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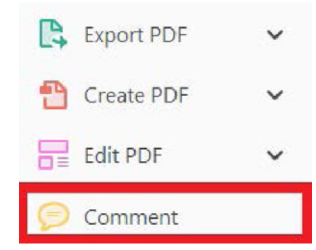

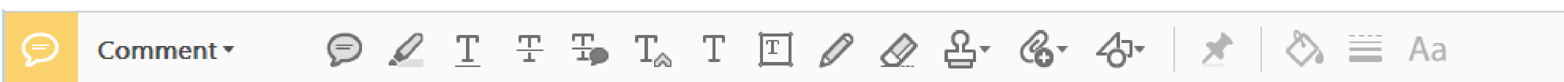

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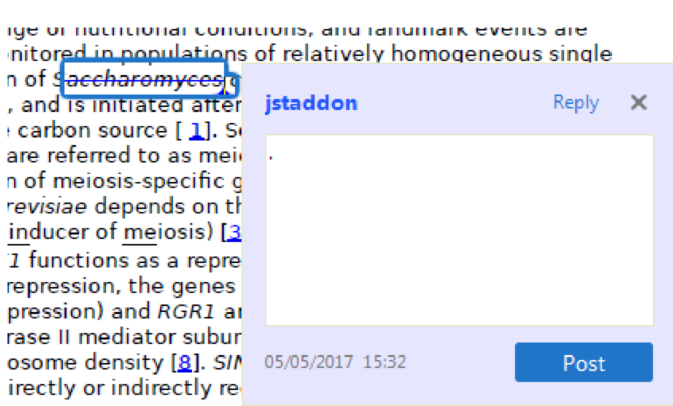

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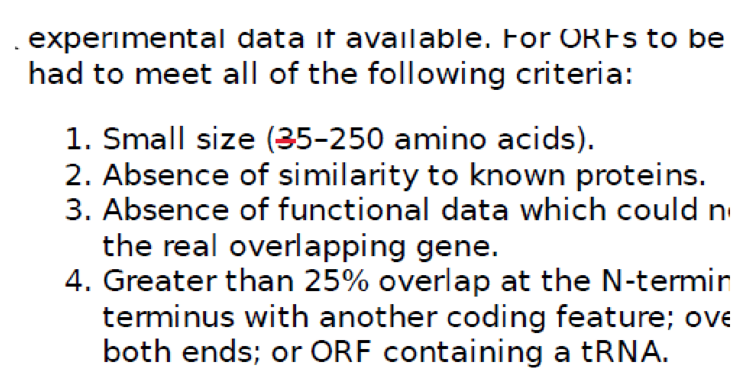

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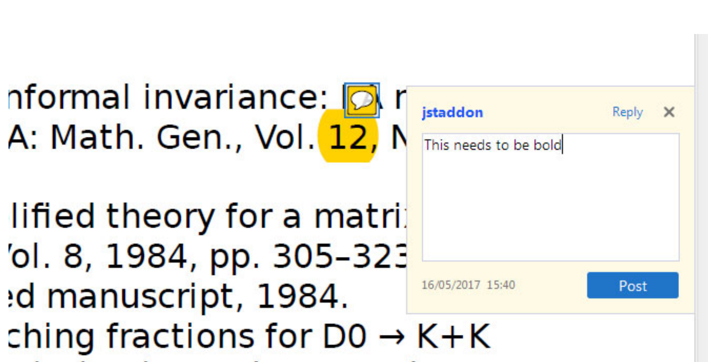

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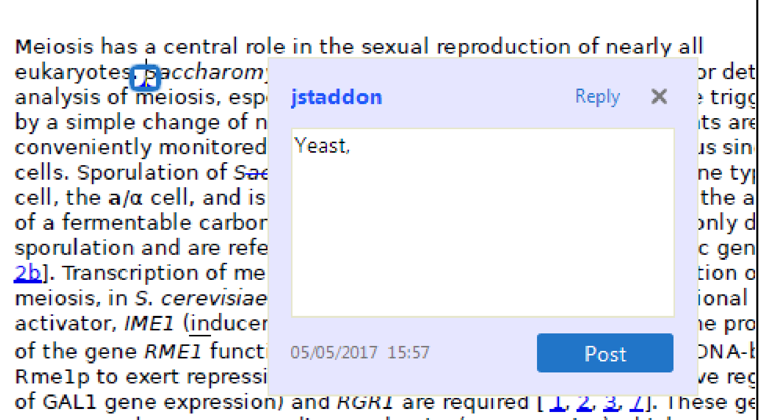

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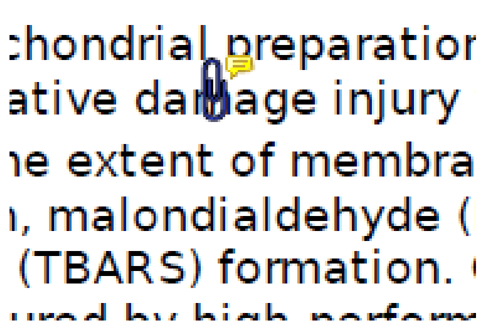

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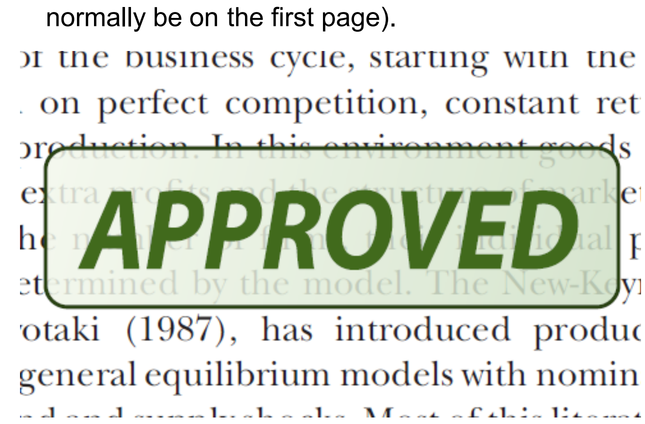

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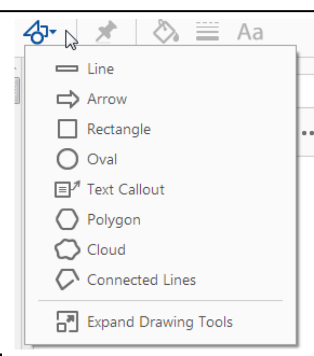

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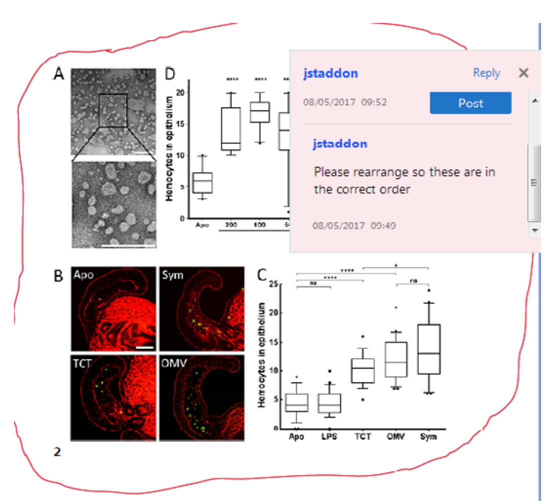

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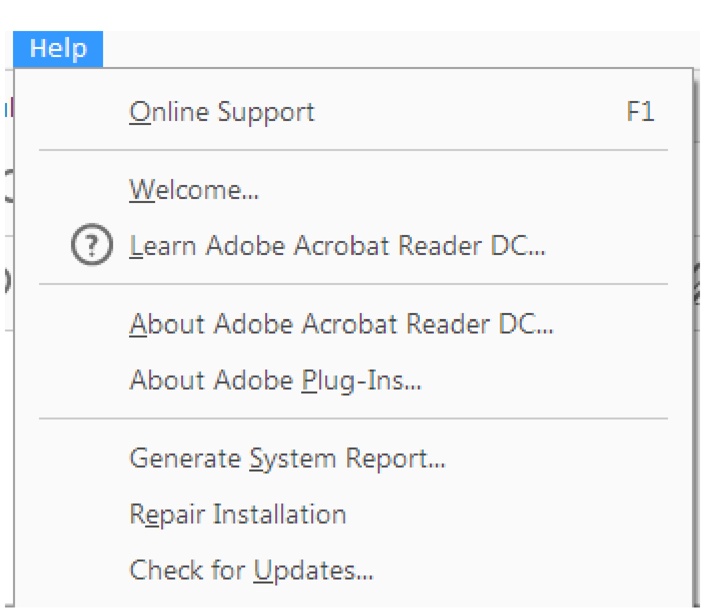

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RESEARCH ARTICLE

Population density and developmental stress in the Neolithic: A diachronic study of dental fluctuating asymmetry at Çatalhöyük (Turkey, 7,100–5,950 BC)

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Abstract

Objectives: The transition from foraging to farming is usually associated with unprecedented population densities coupled with an increase in fertility and population growth. However, little is known about the biological effects of such demographic changes during the Neolithic. In the present work, we test the relationship between diachronic changes in population size, relative exposure to developmental stressors, and patterns of dental fluctuating asymmetry in the Neolithic population of Çatalhöyük (Turkey, 7,100–5,950 cal BC).

Materials and Methods: We calculate fluctuating asymmetry of mesio-distal and bucco-lingual diameters of upper and lower permanent canines and first and second molars on a large (N = 259) sample representing adults of both sexes and various age classes.

Results: Results show only a moderate decrease of fluctuating asymmetry during the late phase of occupation of the site, possibly linked to a decrease in population density, and no differences in asymmetry between sexes.

Discussion: Though preliminary, our data reflect the presence of developmental stressors throughout the occupation of the site, albeit with a slight improvement in living conditions during the latest periods of occupation. At the same time, these data confirm the key role of diet as buffer against the detrimental effects of fluctuating demographic pressures on the biology of prehistoric human populations.

KEYWORDS

developmental stress, fluctuating asymmetry, neolithic, population density

1 | INTRODUCTION

The transition from foraging to farming is associated with the "…first human experiment in unprecedented population concentrations" (Bocquet-Appel, 2008). High energetic inputs due to calorie-rich food availability and a concomitant decrease in energy expenditure prefigured a shift in the energetic equilibrium of fertile women, resulting in an increase in fertility and birthrates, with unprecedented demographic effects (Bocquet-Appel, 2002, 2008, 2011). On the other hand, while these increases in fertility are today widely recognized due to convincing bioarchaeological and ethnological data, there is also growing evidence of an increase in infant mortality, and of alternating patterns of boom-and-bust demographic changes during the early-mid Holocene of the Near East and Western Europe (Bocquet-Appel, 2008; Shennan et al., 2013).

Higher population densities resulted in increasingly complex social networks, increased social tensions, and the unprecedented flourishing of ritual and symbolism (Garfinkel, 1987; Kuijt & Goring-Morris, 2002; Pearson & Meskell, 2015; Rollefson, 2002; Wright, 2014). These patterns, in addition to their specific bearing on prehistoric archaeology and palaeodemography, have wider consequences, forming the basis of later phenomena such as social differentiation, social stratification, and the rise and development of social inequality

(Powers & Lehmann, 2014; Powers, van Schaik, & Lehmann, 2016; Price, 1995).

The transition to farming is associated by various authors with a decrease in health, differential patterns and sex-based division of physical activity, and a variety of micro-evolutionary processes (González-José et al., 2005; Katz, Grote, & Weaver, 2017; Larsen, 1995; O'Brien et al., 2012; Paschetta et al., 2010; Pinhasi, Eshed, & Shaw, 2008; Pinhasi, Eshed, & von Cramon-Taubadel, 2015; von Cramon-Taubadel, 2011, 2017). The greater proximity of people to animals that this transition brought and the closeness of living quarters to waste disposal areas are recognized as the causes of the so-called "first epidemiological transition," generally characterized by the earliest appearance of infectious and parasitic diseases among human populations (Armelagos, Brown, & Turner, 2005; Larsen, 1995). All these factors, together with nutritional (especially protein) deficiencies stemming from a narrower dietary niche, are the basis of well-documented social changes coinciding with the Palaeolithic to Neolithic transition. Previous bioarchaeological comparisons between hunter-gatherer and farming communities highlight a general worsening of skeletal and dental health, a pattern consistent with an increase in socio-environmental stressors with the adoption of farming (Cohen & Armelagos, 1984; Larsen, 1995). It should be stressed, however, that the above pattern was probably not ubiquitous but rather characterized by a certain diachronic and regional heterogeneity (Cohen & Crane-Kramer, 2007; Starling & Stock, 2007; Stock & Pinhasi, 2011). Also, biocultural reconstructions based on paleopathological patterns need to be considered with caution, given the possible mismatch between observed frequencies of skeletal lesions and actual health of the individual/population (Wood, Milner, Harpending, & Weiss, 1992—but see Goodman, 1993).

The above features raise the question of the types of biocultural adaptive strategies adopted by humans during the Neolithic transition, and, more specifically, of the socio-cultural and biological evolutionary processes triggered by the new environmental challenges associated with sedentism (Hawks, Wang, Cochran, Harpending, & Moyzis, 2007; Holden & Mace 1997; Laland, Odling-Smee, & Myles, 2010; Mace, 2009; Naugler, 2008; O'Brien et al., 2012). An interesting angle from which to approach this issue is the exploration of possible relationships between changes in population densities, deviations in human developmental trajectories, and the evolution of developmental and/or behavioral buffers to such stressors over time.

Developmental stressors consist of any genetic and/or environmental factor hampering a specific genotype to reach its target phenotype, given a particular growth environment (Palmer & Strobeck, 2003). Examples include (among others) inbreeding, nutritional deficiencies, and infectious and metabolic diseases (Parsons, 1990). Independently from the type of stressors, threats to physiological homeostasis may result in deviations from the expected developmental trajectories under given environmental conditions. Accordingly, such deviations are potentially informative on two levels: about the relative developmental stability (or instability—DI) of an organism (Møller & Swaddle, 1997), and about the number of stressors to which the organism is exposed during growth and development.

Studies of stress in past populations are most often based on a suite of skeletal and dental features (e.g., enamel hypoplasia, *cribra orbitalia*, periostotic lesions, and long bone dimensions) associated either with developmental disruptions, non-specific bone reactive processes, or nutritional deficiencies. An additional proxy of developmental stress, widely used in biology, is fluctuating asymmetry (FA). FA is defined as subtle, random deviations from symmetry in bilateral traits and is usually adopted in developmental biology as a proxy for developmental instability (Klingenberg, 2003). FA differs from the two other types of bilateral asymmetry, anti-symmetry (AS), and directional asymmetry (DA). In AS a population shows a mean difference between sides for bilateral traits, but it is composed of both left- and right-biased individuals. In DA, on the other hand, individuals present a bias in bilateral traits consistently favoring one side over the other. Mathematically, FA, AS, and DA are defined, respectively, by a normal and a platykurtic or bimodal distribution about a mean of zero, and by a normal distribution about a mean other than zero. The rationale for the use of FA in studies of developmental stress is that random, localized perturbations differently affect the development of the two sides of symmetric traits otherwise sharing the same genotype, resulting in asymmetry (Van Valen, 1962). Differences between sides can therefore be interpreted as proxy for developmental instability, and correlated with the presence of stress-induced developmental noise.

Though largely under-represented in the bioarchaeological literature, previous studies have already explored the use of dental, craniofacial, and skeletal FA in testing patterns of developmental stress in both living and past populations, with results that overall confirm this parameter as a useful tool when investigating developmental stress in past populations (Albert & Greene 1999; Barrett, Guatelli-Steinberg, & Sciulli, 2012; Costa, 1986; DeLeon, 2007; Doyle & Johnston, 1977; Gawlikowska-Sroka, Dabrowski P. Szczurowski, Dzieciolowska-Baran, & Staniowski, 2017; Gawlikowska-Sroka, Dąbrowski, Szczurowski, & Staniowski, 2013; Greene, 1984; Hoover, Corruccini, Bondioli, & Macchiarelli, 2005; Hoover & Matsumura, 2008; Kieser, Groeneveld, & Preston, 1986; Kujanova, Bigoni, Veleminska, & Veleminsky, 2008; Perzigian, 1977). FA offers advantages over classic osteological markers of stress, namely that FA is a quantitative variable, and it is not linked to episodes of stress (as is the case with enamel hypoplasia); but represents the outcome of continuous alterations in physiological homeostasis. Collectively, these attributes make analyses of FA less biased by the analytical problems typically affecting qualitative features and are more suited to discussions of long-term patterns of developmental stress.

Many bioarchaeological studies of stress in past populations compare skeletal assemblages representing different social statuses and contrasting socio-economic strategies, with others focused on the analysis of differences in stature and/or skeletal and dental morphological changes between different social groups and between foragers and farmers (Bigoni, Krajicek, Sladek, Veleminsky, & Veleminska, 2013; Cardoso & Gomes, 2009; Cohen & Armelagos, 1984; Cohen & Crane-Kramer, 2007; Larsen, 1995; Pinhasi & Stock, 2011; Sakashita, Inoue, Inoue, & Zhu, 1997; Starling & Stock, 2007; Temple & Larsen, 2007). In addition to demonstrating the usefulness of dental and skeletal changes when testing biocultural hypotheses, results of these studies are, in general, consistent in highlighting a general decrease in quality of life and increase in environmental stressors associated with the adoption of a sedentary lifestyle and farming economy. On the other hand, much less is known about the biological effects of fluctuating population densities in Neolithic communities after the transition to farming (but see Larsen et al., 2015). This study applies a more fine-grained approach by exploring the relationship between changes in population density and patterns of developmental stress in a single archaeological setting—Neolithic Çatalhöyük in Central Anatolia—characterized by changes in population size in the context of a millennium-long occupation of a large village setting.

1.1 | Biocultural context

Neolithic Çatalhöyük (7100–5,950 cal BC—Bayliss et al., 2015) is one of the most important settlements of the Near Eastern Pre-Pottery or Aceramic Neolithic, being characterized by a large occupation footprint (13 ha), long-standing occupation (ca., 1,150 years) and archaeological features consistent with the presence of complex sociocultural traditions.

The exceptional archaeological and bioarchaeological contextualization of this site (e.g., Hodder, 2014a), unmatched by any other Neolithic context in the Old World, permits a unique opportunity to test central hypotheses about the biocultural changes associated with large population agglomerations in a key geographic area for the study of subsequent Neolithic processes.

Two main excavation areas are represented at Çatalhöyük (North and South—including TP and TPC areas) (Hodder, 2014b). Stratigraphic levels at Çatalhöyük, from the start of the occupation to the abandonment of the site, are subdivided into four diachronic phases: early (7,100–6,700 BC), middle (6,700–6,500 BC), late (6,500–6,300 BC), and final (6,300–5,950 BC) (I. Hodder, personal communication, and forthcoming). Current estimates based on architectural features (Cessford, 2005) indicate a population of 3,500–8,000 individuals, while previous archaeological and paleodemographic data (number of buildings, number of buried individuals per building, juvenility indices) suggested the presence of salient demographic fluctuations throughout the occupation of the site (Cessford, 2005; Düring, 2001; Larsen et al., 2015). Similarly, estimates of percentage of open spaces and number of building per excavated area, suggest a progressive increase of building dispersal ~~throughout~~ time (Düring, 2001: Table 1; Hodder, 2014a).

As for paleodemographic patterns, previous calculation of juvenility indices (used as proxy for fertility) (Larsen et al., 2015) describe in clear fashion an increase in population size and fertility throughout the early and middle phases of occupation, with a peak occurring around 6,610–6,250 BC, followed by a significant decrease (Early = .29, Middle = .46, Late = .29). This pattern, taken together with archaeological sites in the Konya plain pre-dating the site at Çatalhöyük (Baird, 2005; Baird et al., 2018) represented by typically small and rather dispersed settlements fits a scenario of population agglomeration, with demographic growth mainly driven by increases in fertility and birthrate. Conversely, the demographic decline estimated for the later phases could be related to the progressive abandonment of the site, likely due to a complex mosaic of factors, possibly including environmental changes driven by human activity and over-exploitation of resources (Doherty, 2013, Orton et al. 2018).

The presence of demographic fluctuations in a relatively narrow chronological interval raises the question of their possible impact on the members of the Çatalhöyük community, the question being which kind (if any) of effects these changes had on population density (and its biocultural correlates) of the settlement. Previous research highlighted diachronic patterns in the frequency of periostotic lesions mirroring the postulated changes in population size at the site, a result interpreted as a result of differential exposures to pathogens through time due to variable population densities (Larsen et al., 2015). This hypothesis seems supported by both isotopic and biomechanical data, which converge in suggesting the presence during the later phase of occupation of a more mobile and dispersed population, a factor that would have led to a reduced exposure to pathogens.

Conversely, reconstructed growth trajectories of both stature and body mass seem to contradict such a scenario, equating to an overall "healthy" population, a result interpreted as due to the buffering role of an adequate nutrition against the detrimental effects of environmental stressors (e.g., parasitic diseases, infections) on development (Larsen et al., 2015). These contrasting results stress the need for further research into the type of demographic changes (population size and density) characterizing the occupation of Çatalhöyük, and on their biological and cultural effects on the occupants of the settlement.

Here, we use Çatalhöyük as a natural experiment to explore the biological correlates of population changes associated with the Neolithic transition. More specifically, we focus on the developmental effects of such changes using dental fluctuating asymmetry (DFA) as a proxy for differential exposure to environmental stressors to test three main hypotheses:

TABLE 1 Sample size by sex, age, and occupation phase

	Early			Middle			Late/final			Unstratified Neolithic			
	F	M	NA	F	M	NA	F	M	NA	F	M	NA	Total
Infant (2 months–3 y)	0	0	0	0	0	3	0	0	1	0	0	0	4
Child (3–12 y)	0	0	5	0	0	58	0	0	13	0	0	5	81
Adolescent (12–19 y)	0	1	1	3	2	17	2	1	5	0	1	3	36
Young adult (20–34 y)	2	2	1	13	12	1	5	4	0	2	0	2	44
Mature adult (35–50 y)	2	2	0	13	10	0	7	7	1	2	1	1	46
Older adult (>50 y)	2	2	0	7	2	1	0	3	0	0	0	0	17
Adult (>20 y)	1	0	0	6	6	2	3	6	3	1	1	2	31
Total	7	7	7	42	32	82	17	21	23	5	3	13	259

Y = years; M = males; F = females; NA = undetermined sex.

Hp1: Given a correlation between population density (and fertility) and relative exposure to environmental stressors, mean DFA values will correlate with fluctuations in population size (and fertility), and will be characterized by an increase throughout the early and middle phases followed by a decrease.

Hp2: Given the hypothesized higher developmental buffering and greater genetic control of odontogenesis in females (Garn, Lewis, & Kerewsky, 1967; Garn, Lewis, Kerewsky, & Jegart, 1965; Stinson, 1985), males will exceed females in expressing developmental disturbance.

Hp3: Because of the expected correlation between FA and developmental stress, there will be an inverse correlation between asymmetry and age-at-death in this setting.

2 | MATERIALS AND METHODS

Before proceeding with the analysis of asymmetry, we determined if inclusion of the skeletal remains excavated in 2016 and 2017 altered the juvenility index estimates proposed by Larsen et al. (2015), and recalculated the number of buildings and buried individuals per building including data not available for previous estimates. For the latter purpose, only primary and primary disturbed burials were considered. Note that the use of the term buried individuals rather than burials id preferred here since burials at Çatalhöyük may represent both single and multiple interments.

The juvenility index D3–19/D3+ (the ratio between individuals aged between 3 and 19 years and the total of individuals above 3 years of age) was calculated on a sample of 324 individuals from primary and primary disturbed burials from all occupation levels at Çatalhöyük. In this and the following age-at-death and sex were determined according to standard protocols (Buikstra & Ubelaker, 1994).

Analyses of DFA were performed on a sample representing all stratigraphic phases of Çatalhöyük and composed of individuals selected on the basis of the presence of the following antimeric permanent teeth: canines (C), first molars (M1), and second molars (M2) of both maxillae and mandibles. These teeth were chosen in order to be able to study developmental stress for a relatively long period of individual growth and development. The choice to consider both molars was suggested by the possible differences in developmental stability between polar versus non-polar teeth of a dental field (Dahlberg, 1945; Goodman, 1989; Goodman & Armelagos, 1985). On each tooth, bucco-lingual (BL) and mesio-distal (MD) diameters were taken according to Hillson, Fitzgerald, & Flinn (2005) with a Mitutoyo digital calipers (accuracy = .01). Teeth with incomplete crown formation, caries, intra-vitam and post-mortem damage, high degrees of calculus (calcified plaque) deposition, and wear were excluded from the study. In total, the sample is composed of 259 individuals representing both sexes and various age classes (Table 1).

Because of the need to maximize the sample size in the context of time constraints, data collection was subdivided between two observers (MM and ID). Both observers measured each tooth two times, with an interval of a week between observations. This strategy, while unavoidable, exposes the resulting dataset to possible biases due to inter-observer error. To control for this error, both observers independently measured 51 specimens taken from the identified collection of "Fiorentini" (individuals of both sexes who died in the Florentine area of Italy during the second half of the 19th century AD), housed at the Museum of Natural History of the University of Florence (Moggi-Cecchi, Pacciani, & Pinto-Cisternas, 1994) (Table 2). This sample was chosen due to the lack of available time for performing the same analysis in the field at Çatalhöyük, and on the basis of its excellent preservation, which maximized the sample size for error analysis. The relative amount of variance due to FA versus interobserver error was estimated by means of a two-way, mixed-model analysis of variance (ANOVA) with individuals as the random factor and sides as fixed. Traits showing nonsignificant FA when controlling for interobserver error where excluded from the dataset.

Further analyses were developed according to the following steps, based on the work of Palmer and Strobeck (2003):

1. The presence of outliers possibly inflating FA values was first assessed by visual inspection by R-L scatterplots, and tested by means of a Grubb's test.
2. Because FA analyses may be biased by the presence of antisymmetry or directional asymmetry, we determined the presence of deviations from normality of the difference (R-L) in each trait, after computing the average of two observation sessions. Directional asymmetry and antisymmetry were tested by means of a D'Agostino-Pearson omnibus test (cf., Barrett et al., 2012).
3. We performed a two-way mixed-model analysis of variance (ANOVA) with individuals as the random factor and sides as fixed to assess the relative amount of variance due to FA versus measurement error (ME).
4. We used a Spearman test for testing the correlation between $|R - L|$ and $|(R + L)/2|$ and possible allometric patterns in asymmetry.
5. To assess diachronic and demographic patterns in fluctuating asymmetry, we first calculated a trait-specific index $|(R - L)|$ (Palmer & Strobeck, 2003) for each individual. Owing to missing data, we did not attempt to calculate a composite index of FA. Because calculations of inter-observer error are influenced by the relative weight of the latter versus asymmetry, we also compared the asymmetry of each trait between the Fiorentini and Çatalhöyük samples by means of a Wilcoxon test. Owing to the small size of the Fiorentini sample, we did not attempt to test for differences controlling for age and/or sex.

Potential differences in FA between periods, age groups, and sexes were tested by means of Kruskall Wallis and Kendall Tau correlation tests. Because of unbalanced sample sizes, the Late and Final

TABLE 2 Size and age distribution of the sample used for the calculation of the inter-observer error

	F	M	NA	
≥18 years	23	24	0	
<18 years	2	1	1	
Total	25	25	1	51

F = females; M = males; NA = undetermined sex.

phases were combined into one subsample. Correlation tests were undertaken after chronologically ordering each phase from 1 (earliest) to 3 (latest).

The possible association between FA and age-at-death was tested using both the original age classes and after splitting the sample into two groups: subadults (up to 19 years of age) and adults (from 20 years of age). The latter strategy was dictated by the small sample sizes of individual age classes, and in order to include in our calculation 31 adults in this study who were not assigned to specific age classes due to their poor preservation. Correlation between FA and age classes was tested with a Kendall Tau correlation test, whereas possible differences between adults and subadults were checked with a Wilcoxon test. Difference in asymmetry among traits was tested by means of a Wilcoxon test. Comparisons were made only between asymmetry values calculated using the same procedure (i.e., standardized or unstandardized by size). All statistical analyses were performed in R version 3.4.1, setting alpha at .05.

3 | RESULTS

3.1 | Diachronic patterns of fertility, number of buildings and individuals buried per building

The new juvenility indices calculated as part of this study (early = 9/29 [.31], middle = 96/218 [.44], late/final = 20/77 [.26]) are consistent with those presented by Larsen and collaborators in their earlier study (Larsen et al., 2015) (early = .29, middle = 0.46, late =.29). These findings confirm a diachronic pattern of increased fertility from the early to middle phases of occupation of the site, followed by a decrease in the late-final phase.

The number of buildings and of individuals buried per building for the North, South, TP, and TPC areas of the site increase from the early occupation phase, reach a peak in the middle, and decrease during the late and final phases (Figure 1, Supporting Information Table S1), a pattern in overall agreement with previous studies and confirming the

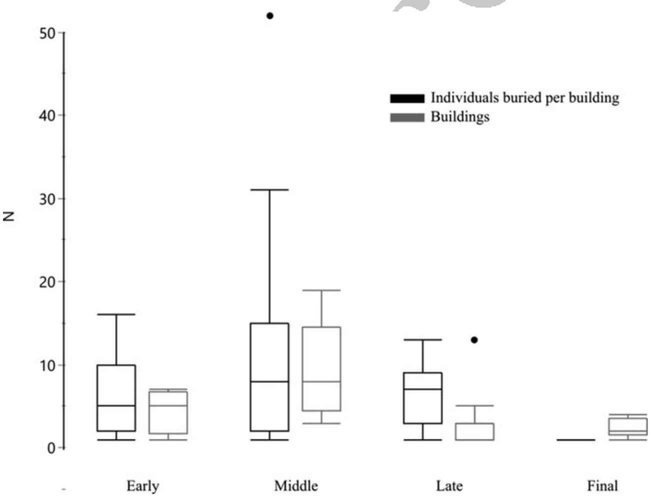

FIGURE 1 Temporal changes in number of buildings and buried individuals per building at Çatalhöyük. Data include all main excavation areas (north, south, TPC and TP), and only primary and primary disturbed burials

postulated increase in population size followed by a decline until the final abandonment of the site. The possibility of the above trend being a by-product of differences in the extent of excavation or differential preservation can be dismissed since excavation of the site is by stratigraphic layers (i.e., following the contours of the layered deposits and not arbitrary layers of similar thicknesses), and skeletal preservation is uniformly good to excellent throughout the stratigraphic layers of Çatalhöyük. This means that buried individuals coming from the same phase are of the same relative date across the excavated area of the site. Note also that the perimeter of the excavated areas did not change throughout the field seasons.

3.2 | Interobserver error, deviation from normality, measurement error, and size effect

On the basis of the ANOVA results, five traits were excluded due to their high inter-observer error: UM1 (MD and BL), UCMD, LM1BL, and LCBL (Supporting Information Table S2). LM2MD and UCBL were further excluded due to the significant deviation from normality of their asymmetry values. In addition, the test for outliers by means of Grubb's test suggested exclusion of a number of observations (max: 31, min: 7) from each trait-specific set.

All the remaining traits showed significant FA after controlling for measurement error (Table 3: Interaction Individual × Side), therefore ensuring that differences between sides in each trait were not due to directional asymmetry, antisymmetry, or observer error. Regression of asymmetry on size (see methods section) points to only two cases (LM2BL and LCMD) exhibiting a significant correlation between these variables (Table 4). Thus, we decided to use two different FA indices in the following analyses: $|(R - L)|$ for traits showing no correlation between asymmetry and size (UM2MD, UM2BL, and LM1MD) and $|R - L| \ / \ |(R + L)/2|$ for traits with asymmetry and size correlations (LM2BL and LCMD).

A comparison of these indices between the Fiorentini sample and the Çatalhöyük dataset (Supporting Information Table S3) provides only one (LM1MD) significant difference.

3.3 | Temporality, age-at-death, sex, and trait

A comparison between chronological phases indicates a general decrease in asymmetry with time, a pattern that reaches significance, however, only when considering sexes separately and only for LM2BL in females (Tables 5–7). As for age, the Kendall's Tau test on FA versus age classes highlights one trait (UM2MD) showing a positive correlation between asymmetry and age-at-death, and two traits (LM2BL, LCMD) characterized by a negative correlation (Table 8, Figure 2). When grouping the individuals into two age groups, subadults show significant higher asymmetry values for LM2BL, LM1MD, and LCMD (Table 9, Figure 3). As for sex, no trait shows significant differences between males and females, both considering each period separately and without chronological subdivisions (Table 10). Finally, when comparing traits to each other, average asymmetry is significantly different between UM2MD versus LM1MD and between UM2BL and LM1MD (Table 11). Interestingly, these differences favor maxillary teeth in both cases.

TABLE 3 Results of two-way mixed-model ANOVA (two repeated measurements)

		Df	SumSq	MeanSq	*F*	*p*
UM2MD	Individual	115.00	218.20	1.90	42.18	<.001
	Side	1.00	0.24	0.24	5.28	.023
	Individual x side	101.00	11.01	0.11	2.42	<.001
	Residuals	226.00	10.17	0.05		
UM2BL	Individual	109.00	226.39	2.08	76.88	<.001
	Side	1.00	0.28	0.28	10.40	.001
	Individual x side	94.00	7.00	0.07	2.76	<.001
	Residuals	213.00	5.75	0.03		
LM2BL	Individual	99.00	105.56	1.07	185.68	<.001
	Side	1.00	0.01	0.01	0.99	.321
	Individual x side	81.00	3.94	0.05	8.47	<.001
	Residuals	183.00	1.05	0.01		
LM1MD	Individual	102.00	218.59	2.14	99.54	<.001
	Side	1.00	0.01	0.01	0.52	.471
	Individual x side	89.00	4.64	0.05	2.42	<.001
	Residuals	202.00	4.35	0.02		
LCMD	Individual	102.00	60.61	0.59	175.01	<.001
	Side	1.00	0.07	0.07	20.33	<.001
	Individual x side	79.00	2.09	0.03	7.79	<.001
	Residuals	183.00	0.62	0.00		

~~UM2MD~~; second upper molar; LM2: second lower molar; LM1: first lower molar; LC: lower canine; MD = mesio-distal diameter; BL = bucco-lingual diameter.

4 | DISCUSSION

Before discussing the results of this study, we first address some theoretical and methodological issues regarding FA studies. A straightforward interpretation of FA as a measure of stress has been recognized as inadequate (~~Dongen~~, 2006; Leamy & Klingenberg, 2005), especially due to the current poor understanding of the genetic background of developmental instability, and the difficulty of estimating the latter from single traits. However, for this study, the risk of a genetic bias should be reduced by focusing on a single population (note also that patterns of nonmetric dental traits suggest a substantial lack of gene flow at Çatalhöyük (Pilloud & Larsen, 2011). Another issue, possibly more serious, is represented by the sample used for the test of inter-observer error. Although the use of a population different from that of Çatalhöyük was unavoidable, it is obvious that the use of a single observer, and the test for any measurement error on a single sample would have been ideal. To better accommodate these potential sources of bias inter-observer error as measured in this study is quantified with respect to the amount of variance due to asymmetry. In this sense, our error estimates appear rather solid in light of the large overlap in asymmetry values between the Çatalhöyük and Fiorentini samples.

Also, the exclusion of a number of traits characterized by unacceptable levels of inter-observer error led to a sensible decrease of sample size, already constrained by the need to exclude those teeth not preserving maximum crown diameters. Dental pathological conditions and loss of dental hard tissue due to wear (e.g., due to attrition and abrasion), represent two of the principal causes that affect the dimensions of a tooth. Mastication and the use of teeth as tools in working of materials (paramastication), are among the major factors of abrasion (e.g., Larsen, 1985; Molnar, 1972).

Both issues (exclusion of traits due to interobserver error and exclusion of individuals due to missing data) pose the question of the real representativeness of our data for the whole population. This is especially relevant for the first and last chronological phases of Çatalhöyük, represented in some cases by relatively few individuals, but demographically extremely relevant (representing the beginning and end of occupation). In addition, the small and unbalanced sample sizes prevented the use of a composite index, with a resulting decrease in our ability to capture nuanced but possibly relevant asymmetry patterns. Finally, the reduced sample sizes also hindered detailed analysis of developmental trajectories of asymmetry, and of polar versus antipolar teeth sensitivity to stress. Because of these (unavoidable) problems, this work must be considered as a preliminary test of our starting hypotheses, to be integrated in the future by the inclusion of additional data (e.g., enamel hypoplasia, Harris lines). On the other hand, when considered with the caution and criticism required by the

TABLE 4 Correlation between asymmetry and size

	n	Spearman ρ	*p*
LM1MD	108	.00	.977
LCMD	89	.49	<.001
LM2BL	87	.51	<.001
UM2BL	111	.08	.426
UM2MD	114	.13	.163

~~UM2MD~~; second upper molar; LM2: second lower molar; LM1: first lower molar; LC: lower canine; MD = mesio-distal diameter; BL = bucco-lingual diameter.

TABLE 5 Results of Kruskall-Wallis test on asymmetry values between periods

	F							M						
	Early		Middle		Late-final			Early		Middle		Late-final		
	n	Median	*n*	Median	*n*	Median	*p*	*n*	Median	*n*	Median	*n*	Median	*p*
UM2MD	1	0.430	21	0.255	5	0.070	0.247	4	0.540	18	0.368	4	0.155	0.158
UM2BL	1	0.325	21	0.135	4	0.283	0.477	4	0.203	18	0.143	3	0.135	0.536
LM2BL	1	0.054	17	0.034	7	0.007	0.017 (0.011 2vs3)	3	0.043	13	0.028	7	0.011	0.307
LM1MD	1	1.170	16	0.250	7	0.350	0.307	0		14	0.185	7	0.155	0.279
LCMD	3	0.046	18	0.025	7	0.007	0.425	2	0.033	15	0.011	6	0.012	0.811

M = males; F = females (NA individuals not included).

aforementioned issues, we believe that our results are nonetheless able to identify some general patterns. These can be summarized as:

1. Homogenous levels of asymmetry throughout the occupation of the site, with the only diachronic change (i.e., decrease over time) observed in females for a single trait only.
2. Higher asymmetry in subadults versus adults.
3. No differences in asymmetry between the sexes.

Our first hypothesis postulated a decrease in dental asymmetry across chronological phases, and, specifically, an inverse correlation between developmental stress and postulated population density at the site. Results of both the Kruskall-Wallis and the Kendall tests, while indicating a slight decrease in FA with time, point to only a single case, LM2BL in females, for which this trend is significant (Table 5). Among the factors underpinning these results, three may play a relatively important role: (1) variable developmental buffering among different teeth, (2) a complex relationship between population density and developmental stress, and (3) a lack of correlation between calculated population size and inferred population density at the site.

Differences in asymmetry between tooth classes have been previously reported and their developmental background extensively discussed (Bailit, Workman, Niswander, & Maclean, 1970; Garn & Bailey, 1977; Garn, Lewis, & Kerewsky, 1966; Garn et al., 1967; Guatelli-Steinberg, Sciulli, & Edgar, 2006; Harris & Nweeia, 1980; Hershkovitz Livshits, Moskona, Arensburg, & Kobyliansky, 1993; Perzigian, 1977; Sofaer, Bailit, & MacLean, 1971). Among the causes of such variability, one can mention differences in developmental stability of polar versus distal teeth (Hershkovitz et al., 1993; Townsend, Brook, Yong, & Hughes, 2015), upper versus lower dentitions (see Guatelli-Steinberg et al., 2006; Hershkovitz et al., 1993), and between MD and BL dimensions on the same tooth (Kolakowski & Bailit, 1981; Potter & Nance, 1976).

An additional possibility to consider may also be a lack of marked differences in stressors between periods. Thus, different degrees of developmental stability contributed to obscure possible diachronic patterns of developmental disruption. However, acknowledging such differences among traits, our data clearly indicate, overall, an absence of chronological differences in FA at Çatalhöyük. This result may shed some light on the biological correlates of local demographic changes in the prehistoric community. Bioarchaeologists postulate a link between the increase in population densities and worsening life conditions (e.g., unprecedented levels of zoonotic diseases, infections, and malnutrition) characterizing the Neolithic transition (Armelagos et al., 2005; Larsen, 1995). Investigations on a smaller scale focused on local shifts in population densities are fewer, and their results less clear. From this perspective, skeletal and biochemical data from Çatalhöyük depict a complex picture. That is, diachronic patterns of periostosis show a sudden decrease in skeletal lesions in the late phase of occupation of the site, whereas estimates of stature and body mass fail to highlight changes in these parameters through time. At the same time, juvenile $\delta^{15}N$ values are consistent with a relatively "premature" start of weaning (at about one year and-a-half—Larsen et al., 2015). Previous interpretations of these data postulated a diachronic worsening of life conditions due to increasing population densities, coupled with a weak immune response to environmental stressors due to early weaning. The parallel lack of abrupt deviations in body size, body mass, and cortical bone mass from those expected from a "healthy" population was further interpreted as the result of the access to cereal grains and animal (caprine) proteins, which would have acted as a buffer against these potential sources of stress (Larsen et al., 2015). Our results confirm the lack of marked temporal changes in developmental disruption at the site (therefore in agreement with data on stature), and are in only slight agreement with previous hypotheses about a decrease of exposure to stressors during the late phase of occupation (as evidenced by diachronic frequencies of periostosis). This result may strengthen the hypothesis of Larsen et al. (2015) about the buffering effect of diet versus the potential developmental effects of population crowding during the early-mid occupation of Çatalhöyük. Results on FA suggest a complex scenario, namely the possibility of a moderate amount of environmental stressors throughout the entire occupation of the site (therefore even in a situation of decreased population density), though mitigated by the effects of diet. A comparison of our data with those from previous work on dental FA is unwarranted due to methodological and

TABLE 6 Results of Kendall's test on asymmetry versus periods

	M			F		
	n	Tau	*p*	*n*	Tau	*p*
UM2MD	26	−.312	.053	27	−.259	.110
UM2BL	25	−.109	.511	26	.011	.948
LM2BL	23	−.230	.178	25	−.488	.004
LM1MD	21	−.203	.279	24	−.068	.693
LCMD	23	−.066	.704	28	−.171	.270

M = males; F = females (NA individuals not included).

TABLE 7 Results of Kruskall-Wallis and Kendall's test on asymmetry versus periods

	Early		Middle		Late-final				
	n	Median	*n*	Median	*n*	Median	*p* ~~(Wilcoxon)~~	Tau	~~Pkendall~~
UM2MD	9	.155	78	.240	20	.225	.530	−.088	.276
UM2BL	9	.130	77	.185	18	.225	.567	.075	.368
LM2BL	8	.044	48	.036	22	.014	.181	−.150	.121
LM1MD	8	.335	66	.250	24	.283	.397	−.042	.626
LCMD	9	.053	53	.029	20	.015	.387	−.054	.571

Pooled sexes—M, F, and NA. ~~UM2MD:~~ second upper molar; LM2: second lower molar; LM1: first lower molar; LC: lower canine; MD = mesio-distal diameter; BL = bucco-lingual diameter. UM2MD, UM2BL, LM1MD asymmetry index = |(R-L)|. LM2BL, LCMD asymmetry index = |R-L| / |(R + L)/2|.

biological discrepancies. First, the comparability between results would be hampered by the use of different statistical protocols from the one adopted here. Moreover, comparing FA values between populations representing different gene pools (and developmental stability) and environments (and environmental stressors) would be problematic.

A better approach would be the analysis of dental FA on samples predating the occupation of Çatalhöyük and theoretically representing the same biological population (the ideal candidate being the nearby but the earlier site of Boncuklu—see Baird et al., 2018). Such a study would provide essential data for further testing our interpretations.

A potential issue affecting all these reconstructions is the hypothesized correspondence between population size and population density at Çatalhöyük. It is indeed likely that the extent of occupation at the community changed through time (cf., Cessford, 2005), and these fluctuations had significant consequences for population densities and their biological correlates. Furthermore, the observed lack of correspondence between the frequency of periostosis and the temporal trends in stature and FA is hardly unexpected, given both the multifaceted nature of physiological stress (Reitsema & McIlvaine, 2014; Temple & Goodman, 2014), and the complex and not necessarily co-occurring series of variables influencing these features (e.g., time and duration of disruption, type of stress, genetic and epigenetic factors).

Our second and third hypotheses postulated, respectively, the presence of sexual differences in FA, and a negative correlation between FA and age-at-death. Comparisons between males and females fail to highlight any significant contrast in asymmetry values, a result that contradicts our expectations based on a suspected greater developmental buffering (Stinson, 1985) and more robust genetic control of odontogenesis (Garn, Lewis, & Kerewsky, 1965; Garn et al., 1967) in females, and on clinical and epidemiological data indicating a lower immunocompetence in males (Guerra-Silveira & Abad-Franch, 2013; Jansen, Stark, Schneider, & Schoneberg, 2007; Klein, 2000, 2004; Leone et al., 2004; Markle & Fish, 2014; Muenchhoff & Goulder, 2014; Owens, 2002; Pennell, Galligan, & Fish, 2012). Though apparently counter-intuitive, our results are nonetheless consistent with those from other studies (e.g., Guatelli-Steinberg et al., 2006; Kieser et al., 1986). In a recent study of dental fluctuating asymmetry in a contemporary African-American population, Guatelli-Steinberg et al. (2006) found that the only significant difference between sexes was due to higher FA values for the permanent mandibular canine in females, with no apparent sexual dimorphism for the maxillary canine. In discussing these contradictory results, these authors postulated that sexual differences in developmental buffering might have obscured by the presence of relatively high levels of developmental noise (and the possible presence of sex-biased childcare practices).

In the present analysis, we previously mentioned the possibility of a relatively homogenous exposure to developmental stressors throughout the occupation of the site as the main factor responsible of the weak diachronic decrease in FA. Isotope data also indicates a lack of differences in diet between the sexes at Çatalhöyük (females:

TABLE 8 Results of Kendall's test on asymmetry versus age classes (unspecified adults ~~>~~20 not included)

	n	Tau	*p*
UM2MD	104	.16	.0348
UM2BL	102	.03	.7324
LM2BL	77	−.24	.0043
LM1MD	97	−.14	.0778
LCMD	79	−.25	.0033

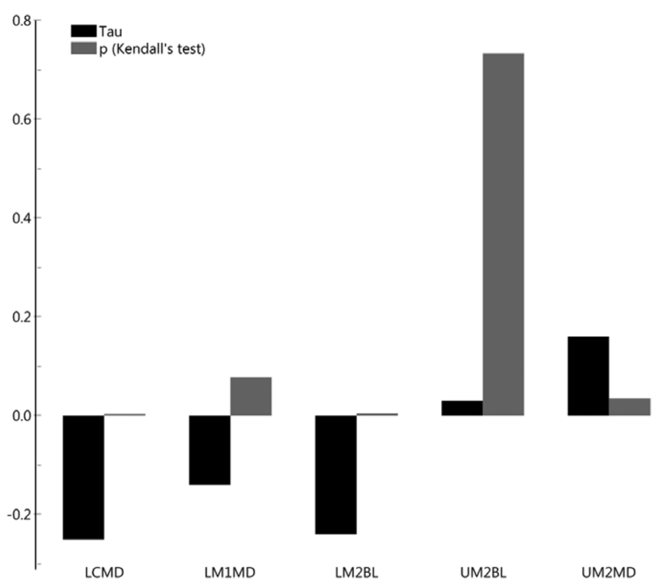

FIGURE 2 Results of Kendall's test of dental fluctuating asymmetry vs. age classes. Significant correlations are all negative (see also Table 5)

TABLE 9 Results of Wilcoxon test on asymmetry among adults and subadults

	Adult		Subadult		
	n	Median	*n*	Median	*p* (Wilcoxon)
UM2MD	56	.270	58	.213	.0874
UM2BL	54	.178	57	.210	.6904
LM2BL	57	.020	31	.053	.0076
LM1MD	53	.220	55	.330	.0097
LCMD	55	.012	35	.050	.0014

UM2MD: second upper molar; LM2: second lower molar; LM1: first lower molar; LC: lower canine; MD = mesio-distal diameter; BL = bucco-lingual diameter. UM2MD, UM2BL, LM1MD asymmetry index = |(R-L)|. LM2BL, LCMD asymmetry index = |R-L| / |(R + L)/2|.

$\delta^{13}C = -18.8\%$, $\delta^{15}N = 12.6\%$; males: $\delta^{13}C = -18.6\%$, $\delta^{15}N = 12.7\%$) (Larsen et al., 2015), therefore suggesting the absence of sex-biased childcare practices in this community. Altogether, these results strengthen the hypothesis of a weak influence of population size on actual exposure to developmental stress. Rather, applying the argument of Guatelli-Steinberg et al. (2006) we suggest that continuous exposure to relatively high developmental stressors obscured possible sexual differences in immunocompetence and fragility.

With regard to our third hypothesis, patterns of FA across age classes and between adults and subadults tend to confirm the expected correlation between high FA and premature mortality. Several studies identify an association between FA and various health variables, such as parasitism, chromosomal abnormalities, and genetic diseases (Kieser, Groeneveld, & Da Silva, 1997; Møller, 2006; Thornhill & Møller, 1997), and the link between assaults on the immune system and the development of asymmetrical phenotypes (Fair, Hansen, & Ricklefs, 1999; Møller, 2006; Whitaker & Fair, 2002). In addition, age-at-death profiles of individuals showing dental effects of high exposure to early life stressors (i.e., enamel defects) are overall consistent with a link between developmental disruptions and higher fragility (Amoroso, Garcia, & Cardoso, 2014; Armelagos, Goodman, Harper, & Blakey, 2009). The observed contrast between adults and subadults in FA at Çatalhöyük is relevant since it supports the interpretation of this parameter as a marker of developmental stress. Accordingly, it justifies the socio-ecological interpretation of the data proposed in the present investigation. Also, note that this result is in agreement with the age distribution and relative prevalence of periostosis at Çatalhöyük (higher incidence in subadults), as well as with biochemical reconstructions suggesting a condition of weakened immunocompetence in juveniles (Larsen et al., 2015).

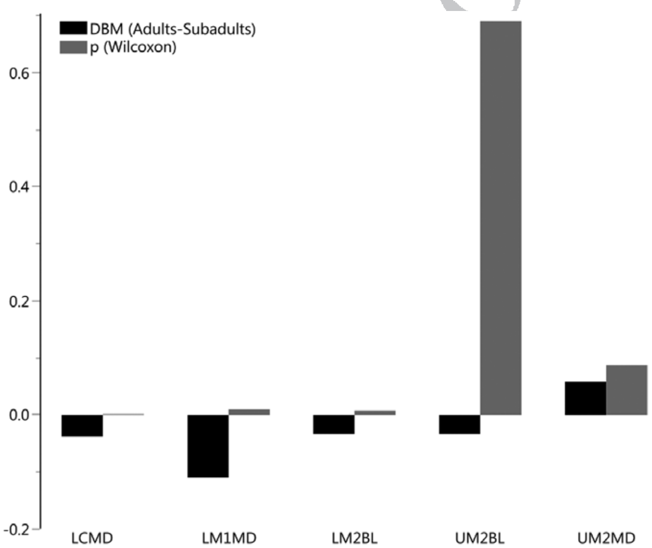

FIGURE 3 Differences between medians (DBM) of adults and subadults, and p values of the Wilcoxon tests. Note that all significant differences show higher FA in subadults

TABLE 10 Results of Wilcoxon test on asymmetry between sexes

	F		M		
	n	Median	*n*	Median	*p* (Wilcoxon)
UM2MD	29	.255	27	.345	.1584
UM2BL	28	.210	26	.153	.9931
LM2BL	30	.014	25	.021	.7353
LM1MD	27	.250	23	.175	.0643
LCMD	29	.016	25	.011	.4932

M = males; F = females (NA individuals not included)

5 | CONCLUSION

We examined the relationship between diachronic changes in population size, relative exposure to developmental stressors, and patterns of dental fluctuating asymmetry in the Neolithic population of Çatalhöyük (Turkey, 7,100–5,950 cal BC). Though preliminary, our results are consistent with the presence of developmental stressors throughout the occupation of the site, though with a slight improvement in living conditions during the latest periods of occupation. Moreover, our data agree with the results of previous research suggesting the important role diet played as a developmental buffer at Çatalhöyük, and overall demonstrates the usefulness of dental fluctuating asymmetry as an analytical tool in biocultural reconstructions of health and living conditions. More work is needed in order to further test our hypotheses (e.g., combine data on dental fluctuating asymmetry with patterns of enamel hypoplasia and Harris lines). On a more general level, our study highlights the complex and multifaceted nature of developmental stress and the usefulness of a multipronged approach

TABLE 11 Results of Wilcoxon test on asymmetry between traits

			Z	*p*
UM2MD	vs.	UM2BL	1.41	.159
UM2MD	vs.	LM1MD	−2.05	.040
UM2BL	vs.	LM1MD	−3.39	.001
LM2BL	vs.	LCMD	−.21	.833

UM2MD: second upper molar; LM2: second lower molar; LM1: first lower molar; LC: lower canine; MD = mesio-distal diameter; BL = bucco-lingual diameter. UM2MD, UM2BL, LM1MD asymmetry index = |(R-L)|. LM2BL, LCMD asymmetry index = |R-L| / |(R + L)/2|. Only asymmetry indices calculated with the same formula are compared.

to developmental studies, while stressing the need for new palaeodemographic models that permit more informed discussions of the links between environment, growth, and development in the past.

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