



Variation in ontogenetic trajectories of limb dimensions in humans is attributable to both climatic effects and neutral evolution

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ABSTRACT

Previous studies showed that there is variation in ontogenetic trajectories of human limb dimensions and proportions. However, little is known about the evolutionary significance of this variation. This study used a global sample of modern human immature long bone measurements and a multivariate linear mixed-effects model to study 1) whether the variation in ontogenetic trajectories of limb dimensions is consistent with ecogeographic predictions and 2) the effects of different evolutionary forces on the variation in ontogenetic trajectories. We found that genetic relatedness arising from neutral (nonselective) evolution, allometric variation associated with the change in size, and directional effects from climate all contributed to the variation in ontogenetic trajectories of all major long bone dimensions in modern humans. After accounting for the effects of neutral evolution and holding other effects considered in the current study constant, extreme temperatures have weak, positive associations with diaphyseal length and breadth measurements, while mean temperature shows negative associations with diaphyseal dimensions. The association with extreme temperatures fits the expectations of ecogeographic rules, while the association with mean temperature may explain the observed among-group variation in intralimb indices. The association with climate is present throughout ontogeny, suggesting an explanation of adaptation by natural selection as the most likely cause. On the other hand, genetic relatedness among groups, as structured by neutral evolutionary factors, is an important consideration when interpreting skeletal morphology, even for nonadult individuals.

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1. Introduction

Past studies have shown that variation reflective of population history is preserved in the postcranium, including transitions in subsistence strategies (Ruff et al., 1984; Ogilvie, 2004; von Cramon-Taubadel et al., 2013; Ruff et al., 2015), climatic selection (Betti et al., 2015; Roseman and Auerbach, 2015) as a result of expansion out of Africa (Ruff, 1994; Holliday, 1997; Holliday and Ruff, 2001; Betti et al., 2012), and signatures of neutral (nonselective) evolution (Roseman and Auerbach, 2015; Agostini et al., 2018). Specifically, geographically patterned variation in human body form (body size, body dimensions, limb shape and size, and the relative proportions among these components) is often interpreted as the result of

climatic adaptation (Ruff, 1991, 1993, 1994; Pearson, 2000). The primary explanation is that human groups living in colder climates evolved body proportions that minimize heat dissipation and maximize heat retention, as a lower surface-area-to-volume ratio promotes these processes (Ruff, 1993; Lieberman, 2015). Comparison of body breadth among modern human groups showed an increase in absolute body breadth with increasingly colder climates (Ruff, 1991, 1993, 1994; Weaver, 2003). The increase in body breadth corresponds to an increase in volume when the body is modeled as a cylinder (Ruff, 1991, 1994), thereby decreasing the surface-area-to-volume ratio. Comparison of limb length relative to overall body size or body size proxy also seemingly confirmed the thermoregulatory hypothesis. Studies generally showed that groups living in warmer areas tend to have relatively longer limb lengths than groups living in colder areas (Roberts, 1953; Ruff, 1994; Holliday and Falsetti, 1995; Holliday, 1997; Katzmarzyk and Leonard, 1998). Furthermore, past studies have also identified

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that variation in relative limb length among modern human groups is largely due to variation in distal limb elements (Trinkaus, 1981; Ruff, 1994). Modern humans in warmer areas (the tropics) tend to have higher intralimb indices (i.e., brachial and crural indices) than their counterparts in colder areas (Trinkaus, 1981; Ruff, 1994; Betti et al., 2015). This pattern tends to hold regardless of body size (Kurki et al., 2008) or geographic areas (Temple, 2008; Auerbach, 2012; Seguchi et al., 2017), but not necessarily so when the comparison is limited to a local scale (Kurki et al., 2008; Temple et al., 2008; Seguchi et al., 2017), since comparison on a local scale is often confounded by recent population history and migration (Temple et al., 2008; Auerbach, 2010).

Recently, studies using population genetics models had begun to challenge the view that climatic adaptation is the only driving force behind the variation in human body form, with research showing that different evolutionary forces, including random genetic drift, gene flow (Hruschka et al., 2015; Roseman and Auerbach, 2015; Pomeroy et al., 2021; Savell et al., 2022), and a combination of direct and indirect responses to climatic selection (Savell et al., 2016), all contribute to the variation in human body form. Pomeroy et al. (2021) showed that population history, encompassing neutral evolutionary processes, accounts for a greater and unique proportion of the variance in stature, lower limb length, and sitting height. Savell et al. (2022) demonstrated that, after accounting for the effects of neutral evolution, measurements associated with body breadth (i.e., bi-iliac breadth) were negatively associated with extreme temperatures, suggesting directional selection in response to climatic conditions as the primary driver for variation in body breadth. Signals of directional selection in limb lengths, however, could not be reliably demonstrated. These results affirmed that population structure arising from neutral evolutionary forces is an important consideration when interpreting variation in human body form in the evolutionary context.

While there are many studies available on the variation of human body form in adults, information on nonadults is very limited. Cowgill et al. (2012) showed that ecogeographic patterns in anthropometric measures occur early in infancy and are maintained throughout growth in a global sample of modern humans. Skeletally, differences in the relative length of long bones showed similar patterns, with groups living in colder areas (at higher latitudes) having lower intralimb indices than those living in warmer areas (at lower latitudes). The relative relationships among different groups are also maintained throughout growth (i.e., groups having higher intralimb indices will always have higher intralimb indices no matter which life history stage they are in; Cowgill et al., 2012). Similar observations have been made by several other studies (Frelat and Mitteroecker, 2011; Temple et al., 2011; Bleuze et al., 2014; Osipov et al., 2016). However, although some of these studies have speculated about the underlying evolutionary processes, none of them have systematically examined the evolutionary significance of immature skeletal morphology using evolutionary theory-informed models. Moreover, traditional statistical tests of association between anthropometric or skeletal measures with latitude or temperature variables do not account for neutral forces of evolution (mutation, gene flow, and random genetic drift). Groups that are closely related genetically will resemble one another because of their shared history and gene flow among them (Relethford et al., 1997; Roseman, 2004; Whitlock, 2008; Stone et al., 2011). The patterns observed in nonadults can arise simply because of genetic divergence among groups. Studying patterns of phenotypic variation in nonadults under a population genetics framework to test hypotheses about different evolutionary forces is therefore necessary to fully understand how different evolutionary forces shape patterns of postcranial trait variation in modern humans.

It is likely that the evolutionary forces that influence adult characteristics are active during the entire life course. Thus, variation among immature populations can arise because of genetic divergence among groups or from selective effects. Studying entire ontogenetic trajectories—changes in phenotype through univariate or multivariate space over the course of ontogeny (Alberch et al., 1979; Alberch, 1980)—using evolutionary models as opposed to standard statistics (e.g., linear regression) is vital when multiple evolutionary forces might have played a role in shaping variation. Doing so allows different evolutionary scenarios to be directly compared, thus aiding in ruling out scenarios that do not fit the data well. In the past, ontogenetic studies of postcranial elements mostly focused on exploring within-group variation (Bastir et al., 2013; Pujol et al., 2014, 2016; Huseynov et al., 2016). Most of these studies found that distinctive ontogenetic trajectories relating to sex differences in different skeletal elements emerge around the onset of puberty. In an among-group comparison, Frelat and Mitteroecker (2011) compared the growth trajectories of the femur and tibia between a European group and an African group and found that, despite the overall similarity, among-group differences in ontogenetic trajectories of bone length and shape can be observed at an early age. This was especially true for the tibia, where group differences in ontogenetic trajectories of bone length were present at birth and diminished in early childhood. A follow-up study on the ontogeny of transverse dimensions of human body form in three groups reported similar findings (Frelat et al., 2017). While there is among-group variation in ontogenetic trajectories, the underlying evolutionary causes of this variation remain unknown.

This study uses a global sample from both contemporary and archaeological groups to test three hypotheses. First, past studies have repeatedly demonstrated that variation in ontogenetic trajectories of limb proportions is consistent with ecogeographic predictions (Temple et al., 2011; Cowgill et al., 2012; Osipov et al., 2016); that is, groups living in colder areas will have lower intralimb indices than those living in warmer areas. We thus hypothesize that in a geographically and temporally diverse sample, we will be able to identify variation in ontogenetic trajectories of limb dimensions associated with climatic conditions. We predict that groups living in colder areas will have shorter limbs compared to groups living in warmer climatic conditions throughout ontogeny, factoring in the effects of body size. Second, we hypothesize that, similar to variation in adult body form (Hruschka et al., 2015; Roseman and Auerbach, 2015; Pomeroy et al., 2021; Savell et al., 2022), body form in nonadults, and its variation throughout ontogeny, are under a variety of evolutionary influences. We expect that neutral evolutionary forces can account for some of the observed variation in ontogenetic trajectories of limb dimensions and proportions. Finally, similar to observations made in previous studies about adult body form (Roseman and Auerbach, 2015; Savell et al., 2022), we hypothesize that, after accounting for neutral evolution, the observed variation in ontogenetic trajectories of limb dimensions and proportions is still associated with climatic factors in the predicted direction. This study aims to tease apart the evolutionary forces underlying variation in ontogenetic trajectories of limb dimensions and ultimately the adult body form, thus providing a deeper understanding of the evolutionary history of modern humans.

2. Methods

2.1. Materials

This study uses the linear measurements of four long bones (humerus, radius, femur, and tibia) from individuals of both sexes

ages 0 (birth) to 16 years. The measurements collected include diaphyseal length, proximal and distal breadth, and midshaft mediolateral (ML) diameter (Table 1). Breadth measurements were included because of their reported correlation with body breadth (Shaw and Stock, 2011; Davies and Stock, 2014) and body size (Ruff, 2007; Squyres and Ruff, 2015; Chu et al., 2022). Research also showed variation in limb breadths across different climatic conditions (Eveleth and Tanner, 1976; Weaver, 2003). Femoral head diameter, although often used as an imperfect proxy for body size (Ruff, 1991; Auerbach and Ruff, 2004), is not included because reliable measurements cannot be taken until the femoral head is fully fused, which does not occur until early puberty (Cunningham et al., 2016). A previous study taking osteometric measurements from medical images also showed that true femoral head size (which appears as a separate epiphysis in young individuals) can only be reliably measured around seven years of age (Ruff, 2007).

Archaeological samples Osteometric data from seven archaeological samples ($n = 556$) were collected previously (Cowgill, 2010). Age for each individual was estimated by Cowgill (2010) using either dental development or diaphyseal length. Detailed descriptions of these samples as well as data collection protocols are published elsewhere (Cowgill, 2010; Temple et al., 2011; Cowgill et al., 2012). To make data comparable to the contemporary samples, only measurements from unfused bones or without epiphyses were included in the final data set. All data from archaeological samples were collected by L.C. and have been deposited in Zenodo (<https://doi.org/10.5281/zenodo.7675357>).

Contemporary samples All data for contemporary samples (total $n = 3637$ stored in the database) were collected from the Subadult Virtual Anthropology Database (for more information, see Stull and Corron, 2022). The data include postmortem computed tomography (CT) scans generated in the United States (Berry and Edgar, 2021), medical CT scans generated in France (Corron, 2016), the Netherlands, and Taiwan (Yim et al., 2021b), osteometric measurements from dry skeletal samples in Columbia, and medical Lodox Statscan (full-body digital X-ray) images generated in South Africa (Stull et al., 2014a). For CT scans, linear measurements were collected from 3D-rendered skeletal models following the protocol described by Stock et al. (2020). Measurements from 3D models and dry bones were acquired either from the Subadult Virtual Anthropology Database (<https://zenodo.org/communities/svad>; Stull and Corron, 2022) or (in the case of the Taiwanese sample) collected by A.D. Y. The agreement between data in the Subadult Virtual Anthropology Database and data collected by A.D. Y. has been tested previously and found to be acceptable (average technical error of measurements was less than 0.05 mm; Yim et al., 2021a). The processes of reconstruction of 3D models allow for the removal of unfused and fused epiphyses, thereby increasing the sample size for the final data set. For Lodox Statscan images, measurements were collected previously (Stull et al., 2014a) following protocols developed by Stull et al. (2014a). The collection and processing of medical images and osteometric data were done retrospectively, with no personal identifiable information being made available to the researchers (Stull and Corron, 2022). This is in

compliance with the Declaration of Helsinki for the protection of privacy and consistent with the ethical principles described in the Belmont Report. The study protocol was reviewed and determined by the Office for the Protection of Research Subjects at the University of Illinois to not meet the criteria for Human Subjects Research. Institutional review board approval is therefore exempt. All data are freely available in the Subadult Virtual Anthropology Database Zenodo community (<https://zenodo.org/communities/svad>).

Past studies demonstrated that the metrics taken from rendered 3D images from CT scans (Stull et al., 2014b; Colman et al., 2019) and Lodox Statscan (Stull et al., 2013) showed no significant difference from those collected from dry bones. Therefore, we combined the two sets of samples in the final data set to increase geographic coverage. We made no attempt to test for interobserver error between the two samples because any systematic shift in measurement between the two should be picked up by including sample type (archaeological or contemporary) as an explanatory variable. Table 2 provides a summary of all samples used in the current study, including sample size, sample location, and corresponding climatic variables. A map of sample distribution is presented in Supplementary Online Material (SOM) Figure S1. A breakdown of the sample size for each bone is presented in SOM Table S1.

2.2. Methods

We used a multivariate mixed model approach to partition the effects of climatic factors and neutral evolution on limb dimensions during growth. A general mixed model takes the form of:

$$Y = XB + ZU + E$$

where Y is the matrix containing all measurements from one bone (proximal and distal breadth, diaphyseal length, midshaft ML diameters), B is the matrix of fixed effects (estimated size proxy and climatic variables), U is the matrix of random effects (phenotypic similarities among groups attributed to shared history), E is a matrix of error terms (the residuals), and X and Z are incidence matrices, relating each effect to Y (Lynch and Walsh, 1998; Hadfield and Nakagawa, 2010). The age of the individual is included as either a fixed effect or a random effect, depending on the model (see below). We used the square root of age to linearize the relationship between age and individual measurement (Stull et al., 2014a). Climatic variables include mean annual temperature, maximum temperature of the warmest month (warmest temperature), and minimum temperature of the coldest month (coldest temperature). Past studies showed that extreme temperatures such as the warmest and coldest temperatures are likely the driving forces behind ecogeographic variation in human skeletal traits (Hubbe et al., 2009; Foster and Collard, 2013; Betti et al., 2014, 2015). On the other hand, a clear association has been shown between mean annual temperature and several human body proportions and/or skeletal traits (Katzmarzyk and Leonard, 1998; Harvati and Weaver, 2006; Leonard and Katzmarzyk, 2010; Cowgill et al., 2012). Moreover, different traits often have different responses to different temperature variables (Stinson, 1990; Pomeroy et al., 2021; Savell et al., 2022), suggesting the inclusion of all the temperature variables is necessary to study the differing independent effects on skeletal traits. These three climatic variables were obtained from WorldClim (Hijmans et al., 2005; Fick and Hijmans, 2017) and PaleoClim (Fordham et al., 2017; Brown et al., 2018) databases. While other studies often exclude data after 1990 when deriving temperature variables as a way to lessen the effects of the recent rise in global temperatures (Cowgill et al., 2012; Savell et al., 2022),

Table 1
Osteometric variables used in this study.

Bone	Osteometric measurements
Femur	Femoral diaphyseal length; femoral midshaft breadth; femoral distal breadth
Tibia	Tibial diaphyseal length; tibial midshaft breadth; tibial proximal breadth; tibial distal breadth
Humerus	Humeral diaphyseal length; humeral midshaft breadth; humeral distal breadth
Radius	Radial diaphyseal length

Table 2

Summary of samples used in the current study, including sample identifier, sample size, latitude, and corresponding climatic variables.

Sample	Sample size	Latitude (°)	Mean annual temperature (°C)	Maximum temperature of the warmest month (°C)	Minimum temperature of the coldest month (°C)
Contemporary					
Columbia	57	6.267	21.1	27.8	14.8
France	578	43.297	14.0	28.3	2.1
The Netherlands	216	52.289	9.3	20.9	−0.2
South Africa	1348	−33.954	17.1	26.8	8.0
Taiwan	117	25.033	21.9	31.8	12.5
United States	1321	35.084	13.3	33.8	−5.5
Archaeological					
Amerindians	120	40.80	8.65	22.05	0.1
Indian Knoll	97	37.268	14.1	33.9	−4.5
Kulubnarti	97	21.070	26.5	42.1	9.1
Mistihaj (Vlakh)	58	43.704	7.4	23.4	−8.9
Dart	68	−26.188	14.4	25.2	−0.5
Luis Lopes	48	38.717	16.2	24.9	9.2
Point Hope (arctic)	68	68.341	−6.6	8.4	−21.3

we used the historical average for the years 1970–2000 from WorldClim. Given that our contemporary samples are very recent, we assume that the recent climatic data are representative of the environmental conditions that these contemporary samples were in, and any effects of rising temperatures are mitigated by taking the long-term average of temperatures recorded over three decades. This approach is supported by a previous study using similarly recent samples (Pomeroy et al., 2021). We chose not to include sex as a fixed effect because past studies on modern humans generally showed little to no sex effects on the ontogenetic trajectories of various linear dimensions of the body (e.g. Wilson et al., 2015; Huseynov et al., 2016; Pujol et al., 2016; García-Martínez et al., 2020), and because estimating sex in nonadults is difficult due to the lack of a standard methodology (Christensen et al., 2013; Moore, 2013).

We included a size proxy in the model to account for the effects of changing linear dimensions as a result of allometric variation. Whenever possible, body mass estimates were derived from the equations provided by Ruff (2007) using the distal femoral breadth. However, it was not possible to estimate body mass for all individuals because femoral distal breadth, which is used to estimate size, is not available for every individual. While an externally defined size proxy such as body mass is ideal, an internally defined size proxy, Mosimann's (1970) 'size variable,' was used as a substitute for body mass when femoral distal breadth was not available. Mosimann's size is the geometric mean of all measurements taken from one single bone, and the relationship between Mosimann's size and estimated body mass is highly and significantly correlated ($r = 0.85$ for humerus and 0.94 for tibia, adjusted $r^2 = 0.90$ and 0.76 for humerus and tibia, respectively, with $p < 0.001$ for both models; SOM Fig. S2; SOM Table S2). Therefore, for the femur models, all individuals have a body mass estimate since all measurements taken from the femur are available for all individuals. For the radius model, since only one measurement from the radius was taken as the response variable, estimated body mass was used as a fixed effect. For the humerus and tibia, Mosimann's size was used as a fixed effect for the corresponding single-bone models, since all individuals in these subsets of data have all measurements from one single bone. Size (body mass or internally defined measure of size) was included as a fixed-effect term because a previous study (Yim et al., 2021b) showed that relationships between body size and long bone diaphyseal metrics are not likely to change across age stages and samples. Furthermore, the inclusion of age as an effect in the models should account for any change in the scaling relationships between bone measurements and size.

The U matrix encodes phenotypic similarities among groups as a result of shared history. It has a mean vector of $0 \rightarrow$ and a variance-covariance (V/CV) structure that can be decomposed into $A \otimes H$, where A is the matrix of group relationships and H is the trait V/CV matrix (similar to G in quantitative genetics) (Katz et al., 2016, 2017). In evolutionary analysis at the species level, A is the correlation among species given the phylogenetic relationships, equivalent to the shared branch length on the phylogeny under consideration, with a maximum (total) length of the tree scaled to one (Lynch, 1991; Hadfield and Nakagawa, 2010). We followed the methods outlined in Katz et al. (2016, 2017) to estimate A directly by first correlating geographic distance with genetic (microsatellite) distance using publicly available genomic microsatellite variation data (Rosenberg et al., 2002; Friedlaender et al., 2008; Pemberton et al., 2013), converting geographic distances among groups in our sample into genetic distances, and then calculating pairwise correlations in the A matrix. A more detailed description of the approach can be found in Katz et al. (2016, 2017).

We fit mixed-effects linear models using the 'brms' package (Bürkner, 2017) in R 4.1.0 (R Core Team, 2021). Four sets of models were fitted for each long bone. The first set of models ('climate-only models') included only the fixed-effect terms (age, sample type, body size, and climatic variables). The models are termed 'climate-only models' because they represent traditional statistical testing of association with variation in ontogenetic trajectories and different climatic variables, and the primary purpose of this study is to address and account for the role of neutral evolutionary forces. Through contrasting goodness of fit statistics among the models and interpreting estimated coefficients, the results of the climate-only models will inform hypothesis 1 (variation in ontogenetic trajectories of limb dimensions is associated with climatic conditions). All possible subsets of climatic variables were used in this step to determine the best-fitting models for the subsequent mixed-effects models. A summary of models and their corresponding fixed-effect terms based on climate-only model fitting results is presented in SOM Table S3. The second set of models included only a random-effect term representing phenotypic similarity due to genetic relatedness but not climatic variables ('population structure-only model'). The third set of models included both climatic and population structure variables ('inclusive model'). This set of models represents both adaptation to climate and neutral evolution as contributing to the differences in growth trajectories. In addition, we fit a random slope and intercept model with estimated body size and climatic variables as fixed effects and both population structure and age as random effects ('inclusive random slope model'). This model allows for differences in the

slopes of growth trajectories to account for distinctive patterns of growth among different groups.

We used the widely applicable information criterion (WAIC; Watanabe, 2010) and leave-one-out (LOO) cross-validation (Vehtari et al., 2017) for model comparison and hypothesis testing. The WAIC is an improved form of the deviance information criterion and a generalized form of the Akaike information criterion and the Bayes information criterion, but for singular statistical models. A Bayesian hierarchical model is generally singular because the probability distributions are dependent on the data. The LOO cross-validation model is designed to test the prediction accuracy of the models and consists of re-fitting models using different training sets, although newer algorithms permit the approximation of LOO without refitting the models (Vehtari et al., 2017). While WAIC is asymptotically equivalent to LOO, LOO is generally considered more robust because WAIC is only a point estimate (van der Linde, 2005; Plummer, 2008), while LOO is calculated with a distribution attached. In cases with weak priors, as is the case in the present study, LOO is preferred (Vehtari et al., 2017). The comparison of model fit statistics among the four sets of models will inform hypothesis 2 (neutral evolutionary forces can account for some of the variation in the ontogenetic trajectories of limb dimensions): if any model with population structure is the best-fitting model, hypothesis 2 is supported.

The 'brms' package implements Bayesian mixed-effects models using the Bayesian inference probabilistic programming language 'Stan' (Stan Development Team, 2015; Carpenter et al., 2017). 'Stan' allows the sampling of the posterior probability distribution of model parameters through Markov chain Monte Carlo (MCMC) to be performed using a Hamiltonian sampler, which greatly improves the sampling efficiency (Homan and Gelman, 2014), thus reducing the number of iterations needed for model convergence. Each model was performed with two parallel sampling Markov chains, each with a 250,000-iteration burn-in, followed by a 250,000-iteration sampling, thinning at a rate of 250. A total of 2000 posterior samples were obtained for inference for each model. All models were fitted with uninformative priors with a continuous uniform distribution for the estimated effects (slopes). The distribution of model coefficients (estimated effects) from the posterior sample forms a 95% credible interval and serves as the basis for interpretation of the effects for different predictor variables (sample type, body size, and climatic variables). The 95% credible interval represents the interval within which the unobserved effects of the variable fall with a 95% probability, given the evidence provided by the observed data. For the best-fitting models, we derived the conditional effects for each temperature variable. The conditional effects show the direct contribution of different temperature variables on the dependent variable (linear measurements) by holding all the random effects and other covariates constant (Gelman et al., 2013; McElreath, 2020). In a simple linear model with multiple predictors, this is done by taking the partial derivative of the response variable with respect to the variable of interest. In a Bayesian model, conditional effects were obtained using the posterior predictive distribution. This was done by marginalizing the distribution of the range of all possible values for the temperature variable under consideration, using the mean values for all other numeric variables, and holding all categorical variables constant (Bürkner, 2017, 2018). This approach accounts for the uncertainty in model parameters. The conditional effects allow for visualization and interpretation of the directional effects of the temperature variables after accounting for the effects of neutral evolutionary forces, thus informing hypothesis 3 (the effects of temperature variables follow ecogeographic predictions after accounting for neutral evolutionary forces). In addition, the posterior distributions of the estimated intercepts and slopes derived from

the best-fitting models were used to demonstrate the relative magnitude of the effects. The effects of among-group variation were taken as a contrast between the estimated group-level intercepts of two groups in our sample with maximum relatedness and minimum relatedness (maximum and minimum correlations in the A matrix).

In addition to temperature variables, we also investigated the relationships between age and different long bone linear measurements using a similar approach but varying group-level effects to obtain group-specific posterior predictive distributions.

3. Results

Without taking neutral evolutionary forces into account (climate-only models; SOM Fig. S3), the association between climatic variables and diaphyseal length measurements mostly fits ecogeographic predictions. An increase in the minimum temperature of the coldest month (coldest temperature) is associated with an increase in the diaphyseal length of the humerus, radius, and femur but a slight decrease in the tibial diaphyseal length. An increase in the maximum temperature of the warmest month (warmest temperature) is associated with an increase in the diaphyseal length of the humerus, femur, and tibia. For breadth measurements, only the femoral distal breadth has a reliably nonzero relationship with the coldest temperature (an increase in the coldest temperature is associated with an increase in the femoral distal breadth). On the other hand, an increase in the mean annual temperature is associated with a decrease in the diaphyseal length of the humerus and femur, as well as the distal breadth of the femur.

Different model fitting statistics are summarized in Table 3, with the model diagnostics for the best-fitting model presented in SOM Figures S4–S9. Models that account for population structure arising from neutral evolution generally outperformed models that do not account for population structure (climate-only models). Models with only random-effect terms (population structure–only models) also outperformed the climate-only models for all bones except the femur. The inclusive random slope model is the best-fitting model for the humerus, femur, and tibia, while the inclusive model is the best-fitting one for the radius. The inclusive model allows the model intercept to vary at both population and group levels, while the inclusive random slope model allows the model

Table 3

Summary of model comparison statistics for the mixed-effect models, with the best-fitting models bolded for each bone. Model selection was based on a combination of information criteria, adjusted r-squared, and posterior predictive check.

Bone	Model	WAIC	LOOCV
Humerus	Climate-only model	19,557.4	19,557.3
	Population structure–only model	19,402.2	19,392.2
	Inclusive model	19,401.7	19,395.7
	Inclusive random slope model	19,018.8	19,016.8
Radius	Climate-only model	13,362.0	13,353.1
	Population structure–only model	13,210.7	13,204.7
	Inclusive model	13,211.4	13,203.9
	Inclusive random slope model	13,212.3	13,214.8
Femur	Climate-only model	31,568.6	31,568.7
	Population structure–only model	31,596.3	31,614.6
	Inclusive model	31,172.3	31,171.9
	Inclusive random slope model	31,072.9	31,072.8
Tibia	Climate-only model	33,234.2	31,972.0
	Population structure–only model	32,900.4	31,633.4
	Inclusive model	32,967.9	31,648.2
	Inclusive random slope model	32,797.6	31,533.8

Abbreviations: WAIC = widely applicable information criterion; LOOCV = leave-one-out cross-validation.

coefficients associated with age to vary at both levels. That is, ontogenetic trajectories are assumed to be largely parallel among groups in the inclusive model, while in the inclusive random slope model, they are assumed to intercept one another. The results indicate that variation in ontogenetic trajectories of long bone linear dimensions is largely a result of both effects from climatic factors and neutral (nonselective) evolution.

Figure 1 shows the estimated effects of different climatic variables on long bone linear dimensions during ontogeny from the best-fitting models (inclusive random slope model for the humerus, femur, and tibia and inclusive model for the radius). While all 95% posterior credible intervals overlap with zero, this plot allows us to infer the association with temperature among groups of linear measurements, considering the confounding effects of population structure: temperatures have virtually no effect on the midshaft breadths and have minimal effects on tibial proximal and distal breadth. On the other hand, there is a weak association with temperature variables among diaphyseal lengths and most distal breadth measurements. An increase in extreme temperatures (minimum temperature of the coldest month and maximum temperature of the warmest month) is associated with an increase in all diaphyseal length measurements and distal breadth measurements of the humerus and femur. An increase in the mean annual temperature has the opposite effect on humeral and femoral diaphyseal lengths and the distal breadth of the femur. Compared with the climate-only models (SOM Fig. S3), where all diaphyseal lengths have reliable nonzero relationships with all temperature variables, population structure arising from shared history has obscured the signals of climatic factors in all measurements.

For all models, age and size are the only two fixed effects that consistently show a reliably nonzero relationship with different osteometric variables. The 95% posterior credible intervals of model coefficients associated with the square root of age for different response variables in the best-fitting single-bone models (inclusive random slope model for the humerus, femur, and tibia and inclusive model for the radius) are shown in Figure 2. This figure shows the distribution of the estimated effects of the square root of age, and it is clear that the effects of age are reliably nonzero for all diaphyseal length measurements (femur, tibia, humerus, and radius), and all femoral breadth measurements, regardless of groups. Figure 3 shows the 95% posterior credible intervals of the estimated effects of size for all osteometric variables. This plot therefore represents the allometric (size-related) component of ontogenetic change in all linear measurements. Size accounts for a small but reliably nonzero contribution to all linear measurements. Compared to Figure 2, it can be inferred that allometric change accounts for most of the variation in ontogenetic trajectories for almost all breadth measurements. That is, age-related change in size is responsible for variation in ontogenetic trajectories for all breadth measurements, while the independent effect of age is weak and cannot be reliably discerned from no effect.

The conditional effects of extreme temperatures are presented in Figure 4. With the exception of the tibia, most diaphyseal lengths show a weak, positive association with increases in the minimum temperature of the coldest month. There is no association between the coldest temperature and tibial diaphyseal length. In contrast, all diaphyseal lengths show a clear positive association with the maximum temperature of the warmest month. On the other hand, both femoral and humeral diaphyseal lengths show a clear negative association with mean annual temperature (SOM Fig. S10). The mean annual temperature was dropped as a fixed-effect term for the radius and tibia during model fitting (SOM Table S3), as the inclusion of this term did not improve model fit statistics. In terms of breadth, the minimum temperature of the coldest month and the maximum temperature of the warmest month show a weak but

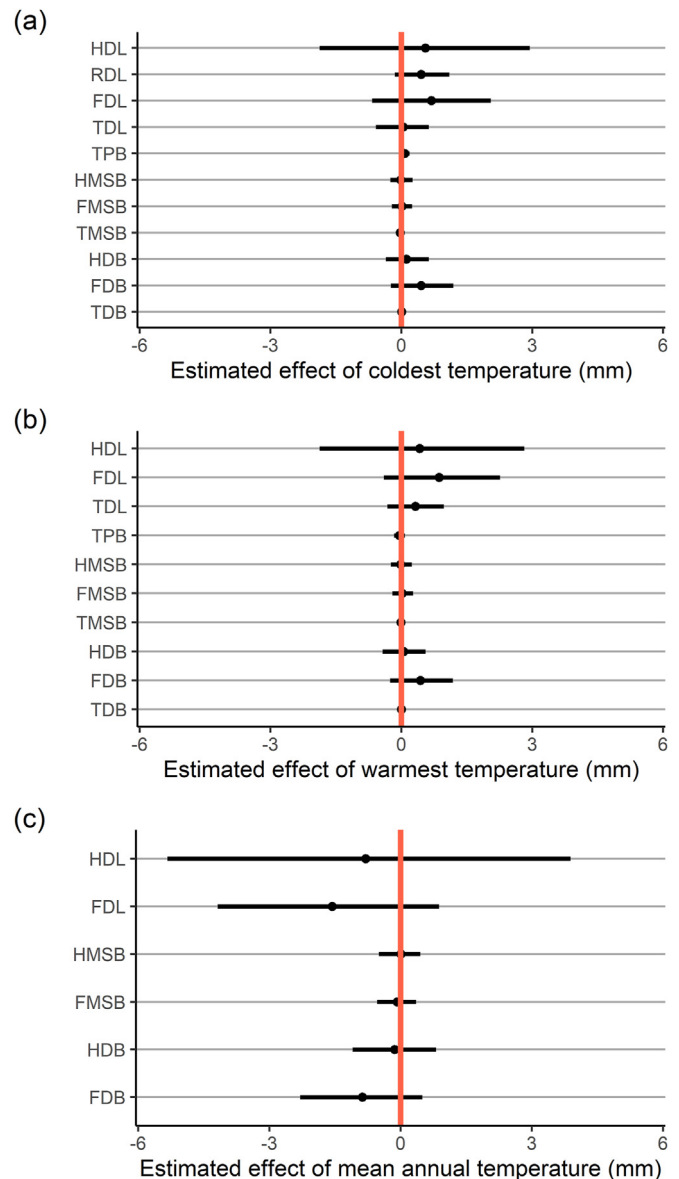


Figure 1. The estimated effects (95% posterior credible intervals for the slope) of different climatic variables on long bone linear measurements during ontogeny. Red vertical line indicates no effect (slope = 0). Abbreviations: HDL, humeral diaphyseal length; RDL, radial diaphyseal length; FDL, femoral diaphyseal length; TDL, tibial diaphyseal length; TPB, tibial proximal breadth; HMSB, humeral midshaft breadth; FMSB, femoral midshaft breadth; TMSB, tibial midshaft breadth; HDB, humeral distal breadth; FDB, femoral distal breadth; TDB, tibial diaphyseal breadth. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

clear positive trend, while the mean annual temperature displays a weak but clear negative trend, similar to the results for diaphyseal length. The breadth measurements with meaningful associations with different variables are presented in SOM Figure S11.

Because of the complexity of the models with varying fixed and random effects on the ontogenetic trajectories of different linear measurements, a comparison of the magnitudes of different effects illuminates the effects of different processes. Figure 5 shows the magnitudes of estimated effects on long bone length for age, sample type (modeled as a binary variable, with archaeological as the baseline [zero] for comparison), climatic variables, and among-group variation. Much of the variation in ontogenetic trajectories of linear long bone length is attributable to age and among-group

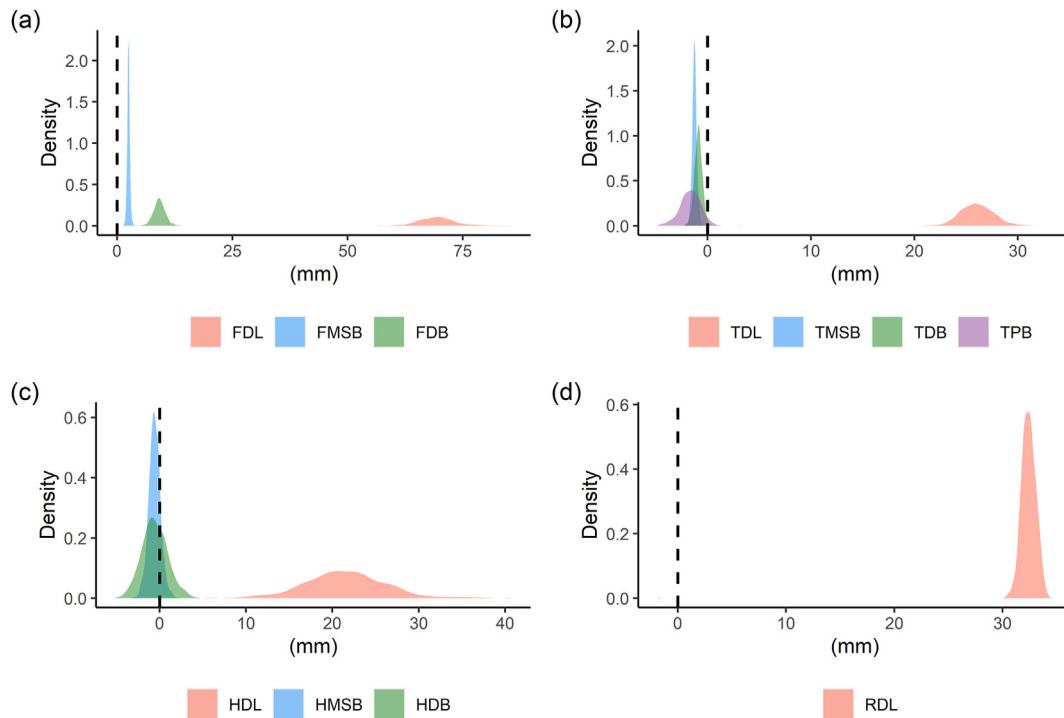


Figure 2. The 95% posterior credible intervals of model coefficients associated with the square root of age for all response variables in the best-fitting models for measurements of the femur (a), tibia (b), humerus (c), and radius (d). Abbreviations: HDL, humeral diaphyseal length; RDL, radial diaphyseal length; FDL, femoral diaphyseal length; TDL, tibial diaphyseal length; TPB, tibial proximal breadth; HMSB, humeral midshaft breadth; FMSB, femoral midshaft breadth; TMSB, tibial midshaft breadth; HDB, humeral distal breadth; FDB, femoral distal breadth; TDB, tibial diaphyseal breadth. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

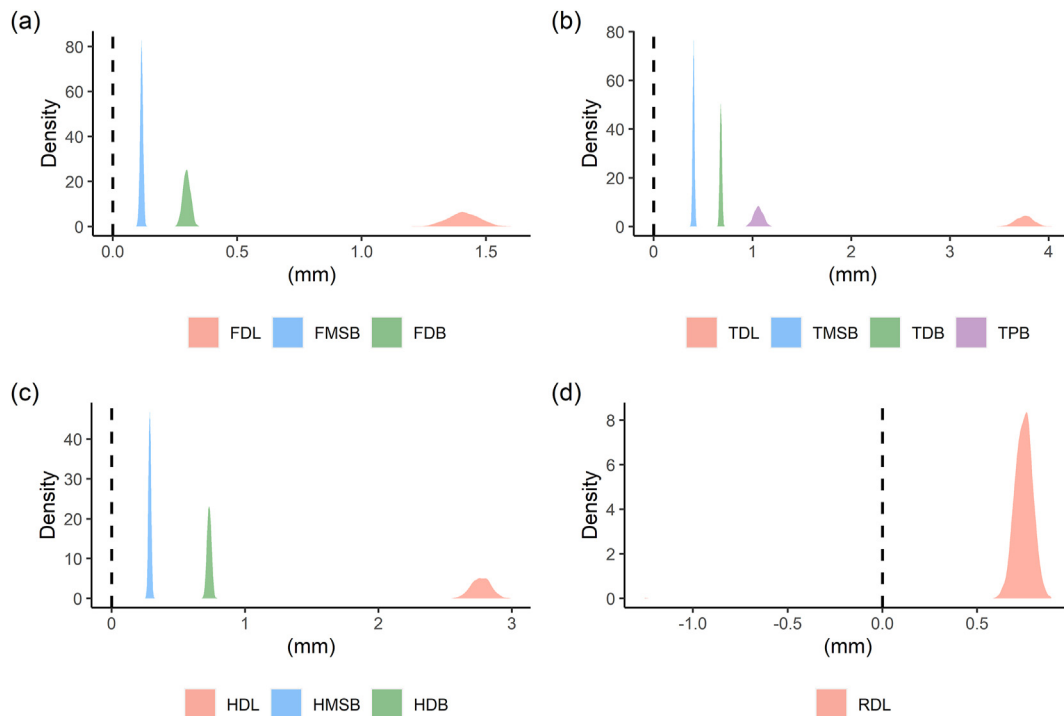


Figure 3. The 95% posterior credible intervals of the fixed-effect coefficients associated with size for all response variables in the best-fitting models for measurements of the femur (a), tibia (b), humerus (c), and radius (d). Abbreviations: HDL, humeral diaphyseal length; RDL, radial diaphyseal length; FDL, femoral diaphyseal length; TDL, tibial diaphyseal length; TPB, tibial proximal breadth; HMSB, humeral midshaft breadth; FMSB, femoral midshaft breadth; TMSB, tibial midshaft breadth; HDB, humeral distal breadth; FDB, femoral distal breadth; TDB, tibial diaphyseal breadth. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

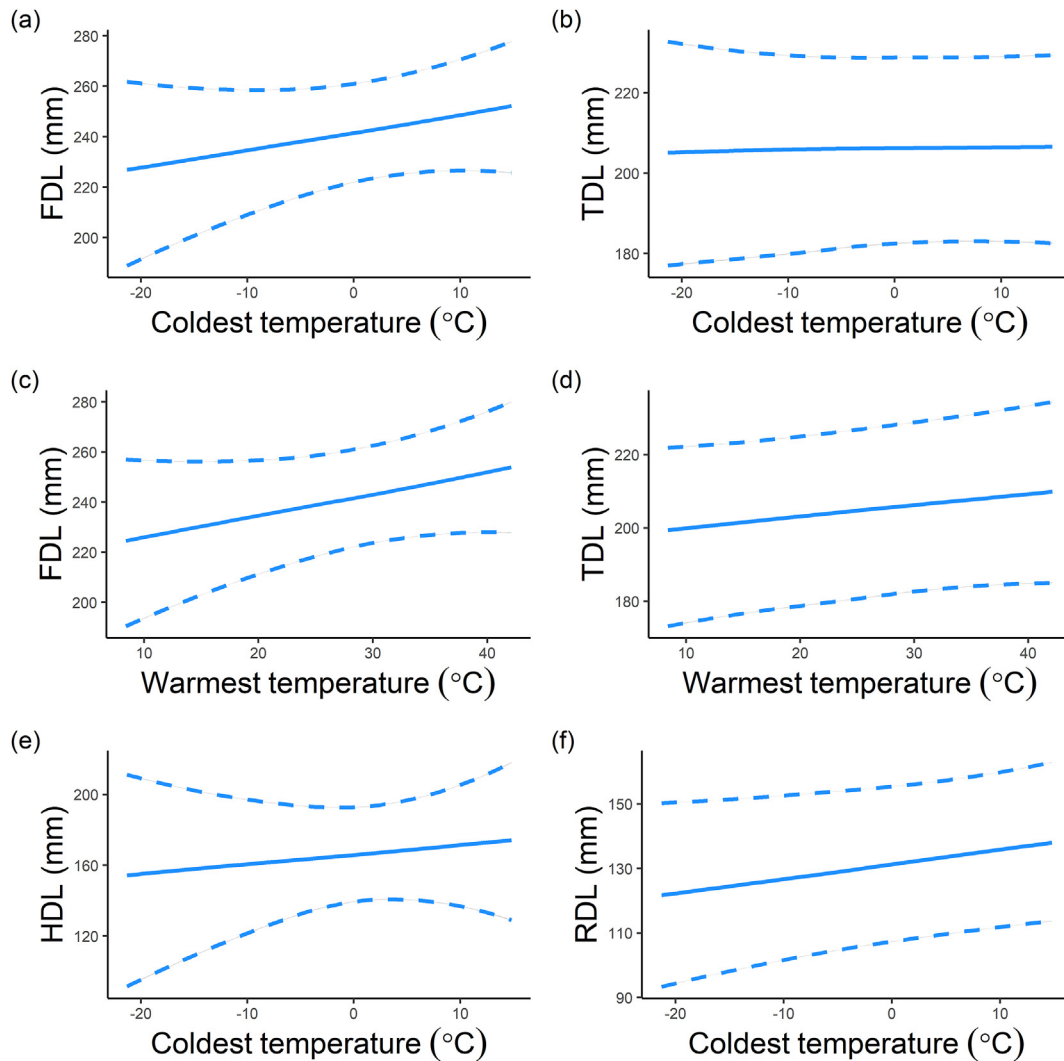


Figure 4. Estimated conditional effects of the minimum temperature of the coldest month (coldest temperature) and the maximum temperature of the warmest month (warmest temperature) on diaphyseal lengths. For humeral diaphyseal length, the effects of the warmest temperature have a similar profile to the effects of the coldest temperature. For radial diaphyseal length, the warmest temperature was dropped as an explanatory variable during initial model fitting. The plots for the warmest temperature are therefore not included here. Abbreviations: HDL, humeral diaphyseal length; RDL, radial diaphyseal length; FDL, femoral diaphyseal length; TDL, tibial diaphyseal length.

variation, while sample type and climatic variables account for a small proportion of the variation. For breadth measurements, much of the variation in ontogenetic trajectories is accounted for by among-group variation (SOM Fig. S12). The results presented here demonstrate that population structure is an important confounding factor for the among-group variation in ontogenetic trajectories, with effects several magnitudes greater than the effects of climatic variables and even sample type. However, given the effects of increasing temperature shown in Figure 4 (see also SOM Fig. S11), it is clear that population structure alone cannot account for all of the observed variation among groups.

4. Discussion

This study investigated the variation in the ontogenetic trajectories of long bone dimensions among different archaeological and contemporary groups using a linear mixed model approach. We showed that there is variation in ontogenetic trajectories of limb dimensions associated with temperature differences. The trend is clearer when population structure arising from neutral evolution is not accounted for. Groups living in colder areas tend to have shorter

limbs compared to groups living in warmer climatic conditions throughout ontogeny. The association between temperature differences and breadth measurements is less clear-cut. The overall results are consistent with previous studies using anthropometric measurements (Cowgill et al., 2012) and intralimb indices (Temple et al., 2011; Cowgill et al., 2012; Osipov et al., 2016), and provide support for our first hypothesis.

Our findings also support hypothesis 2. We showed that population structure arising from neutral evolution, allometric variation associated with the change in size, and directional effects from climatic factors all contributed to the variation in ontogenetic trajectories of all major long bone dimensions in modern humans. While the incorporation of group-level random effects, reflecting shared history and neutral evolutionary forces, may obscure the relationship between climatic variables and long bone linear measurements during ontogeny, they nonetheless represent an important and necessary component in explaining the variation in ontogenetic trajectories. The best-fitting models showed ontogenetic trajectories for linear measurements of the femur, tibia, and humerus vary in both intercept and slope among groups, while the ontogenetic trajectories for radial diaphyseal length vary only in

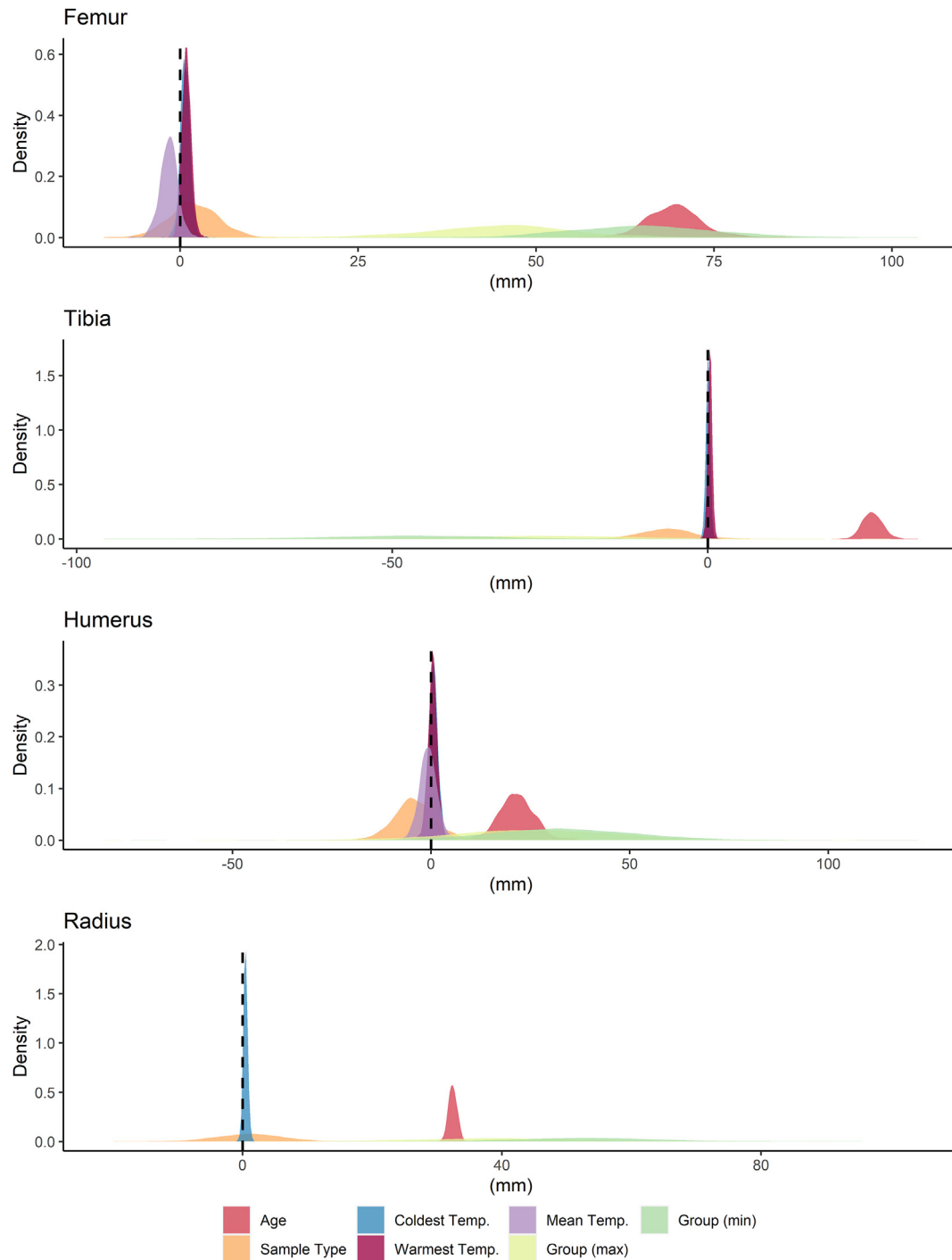


Figure 5. Comparison of effect magnitude for all long bone diaphyseal lengths showing the effects of age, sample type (archaeological vs. contemporary, i.e., how much effect being in the contemporary sample will have compared to being in the archaeological sample [set as 0]), climatic variables (coldest temperature, warmest temperature, and mean annual temperature), and contrasting effects between groups of maximum and minimum relatedness. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

intercept among different groups. However, population structure alone cannot account for all the observed variation in ontogenetic trajectories. Similar conclusions were reached in previous studies on adult body proportions and long bone dimensions and proportions (Betti et al., 2012; von Cramon-Taubadel et al., 2013; Roseman and Auerbach, 2015). Because of neutral evolution, groups that are closely related genetically will resemble one another phenotypically, thereby potentially confounding our

interpretations of skeletal morphology, so the use of limb proportions and dimensions to infer climatic conditions may not be the best practice without considering group relationships and shared history. The importance of neutral evolution in shaping all aspects of human skeletal morphology has been discussed extensively (e.g., von Cramon-Taubadel, 2009; Roseman and Auerbach, 2015; Agostini et al., 2018). We showed that similar consideration must be taken when interpreting the meaning of differing limb

dimensions and presumably proportions among groups in nonadults.

Our best-fitting models suggested that, after accounting for the effects of neutral evolution and holding all other factors under study (i.e., size, sample type, age, and group relationship) equal, an increase in extreme temperatures will be associated with an increase in all diaphyseal lengths throughout growth. Despite the overall weak relationships between extreme temperatures and diaphyseal lengths, our results are in agreement with our hypothesis 3 and consistent with the two ecogeographic rules: Allen and Bergmann's rules (Bergmann, 1848; Allen, 1877), which predict groups living in warmer areas tend to have longer long bones and vice versa. It is reasonable to assume that it is the variation in ontogenetic trajectories that ultimately results in differences in skeletal morphology observed in adults (e.g., Ruff, 1991; Ruff, 1994; Pearson, 2000). Similar to our results, a previous study in adults (Savell et al., 2022) showed that no associations between various long bone lengths and extreme temperatures could be reliably demonstrated (all estimated effects overlap zero), and thus no evidence of temperature-driven directional selection could be concluded. Interestingly, in our study, the relationship between tibial diaphyseal length and warmest temperature is stronger, and a clear trend can be discerned compared to the relationship between tibial diaphyseal length and coldest temperature. This may suggest that the need for heat dissipation (heat stress) exerts stronger long-term selective pressure on tibial length than the need for heat retention (cold stress), consistent with conclusions made in a previous study (Pomeroy et al., 2021). Alternatively, although past studies in adult humans have identified that the length of distal limb elements is more strongly associated with climatic conditions (Trinkaus, 1981; Ruff, 1994), an experimental physiology study in adult humans showed that, after controlling for body mass, variation in femoral length (and not tibial length) correlates more strongly with heat dissipation (Tilkens et al., 2007). This may explain why associations with both extreme temperatures are stronger in the humerus and femur and why the associations with only one extreme temperature are clear for both the radius and tibia.

Interestingly, our models also showed that mean annual temperature has the opposite effect on femoral and humeral diaphyseal lengths, in that an increase in mean annual temperature will be associated with a decrease in femoral and humeral diaphyseal lengths. Mean annual temperature was not selected as an explanatory variable for the tibia and radius during variable selection, as it did not improve the model fit for either single bone model. This suggests that variation in mean annual temperature is potentially responsible for the observed variation in intralimb indices. A previous study by Savell et al. (2016) also showed that in adults, there is little trait-specific (direct) response to climatic selection for femoral length, while humeral length is predicted to lengthen with increasing latitude. It is possible that the combination of the response to extreme temperature differences and the response to mean annual temperature differences in nonadults led to the patterns observed by Savell et al. (2016). Alternatively, Roseman and Auerbach (2015) argued that balancing selection may have contributed to the maintenance of among-group variation in human body form, while Sanjak et al. (2018) suggested that balancing selection is widespread in contemporary humans. The directional response of femoral and humeral diaphyseal lengths to the mean annual temperature detected in this study may reflect balancing selection acting to maintain a phenotypic optimum for limb length. Nonetheless, both the crural index (length of the tibia relative to the femur) and brachial index (length of the radius relative to the humerus) showed significant correlations with climates in modern humans (Trinkaus, 1981; Ruff, 1994; Betti et al., 2015) such that humans in warmer areas (the tropics) have higher crural and

brachial indices. Previous studies also showed this pattern can be observed in infants and children on a large geographic scale (Cowgill et al., 2012), and the relative rank of these indices (i.e., groups in warmer areas have greater intralimb indices) among groups is maintained throughout ontogeny (Frelat and Mitteroecker, 2011; Temple et al., 2011; Cowgill et al., 2012; Bleuze et al., 2014; Osipov et al., 2016). The findings of the current study present a possible scenario for the underlying mechanism of the variation in intralimb indices, namely, the lengths of distal elements are under directional effects from extreme temperatures while the lengths of proximal elements are under the competing effects of both extreme and mean annual temperatures, or under both directional selection and balancing selection.

We also showed that variation in femoral and humeral distal breadths during ontogeny has a similarly weak relationship with different temperature variables to that of diaphyseal lengths. This is to some degree consistent with previous studies showing group differences in knee width (Farrally and Moore, 1975) and epiphysis width of the femur (Frelat and Mitteroecker, 2011). As for association with age, only the breadth measurements associated with the femur have a reliably nonzero relationship. On the other hand, all breadth measurements have a reliably nonzero relationship with size during ontogeny, indicating variation in the ontogenetic trajectories of breadth is largely due to allometric change. This makes sense because, generally speaking, long bone breadth has a strong association with cross-sectional properties (Stock and Shaw, 2007), which in turn is associated with overall body size (Pearson, 2000). Body size is also known to vary with climate (Roberts, 1953; Ruff, 1994; Katzmarzyk and Leonard, 1998; Pearson, 2000; Collard and Wood, 2007), with a decrease in annual temperature associated with an increase in body size (Roberts, 1953; Ruff, 1994; Katzmarzyk and Leonard, 1998; Collard and Wood, 2007). Past studies also showed human groups living in warmer environments have absolutely narrower limbs compared to those living in colder climates (Eveleth and Tanner, 1976; Weaver, 2003). Since variation in most breadth measurements is largely attributable to allometric change, as shown in our study, groups living in colder areas will have greater body size, and as a result, have wider long bones. On the other hand, the direct effects of temperature variables on breadth measurements are opposite of what would be expected under Bergmann's rule. There are two possible explanations: first, the independent effects of temperature variables are smaller than the independent effects of size (Fig. 3; SOM Fig. S12). Therefore, trait-specific response to change in extreme temperatures is likely not detected in previous studies (Eveleth and Tanner, 1976; Weaver, 2003). Previous results showing an association between limb breadths and climates are instead an association between limb breadths and body size, structured by climatic differences. Another possible explanation is that different breadth measurements usually have variance several magnitudes smaller than diaphyseal length. Linear mixed-effects models work by decomposing variance structure among the data into fixed and random effects. Since breadth measurements were measured on a smaller scale than length measurements, there is less variance to be assigned to multiple fixed and random effects. The discrepancies in the magnitude of variance might have contributed to the weak relationship in an unexpected direction between different breadth measurements and factors other than size.

This study is not without limitations. First, it is possible that the lack of a clear association with climate is due to the potential collinearity among the predictor variables. That is, age is associated with size, and size is potentially associated with climatic variables. Given the reliably nonzero association with either age and/or size for most response variables, the independent effect for climatic variables can be difficult to estimate in traditional statistical

models, a problem similar to the identification problem in age-period-cohort analysis in epidemiology (Keyes et al., 2010; Yang and Land, 2013). While the use of a Bayesian model with an MCMC sampler can circumvent this problem, we acknowledge this potential limitation of the current study. Second, our model is unable to distinguish the effects of climatic selection (long-term evolutionary change) and plasticity relating to temperature. Animal models showed temperature has a direct effect on postnatal growth (Serrat et al., 2008; Serrat, 2013), and it is possible that the association with different climatic variables among different osteometric variables during ontogeny observed in this study is a result of plasticity. However, the conditional effects reported in our study also showed that the association of long bone dimensions with climate was present throughout ontogeny. Group differences present at early stages of ontogeny are more likely evolutionary as opposed to plastic because presumably, environmental influences (e.g., mechanical loading) have not had a chance to influence traits present in fetuses and neonates (Weaver, 2009). Therefore, we propose climatic adaptation is one of the most likely underlying causes of the observed variation in ontogenetic trajectories in modern humans. Nonetheless, we cannot make a definitive conclusion regarding the plasticity vs. adaptation debate.

Moreover, there is no doubt that other factors such as humidity, amount of biomass, and nutritional stress have effects on the variation in ontogenetic trajectories of limb dimensions. In adults, there is evidence that increased humidity will render the thermoregulatory role (heat dissipation) of longer limbs ineffective (Cavalli-Sforza, 1986; Pomeroy et al., 2021). In nonadults, lower socioeconomic status (and therefore greater nutritional stress) is associated with shorter diaphyseal length and breadth (Pinhasi et al., 2006, 2014), and the differences are less pronounced in upper limbs than in lower limbs (Pinhasi et al., 2005). In contemporary human groups from similar geographic areas, shorter overall limbs and limb segment lengths during growth are associated with greater ecological and environmental stress (Pomeroy et al., 2012). Previous studies on human body form often used latitude as an explanatory variable (e.g., Cowgill et al., 2012; Roseman and Auerbach, 2015; Savell et al., 2022), and Savell et al. (2022) showed latitude has an independent effect on body and limb proportions. Because latitude is an all-encompassing variable that includes different climatic factors such as temperature, humidity, precipitation, and wind, this study chose to study temperature variables directly in order to understand the direct effects of temperature variation as it relates to ontogenetic trajectories of limb dimensions. However, given the overall weak association with temperature variables, it is reasonable to assume that latitude, which is often used as a proxy for temperature, will have a similar or weaker relationship with the skeletal traits analyzed in this study. Nonetheless, further study is needed to ascertain associations with latitude as well as the effects of other climatic or ecological factors.

In a recent study, Waxenbaum et al. (2019) examined fetal limb proportions in a sample consisting of individuals of European American and African American ancestry from Florida. They found no significant differences between these two groups, therefore raising the question of to what extent ecogeographic patterns can be observed at an early age. A previous study (Weaver et al., 2016) reported differences in diaphyseal end size to shaft length ratios among major long bones between the two groups (individuals of European American and African American ancestry) using a different sample, although which group has the greater ratio is dependent on the bone being compared. The inconsistency between these two studies may be a result of the bones and measurements of choice, as our findings showed differing effect magnitudes associated with different variables for different bones. Variation in long bone lengths during ontogeny is largely attributable to the effects of

age and group relationships, while for breadths, the among-group differences are of several magnitudes greater than other effects. Moreover, our findings also showed that when group relationships are not accounted for, climatic factors will appear as the factor driving group differences for long bone lengths, but not for breadths. Therefore, for comparison between two local groups in a fetal sample, group differences may not be apparent. On the other hand, because group relatedness is the primary driving effect for breadths differences, a comparison between the same two groups involving breadth may yield different results. Nonetheless, the results from these studies (Weaver et al., 2016; Waxenbaum et al., 2019) showed that direct comparisons among groups without accounting for group relationships can be potentially misleading.

5. Conclusions

This study showed that multiple factors likely contributed to the observed variation in ontogenetic trajectories of human long bone linear dimensions. The variation is consistent with previous studies on the distribution of human body proportions, in that an increase in extreme temperatures is associated with an increase in all diaphyseal length measurements. A similar relationship also exists for a few breadth measurements. Population structure, arising from shared history among groups, is an important component of variation in ontogenetic trajectories of long bone dimensions, and the highly structured nature of population relationships can obscure climatic signals. Nonetheless, when interpreting the results as a whole, both the predicted mean effects and the conditional effects of extreme temperatures for all diaphyseal lengths showed a weak but clear positive association during ontogeny, after accounting for the effects of neutral evolution. This is consistent with expectations from ecogeographic rules. Femoral and humeral diaphyseal lengths also showed clear negative associations with mean annual temperature. This relationship likely contributed to the variation in intralimb indices among groups during ontogeny.

Declaration of competing interest

There is no conflict of interest.

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Appendix A. Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2023.103369>.

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