



OPEN Multifactorial drivers of spatial variation in human body form across modern China

Doudou Cao^{1,2}✉, Enrico R. Crema² & Emma Pomeroy²

Human body form reveals cumulative effects of ecological and socio-cultural factors. China provides an exceptional context for investigating these multifactorial influences, not only because of its extensive geographic and cultural diversity, but also because recent decades have been marked by rapid economic development, urbanisation, migration, and the population-level trauma of the Great Famine. Using anthropometric data from >90,000 adults across 213 geo-referenced groups from mid-late-20th and early-21st centuries, we applied Bayesian hierarchical models to assess the roles of climate, altitude, urban–rural status, linguistic affiliation, and time in shaping stature, body mass, relative sitting height, and body breadth. Substantial secular increases in body size, particularly body mass, were associated with recent economic development and urbanisation. Males and females responded similarly across environmental and temporal gradients, indicating limited sex-based differentiation. Northern groups remained taller and heavier than their southern counterparts. Notably, maximum precipitation, not temperature, emerged as the strongest climatic correlate, likely reflecting indirect effects of subsistence and disease burden. Relative sitting height increased modestly over time, while relative body breadth showed a stable east–west gradient, potentially shaped by population history. Regional exceptions, including highland Tibetan and Sherpa populations and northeastern groups, along with widening divergence among linguistic subgroups, underscore the persistent roles of migration, developmental constraints and potential high-altitude adaptation. These findings show that recent changes in human body form in China cannot be understood as simple outcomes of modernisation alone, but instead reflect layered interactions among ecology, population history, socio-economic transformation, and cohort-specific historical experience.

Keywords Stature, Body mass, Body proportion, Growth, Climatic adaptation, China

Author information.

Introduction

Human body form varies markedly across populations, driven by a complex interplay of genetic, environmental, and sociocultural forces^{10,12,20,47,52}. For nearly two centuries, ecogeographic ‘rules’ have guided interpretations of climate-related morphological variation, proposing that larger body sizes⁷ and shorter extremities¹ in colder climates enhance heat conservation. Such patterns have been widely documented among endothermic species, including humans and extinct hominins^{51,53}. However, emerging evidence suggests that temperature, or latitude, often serves as a proxy for broader ecological and socioeconomic factors, such as nutrition, disease burden, and population history, rather than acting as a direct causal driver of body form^{14,32,47}. Developmental plasticity further enables growth adjustments in response to local environmental conditions during early life⁵. Consequently, human morphology rarely conforms neatly to single climatic axis but instead reflects the cumulative outcomes of interacting influences across both evolutionary and developmental timescales⁸.

China’s extensive ecological and cultural diversity provides an exceptional setting for exploring the multifactorial influences shaping human biological variation. This setting is further distinguished by China’s recent history, including the demographic and nutritional disruptions associated with the Great Famine and the rapid urbanisation, economic development, and dietary transitions that followed in the late twentieth and early twenty-first centuries^{17,18,42}. While previous studies have identified latitudinal gradients in body size, most studies have focused narrowly on individual traits, such as stature or body mass, and have often been confined to particular population groups^{17,37,39}. Few examine relative sitting height (a proxy for lower limb length) or lateral

¹Hong Kong Institute for the Humanities and Social Sciences, University of Hong Kong, Hong Kong SAR, China.

²Department of Archaeology, University of Cambridge, Cambridge, UK. ✉email: dcao@hku.hk

dimensions such as bi-iliac breadth, despite their relevance to thermoregulation, locomotion, and childbirth^{54,67}. Furthermore, although existing studies underscore the importance of latitude, nutrition, and socioeconomic conditions^{39,40,42}, there remains a lack of spatially explicit analyses that integrate climatic, geographic, cultural, and historical variables into a unified framework.

Here, we compiled anthropometric data on mean stature, body mass, relative sitting height (trunk-to-height ratio), and relative body breadth (bi-iliac breadth relative to stature) for over 90,000 adults from 223 georeferenced population samples, spanning mid-twentieth to early-twenty-first centuries. These data capture cohorts born during or shortly before/after the Great Famine, and those raised in the post-reform era (Supplementary Table S1), and are paired with ecogeographic predictors (temperature, precipitation, altitude), residential context (urban vs. rural), and linguistic affiliation. Using Bayesian generalised additive mixed models (GAMMs), we model non-linear spatial and temporal variation in body form, while accounting for potential unmeasured factors, such as gene flow and local subsistence.

With a robust database, this study asks how contemporary variation in body form across China has been shaped by long-term ecological adaptation as well as more recent developmental responses to improving living standards and urbanisation.

Results

Spatiotemporal patterns in body size and proportions

Across mid-20th- to early 21st-century Chinese populations, Bayesian predictions indicate a substantial increase in body size over time, especially in body mass, alongside more modest changes in stature and comparatively limited shifts in body proportions (Figs. 1, 2, S1–S8). Despite these increases, large-scale geographic patterning remains broadly stable: stature and body mass retain a pronounced north–south gradient, with northern populations consistently predicted to be taller and heavier than southern populations across both scenarios. By contrast, relative sitting height and relative body breadth show weaker temporal change and more regionally variable spatial structure.

Stature shows the clearest spatial structuring among all traits. In males, early rural predictions range from approximately -1.5 z in southern China, equivalent to around 158.2 cm, to $+1.0$ z in northern China, equivalent to around 168.6 cm (Fig. 1, first row). In the late urban scenario, this gradient persists but shifts upward, with values reaching around $+1.5$ z in the north, approximately 170.5 cm, and around -0.5 z in the south, approximately 162.8 cm. A similar latitudinal pattern is also evident in the environment-only component, defined as the difference between the full and space-only predictions (Figs. S1–S2, first rows), indicating that measured covariates explain an important part of the predicted north–south variation in stature.

Body mass shows a broadly similar spatial pattern to stature but a stronger temporal increase. In early rural males, predicted values are low in southern China, reaching approximately -1.5 z , equivalent to around 50.4 kg relative to the overall male mean of 60.9 kg, whereas northern populations are slightly above the mean, around $+0.3$ z (Fig. 1, second row). In the late urban scenario, body mass increases markedly nationwide, especially in northern and western China, where values exceed $+1.5$ z , equivalent to over 70 kg. Southern values also increase but remain comparatively lower, around -0.3 z , or approximately 58.8 kg.

Relative sitting height shows more limited temporal change (Fig. 1, third row). In early rural males, predicted values are negative across much of western and southwestern China, reaching around -1.2 z and indicating proportionally longer lower limbs, whereas parts of the northeast show relatively longer trunks. By the late urban scenario, values converge closer to the overall sample mean, approximately 53.5% of stature, although southern and southwestern regions remain relatively lower.

Relative body breadth shows clearer spatial structure than relative sitting height (Figs. 1 and 2, fourth row). In early rural males, higher values cluster in the northwest and Tibetan Plateau, around $+1.0$ to $+1.5$ z , corresponding to approximately 17.6–17.9% of stature. Coastal and northeastern regions show lower values, around 0 to -1 z . This west–east and highland–lowland contrast persists in late urban males, with highland regions reaching $+1.5$ to $+2.0$ z , approximately 17.9–18.2%, while southeastern regions remain comparatively narrower. Space-only predictions capture the main features of this distribution, whereas environment-only predictions are weaker and less spatially coherent (Figs. S1–S2, fourth rows), indicating that relative body breadth is more strongly associated with broader geographic structure than with the measured environmental covariates alone.

Female spatiotemporal trends broadly mirror those observed in males, both in direction and magnitude (Fig. 2). Northern females are consistently predicted to be taller and heavier than southern females across the early rural and late urban scenarios. Female relative body breadth also shows a similar regional structure, with higher predicted values in western groups and lower values among coastal populations. However, some sex-specific model behaviour is evident. For female stature, space-only predictions diverge from both full and environment-only predictions in the northeast, suggesting that this regional pattern is not fully captured by measured environmental covariates and may reflect local non-climatic factors or other geographically structured processes (Figs. S3–S4, first rows).

Socio-economic and environmental fixed effects

Modelled fixed effects, representing average predictor–trait associations across the full dataset, indicate that socio-economic and environmental predictors were more strongly associated with body size than with body proportions (Fig. 3). Conditional effect plots for the continuous environmental predictors are shown in Figs. S9–S12. Following the terminology summarised in Table S2, 95% highest posterior density intervals (HPDIs) represent the narrowest intervals containing 95% of the posterior probability for each parameter; intervals overlapping zero indicate greater uncertainty in the direction of the association.

For stature, based on 220 male and 218 female groups, urban residence is positively associated with stature in both sexes (Fig. 3, first row). The estimated effect is $\beta = 0.42$ in males (95% HPDI: 0.07 to 0.77) and $\beta = 0.40$

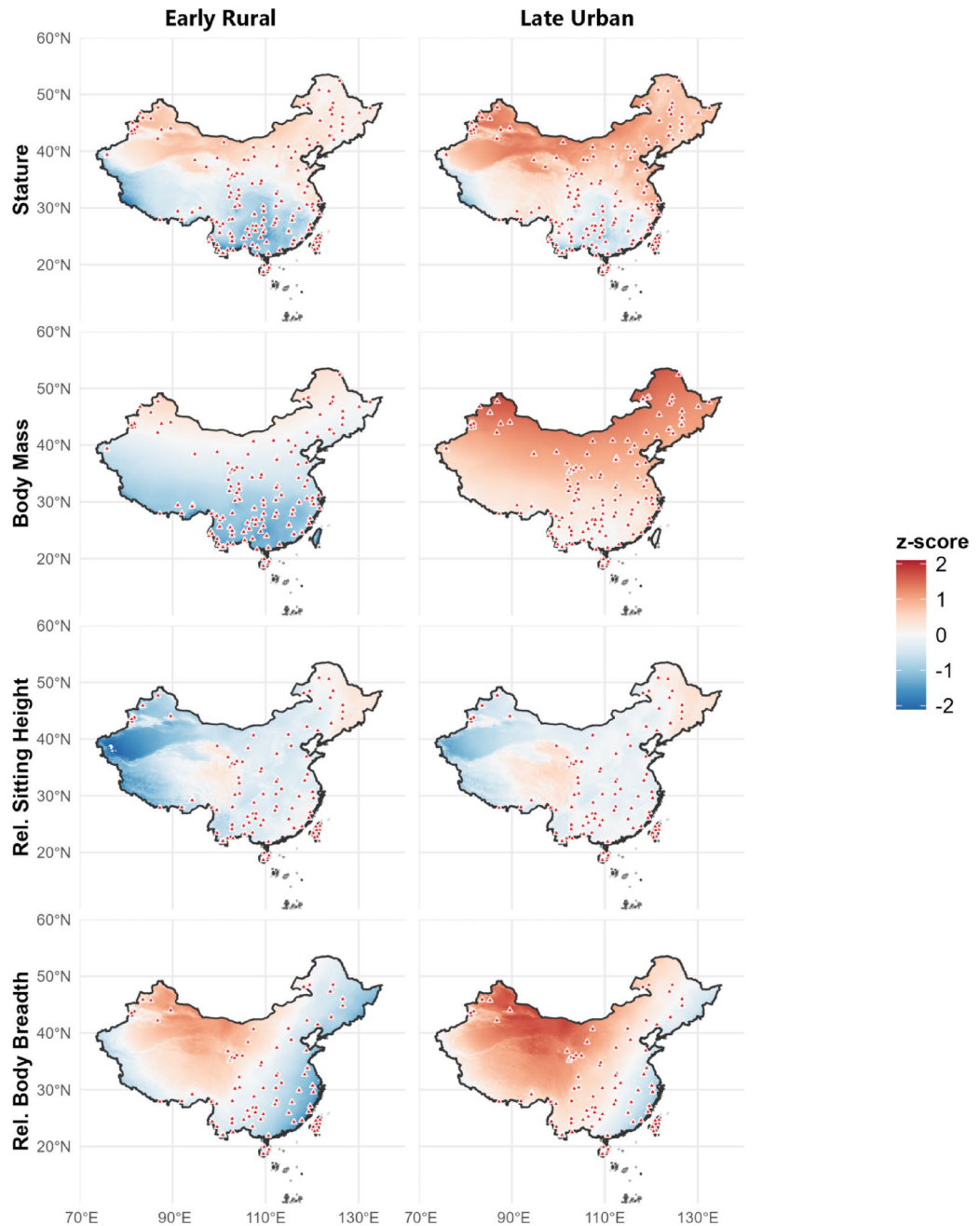


Fig. 1. Predicted spatial variation in male body size and proportions under early rural and late urban scenarios. Maps show male Bayesian full-model predictions for four traits: stature, body mass, relative sitting height, and relative body breadth. Predictions are expressed as z-scores standardised relative to the overall sample mean of each trait. The early rural and late urban scenarios contrast the two most distinct combinations of period and residence in the dataset and therefore reflect both temporal and urbanisation-related differences. The full-model predictions include fixed effects, spatial smoothing, and language subgroup random effects. Note that coastlines may appear visually darker than internal land borders at this map scale because of their more irregular and densely segmented geometry. Maps were generated by the authors in R version 4.3.2 (<https://www.r-project.org/>), with administrative boundary data obtained from Tianditu, the National Platform for Common Geospatial Information Services of China (<https://www.tianditu.gov.cn/>).

in females (95% HPDI: 0.01 to 0.92), with most posterior mass above zero. By contrast, the independent effect of the late period is small and uncertain, with 95% HPDIs overlapping zero. Among environmental predictors, maximum precipitation shows the most consistent negative association with stature, with posterior means of $\beta = -0.42$ in males and $\beta = -0.39$ in females. Altitude and minimum temperature also show weak negative tendencies, but their HPDIs include zero, indicating substantial uncertainty.

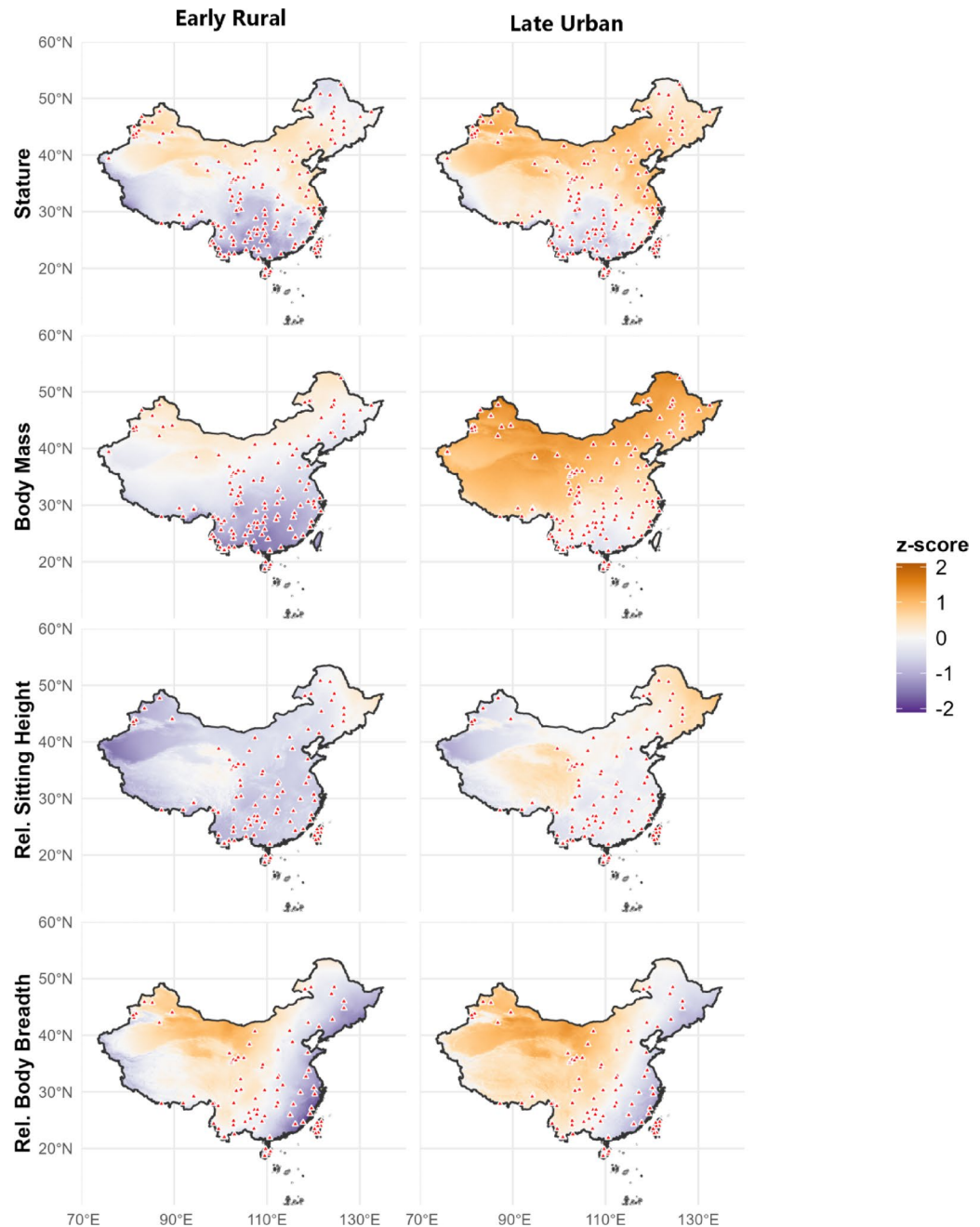


Fig. 2. Predicted spatial variation in female body size and proportions under early rural and late urban scenarios. Maps show male Bayesian full-model predictions for four traits: stature, body mass, relative sitting height, and relative body breadth. Predictions are expressed as z-scores standardised relative to the overall sample mean of each trait. The early rural and late urban scenarios contrast the two most distinct combinations of period and residence in the dataset and therefore reflect both temporal and urbanisation-related differences. The full-model predictions include fixed effects, spatial smoothing, and language subgroup random effects. Note that coastlines may appear visually darker than internal land borders at this map scale because of their more irregular and densely segmented geometry. Maps were generated by the authors in R version 4.3.2 (<https://www.r-project.org/>), with administrative boundary data obtained from Tianditu, the National Platform for Common Geospatial Information Services of China (<https://www.tianditu.gov.cn/>).

For body mass, based on 187 male and 186 female groups, posterior distributions indicate stronger temporal effects than for other traits (Fig. 3, second row). The late period is associated with higher body mass in both sexes, with $\beta = 0.83$ in males (95% HPDI: 0.02 to 1.95) and $\beta = 0.92$ in females (95% HPDI: -0.01 to 1.97). The female estimate is similar in magnitude to the male estimate, although its HPDI marginally crosses zero. Urban residence is also positively associated with male body mass ($\beta = 0.40$), whereas the corresponding female effect is smaller and more uncertain ($\beta = 0.16$; 95% HPDI: -0.01 to 0.34). Environmental associations with body mass

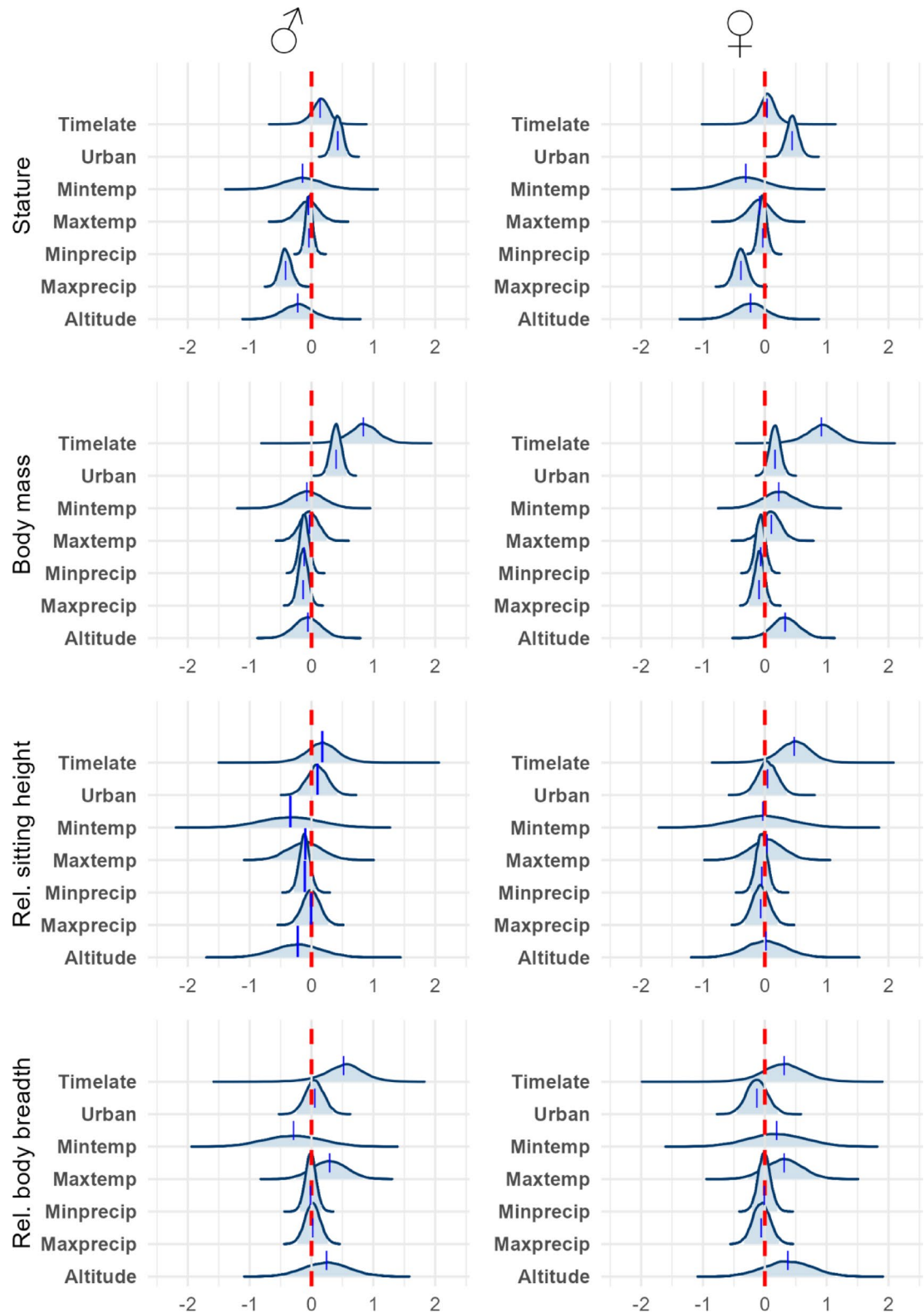


Fig. 3. Posterior distributions of fixed effects on body size and proportions traits (top to bottom): stature, body mass, relative sitting height, and relative body breadth. Predictors include TimeLate (21st-century vs. mid-late 20th-century baseline), Urban (urban vs. rural baseline), scaled climatic variables (minimum/maximum temperature, minimum/maximum precipitation), and altitude. Male (♂) results are on the left, female (♀) on the right. Red dashed lines indicate zero (no effect); blue vertical lines mark posterior means. Distributions whose means and 95% credible intervals (shaded areas) are shifted from zero indicate credible predictor effects.

are generally weaker: precipitation show negative tendencies in males, while altitude and minimum temperature show modest positive tendencies in females, all with wide HPDIs.

Body proportions show weaker and less consistent associations overall. For relative sitting height, based on 140 male and 139 female groups, most predictor effects are small and uncertain, although the late-period posterior mean is more positive in females than in males ($\beta = 0.47$ versus 0.17 ; Fig. 3, third row). For relative body breadth, based on 131 male and 130 female groups, temporal posterior means are slightly larger in males ($\beta = 0.52$) than in females ($\beta = 0.31$), but both HPDIs span zero (Fig. 3, fourth row). Female relative body breadth also show positive tendencies for maximum temperature ($\beta = 0.31$) and altitude ($\beta = 0.38$), although credible intervals remain wide.

Language subgroup variation

Language subgroup variation was assessed using three complementary summaries: random effects, counterfactual early–late contrasts, and ICCs, which address related but distinct questions. Random effects subgroup deviations after accounting for measured predictors and spatial structure: random intercepts capture residual baseline differences among language subgroups (Fig. 4), while subgroup-specific TimeLate slopes capture deviations in later–earlier temporal change (Fig. 5). By contrast, counterfactual early–late contrasts evaluate whether temporal change differed among language subgroups under matched environmental conditions, with continuous environmental covariates fixed at their means and rural residence used as the baseline (Figs. S5–S8). This distinction clarifies that the analysis does not simply compare language subgroups at one time point, but also assesses whether subgroup-specific temporal trajectories differed after standardising environmental conditions.

Overall, language subgroup variation was present but generally modest after accounting for measured predictors and spatial structure (Fig. 4). For stature, subgroup-specific posterior early–late contrasts were small overall (Fig. 5, first row), and the corresponding posterior early–late contrasts were likewise limited (Fig. S5). Sinitic males showed the clearest positive contrast: 1.26 cm [95% HPDI: $0.46, 2.09$], indicating a credible increase above zero (Fig. S5). Mon-Khmer and Tungusic males showed smaller positive median posterior contrasts of 0.87 and 0.73 cm, respectively, while most other male subgroups fell within ± 0.5 cm. Female contrasts were smaller and showed greater posterior uncertainty: Sinitic females had a median contrast of 0.27 cm [95% HPDI: $-0.43, 1.02$], and all female subgroup HPDIs included zero.

For body mass, posterior early–late contrasts were larger and more consistently positive (Fig. 5, second row), as were the posterior early–late contrasts shown in Fig. S6. All language subgroups showed positive median posterior contrasts, with the largest increases in Mongolic and Sinitic groups: approximately 9.9 – 12.2 kg in males and 7.2 – 10.3 kg in females. Tibeto-Burman, Turkic, Tungusic, and Mon-Khmer groups showed intermediate increases of approximately 4 – 6 kg across sexes, whereas Hmong-Mien and Kra-Dai showed the smallest increases, around 2.8 – 3.6 kg in males and 1.6 – 1.7 kg in females. For most subgroups, 95% HPDIs excluded zero, providing stronger posterior evidence for temporal increases in body mass. Hmong-Mien and Kra-Dai were the main exceptions, with HPDIs overlapping zero.

For relative sitting height, counterfactual contrasts indicated minimal temporal change across most subgroups (Fig. 5, third row), and counterfactual contrasts indicated minimal temporal change across most subgroups (Fig. S7). Among males, Sinitic and Turkic populations showed the largest median contrasts, approximately $+0.25$ and $+0.22\%$ points, respectively. Most other male subgroups fell between approximately $+0.06$ and $+0.16\%$ points, while Hmong-Mien showed a slightly negative median. Female contrasts were slightly larger, reaching approximately $+0.59\%$ points in Sinitic groups and $+0.53\%$ points in Turkic groups. For nearly all subgroups, 95% HPDIs were broad and included zero, except for Sinitic and Turkic females, whose intervals lay entirely above zero.

Relative body breadth also showed limited subgroup-specific temporal divergence, with most language subgroups centred close to zero; Mon-Khmer was also close to zero, while Mongolic showed a slightly negative tendency (Fig. 5, fourth row). However, the posterior counterfactual early–late contrasts under matched covariate conditions indicated modest positive shifts in some groups (Fig. S8). Turkic groups showed the largest median posterior contrast, at $+0.66\%$ points [95% HPDI: $0.14, 1.49$], followed by Sinitic groups at $+0.50\%$ points [95% HPDI: $0.16, 0.93$]. Hmong-Mien and Mon-Khmer groups showed moderate positive contrasts, particularly among females, whereas Tibeto-Burman, Tungusic, Kra-Dai, Mongolic, and Austronesian groups generally had smaller contrasts below 0.3% points, with wide HPDIs spanning zero.

Intraclass correlation coefficients (ICCs) were generally modest (Table S3). As defined in Table S2, ICC refers to the proportion of total modelled variance attributable to language subgroup-level variation. Some traits, particularly body mass and relative body breadth, showed higher ICCs in the late period. Because ICC is a ratio, higher values may reflect increased between-subgroup variance, reduced within-subgroup variance, or both. Therefore, the higher late-period ICCs indicate a greater relative contribution of language subgrouping to total variance, rather than direct evidence of increased between-group divergence.

Additionally, highland groups show population-specific variation within these broader subgroup patterns. Indigenous Tibetan populations have consistently greater body mass than both northern and southern Han Chinese, despite relatively smaller stature in earlier periods (Fig. 6). By contrast, Sherpa populations from the southern Tibetan Plateau show lower predicted stature and body mass despite living at comparable elevations. They also show relatively shorter trunk length and narrower body breadth, consistent with the lower predicted values for the southwestern Tibetan Plateau in the relative sitting height and relative body breadth maps (Figs. 1 and 2, third and fourth rows).

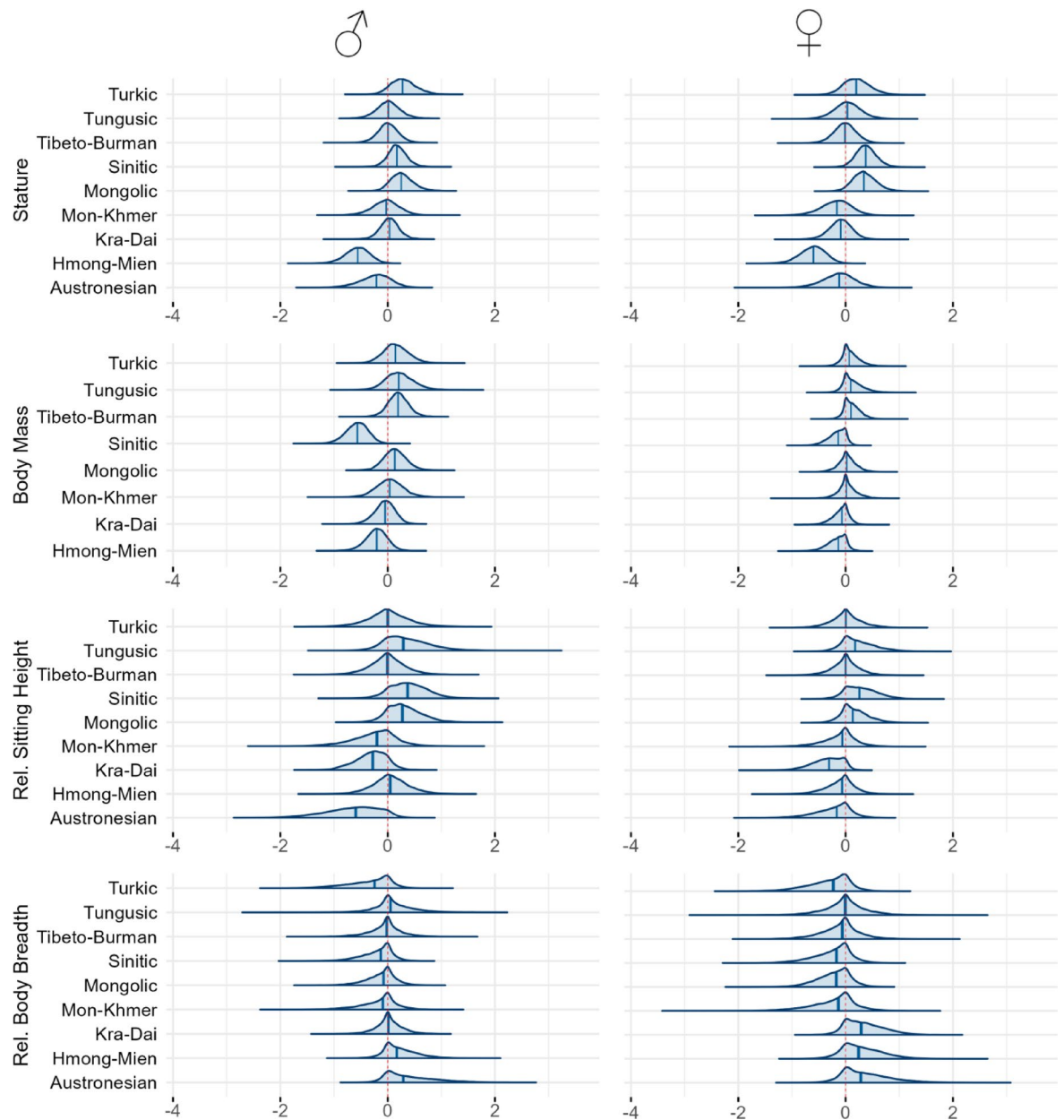


Fig. 4. Posterior distributions of random intercepts by language subgroup. Traits (top to bottom): stature, body mass, relative sitting height, and relative body breadth. Intercepts represent subgroup-specific baseline values. Male results (♂) are on the left, female (♀) on the right. Red dashed lines mark the grand mean ($z = 0$); blue vertical lines show posterior means. Distributions whose means and 95% credible intervals (shaded areas) are shifted from zero suggest credible subgroup-level differences. Positive values indicate above-average baseline values for the trait; negative values indicate below-average.

Discussion

Secular increases in body size within persistent geographic structure

Drawing on a large georeferenced dataset and a Bayesian spatial modelling framework, this study reveals a complex and multilayered pattern of human morphological variation in modern China. The clearest finding is a widespread secular increase in body size from the mid-20th to early 21st century, particularly in body mass and, to a lesser extent, stature. These gains are likely linked to China's economic growth, improved nutrition, better healthcare, and changing living conditions following market reforms^{17,42}, and are consistent with global patterns linking development and physical growth^{12,24}. Urban residents tend to be taller and heavier than rural populations, which may reflect both increased caloric intake and reduced physical activity³⁰. However, southern populations remained shorter and lighter than northern populations, indicating that recent development has modified but not erased long-standing geographic disparities.

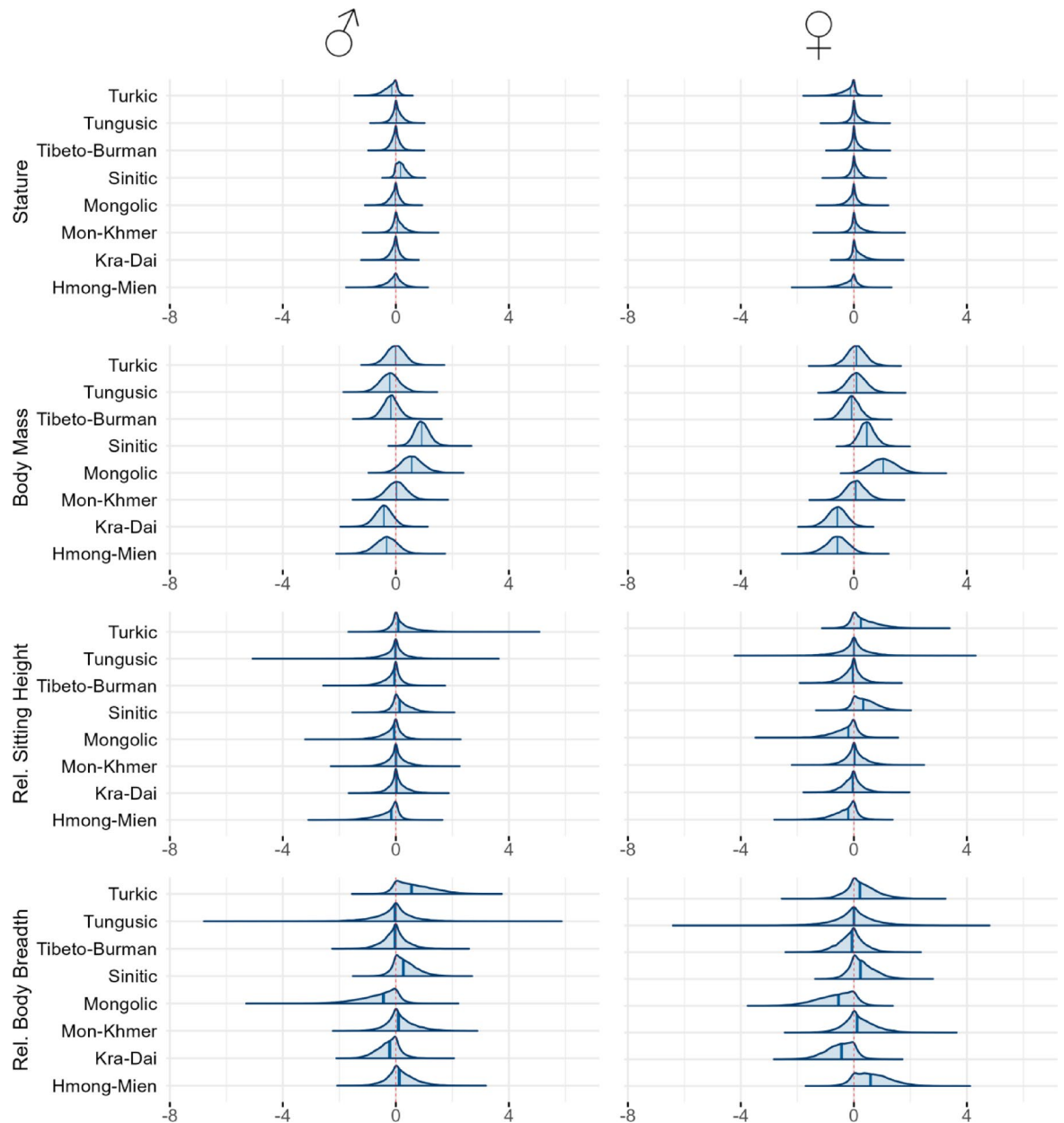


Fig. 5. Posterior distributions of random slopes for temporal change by language subgroup. Traits (top to bottom): stature, body mass, relative sitting height, and relative body breadth. Slopes estimate subgroup-specific effects of TimeLate (21st-century vs. mid-late 20th-century baseline). Male (♂) results are on the left, female (♀) on the right. Red dashed lines indicate the overall mean slope; blue vertical lines mark posterior means. Distributions whose means and 95% credible intervals (shaded areas) are shifted from zero indicate credible subgroup-level differences in the rate or direction of temporal change. Positive values indicate above-average increases over time; negative values indicate below-average or negative change.

The persistence of a north–south gradient in stature and body mass is one of the most robust findings of this study. Stature showed the clearest spatial structuring among all traits, with northern populations consistently predicted to be taller than southern populations across both early rural and late urban scenarios. While this pattern superficially resembles ecogeographic expectations under Bergmann’s rule, our models indicate that neither minimum nor maximum temperature function as strong independent predictors, consistent with previous studies^{47,58}. Instead, maximum precipitation emerged as a negative predictor of stature, with higher rainfall potentially enhancing agricultural productivity but also increasing pathogen loads in humid tropical climates that may suppress growth^{32,47}. More broadly, thermoregulatory explanations may be most applicable at climatic extremes, whereas much of China’s Holocene and recent climatic variation falls within ranges where ecology, subsistence, disease ecology, population history, and socio-economic conditions are difficult to separate^{14,23}.

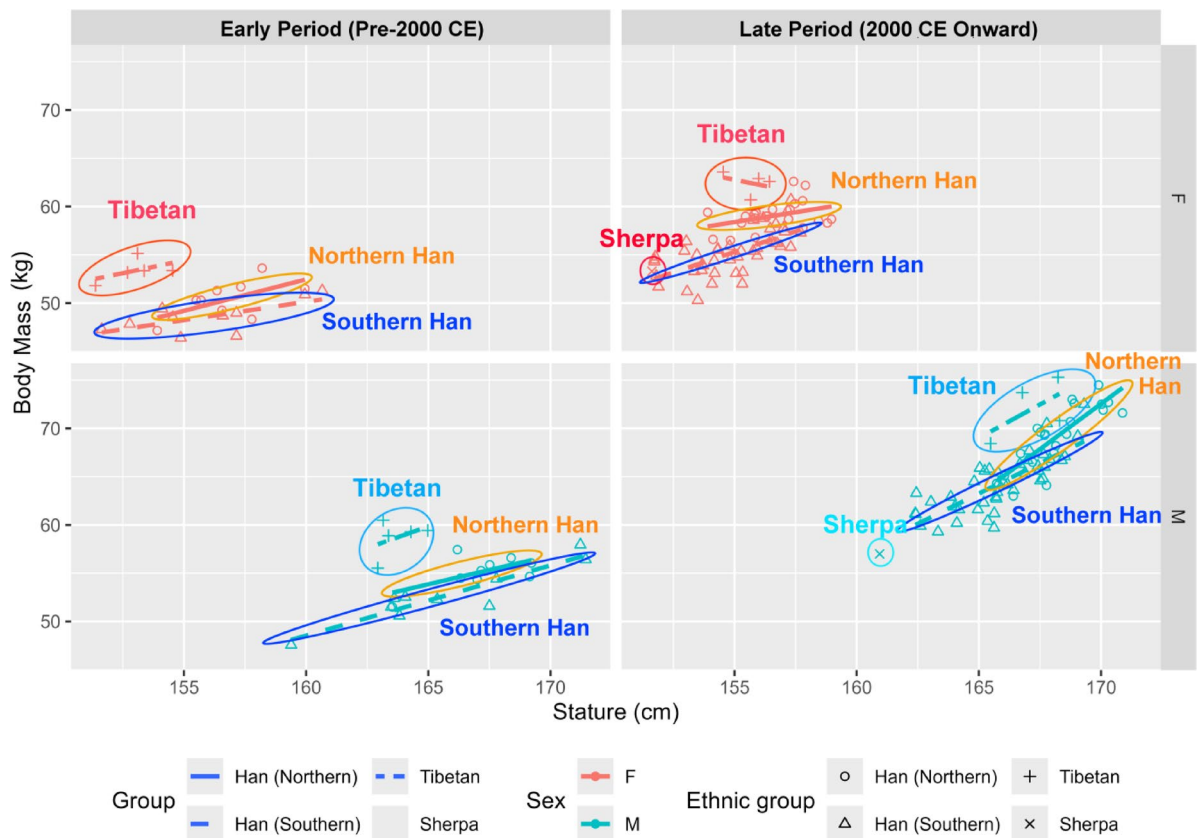


Fig. 6. Body size variation across highland groups and lowland Han Chinese groups. M: male; F: female. “Northern” and “Southern” refer to regions north and south of the Qinling–Huaihe Line ($\sim 34^{\circ}\text{N}$), respectively⁷². Note that Tibetan individuals consistently lie above the Han regressions, indicating relatively greater body mass for a given stature. Sherpa, shown only in the late period, cluster at lower stature and body mass despite comparable high-altitude residence. Secular increases in body size are evident across Han and Tibetan groups; Northern Han remain taller and heavier than Southern Han in both periods.

Importantly, the persistence of this latitudinal gradient in the spatial residuals, even after including environmental covariates, may also reflect partial spatial confounding: large-scale geographic structure and climate share overlapping variation, making their independent effects difficult to fully separate.

The similar latitudinal pattern observed in the environment-only component suggests that measured covariates account for part of the predicted north–south stature gradient. However, the persistence of spatial structure beyond these covariates indicates that geography also captures unmeasured or historically structured processes. Climate, geography, subsistence history, migration, and ancestry are spatially correlated, creating partial spatial confounding in models that attempt to separate environmental and geographic effects. In northern China, colder and drier environments historically supported millet and wheat agriculture, pastoralism, and greater consumption of livestock products, including meat and dairy^{27,60}. These subsistence strategies coincided with sustained cultural and genetic exchange with populations across northern Eurasia, likely facilitated by shared climatic conditions and geographic connectivity^{21,43,49}. In contrast, southern populations have historically practiced rice agriculture adapted to warmer, more humid environments^{27,60}, and maintained closer links with groups in South and Southeast Asia^{26,38}. These long-standing north–south differences in lifestyles and interactions are also mirrored in a genetic north–south gradient, reflecting long-term regional differentiation and episodes of demic diffusion that may have contributed to persistent geographic variation in body size^{39,40,74}.

Recent socioeconomic development appears to have modified but not removed these older geographic patterns. While a north–south stature gradient persists, the gap has narrowed modestly (~ 2 cm), likely due to more rapid stature gains among some economically advantaged southeastern coastal provinces^{30,42}. Internal migration may also play a role: the movement of taller individuals from the north into southern urban centres could elevate local population averages⁴¹. In contrast, body mass is more strongly linked to temporal and urbanisation effects, emphasising its sensitivity to recent socioeconomic shifts and life-course exposures²⁴. This is consistent with the larger and more consistent early–late contrasts in body mass across language subgroups, compared with the weaker subgroup contrasts in stature and body proportions.

Residual spatial patterns also highlight regional nuances. In northeastern China, female stature estimates from spatial-only models differ from those incorporating environmental predictors, indicating the influence of additional factors not captured by the included variables. One relevant historical process is the ‘Chuangguandong (闯关东)’ migration, which brought a substantial number of Han settlers (~ 8.7 million) from northern China,

particularly the Shandong Peninsula and Zhili region, including today's provinces of Hebei, Henan, and Shandong, as well as the municipalities of Beijing and Tianjin, into Manchuria (the northeastern provinces of Heilongjiang, Jilin, and Liaoning) during the late nineteenth and early twentieth centuries⁵⁰. Although the migration increasingly involved entire families, it was male-biased, particularly in its early waves. This demographic asymmetry may have promoted greater genetic admixture among males, aligning male stature more closely with northern donor populations, while females, less directly affected by incoming ancestry in the initial generations, retained distinct local traits⁷⁶. However, such sex-specific effects would be expected to persist for only a few generations (i.e., until admixture equilibrated), suggesting that additional or more recent influences, whether environmental, socioeconomic, or nutritional, are also likely involved. As spatial residuals capture any unmeasured, geographically structured factors, including omitted environmental variables or historically patterned processes, part of the remaining signal may therefore reflect shared geographic and environmental gradients rather than a fully independent signal.

High-altitude exceptions

Tibetan populations residing at high altitudes historically exhibited short stature, with recent increases likely reflecting improvements in nutrition and socioeconomic conditions. However, their consistently elevated body mass relative to both lowland and other highland groups may indicate distinctive metabolic adaptations^{3,6}. Bayesian GAMMs reveal a positive, albeit non-significant, association between altitude and female body mass, supporting hypotheses that link increased adiposity to enhanced reproductive fitness in ecologically demanding environments^{65,66}. Evidence from physiology and genetics strengthens this interpretation: modern Tibetans exhibit similar basal metabolic rates to lowlanders but maintain higher body fat levels⁶, and carry genetic variants associated with efficient lipid metabolism³⁵ and the broader adaptive functions of adiposity, including energy buffering, thermoregulation, and reproductive support at high altitudes⁶⁶. High dietary intake of animal products and associated metabolic pathways may also contribute³.

By contrast, Sherpa populations on the southern Tibetan Plateau exhibit smaller body size than other highland groups, even after accounting for climatic and altitudinal influences. This persistent pattern likely reflects complex interactions between local adaptation, population history and lifestyles^{29,73,75}. Genomic studies show that while both Sherpas and Tibetans are closely related to other East Asians, Sherpas carry more South Asian ancestry, whereas Tibetans show stronger East and Central Asian signals, supporting a model of multiple migration waves and differential admixture^{28,75}. Importantly, comparative studies of South Asian populations have documented persistently low lean mass and reduced overall body mass^{46,55}, suggesting that inherited growth trajectories linked to population history may contribute to the smaller body size observed in Sherpas. These ancestral patterns may be further reinforced by development constraints related to labour-intensive livelihoods and limited access to nutritional buffering in high-altitude environments⁷³.

Stable but patterned body proportions

Patterns in body proportions appear more stable across time and space. Relative sitting height shows modest increases over time, suggesting that trunk length rather than lower limb length has contributed more to recent stature gains, in contrast with some previous research^{13,63}. This may not indicate greater plasticity of the trunk, but rather its later developmental window, allowing it to better take advantage of improving growth environment, especially when lower limb growth potential has plateaued². Nutritional transitions, particularly rising obesity and earlier maturation, may also influence the balance between trunk and limb growth^{2,15}. Regionally, northeastern groups in colder environments display higher relative sitting height, consistent with thermoregulatory expectations, but other northern populations diverge from Allen's rule by showing comparatively shorter trunks. Environmental variables explain little of this variation, with only a weak latitudinal gradient, implying that climate, genetics, development, and cultural history exert overlapping and sometimes counteracting effects^{52,57}.

Relative body breadth follows a consistent east–west gradient, with broader torsos in inland and highland areas and narrower torsos along the southeastern coast. While this pattern may relate to thermoregulatory pressures, Bayesian models did not find temperature to be a significant predictor. Notably, northeastern populations defy ecogeographic expectations by showing narrower pelvises despite cold climates. This deviation is consistent with prior research indicating that pelvic morphology is less developmentally plastic than limb proportions and is more likely shaped by neutral evolutionary processes, such as genetic drift and migration, rather than direct climatic adaptation¹⁰.

At the same time, the pelvis is a complex structure shaped by multiple, partly competing demands, including thermoregulation, body size, and childbirth. Compared with limb length, pelvic form is likely to be more developmentally and functionally constrained, but this does not mean that all pelvic dimensions are entirely fixed or equally canalised^{9,11}. Bi-iliac breadth, as used here, captures external pelvic breadth rather than the dimensions of the obstetric canal itself; it therefore cannot be interpreted as a direct measure of pelvic aperture or birth-canal capacity. Nevertheless, it remains relevant to childbirth-related constraints, because external body-breadth measures and pelvic canal dimensions are not entirely independent. For example, smaller-bodied female skeletal samples have been reported to show higher frequencies of pelvic canal contraction, and pelvic canal breadth has been shown to correlate positively with body-size and body-breadth measures, including femoral head diameter and bi-iliac breadth^{33,34}. Studies of living populations likewise suggest that maternal pelvic dimensions are associated with neonatal size, although dimensions more directly related to the obstetric canal, such as conjugate and interspinous diameters, are more informative than external breadth measures^{67,68}. Some pelvic dimensions also retain developmental responsiveness to growth conditions, as markers of linear growth have been associated with adult pelvic dimensions⁵⁹. Dietary factors are relevant as well: dairy consumption, more common among northern and highland pastoralists, may support skeletal growth, including pelvic dimensions, under nutritional constraints^{20,69}. Sherpa groups remain exceptional, displaying narrow

pelves despite high-altitude residence, possibly due to a combination of genetic ancestry, subsistence demands, and growth constraints^{73,75}. In this sense, relative body breadth appears to reflect layered influences, including population history, ecological context, growth conditions, and reproductive constraints, rather than a single process of climatic adaptation, developmental plasticity, or canalisation.

Sex-specific and language subgroup variation

Sex-specific patterns were broadly similar, with few clear differences in response to environmental or socioeconomic gradients, contrary to prior research suggesting greater male sensitivity to environmental stressors^{62,64}. One possible explanation is that improved living standards, expanded healthcare, and reduced sex bias in resource allocation have narrowed sex-specific growth differences in recent decades, particularly under the one-child policy^{17,36}. Nevertheless, some sex-specific model behaviour was evident, including the northeastern female stature residual pattern and slightly stronger late-period tendencies in female relative sitting height. These effects were generally modest or uncertain and should not be overinterpreted. Urbanisation also showed a stronger association with male body mass, suggesting that lifestyle changes involving diet, occupation, and physical activity may have affected male body mass more strongly.

Bayesian models also reveal persistent differences in body size among language subgroups, particularly in stature. Northern groups (e.g., Turkic, Mongolic) tended to be larger-bodied, consistent with pastoralist subsistence and connections to northern Eurasia, whereas smaller-bodied southern groups (e.g., Hmong-Mien, Kra-Dai) practiced rice agriculture in warm, humid environments with stronger ties to Southeast Asia^{31,43}. These long-standing ecological and cultural contrasts likely continue to shape present-day variation in body form among linguistic groups.

However, linguistic categories should not be treated as direct proxies for genetic ancestry, culture, or socioeconomic experience. Each language subgroup contains substantial internal heterogeneity in ancestry, geography, subsistence, migration history, urbanisation, and living conditions. The late-period increase in ICC values also requires caution. ICC represents the proportion of total modelled variance attributable to language subgrouping; therefore, higher ICCs may result from increased between-subgroup variance, reduced within-subgroup variance, or both. Rather than indicating that language groups necessarily became more divergent, higher late-period ICCs suggest a greater relative contribution of language subgrouping to total variance. This pattern may reflect uneven socioeconomic development, selective migration, assortative marriage, internal homogenisation within some subgroups, or a combination of these processes^{41,42,45}.

More broadly, these findings show that human morphological variation in modern China is not simply a biological response to climate or a passive outcome of economic development, but a dynamic archive of ecological inheritance, population history, developmental plasticity, and social transformation. Contemporary China offers a particularly informative biocultural case, because rapid urbanisation, economic development, and nutritional transition have unfolded against a background of marked regional ecological diversity and long-standing historical and population structure. The persistence of older geographic and population-structured patterns alongside recent secular increases in body size suggests that modernisation reshapes, but does not erase, the biological traces of ecology and population history. Morphological variation is therefore layered and context-dependent, preserving signals of longer-term ecological and population-historical legacies while also reflecting the more recent imprint of socioeconomic change.

Limitations and implications

While our study draws on a large, georeferenced dataset and a flexible Bayesian modelling framework, some limitations remain. Certain regions, particularly those with smaller ethnolinguistic populations, are underrepresented, potentially biasing spatial predictions and limiting resolution within subgroups. The early-period dataset also includes some school-based samples, including individuals aged 18 years or older. These samples may not fully represent the general adult population of the mid-20th century, because access to schooling was uneven across regions and socioeconomic backgrounds. In this respect, school-based samples are likely to have overrepresented individuals from relatively advantaged socioeconomic backgrounds, especially before the Great Famine and in rural or less developed regions where educational access was more limited. This bias should therefore be considered when interpreting early-period body size estimates. However, if school-based samples disproportionately captured individuals with better nutritional and socioeconomic conditions, then the observed temporal increases in stature and body mass are likely to represent conservative estimates rather than inflated ones. In other words, the inclusion of relatively advantaged individuals in the early-period sample would tend to reduce, rather than exaggerate, the magnitude of secular change. Older students in elementary or middle-school records should also be interpreted in the historical context of delayed or interrupted schooling and the expansion of adult and remedial education in mid-20th-century China. Such individuals may therefore include older youths or adults whose education had been postponed or resumed. Because this study focuses mainly on broad spatial and temporal patterns rather than individual growth trajectories, and because the models include period, residence, geography, and subgroup structure, this sampling issue is unlikely to fully account for either the large-scale temporal shifts or the persistence of spatial patterning observed here.

Linguistic categories, though analytically useful, encompass substantial internal heterogeneity, spanning both ancestral differences and socioeconomic gradients. Moreover, while GAMMs model spatial and nonlinear effects well, they cannot capture all life-course dynamics or contextual interactions, such as those linked to education, early-life conditions, or intergenerational trauma (e.g., famine exposure). Additionally, proxies like relative sitting height and bi-iliac breadth, though informative, are not direct measures of limb or body composition and may obscure finer variation. Inconsistencies in measurement across datasets may also introduce noise, although the modelling framework helps to mitigate this. Lastly, the focus on population means may overlook important within-group and individual-level variation.

Despite these caveats, this study provides one of the most spatially detailed and multifactorial analyses of modern human body size and proportions in China. By integrating climatic, geographic, historical, and cultural variables, it advances understanding of how human biological variation reflects both long-term ecological adaptation and recent sociopolitical change. More broadly, the Chinese case offers a particularly valuable window into the complexity of biological change over short historical timescales. Rapid urbanisation, economic development, nutritional transition, and population movement have unfolded against a background of marked ecological diversity, cultural heterogeneity, and major population-level disruption, including the Great Famine. This setting makes it possible to examine not only which aspects of body size and proportion changed within a few decades, but also which spatial and population-structured patterns persisted despite rapid development.

Future research would benefit from longitudinal and cohort-based data that can more directly capture life-course dynamics and intergenerational change. In particular, spatially mapped cohort data on age-specific fertility, infant and juvenile mortality, and younger adult mortality could provide an important extension of the present analysis, especially given the demographic consequences of the Great Famine, uneven regional development, and subsequent family-planning policies^{18,25}. Such data would allow future work to examine whether regional variation in body size and proportions corresponds to broader cohort-level patterns in fertility, early-life survival, and mortality risk. Integrating these demographic records with anthropometric, socioeconomic, genetic, and epigenetic data would help disentangle inherited population structure from environmental and developmental effects. Expanding datasets to include measures such as limb segment lengths, craniofacial dimensions, and body composition, while improving representation of understudied groups and socioeconomic detail, would further enrich interpretations of long-term adaptation, developmental plasticity, and the biological consequences of rapid social transformation.

Methods

Stature, body mass, relative sitting height, and relative body breadth (bi-iliac breadth relative to stature) from over 90,000 adults representing 213 groups were sourced from publications and analysed across two periods based on the time of data collection (Supplementary Table S1). The two periods are: (1) Mid-to-late 20th century (1949–1999), including individuals born during the Great Chinese Famine (1959–1961), a period of severe malnutrition and food shortages with lasting impacts on growth and health¹⁸, and (2) Early 21st century (after 2000), representing individuals born following China's 1978 economic reform, whose childhood and adolescence further improved living standards, healthcare, and nutrition resulting from further socioeconomic developments in the 21st century^{17,42}. We further distinguished groups by urbanism, following the classifications in the original reports. Urban groups refer to those sampled in cities and towns, while rural groups refer to those from villages and county-level communities. Ethical approval for the secondary use of published anthropometric data was obtained from the Human Research Ethics Committee of the University of Hong Kong (Ref: EA260329). All data used in this study were derived from previously published sources and contained no personally identifiable information.

The dataset includes groups from different ethnic backgrounds across 12 language subgroups. Language classifications were cross-checked and verified using Ethnologue (<https://www.ethnologue.com/>) and Glottolog (<https://glottolog.org/>) to ensure consistency and accuracy. Notably, 'ethnic background' here incorporates both officially recognised and socially identified groups, capturing biological (shared ancestry, population history, and long-term adaptations) and sociocultural dimensions such as language and self-identification⁴. Only individuals aged over 18 years were included, as most people reach final adult stature by this stage, with minimal growth thereafter despite some variability in growth rates¹². Adult stature and body mass may decline in older age due to vertebral compression, osteoporosis, and muscle loss^{19,56}. Because systematic age data were not available, this effect could not be directly controlled, though no dataset consisted solely of older individuals, reducing the likelihood of major bias.

Environmental variables, including minimum and maximum annual temperatures, precipitation during the driest and wettest quarters, and altitude, were extracted at each sample location using WorldClim 2.1 raster datasets with 30 arc-second resolution²². Records missing environmental or geographic data were excluded, and to ensure reliable statistical estimation, analyses were restricted to language subgroups represented by at least three population groups. Data were then analysed separately by sex to account for sex-specific differences.

Each anthropometric trait (separately by sex) was analysed using Bayesian generalised additive mixed models (GAMM) implemented in the *brms* package in R version 4.3.2¹⁶; R Core Team⁴⁸. Both environmental variables and anthropometric traits were z-standardised (mean = 0, SD = 1), enabling direct comparison of effect sizes across traits and sexes. Model structures included:

1. A tensor product smooth term for longitude and latitude to capture spatial autocorrelation.
2. Climatic variables: minimum/maximum temperatures and minimum/maximum precipitation.
3. Topographic variable: altitude.
4. Sociocultural covariates: time period and urbanism.

Group-specific variability was modelled using random intercepts and random slopes for time period across nine language subgroups (three subgroups were excluded due to having fewer than three samples), thus employing mixed models. A Student's *t*-distribution was specified for robustness against outliers. Priors were set as follows: Normal(0,1) for fixed effects to gently regularise estimates toward zero without overly constraining them, Cauchy(0,1) for variance parameters to allow for larger variability while preventing extreme values, and Gamma(2,0.2) for degrees of freedom to favour moderately heavy tails for the *t*-distribution, enhancing robustness to outliers. Each model was run for four MCMC chains of 4,000 iterations (1,000 warm-up), ensuring convergence ($\hat{R} < 1.01$) and sufficient effective sample sizes. Posterior draws of fixed and random effects were

extracted to visualise estimates and uncertainty intervals. Conditional effects plots were generated to visualise the modelled relationships between individual predictors and each body dimension, along with observed predictor ranges. The ICCs were also computed to quantify the proportion of total variance attributable to subgroup-level clustering. Key model outputs and interpretive terms are summarised in Table S2.

To clarify spatial and environmental influences independently of group-specific variation, we generated three complementary prediction maps based solely on fixed effects, i.e., setting $re_formula = \sim 0$ to exclude contributions from random effects during prediction. This approach isolates broad ecological gradients without confounding from language-group-specific deviations modelled through random intercepts and slopes. Specifically:

1. Full prediction maps based on both spatial and environmental effects (coordinates, climatic, and altitude data included), reflecting the actual predicted anthropometric variation across China for different time periods and urban/rural scenarios. Coordinates were obtained from the original studies, or, if absent, inferred from reported location names.
2. Coordinate-only prediction maps created by holding environmental covariates constant at their mean (scaled mean = 0), allowing only spatial coordinates to vary. These maps highlight the residual geographic structure not explained by climate or altitude, potentially reflecting unmeasured environmental, genetic, or sociocultural influences.
3. Environmental effect maps, computed by subtracting coordinate-only predictions from full-model predictions. The resulting maps directly visualise the spatial distribution of the net environmental contribution to trait variation, independent of pure geographic structure.

To highlight contrasts, we compared early rural and later urban populations, representing two socioeconomic extremes: the former shaped by widespread undernutrition and limited healthcare, and the latter by improved nutrition, healthcare, and urban infrastructure following economic reforms. All analyses were scripted in R version 4.3.2 (R Core Team⁴⁸). Data wrangling and restructuring were conducted using *tidyverse* packages⁷¹, and plotting and map visualisation were carried out using *ggplot2*⁷⁰. Bayesian GAMMs were fitted using *brms*¹⁶ via *Stan* (Stan Development Team⁶¹). Spatial data processing and map generation were conducted using *sf*⁴⁴, with *raster* and *terra* used for environmental raster processing. Fully reproducible code for the analyses, figures, and maps is available in the online repository archived on Zenodo at <https://doi.org/10.5281/zenodo.20550013>.

Data availability

The aggregated, group-level anthropometric dataset and all R scripts used for data cleaning, statistical modelling, and figure generation are available in the GitHub repository [https://github.com/CarolDoudouCao/ModernBodyForm_China] (https://github.com/CarolDoudouCao/ModernBodyForm_China). Climate-raster layers for temperature, precipitation, and elevation were obtained from WorldClim v2.1 (Fick & Hijmans 2017; [<https://www.worldclim.org/data/worldclim21.html>] (<https://www.worldclim.org/data/worldclim21.html>))

Code availability

The code used to perform the statistical analyses and generate the figures and maps in this study is available from GitHub and has been archived on Zenodo at <https://doi.org/10.5281/zenodo.20550013>.

Received: 11 February 2026; Accepted: 8 June 2026

Published online: 12 June 2026

References

1. Allen, J. A. The influence of physical conditions in the genesis of species. *Radic. Rev.* **1**, 108–140 (1877).
2. Ashizawa, K. Leg length increase/decrease in Japanese in the latter half of the 20th Century. *Anthropol. Sci.* **110** (3), 279–292. <https://doi.org/10.1537/ase.110.279> (2002).
3. Bao, J. et al. A study of Weizang and Kham Tibetans' somatotype by Heath-Carter method 卫藏藏族与康巴藏族的Heath-Carter法体型. *Acta Anthropol. Sin. 人类学学报.* **40** (5), 834–846. <https://doi.org/10.16359/j.cnki.cn11-1963/q.2020.0038> (2021).
4. Barth, F. & Bergen, U. *Ethnic groups and boundaries: the social organization of culture difference* (Little, 1969).
5. Bateson, P. et al. Developmental plasticity and human health. *Nature* **430** (6998), 419–421. <https://doi.org/10.1038/nature02725> (2004).
6. Beall, C. M., Henry, J., Worthman, C. & Goldstein, M. C. Basal metabolic rate and dietary seasonality among Tibetan nomads. *Am. J. Hum. Biol.* **8** (3), 361–370 (1996).
7. Bergmann, C. Über die Verhältnisse der warmekonomie der Thiere zu über Grosse. *Gottinger studien.* **3**, 595–708 (1847).
8. Bernstein, R. M. The big and small of it: how body size evolves. *Am. J. Phys. Anthropol.* **143** (S51), 46–62. <https://doi.org/10.1002/ajpa.21440> (2010).
9. Betti, L. Human variation in pelvic shape and the effects of climate and past population history. *Anat. Rec.* **300** (4), 687–697. <https://doi.org/10.1002/ar.23542> (2017).
10. Betti, L., Cramon-Taubadel, N. V. & Lycett, S. J. Human pelvis and long bones reveal differential preservation of ancient population history and migration out of Africa. *Hum. Biol.* **84** (2), 139–152. <https://doi.org/10.3378/027.084.0203> (2012).
11. Betti, L., Lycett, S. J., von Cramon-Taubadel, N. & Pearson, O. M. Are human hands and feet affected by climate? A test of Allen's rule. *Am. J. Phys. Anthropol.* **158** (1), 132–140. <https://doi.org/10.1002/ajpa.22774> (2015).
12. Bogin, B. Chapter 20 - Human growth and development. In M. P. Muehlenbein (Ed.), *Basics in human evolution* (pp. 285–293). Academic Press. <https://doi.org/10.1016/B978-0-12-802652-6.00020-7>. (2015).
13. Bogin, B., Smith, P., Orden, A. B., Silva, V., Loucky, J. & M. I., & Rapid change in height and body proportions of Maya American children. *Am. J. Hum. Biol.* **14** (6), 753–761. <https://doi.org/10.1002/ajhb.10092> (2002).
14. Bogin, B., Hermanussen, M. & Scheffler, C. Bergmann's rule is a just-so story of human body size. *J. Physiol. Anthropol.* **41** (1), 15. <https://doi.org/10.1186/s40101-022-00287-z> (2022).
15. Brannsether, B., Eide, G. E., Roelants, M., Bjerknes, R. & Júlíusson, P. B. Interrelationships between anthropometric variables and overweight in childhood and adolescence. *Am. J. Hum. Biol.* **26** (4), 502–510. <https://doi.org/10.1002/ajhb.22554> (2014).

16. Bürkner, P. C. brms: An R Package for Bayesian multilevel models using stan. *J. Stat. Softw.* **80** (1), 1–28. <https://doi.org/10.18637/jss.v080.i01> (2017).
17. Chae, M., Hatton, T. J. & Meng, X. Explaining trends in adult height in China: 1950 to 1990. *World Dev.* **161**, 106075. <https://doi.org/10.1016/j.worlddev.2022.106075> (2023).
18. Chen, Y. & Zhou, L. A. The long-term health and economic consequences of the 1959–1961 famine in China. *J. Health Econ.* **26** (4), 659–681. <https://doi.org/10.1016/j.jhealeco.2006.12.006> (2007).
19. Cline, M. G., Meredith, K. E., Boyer, J. T. & Burrows, B. Decline of height with age in adults in a general population sample: estimating maximum height and distinguishing birth cohort effects from actual loss of stature with aging. *Hum. Biol.* **61** (3), 415–425 (1989).
20. Cox, S. L. et al. Effects of ancestry, agriculture, and lactase persistence on the stature of prehistoric Europeans. *Curr. Biol.* **35** (22), 5654–5665e5653. <https://doi.org/10.1016/j.cub.2025.10.054> (2025).
21. Dong, G., Liang, H., Lu, Y. & Wang, J. Different trajectories of livelihood transformations in response to the trans-Eurasian exchange in agricultural, pastoral, and agro-pastoral regions of north China during the late Neolithic and Bronze Age. *J. Geog. Sci.* **34** (4), 681–698. <https://doi.org/10.1007/s11442-024-2223-1> (2024).
22. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37** (12), 4302–4315. <https://doi.org/10.1002/joc.5086> (2017).
23. Foster, F. & Collard, M. A reassessment of Bergmann's rule in modern humans. *PLoS One.* **8** (8), e72269. <https://doi.org/10.1371/journal.pone.0072269> (2013).
24. Fox, A., Feng, W. & Asal, V. What is driving global obesity trends? Globalization or modernization? *Glob. Health* **15** (1), 32. <https://doi.org/10.1186/s12992-019-0457-y> (2019).
25. Gørgens, T., Meng, X. & Vaithianathan, R. Stunting and selection effects of famine: A case study of the Great Chinese Famine. *J. Dev. Econ.* **97** (1), 99–111 (2012).
26. Guo, J. et al. Genomic insights into Neolithic farming-related migrations in the junction of east and southeast Asia. *Am. J. Biol. Anthropol.* **177** (2), 328–342. <https://doi.org/10.1002/ajpa.24434> (2022).
27. He, K., Lu, H., Zhang, J., Wang, C. & Huan, X. Prehistoric evolution of the dualistic structure mixed rice and millet farming in China. *Holocene* **27** (12), 1885–1898 (2017).
28. He, G. L. et al. Peopling history of the Tibetan Plateau and multiple waves of admixture of Tibetans inferred from both ancient and modern genome-wide data. *Front. Genet.* **12** <https://doi.org/10.3389/fgene.2021.725243> (2021).
29. He, G. et al. Ancient genomes give insight into 160,000 years of East Asian population dynamics and biological adaptation. *Genome Biol.* **26** (1), 420. <https://doi.org/10.1186/s13059-025-03859-1> (2025).
30. Hu, Y. et al. Trends in urban/rural inequalities in physical growth among Chinese children over three decades of urbanization in Guangzhou: 1985–2015. *BMC Public Health.* **20** (1), 1190. <https://doi.org/10.1186/s12889-020-09239-7> (2020).
31. Huang, X. et al. Genomic insights into the demographic history of the southern Chinese. *Front. Ecol. Evol.* **10**, 853391. <https://doi.org/10.3389/fevo.2022.853391> (2022).
32. Katzmarzyk, P. T. & Leonard, W. R. Climatic influences on human body size and proportions: Ecological adaptations and secular trends. *Am. J. Phys. Anthropol.* **106** (4), 483–503 (1998).
33. Kurki, H. K. Protection of obstetric dimensions in a small-bodied human sample. *Am. J. Phys. Anthropol.* **133** (4), 1152–1165. <https://doi.org/10.1002/ajpa.20636> (2007).
34. Kurki, H. K. Compromised skeletal growth? Small body size and clinical contraction thresholds for the female pelvic canal. *Int. J. Paleopathol.* **1** (3), 138–149. <https://doi.org/10.1016/j.ijpp.2011.10.004> (2011).
35. Li, X. et al. Novel insight into the genetic signatures of altitude adaptation related body composition in Tibetans. *Front. Public Health* **12**, 1355659. <https://doi.org/10.3389/fpubh.2024.1355659> (2024).
36. Liang, Y. & Gibson, J. Do siblings take your food away? Using China's One-Child Policy to test for child quantity-quality trade-offs. *China Econ. Rev.* **48**, 14–26 (2018).
37. Liu, X. et al. Geographical distribution of stature and body mass of rural Chinese Han adults 中国汉族乡村成年人的身高与体质量的地理性分布. *Acta Anthropol. Sin.* 人类学学报 **37** (3), 484–495 (2018).
38. Liu, Y. et al. Genomic insights into the population history and biological adaptation of southwestern Chinese Hmong–Mien people. *Front. Genet.* **12–2021** <https://doi.org/10.3389/fgene.2021.815160> (2022).
39. Lu, G. et al. Geographic latitude and human height: Statistical analysis and case studies from China. *Arab. J. Geosci.* **15** (4), 335. <https://doi.org/10.1007/s12517-021-09335-x> (2022).
40. Ma, L., Cao, Y., Xu, J. & He, J. The relationship between the stature and the geo-environmental factors of 102 populations in China 中国102个人群的身高与地理环境相关性研究. *Acta Anthropol. Sin.* 人类学学报 **27** (3), 9 (2008).
41. Meng, X. Rural-urban migration in China. In *The Oxford companion to the economics of China* (382–387). Oxford University Press. (2014).
42. Morgan, S. L. Richer and taller: Stature and living standards in China, 1979–1995. *China Journal (Canberra, A.C.T.)* **44**, 1–39. (2000). <https://doi.org/10.2307/2667475>
43. Ning, C. et al. Ancient genomes from northern China suggest links between subsistence changes and human migration. *Nat. Commun.* **11** (1), 2700. <https://doi.org/10.1038/s41467-020-16557-2> (2020).
44. Pebesma, E. Simple features for R: Standardized support for spatial vector data. *R J.* **10** (1), 439–446. <https://doi.org/10.32614/RJ-2018-009> (2018).
45. Pisanski, K. et al. Assortative mate preferences for height across short-term and long-term relationship contexts in a cross-cultural sample. *Front. Psychol.* **13**, 937146. <https://doi.org/10.3389/fpsyg.2022.937146> (2022).
46. Pomeroy, E., Mushrif, V., Cole, T., Wells, J. & Stock, J. Ancient origins of low lean mass among South Asians and implications for modern type 2 diabetes susceptibility. *Sci. Rep.* **9** <https://doi.org/10.1038/s41598-019-46960-9> (2019).
47. Pomeroy, E., Stock, J. T. & Wells, J. C. K. Population history and ecology, in addition to climate, influence human stature and body proportions. *Sci. Rep.* **11** (1), 274. <https://doi.org/10.1038/s41598-020-79501-w> (2021).
48. R Core Team. in *A language and environment for statistical computing*. (eds Vienna) (R Foundation for Statistical Computing, 2023).
49. Rawson, J. China and the steppe: reception and resistance. *Antiquity* **91** (356), 375–388. <https://doi.org/10.15184/aqy.2016.276> (2017).
50. Reardon-Anderson, J. *Reluctant pioneers: China's expansion northward, 1644–1937* (Stanford University Press, 2005).
51. Roberts, D. F. Body weight, race and climate. *Am. J. Phys. Anthropol.* **11** (4), 533–558. <https://doi.org/10.1002/ajpa.1330110404> (1953).
52. Roseman, C. C. & Auerbach, B. M. Ecogeography, genetics, and the evolution of human body form. *J. Hum. Evol.* **78**, 80–90. <https://doi.org/10.1016/j.jhevol.2014.07.006> (2015).
53. Ruff, C. B. Climate and body shape in hominid evolution. *J. Hum. Evol.* **21** (2), 81–105 (1991).
54. Ruff, C. B. Morphological adaptation to climate in modern and fossil hominids. *Am. J. Phys. Anthropol.* **37** (S19), 65–107 (1994).
55. Rush, E. C., Freitas, I. & Plank, L. D. Body size, body composition and fat distribution: comparative analysis of European, Maori, Pacific Island and Asian Indian adults. *Br. J. Nutr.* **102** (4), 632–641 (2009).
56. Samaras, T. T., Bartke, A. & Rollo, C. D. *Human Body Size and the Laws of Scaling: Physiological, Performance, Growth, Longevity and Ecological Ramifications* (Nova Science, 2007).

57. Savell, K. R. R., Auerbach, B. M. & Roseman, C. C. Constraint, natural selection, and the evolution of human body form. *Proc. Natl. Acad. Sci.* **113** (34), 9492–9497. <https://doi.org/10.1073/pnas.1603632113> (2016).
58. Savell, K. R. R., Katz, D. C., Weaver, T. D. & Auerbach, B. M. Mixed models for the relationship between latitude, temperature, and human postcranial form. *Am. J. Biol. Anthropol.* **179** (3), 431–443. <https://doi.org/10.1002/ajpa.24586> (2022).
59. Shirley, M. K., Cole, T. J., Arthurs, O. J., Clark, C. A. & Wells, J. C. K. Developmental origins of variability in pelvic dimensions: Evidence from nulliparous South Asian women in the United Kingdom. *Am. J. Hum. Biol.* **32** (2), e23340. <https://doi.org/10.1002/ajhb.23340> (2020).
60. Song, F. & Cho, M. S. Geography of food consumption patterns between South and North China. *Foods* **6** (5). <https://doi.org/10.3390/foods6050034> (2017).
61. Stan Development Team. *Stan modeling language users guide and reference manual*. (2023). <https://mc-stan.org>
62. Stinson, S. Sex differences in environmental sensitivity during growth and development. *Am. J. Phys. Anthropol.* **28** (S6), 123–147 (1985).
63. Tanner, J. M., Hayashi, T., Preece, M. A. & Cameron, N. Increase in length of leg relative to trunk in Japanese children and adults from 1957 to 1977: comparison with British and with Japanese Americans. *Ann. Hum. Biol.* **9** (5), 411–423 (1982).
64. Thurstans, S. et al. Boys are more likely to be undernourished than girls: a systematic review and meta-analysis of sex differences in undernutrition. *BMJ Glob. Health.* **5** (12), e004030 (2020).
65. Wells, J. C. K. Sexual dimorphism in body composition across human populations: associations with climate and proxies for short- and long-term energy supply. *Am. J. Hum. Biol.* **24** (4), 411–419 (2012).
66. Wells, J. C. K. Natural selection and human adiposity: crafty genotype, thrifty phenotype. *Philos. Trans. R. Soc. B Biol. Sci.* **378** (1885), 20220224. <https://doi.org/10.1098/rstb.2022.0224> (2023).
67. Wells, J. C. K., DeSilva, J. M. & Stock, J. T. The obstetric dilemma: An ancient game of Russian roulette, or a variable dilemma sensitive to ecology? *Am. J. Phys. Anthropol.* **149** (S55), 40–71. <https://doi.org/10.1002/ajpa.22160> (2012).
68. Wells, J. C. K., Figueiroa, J. N. & Alves, J. G. Maternal pelvic dimensions and neonatal size: Implications for growth plasticity in early life as adaptation. *Evol. Med. Public. Health.* **2017** (1), 191–200. <https://doi.org/10.1093/emph/eox016> (2017).
69. Wells, J. C. K., Pomeroy, E. & Stock, J. T. Evolution of lactase persistence: turbo-charging adaptation in growth under the selective pressure of maternal mortality? *Front. Physiol.* **12**, 696516 (2021).
70. Wickham, H. *ggplot2: Elegant graphics for data analysis* (Springer, 2016). <https://ggplot2.tidyverse.org>
71. Wickham, H. et al. Welcome to the tidyverse. *J. Open. Sour. Softw.* **4** (43). <https://doi.org/10.21105/joss.01686> (2019). Article 1686.
72. Wu, C. *Geography in China* 中国地理 (Science, 1984).
73. Xiang, X., Du, H., Yu, K. & Zheng, L. Characteristics and comparison of body composition of the Monba, Lhoba and Sherpa peoples 门巴族、珞巴族与夏尔巴人身体成分特点及比较. *Acta Anthropol. Sin. 人类学学报.* **40** (1), 109–117 (2021).
74. Yang, M. A. et al. Ancient DNA indicates human population shifts and admixture in northern and southern China. *Science* **369** (6501), 282–288. <https://doi.org/10.1126/science.aba0909> (2020).
75. Zhang, C. et al. Differentiated demographic histories and local adaptations between Sherpas and Tibetans. *Genome Biol.* **18**, 1–18 (2017).
76. Zhou, J. et al. Genetic structure and demographic history of Northern Han people in Liaoning Province inferred from genome-wide array data. *Front. Ecol. Evol.* **10** <https://doi.org/10.3389/fevo.2022.1014024> (2022).

Acknowledgements

We thank the Harding Distinguished Postgraduate Scholarship Programme at the University of Cambridge for funding the doctoral research of D.C.

Author contributions

D.C. conceived the study, compiled and harmonised the dataset, conducted the statistical analyses, developed the modelling framework, and wrote the first draft of the manuscript. E.R.C. contributed to the development of the analytical strategy, provided guidance on Bayesian modelling and spatial analysis, and critically revised the manuscript. E.P. contributed to the conceptual framing of the study, interpretation of the osteological and anthropological results, and substantially revised the manuscript. All authors discussed the results and approved the final version of the manuscript.

Funding

This research received no specific funding.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-026-57537-8>.

Correspondence and requests for materials should be addressed to D.C.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2026