 5 – Linear Enamel Hypoplasia relative frequencies in the permanent dentition of the Natufian, PPNB, PPNC and early PN sample.

<table>
<thead>
<tr>
<th>Period</th>
<th>Child (5-9 years)</th>
<th>Adolescent (10-19 years)</th>
<th>Young Adult (20-29 years)</th>
<th>Older Adult (≥ 30 years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natufian 13,000-11,000 BC</td>
<td>0.08</td>
<td>0.18</td>
<td>0.20</td>
<td>0.15</td>
</tr>
<tr>
<td>PPNC/PN 7,000-6,000 BC</td>
<td>0.39</td>
<td>0.53</td>
<td>0.52</td>
<td>0.33</td>
</tr>
</tbody>
</table>

### Fig. 5 – Prevalence of linear enamel hypoplasia in teeth, the crowns of which form mainly between one and five years, \( P(\text{LEH}_{1-5}) \), plotted by age at death—here, divided into the four life-stages shown. Compared are the pooled Natufian hunter-gatherer sample (ca. 13,000-10,000 BC), the early agricultural PPNB sample (ca. 9,000-7,000 BC), and the pooled PPNC/Pottery Neolithic (PN) sample (ca. 7,000-6,000 BC).

### DISCUSSION

When Cohen and Armelagos (1984) presented their seminal edited volume of geographically focused syntheses, the Paleopathology at the Origins of Agriculture contributors discussed then available human osteological observations, sketching a robust, straightforward pattern. Agriculture
immediately brought with it multiple, increasingly prevalent sources of morbidity (Cohen and Armelagos 1984). Compared to earlier hunter-gatherer populations in the same region, the first-adopters of farming often exhibited archaeologically preserved skeletal lesions—markers of serious or recurrent stress and inflammation—regardless of life-stage at death (Larsen 1995; Pinhasi and Stock 2011). There are profound, still-debated paleodemographic challenges in interpreting archaeological life-stage-at-death distributions (Bocquet-Appel and Masset 1982; Sattenspiel and Harpending 1983; Paine and Harpending 1996; Bocquet-Appel 2002; Bocquet-Appel and Naji 2006; Bocquet-Appel and Bar-Yosef 2008; Gage and DeWitte 2009). It has remained difficult to establish that the agriculturally associated increase in morbidity actually led to increased mortality (Gage and DeWitte 2009).

More recently, Bogin and colleagues have stated, “Even under good conditions, the stages of human life history are replete with trade-offs for survival, productivity, and reproduction” (Bogin et al. 2007: 631). Disparities in early-life exposures to stress can drive very different investments in growth versus survival, generating population-scale heterogeneity in frailty. We suggest that our results—when considered in light of the DOHaD framework—constitute a new line of evidence, supporting the argument that, broadly across the Levant in the 7th millennium BC, rising rates of early-childhood stress were significantly tied to mortality later in childhood, adolescence, and younger adulthood. Our analysis has revealed strong statistical associations between early-childhood stress-exposure and life-stage at death. In light of the DOHaD framework, population-level heterogeneity in biological well-being (sensu Wood 1998) appears to have generally increased, from the Natufian to the PPNC/Early PN timeframes. Yet, average well-being likely began to deteriorate across the Levant, as domesticated plants and animals were extensively integrated into Neolithic economies, and as villages with more densely packed household structures were settled in the Late PPNB, ca. 7,500-7,000 BC. Our results most strongly suggest that the negative impact on biological well-being took hold across the Levant in the PPNC/Early PN, from ca. 7,000-6,000 BC (Kuijt 2008; Asouti and Fuller 2013; Arranz-Otaegui et al. 2016; Munro et al. 2018).

This main conclusion is consistent with previous and ongoing work. Our life-stage-at-death-specific LEH data for the Levant mirror the picture of relatively poor health among the 7th millennium BC people who inhabited the Pottery Neolithic village of Çatalhöyük in central Anatolia (Larsen et al. 2019). In the southern Levant, evidence for a decline in average health continues into the succeeding Chalcolithic period (ca. 4,500-3,500 BC; Smith and Horwitz 2007). Bocquentin et al. (in press) have carried out an analysis of carious lesions and ante-mortem tooth loss in this study’s pan-Levantine sample. They observe an accelerating, long-term rise in the overall rates of caries formation, from the Early Natufian to the PPNC/PN time periods. They also see that ante-mortem tooth loss actually declined from the PPNB to the PPNC/PN periods. While dental caries formed more often in PPNC/PN individuals, the lesions tended to be smaller than those in the preceding Levantine PPN sample. The trends they observe may more narrowly track the progressive addition of starch, as Neolithic diets became less variable. Bocquentin, Chamel, and Anton observe that overall somatic health can affect the individual’s susceptibility to carious lesions and other oral infections. They argue that there was likely an interplay between an overall decline in somatic health, in general, and oral health, in particular. This would account for the spike in population-level caries rates and stress that emerged by the 7th millennium BC across the Levant (Bocquentin et al. in press).

In this discussion we consider how the development and adoption of agriculture and settlement dynamics may have interacted with the demographic effects of increasingly prevalent early childhood stress, especially from the Late PPNB onward. We then address our finding of likely rising mortality in the PPNC/Early PN timeframe, viewed in light of Bocquet-Appel’s influential “Agricultural Demographic Transition” model.

DECLINING BIOLOGICAL WELL-BEING AND THE NEAR EASTERN TRANSITION TO AGRICULTURE

As we have emphasized above, recent research has highlighted that Near Eastern neolithization involved complex, long-term biocultural processes (Bocquentin in press; Kuijt 2008; Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Asouti 2013; Belfer-Cohen and Goring-Morris 2014; Chamel 2014; Asouti et al. 2015; Flohr et al. 2016; Ibáñez et al. 2018). In the southern Levant archaeobotanical evidence hints that—long prior to domestication—late Upper Paleolithic hunter-gatherers (ca. 21,000 BC) may have engaged in small-scale cultivation of wild-type wheat, barley, and oat plants (Snir et al. 2015). Because substantial carbonized seed assemblages are so rare in Pleistocene contexts, it is unclear whether this was a briefly adopted strategy to cope with Last Glacial Maximum environments, or whether it was the beginning of a very slow process of integrating horticulture into hunting, gathering and fishing economies. During the
subsequent Epipaleolithic (ca. 20,000-10,000 BC), a mosaic of hunting, trapping, gathering and fishing practices reflected, in part, variations in local ecology (Horwitz and Goring-Morris 2000; Munro 2004; Stutz et al. 2009; Grosman et al. 2016; Munro et al. 2016; Martin et al. 2016; Yeomans et al. 2017; Yeshurun and Bar-Oz 2018; Sharon et al. 2020). It is clear, though, that in zones of relatively high biomass productivity—with more rainfall and milder winter temperatures—Early and Late/Final Natufian populations, alike (ca. 13,000-10,000 BC), sustained strong hunting pressure on slower-growing or slower-reproducing game, from land tortoise (Testudo graeca) to diverse ungulate prey (Munro 2004; Stutz et al. 2009; Munro et al. 2016; Munro et al. 2018). This reflects a significant degree of long-term human population increase, from the Late Upper Paleolithic through the Natufian period—again, at least in more productive ecological zones, including southern Levantine Mediterranean vegetation zones and the wetland-dominated southern Rift Valley (Stiner 2005; Stutz et al. 2009; Munro et al. 2016; Stutz 2019). We face an important outstanding question. In the Natufian time-frame, key social and technological factors—including land-tenure, logistical mobility and investment in durable architecture—interacted with broad-spectrum resource exploitation and residential mobility between biomass-productivity zones. How did the feedbacks constituting such complex human systems influence pre-domestication cultivation (Weiss et al. 2006; Asouti 2013; Snir et al. 2015) and, eventually, the domestication of goat and sheep? (Munro et al. 2018) It is clear that Early Natufian foragers exploited a range of legumes that included the putative ancestor to domesticated fava beans (Vicia faba; Caracuta et al. 2016). Early Natufian food preparation technologies already involved winnowing, grinding, and sifting dried grains into flour, which was mixed in a dough with other wild starchy plant foods, baked as a bread (Arranz-Otaegui et al. 2018). Wild grain, legume, and grass seed collection and processing appears to have significantly increased in economic importance during the Late Natufian period across the Levant (Anderson 1999; Moore et al. 2000; Dubreuil 2004; Asouti and Fuller 2012, 2013), a pattern also seen in Younger Dryas settlements in southeastern Anatolia and in the hilly margins of lower Mesopotamia (Savard et al. 2006; Riehl et al. 2015; Rössner et al. 2018).

Subsequently, small-scale pre-domestication cultivation of locally available cereals and legumes clearly expanded during the PPNA period across the wider Near East (Willcox 2012; Asouti and Fuller 2013; Rössner et al. 2018). However, broad-spectrum cereal, legume, nut, fruit, grass-seed and wetland root foraging remained remarkably economically important, from the final Epipaleolithic to the early Pre-Pottery Neolithic, ca. 11,000-9,000 BC (Hillman 2000; Savard et al. 2006; Willcox 2012; Asouti 2013; Riehl et al. 2015; Asouti et al. 2015). The association of iconographically rich monumental architecture with persistent broad-spectrum foraging in PPNA and early Pre-Pottery Neolithic B (EPPNB) southeastern Anatolia highlights how the collective investment in durable aggregation-site architecture, public storage, and ritualized gatherings—including communal feasting—were likely important in mediating mobility, social networks, and land tenure, in a flexible food economy that variably involved foraging, hunting, and small-scale pre-domestication cultivation (Dietrich et al. 2012). This pattern of negotiated, intense resource management, communal food processing, collective storage, feasting, and commemorative mortuary ritual appears to be a wider Near Eastern pattern in the PPNA (ca. 10,000-9,000 BC; Stordeur et al. 2000; Stordeur and Abbès 2002; Kuijt and Finlayson 2009; Finlayson et al. 2011; Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2012; Asouti 2013).

Only later—from the MPPNB (ca. 8,000-7,500 BC) onward—do we see that fully domesticated cereals and legumes are consistently associated with Near Eastern archaeobotanical assemblages (Asouti and Fuller 2012, 2013; Arranz-Otaegui et al. 2016; Rössner et al. 2018). At roughly the same time, domesticated sheep and goat become important in archaeofaunal assemblages (Zeder 2012; Munro et al. 2018). By ca. 7,500 BC, agricultural production and animal herd management took on a significant economic and nutritional importance across the Levant, as PPNB economic systems began to structure anthropogenic vegetation regimes at a wider landscape scale, at least in Anatolia and the southern Levant (Asouti and Kabukcu 2014; Asouti et al. 2015). As we note above, it remains unclear how innovations in food economies, co-residence strategies, and social networks interacted with human demographic change. We emphasize that it is especially difficult to identify systemic feedbacks—that is, the complex causality—driving the adoption of domesticates, the emergence of agricultural production, the settlement of larger, more densely built Neolithic villages, and the incorporation of private household storage and food-processing equipment. It is clear, though, that LPPNB, PPNC and Early PN communities were materially constituted quite differently, when compared with preceding Epipaleolithic and initial Pre-Pottery Neolithic societies (Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Wright 2014).

As shown in figures 4 and 5, our PPNB skeletal sample captures a key trend. According to the DOHaD framework, long-term, population-level early-childhood health deteriorated...
across the transition to agriculture. We suggest that this trend already had an impact on rising mortality in the PPNB timeframe, by ca. 9,000-7,000 BC. An ad hoc G-test of independence (Sokal and Rohlf 1995) between LEH formation and time period for Natufian versus PPNB juveniles (5-19 years) yields a G-statistic of 104, and with one degree of freedom, the one-tailed p-value is a very highly significant $1.8 \times 10^{-24}$. Early-childhood LEH formation is strongly associated with PPNB juvenile mortality, when compared with Natufian mortality. However, among the PPNB adults interred in the Levantine sites in our sample—and especially among those dying as older adults—the frequency of LEH is not significantly higher than that observed for Natufian older adults (G-statistic = 0.89, $p = 0.35$). Part of the complex causality we seek to elucidate, then, appears to involve an incipient deterioration in health, driven by early-life stress, that had already taken hold by PPNB times, during the 8th millennium BC.

Subsequently, during the 7th millennium BC (the PPNC/ Early PN timeframe) in the Levant, early-life stress became ever more prevalent, apparently increasing frailty to an extent that raised mortality among older juveniles and adults. More specifically, high LEH frequencies are associated with death in the juvenile, adolescent, and younger adult life-stages, alike (table 4). More broadly, when compared with hunter-gatherers interred at least 3000 years prior—that is, among those interred in Natufian sites (ca. 13,000-10,000 BC)—we see that a higher proportion of PPNC/PN individuals experienced early-life stress, which constituted a significant predictor of death before the age of 30 (fig. 5). An ad hoc G-test of independence between LEH formation and time period, comparing those reaching the older-adult lifestage ($\geq$ 30 years) during the Natufian versus PPNC/PN timeframes, yields a G-statistic of 23, with a highly significant $p$-value of $1.4 \times 10^{-6}$ (one degree of freedom). At this time, even those surviving past 29 years had already suffered elevated rates of early-life stress. This has an important implication. With greater exposure to nutritional stress or infectious disease in early childhood, PPNC/PN populations were subject to wider heterogeneity in frailty—resulting in stronger mortality selection—between those dying before 30 and those surviving to at least 30 years.

Following Paine and Boldsen (Paine and Boldsen 2002), we suggest that the particularly strong PPNC/PN associations among high LEH prevalence and mortality in the younger-juvenile, adolescent, and younger-adult lifestages (table 5) are most parsimoniously, immediately explained by the emergence of higher endemic infection rates, combined with more frequent infectious disease outbreaks. Episodes of nutritional stress could have contributed to rising average frailty during neolithization, but the statistical association between early-life stress and premature mortality among individuals ritually interred in PPNB and PPNC/PN Levantine village settlements could be entirely explained by more frequent exposure to food or waterborn gastrointestinal parasites, which could cause and further be transmitted by diarrhea. Still, Smith and Horwitz have emphasized that animal domestication in the PPNB would have led to increasing exposure to zoonotic pathogens (Horwitz and Smith 2000; Smith and Horwitz 2007). Goring-Morris and Belfer-Cohen raise the possibility that contagious disease outbreaks contributed to the abandonment or reorganization of several PPNC settlements in the later 7th millennium BC (Goring-Morris and Belfer-Cohen 2011). Our current sample is insufficient to evaluate this suggestion in detail, but community-level health would have tended to affect settlement history.

Although the strong observed association between LEH formation and premature mortality may have been immediately caused by repeated exposure to infectious disease outbreaks, we can identify wider biocultural, systemic factors favoring elevated human morbidity. As Prentiss and colleagues have recently suggested, community-level investment in sedentary settlement and food storage can catalyze positive-feedback cycles, accelerating human harvesting pressure on resources, creating greater vulnerability to more intense episodic food-resource shortfalls, raising infant mortality, and amplifying any existing heterogeneity in frailty (Prentiss et al. 2014; Prentiss et al. 2018; Prentiss et al. 2018). Puleston, Winterhalder and colleagues have presented complementary theoretical analyses, carefully validated by computerized simulations of a demographic model under conditions of limited productive land-area (Lee and Tuljapurkar 2008; Puleston and Tuljapurkar 2008; Lee et al. 2009; Puleston et al. 2014; Winterhalder et al. 2015; Puleston and Winterhalder 2019). They find that, under cultural systems of agricultural production and food storage, human demography can follow rapid expansion dynamics, quickly encountering Malthusian population constraints, largely without warning to the people constituting those populations (Puleston et al. 2014). Moreover, Puleston et al. infer that agricultural set-asides for next year’s seed, while necessary for sustainable interannual farming yields, can dampen per capita calorie availability (Winterhalder et al. 2015), further driving pressures that would widen population-level heterogeneity in frailty.

We argue that our results confirm a fundamental aspect of neolithization in the Near East. The adoption of domestication technologies, the development of agricultural economies and land-resource management practices, and the settlement of
larger, more organizationally complex villages occurred despite long-term costs to community-level biological well-being (Larsen 2006; Larsen et al. 2019). However, this hallmark neolithization process—which extended from the late Upper Paleolithic through the PPNC/PN period—occurred via gradual, if geographically patchy, anthropogenic depression of wild ungulate populations (Munro et al. 2018), development of caprine domestication and herd management (Zeder 2012; Munro et al. 2018), landscape-scale transformation of vegetation regimes (Asouti and Kabukcu 2014; Asouti et al. 2015), expansion of small-scale agricultural fields (Asouti 2013; Asouti and Fuller 2013), and successive investment in settlements with durable, increasingly complex architecture, private storage and food-processing equipment (Goring-Morris and Belfer-Cohen 2008; Kuijt 2008; Wright 2014; Ibáñez et al. 2018).

Following Prentiss et al. (Prentiss et al. 2014; Prentiss et al. 2018; Prentiss et al. 2018), we would expect that sporadic, recurring food-resource shortfalls would have reduced biological well-being within communities, leading to settlement-reorganization and occasional abandonment. Yet, Neolithic landscapes underwent progressive, human-induced transformation, involving larger and marginally more densely distributed settlements. As cycles of settlement formation, abandonment, and new settlement unfolded, ecological refugia for hunting and gathering would have dwindled. This dynamic is arguably a continuation of a foraging-territory compression process that may have contributed to sedentary settlement among Late Epipaleolithic hunter-gatherers (Rosenberg 1998; Munro 2004; Yeshurun and Bar-Oz 2018). In the PPNB and PPNC timeframe (ca. 9,000-6,000 BC), reorganization of existing settlements or establishment of new ones would have depended on plant food storage and accessible agricultural fields. Food management technology and arable land would have initially offered relatively highly viable opportunities for increasing yields. Yet, as Winterhalder et al. have found, this would have quickly returned communities to strained, vulnerable Malthusian conditions, within only a few generations (Puleston et al. 2014; Winterhalder et al. 2015). Local biocultural systemic feedbacks among more frequent Neolithic food-insecurity episodes, susceptibility to infectious disease outbreaks, settlement abandonment/reorganization, and resettlement would have been intimately part of the Near Eastern transition to agriculture.

In this setting, wider social networks—and the cultural landscapes and repertoires that constituted social strategies and relationships, from close-kinship to regional scales—would have critically shaped the establishment and growth of those new or reorganized settlements. From this perspective, rising average PPNC/PN mortality would not have simply been a byproduct of agricultural adoption. Rather, the long-term, archaeologically visible trend we interpret as poorer health and higher mortality would have been underlain by a more intricate biocultural dynamic, in which local communities more quickly and more often ended up subject to elevated heterogeneity in frailty and higher mortality.

THE PPNB/PPNC/PN INCREASE IN MORTALITY: REVISITING THE AGRICULTURAL DEMOGRAPHIC TRANSITION

Theoretical expectations in demography establish that differences in age-at-death distributions between mortality samples—from different sites or across time periods—are often more informative about shifts in fertility rates. Other things being equal, a burial sample with a relatively high proportion of juveniles (relative to all individuals) is expected to reflect higher fertility, rather than high early-life mortality (Bocquet-Appel and Masset 1977; Sattenspiel and Harpending 1983; Bocquet-Appel 2002, 2011; Bocquet-Appel and Bar-Yosef 2008). Still, Gage and DeWitte caution that the proportion of juveniles in an unbiased death assemblage could be variably influenced by the balance between fertility, mortality, and migration—that is, the local population growth rate (Gage and DeWitte 2009). The proportion of juveniles in an archaeological mortuary sample, in turn, is the result of a palimpsest of fluctuations in fertility, across social networks and settlements, over multiple generations. An archaeologically measured value of the proportion of juveniles does not necessarily—or even likely—correspond to a particular long-term average fertility rate. More cautiously stated, other things being equal, directional differences in the proportion of juveniles, observed among chronologically ordered mortuary samples, may only generally reflect corresponding directional changes in fertility rates.

In developing his widely influential “agricultural demographic transition” (ADT) framework, Bocquet-Appel compiled historical demographic records, observing a very high correlation between recorded fertility rates and the proportion of juvenile mortality (aged 5-19 years) among all deaths. He further employed a simulation methodology, conducting a sensitivity analysis of model preindustrial life tables. These results validated earlier theoretical analyses, along with the observed correlations between juvenile (5-19 years) mortality and fertility rates in the living population.
(Bocquet-Appel 2002). Demonstrating that 5-19 year-olds become relatively more common in cemeteries post-dating the adoption of agriculture, Bocquet-Appel has situated his observations about agriculture and fertility in the context of a changing balance in metabolic load. He has argued that fertility would have rapidly risen in Neolithic biocultural systems. Mobility-related activity would have fallen with sedentism, and calorie-rich starchy diets would have helped reduce birth spacing. In his words, agricultural emergence would have fed a sustained Neolithic “baby boom” (Bocquet-Appel 2008: 35).

In measuring the index \( p_{15} \) (that is, the demographic notation for the proportion of deaths between 5-19 years among all deaths) in archaeological skeletal series, Bocquet-Appel and colleagues argue that they have identified an accurate paleoanthropological proxy for fertility rates (Bocquet-Appel 2002; Bandy 2005; Bocquet-Appel and Naji 2006; Bocquet-Appel 2008; Guerrero et al. 2008; Bocquet-Appel 2011). An empirical synthesis of \( p_{15} \) changes in regional transitions may be interpreted as a decline in fertility in the centuries just prior to agricultural adoption, followed by a rapid rise in fertility, which possibly persists up to several millennia after agricultural economies gain a foothold. Archaeologists have largely taken as an article of faith that the “Neolithic demographic transition” scenario—as outlined by Bocquet-Appel in a series of articles and a key edited volume (Bocquet-Appel 2002, 2011; Bocquet-Appel and Naji 2006; Bocquet-Appel and Bar-Yosef 2008)—is reliably in evidence (Bocquet-Appel and Bar-Yosef 2008; Pinhasi and Stock 2011). We suggest that our results contribute to an updated evaluation of how the ADT model may fit the Levantine case.

As illustrated in figure 6, the average \( p_{15} \) values per cross-sectional time period in our Levantine sample confirm previous results for a more restricted Levantine skeletal series (Guerrero et al. 2008). The pattern in figure 6 conforms with Bocquet-Appel’s expectations for how this paleodemographic index should directionally vary across the transition to agriculture. How do we consider the diachronic trend in the proportion of juveniles (5-19 years) in Levantine burials? As emphasized above, we cannot easily rule out alternative explanations to the agricultural demographic transition scenario, including ones involving changing social biases in funerary recruitment. Still, in considering fit to the ADT model, the data—illustrated in figure 6—are tantalizing. Gage and DeWitte (Gage and DeWitte 2009: 652) suggest that Bocquet-Appel’s “death ratio” measures “pick up consistent, albeit weak, signals indicating a change in demographic regime during the transition to agriculture. It is even likely that this is due to changes in fertility, because ethnographic analogies suggest that the fertility of sedentary agriculturalists is higher than that of foragers…” (cf. Hewlett 1991; Bentley et al. 1993).

A more recent, phylogenetic approach to analyzing variation in fertility rates between ethnographically documented agricultural and foraging societies confirms this general pattern. While hunter-gatherer and farming society fertility rates overlap, farmers and pastoralists tend to achieve statistically significantly higher completed fertility rates, typically involving one additional live birth per adult woman surviving to post-reproductive age (Sellen and Mace 1997). This agriculturally linked increase in fertility is significant but marginal. It is substantially smaller than that modeled by Bocquet-Appel (2008). Among the fundamental factors affecting fertility, sedentism would have already impacted maternal activity levels by the Early Natufian timeframe (Weissbrod et al. 2017; Yeshurun et Bar-Oz 2018; Liu et al. 2020), and the starch component of the diet probably already began to rise among Natufian hunter-gatherers (Dubreuil 2004; Arranz-Otaegui et al. 2018). Considered in long-term context, Natufian developments would have likely initiated a gradual decline in

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Footnote 5: In minor contrast with Guerrero et al.’s (2008) results, we observe a PPNA (ca. 10,000-9,000 BC) trough in the proportion of juveniles, across the cross-sectional time-period subsamples. Guerrero and colleagues illustrate a possible \( p_{15} \) minimum already during the Late/Final Natufian period, ca. 11,000-10,000 BC. However, it is much better documented now that domestication, agricultural production, and sedentary village settlement only came to dominate during the PPNB timeframe (Belfer-Cohen and Goring-Morris 2008; Kuijt 2008; Goring-Morris and Belfer-Cohen 2011; Asouti and Fuller 2013; Arranz-Otaegui et al. 2016; Edwards 2016). Thus, the timing of the observed PPNA trough in figure 6 also fits Bocquet-Appel’s (2008) general model, involving a dip in \( p_{15} \) values just prior to the PPNB agricultural transition (see also Bocquet-Appel 2002 and 2011; Bocquet-Appel and Naji 2006).
average birth spacing, with a concomitant slow rise in total fertility rates, from ca. 13,000-8,000 BC. As domestication and agriculture rapidly expanded in economic and dietary importance in the Middle and Late PPNB, ca. 8,000-7,000 BC, the increase in average fertility would likely have accelerated.

Common cautions about culturally biased funerary recruitment do apply for our results, however. Relative to actual deaths in the societies creating the archaeological record, those individuals buried in the on-site mortuary features that archaeologists excavate and study are not necessarily representative. Bocquentin’s contextual analyses of changing burial practices in the Natufian periods (ca. 13,000-11,000 BC) document persistent gender-biased recruitment favoring males, while juveniles were not as likely to be interred in mortuary features in the Late Natufian period as in the Early Natufian period. This is despite the fact that infant and young juvenile burials do not show evidence of underrepresentation due to bone-density-dependent attrition (Bocquentin 2003, 2007). Given the rich variability in mortuary rituals in the Natufian and Neolithic periods across the entirety of the Levant (Kuijt 2000; Goring-Morris and Horwitz 2007; Maher et al. 2011; Nadel et al. 2013; Ortiz et al. 2013; Bocquentin 2014; Chamel 2014; Khawam 2014; Edwards et al. 2018; Benz et al. 2019; Richter et al. 2019; Chamel and Cocqueuguinot 2020; Bocquentin in press), we confirm that the interpretation of long-term change in life-stage-at-death profiles themselves is especially challenging. Under conditions of heightened mortality, it could have been ritually efficacious for a community to handle the deaths of younger individuals by preferentially burying them within settlements. Across the Near East, mortuary ritual appears to have played a central role in how individuals, corporate groups, and whole communities negotiated complex co-residential, land tenure, and social network possibilities and dilemmas—especially as they faced changing variability in biological well-being. Thus, those who lived, died, and were ritually interred in Natufian and early Neolithic sites would have been part of a dialectic among culturally constituted and experienced worlds, social practice, and complex variations in environmental exposures and health outcomes. It remains difficult, quite simply, to tease out significant changes in fertility from our bioarchaeological observations.

We suggest that, if the time-period-specific values in the proportion of juveniles (5-19 years) “pick up consistent, albeit weak, signals” of change in fertility rates (Gage and DeWitte 2009), then according to the DOHaD model, our results track a rise in mortality that was closely, systemically tied to a PPNB-PPNC/Early PN increase in fertility. Bocquet-Appel and colleagues have emphasized that empirical bioarchaeological observations confirm the metabolic load model’s theoretical expectations; with higher population densities, earlier weaning ages, and lower dietary quality, agriculture would have brought an initial rise in fertility, followed by declining health and rising mortality (Bocquet-Appel and Naji 2006; Bocquet-Appel 2008, 2011; Bocquet-Appel et al. 2008). Bocquet-Appel has specifically proposed that, in the Near East—where the social organization and knowledge involved in agricultural production and management were developed and adopted over centuries or millennia—the joint increases in fertility and mortality would have occurred more slowly than in areas of secondary adoption (Bocquet-Appel 2011). Our results suggest that the demographic feedbacks between fertility and mortality were likely very closely, systemically coupled.

From this perspective, we observe that settlement sizes, household complexity, and site distributions are consistent with millennial-scale Neolithic population growth across the entirety of the Levant. Over this long time-frame, local and regional populations were hardly stationary. On the one hand, fluctuations in local populations were likely substantial. On the other hand, at a broad geographic scale, long-term average birth rates tended to be significantly—if only slightly—greater than death rates (Kuijt 2008; Flohr et al. 2016; Ibáñez et al. 2018). While stratigraphic evidence details how individual settlements underwent dynamic histories of growth, reorganization and abandonment, we note that recent analyses of a wide corpus of radiocarbon dates from Near Eastern Neolithic contexts have found no clear evidence for episodes of population explosion; nor have such summed calibrated date probability density distribution (SCDPD) analyses identified signals of population crashes, regional abandonments, or migrations (Borrell et al. 2015; Flohr et al. 2016). The contextual radiocarbon calibration evidence is consistent with a pattern of largely local population continuity, although dramatic changes in settlement, co-residence, mobility, monument construction, storage technologies, food management, and ritual practice unfolded in mosaic fashion across the Near East (Asouti 2013; Asouti and Fuller 2013; Flohr et al. 2016; Belfer-Cohen and Goring-Morris 2011). There is arguably a surprising degree of social and demographic resilience in the face of early Holocene climatic fluctuations (Flohr et al. 2016). There are, however, important exceptions. Borrell et al. identify a possible period of dispersed or falling population in the northern Fertile Crescent in the transition from the Early to Middle PPNC, ca. 8,000 BC (Borrell et al. 2015). More strikingly, the western Jordan region shows signs of major settlement decline over several centuries in the 7th millennium BC.
Long argued to be a total hiatus in Neolithic occupation (e.g., Perrot 1968), PPNC phases have recently been documented at several sites (Bocquentin et al. 2020; Vardi 2020).

The limited paleogenomic data from Epipaleolithic and Neolithic individuals in Anatolia, Syria, and the southern Levant are generally consistent with a resilient geographically structured population network that experienced genetic isolation by distance (Fix 1999; Lazaridis et al. 2016; Loosdrech et al. 2018; Fregel et al. 2018). Although we have presented evidence consistent with increasingly frequent infectious disease outbreaks, there is no indication of an emergent southwestern Asian pandemic that could have thoroughly shaped regional population turnover. As critically emphasized in the human population genetics literature, it is also theoretically challenging to quantify the actual long-term average rate of population growth under neolithization, which would have involved not only gradual demographic increase in the Near East, but also long-distance migration into neighboring areas, from north Africa to central Asia to Europe (Fix 1999). Local fertility and mortality rates would have fluctuated, primarily in response to immediate, contextual factors affecting food availability, workloads, and pathogen exposure. At the same time, regional social network connectivity—and the practices, material culture, and ideologies that mediated long-distance visits, exchange, and kinship alliances—would have had substantial impacts on demographic resilience.

It is plausible, then, that long-term trends in mobility and nutrition were sufficient to raise fertility, especially during periods when settlements were established or reorganized. In turn, population growth would have rapidly led to Malthusian constraints, raising mortality (Winterhalder et al. 2015; Puleston and Winterhalder 2019). In light of such inferred conditions, our results conform to the expectation of a time-averaged archaeological signal, in which mortality and fertility increased in tandem (figs. 4-6). High resolution stratigraphic data from individual Neolithic sites may elucidate the interplay—at centennial scale—among settlement, economic productivity, living conditions, fertility, and mortality.

CONCLUSION

This study has utilized Natufian and Neolithic human skeletal series from 24 separate sites, constituting the largest sample of mortuary features yet analyzed from communities spanning the emergence of agricultural food economies in the Levant. We aggregated skeletons interred in different sites, from the southern and northern Levant, into chronologically cross-sectional samples, in order to maximize statistical power. This study’s analytical methodology, based on theoretical considerations from the DOHaD model, yields robust results. We identify a highly significant average drop in regional, population-level biological well-being, involving an increase in mortality in the Neolithic transition to agriculture (figs. 4-5). Our results cannot yield a detailed quantification of life-stage-specific mortality rates. We can only demonstrate a statistically well-documented directional trend, involving rising mortality at least from the PPNB through the beginning of the PPNC/PN timeframe (ca. 7,000-6,000 BC). This agricultural-associated mortality increase occurred after a period of relatively good health and lower mortality during the Early and Late/Final Natufian periods (ca. 13,000-10,000 BC). Because the cemetery sample from the 9th millennium BC is so small, it remains statistically unclear whether PPNA populations (ca. 10,000-9,000 BC) already began to suffer more frequent early-life stress than their Natufian hunter-gatherer predecessors.

Based on our results, we encourage further contextual interdisciplinary inquiry, in order to resolve more finely the causes and interactions among fertility, mortality, migration, and prevailing biocultural conditions. In focusing on the developmental origins of health and disease (DOHaD), our analysis has highlighted how community heterogeneity in early-life environmental exposures likely played an important role in the Levantine transition to agriculture. Whether structured within settlements and their immediate resource catchments, or at a wider spatial scale, variation in stress exposure appears to have forced concomitant variation in health, shaping feedbacks among life-stage-specific survival chances and mortality risks, in turn, affecting the social alliances that mediated architectural construction, land-resource management, food economies, mobility, and co-residence that, together, underpinned early agricultural societies.

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