Beyond Bergmann's rule: global variability in human body composition is associated with annual average precipitation and annual temperature volatility

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Short title: Climate and human body composition

Research article accepted by the *American Journal of Physical Anthropology*

15th June 2019

Abstract

Objectives: Human populations exhibit substantial geographical variability in body size and shape. However, the ecological stresses underlying this morphological variability remain poorly understood. The prevailing evolutionary explanation, 'Bergman's rule', assumes that morphological variability represents an adaptive response to average thermal conditions. We hypothesised that other climate factors - annual average precipitation, a marker of ecological productivity and inter-annual temperature volatility, a marker of infectious disease spikes - may also contribute to variability in body composition.

Materials and methods: We explored this hypothesis by examining associations between these climate factors and geographic variability in body composition across 133 male and 105 female populations from non-industrialized settings. We used monthly climate data over 113 years (1901-2013) to develop new climate indices for all worldwide land areas. We stratified our analyses by hot/cold setting (>/<20°C).

Results: In hot environments, lean mass increased as predicted in association with ecological productivity, and decreased in association with ecological volatility. Conversely, levels of body fat increased in association with temperature volatility and precipitation. However, in cold settings, equivalent associations were only partially consistent with our hypotheses, and there was suggestive evidence of sex differences in these associations.

Discussion: Beyond associations with mean annual temperature predicted by Bergmann's rule, variability in human body composition is also associated with mean annual temperature and inter-annual temperature volatility, with these associations further differing between hot and cold settings. Collectively, our results suggest that associations of human body composition with climate are complex for both physique (fat-free mass) and energy stores (adiposity).

Keywords: body composition, global variability, climate, adaptation, sex differences.

Introduction

Fossil evidence points to modern humans evolving in Africa within the last few hundred thousand years (Hublin et al., 2017) and then dispersing across most of the Earth's land-mass. Many studies have reported large geographical variability in human morphology (body size and shape), assessed by simple measures such as the ratio of surface area to body mass (Schreider, 1950), or mass relative to height (Katzmarzyk & Leonard, 1998; Roberts, 1953). For example, the average body mass index (BMI, calculated as mass/height^2) among the Turkana of East Africa is below 18.5 kg/m^2 in both sexes (Little et al., 1983), whereas among Tongan Islanders of similar average height it exceeds 30 kg/m^2, indicating ~70% greater body mass (Craig et al., 2001). Such geographical patterning extends to the two primary components of mass, namely fat and lean mass (Wells, 2012a). In turn, this somatic variability is associated with a differential risk in contemporary populations of developing chronic non-communicable diseases (Dulloo et al., 2010; Wells, 2016). For example, South Asians have an elevated risk of developing type 2 diabetes and coronary heart disease, despite low levels of obesity according to BMI cut-offs developed for Europeans (Misra & Khurana, 2009). A key mediating factor is that South Asians have lower levels of lean mass and hence greater fatness for any given BMI value, compared to Europeans (Deurenberg et al., 2002).

Geographical variability in human morphology has been reported to track genetic population structure (Hruschka et al., 2015), though secular trends in BMI (Katzmarzyk & Leonard, 1998) also indicate a contribution of plasticity. However, there is poor understanding of the selective pressures that have shaped morphological variability. In the 19th century, it was proposed that as temperature declined across geographical space, the body size of warm-blooded animals would increase (Bergmann’s rule) (Bergmann, 1847) while the size of body extremities would fall (Allen’s rule) (Allen, 1877). These two so-called ‘ecological laws’ reflect physical principles that relate heat production to body mass or volume, and heat loss to surface area. On this basis, colder environments favour larger animals with smaller extremities to conserve heat, and warmer habitats favour contrasting traits to promote heat loss.

Consistent with these hypotheses, variability in body mass and shape has been associated with the thermal environment in mammals, birds and some amphibians (Ashton, 2002; Ashton & Feldman, 2003; Ashton et al., 2000). In humans, both laws are supported for body mass and limb lengths

(Katzmarzyk & Leonard, 1998; Roberts, 1953), though the effects are most apparent over broad ranges of latitude (Foster & Collard, 2013). Furthermore, variability in both fat and lean mass is consistent with Bergman's hypothesis (Wells, 2012a), though the associations vary subtly by sex (Wells, 2012c). The notion that variability in human morphology indicates thermodynamic adaptation is sufficiently well accepted that it is the primary lens through which broader hominin morphological variability is interpreted (Ruff, 2002; Weaver, 2009).

Nevertheless, a previous analysis of human body composition data found that annual average temperature explained <10% of the geographical variance in contemporary lean mass variability among non-industrialised human populations, and <15% of the variance in adiposity, measured by subcutaneous skinfold thickness (Wells, 2012a). Moreover, these associations only held if Polynesians were omitted from the analyses, for their BMI, lean mass and adiposity are substantially greater than expected given the annual average temperature of their geographical region. It has been suggested that Polynesians might be 'cold-adapted', due to exposure to wind-chill during either oceanic migrations or subsistence activities (Houghton, 1990).

Surprisingly little attention has been given to examining whether there are other climatic factors that might also explain geographic variance in human morphology or body composition. For example, annual average precipitation may provide a robust marker of ecological productivity (Schuur, 2003), and it has recently been proposed to be a more important selective pressure than temperature across global plant and animal populations (Siepielski et al., 2017). For humans, this could relate to the supply of food; for example, greater rainfall has been linked with improved rates of children's growth (Shively, 2017). Furthermore, inter-annual volatility in climate has recently been proposed as a marker of the risk of periodic food insecurity, and has also been widely associated with changes in the geographical distribution of disease vectors, potentially provoking temporary epidemics (World Health Organization, 2005). Consideration of multiple indices of climate would allow both thermodynamic and bio-energetic stresses to be addressed. This would offer a broader analytical framework that is more compatible with evolutionary life history theory, that models how energy is invested across competing functions and tissues in association with ecological factors (Hill, 1993).

Evolutionary life history theory assumes that all organisms are under selective pressure to harvest resources from the environment, and to allocate them to biological functions to maximise fitness

(Stearns 1992; Hill et al., 1993). Energy is allocated in competition between the functions of ‘maintenance’, ‘growth’, ‘reproduction’ and ‘defence’ against pathogens and predators (Hill 1993; Wells et al., 2017). Increased investment in any one of these functions reduces the allocation of energy to the others, resulting in trade-offs between them (Hill 1993). In each sex, fat and lean tissue can be considered as potential targets for investment, with implications for both survival and reproduction, though the two sexes also differ in the optimal relative allocations between these two tissues (Wells 2012c; Shirley et al., 2017).

Here, we test the following new predictions regarding variability in human morphology and body composition. First, we hypothesised that lean mass, incorporating metabolically expensive tissues such as muscle and organs (Aiello & Wheeler, 1995; Shirley et al., 2018), should increase in association with average annual precipitation (a marker of food supply), and decrease in association with inter-annual volatility in temperature (a marker of food insecurity or infectious disease spikes). Second, we hypothesised that subcutaneous adiposity, representing a metabolically cheap form of energy-insurance (Wells, 2012b), should increase in association both with average precipitation, and with volatility in temperature. Third, we hypothesised that while associations between climate and body composition are expected among both sexes, as neither can escape such stresses, those for lean mass should be stronger in males than females, as this tissue benefits male mating opportunities, while those for adiposity should be stronger in females than males, as females utilize fat stores for reproduction (Norgan, 1997; Wells, 2010). These hypotheses are summarised in **Figure 1**.

Materials and methods

This study involved reanalysis of a global database on human body composition from non-industrialized settings previously compiled to test Bergman’s hypothesis (Wells, 2012a), updated with recent anthropometric studies. The database contains data for one or both sexes from small-scale non-western populations, omitting industrialized settings as they tend to have access to technologies that mitigate exposure to ecological stresses associated with climate variability (Wells, 2012a). We assumed that the populations included in the sample remain exposed to both beneficial and adverse components of climate variability, the effects of which may extend to both food supply and infectious disease load.

We used four measures of body composition: body mass index (BMI) which is a composite marker of nutritional status; two skinfolds (Triceps, Subscapular) which are markers of subcutaneous adiposity; and residuals of the regression of BMI on the sum of skinfolds (BMI-residual) which is a marker of height-adjusted lean mass. We extracted data on geographical location for each population, or excluded them from the analysis if such data were unavailable.

We used three indices of climate variability: annual average temperature (°C), annual average precipitation (mm), and inter-year volatility in annual temperature (°C). These indices were computed on a 0.5 degree latitude/longitude grid (equivalent to spatial resolution of ~55 km) over all land territories worldwide except Antarctica. The raw data comprised monthly gridded land air temperature data at a height of 2 m and land precipitation data for the period 1901-2013, representing 113 years (Harris et al., 2014; New et al., 2000). Here, 'inter-year volatility' is defined as the difference between 5th and 95th centiles of the annual values. The three indices of climate variability are displayed geographically in **Figure 2 (a-c)** for the latitude range between 80°N and 30°S that includes all the human population sites. The large sensitivity of each climate index to geographic location is evident. Restricted to the locations that we analysed, average climate values and their variability, stratified by five global regions, are given in **Supplementary online Table 1**. Oceania had the hottest average temperatures and highest average precipitation, while the Arctic region had the greatest temperature variability and the lowest average precipitation.

Human body composition data were available for 133 male and 105 female populations. The geographical distribution of these population sites is shown in **Figure 2 (d)**. The sample was larger for males as some publications were restricted to this sex, however for the majority of the female populations, matching make data were available (*n*=85 populations)

Each human population comprised data on young adults (minimum *n*=8 per sex, median sample *n*=55, ~85% of samples had *n*>20) for age, weight, height, and triceps and subscapular skinfold. The population data also included the date of study so that potential secular trends in growth or nutritional status could be taken into account. Climate data were assigned to each human population according to their geographical coordinates by using the 'nearest matching cell' method. The raw data are available as **Supplementary online Table 2**.

Data preparation

Weight (kg) and height (m) were combined to give BMI (weight/height^2). Skinfolds were right-skewed, and were natural log-transformed (Ln) before analysis. Skinfolds can be used to predict whole-body fat mass, but these equations are from Europeans (Durnin & Womersley, 1974) and may generate bias in non-Europeans (Dioum et al., 2005). A more robust approach is to analyse raw skinfolds as indices of adiposity, and to adjust BMI for the two skinfolds to give an estimate of relative lean mass (Wells, 2012a). For each sex, we therefore regressed BMI on Ln Subscapular and Ln Triceps and obtained unstandardised regression residuals, using the following equations:

Males: BMI = 8.843 + (6.961 * Ln Subscapular) – (1.563* Ln Triceps)
$r^2 = 0.374$, SEE = 1.977

Females: BMI = 6.822 + (4.876 * Ln Subscapular) + (0.959 * Ln Triceps)
$r^2 = 0.523$, SEE = 2.017

We treat this ‘BMI-residual’ as an index of relative lean mass for height, similar to the ‘lean mass index’ (lean mass/height^2) (VanItallie et al., 1990). Correlations of BMI-residual with actual lean mass index values, calculated from European equations (Durnin and Womersley, 1974), were 0.96 in males and 0.94 in females, both $p<0.0001$. In order to be able to plot data on both triceps and BMI-residual on a single graph, we converted BMI-residual to standardised residuals, and Ln Triceps values to internal *z*-scores, thus matching the two variables in format.

Statistical analyses

Preliminary analysis indicated that across geographical locations, temperature volatility and annual average precipitation were correlated with annual average temperature. We addressed this in two ways. First, we regressed temperature volatility on annual average temperature, and used the regression residuals in subsequent regression models. This removed the correlation between the two temperature indices.

Second, we also stratified the sample of populations into two groups, categorized by annual average temperature above/below 20°C. This allowed testing of whether associations of body composition parameters with average annual precipitation and temperature volatility differed systematically in colder versus hotter settings. The cut-off of 20°C was selected partly from the distribution of the data, but also because it is not far below the lower end of the thermo-neutral range. Both heat and cold stress are established determinants of variability in human morphology and physiology (Schreider 1953; Roberts 1953; Leonard et al., 1999), however it is plausible that other ecological stresses such as those addressed here (climate proxies for food supply and pathogen burden) might not correlate similarly with mean annual temperature in hot versus cold settings, while any resulting life history trade-offs attributable to these proxies might also vary according to thermal conditions.

We first plotted our body composition outcomes against the two climate predictors, stratified by hot/cold setting. We then analysed correlations of body composition outcomes with mean precipitation and temperature volatility for each sex, separately in hot and cold settings, partialling out the effects of population age and study date. For precipitation, we also partialled out any residual associations with annual average temperature. Equivalent regression models were used to determine the adjusted regression coefficients (denoted as ß) and their 95% confidence intervals (CI) of the relationship between climate and body composition outcomes. In these models, precipitation was multiplied by 100 so that results are expressed per 100 mm greater precipitation, while the temperature volatility coefficients are expressed per *z*-score greater volatility, adjusting for mean annual temperature. Finally, we constructed multiple regression models, which in addition to age and study date included a dummy variable for hot/cold setting, and an interaction term for the association of the climate predictor with hot/cold setting. This approach was used to test formally whether associations of climate predictors and body composition differed significantly between hot and cold settings. We also tested for sex differences using the same approach, and ran sensitivity analyses by restricting the sample to populations that had data for both sexes.

Study publication date and average (or median) age of each population were included as potential confounders. Initial analyses used all available data. However, some studies had sampled more than one population (for example, different ethnic groups, or nearby settlements) within a small geographical area, resulting in their being assigned the same climate data using the nearest matching cell method. We therefore re-ran the models after averaging the body composition outcomes of all populations assigned identical climate exposures. Variables were retained in statistical models if $0.05 < p < 0.1$, to enable us to detect trends or adjust for potential confounders that were not quite significant. Analyses were performed using IBM SPSS version 24 (Armonk, New York: IBM Corporation).

Results

BMI was positively associated with average precipitation in both sexes in hot settings (Males: ß = 0.164, CI 0.116, 0.211; Females: ß = 0.095, CI 0.003, 0.156), whereas the association was negative in cold settings and not significant (Males: ß = -0.006, CI -0.195, 0.065; Females: ß = -0.081, CI -0.365, 0.195) (**Figure 3, Table 1A**). Conversely, BMI was positively associated with temperature volatility in both sexes in cold settings (Males: ß = 0.879, CI 0.441, 1.317; Females: ß = 1.125, CI 0.569, 1.682) but not in hot settings (Males: ß = -0.031, CI -0.589, 0.527; Females: ß = 0.693, CI -0.039, 0.426). These contrasting associations between hot and cold settings achieved statistical significance in males ($p<0.05$), but not in females (**Table 1A**). The results were broadly similar when the analysis was restricted to location-averaged data, though the interactions of climate predictors with BMI by setting were no longer significant in males (**Table 1B**).

Hypothesis 1: BMI-residual associations

BMI-residual was positively associated with average precipitation in both sexes in hot settings (Males: ß = 0.109, CI 0.070, 0.147; Females: ß = 0.056, CI 0.015, 0.097), but not in cold settings (Males: ß = -0.055, CI -0.178, 0.067; Females: ß = 0.104, CI -0.129, 0.377) (**Figure 4, Table 1A**). Conversely, in hot settings BMI-residual was negatively correlated with temperature volatility in males (ß = -0.373, CI -0.785, 0.038) but not females (ß = -0.084, CI –0.579, 0.411). In cold settings, temperature volatility was positively associated with BMI-residual, but more strongly in males (ß = 0.686, CI 0.248, 0.125) than females (ß = 0.408, CI -0.178, 0.995). Again, these results were broadly similar when the analysis was restricted to location-averaged data; however the correlations were weaker, as were the interaction terms of climate and BMI by setting (**Table 1B**).

Hypothesis 2: subcutaneous adiposity associations

Ln Triceps skinfold was negatively associated with average precipitation in females (ß = -0.037, CI -0.068, -0.005) but not males (ß = -0.009, CI -0.027, 0.017) in cold settings, but showed no such association in hot settings (Males: ß = 0.001, CI -0.005, 0.007; Females: ß = -0.003, CI -0.012, 0.006) (**Figure 5, Table 1A**). The contrast between settings was significant in females. Conversely, Ln Triceps was positively associated with temperature volatility in both sexes in both cold (Males: ß = 0.076, CI 0.016, 0.136; Females: 0.160, 0.087, 0.233) and hot settings (Males: ß = 0.118, CI 0.063, 0.173; Females: 0.216, 0.126, 0.306). These findings were essentially unchanged when the analysis was restricted to location-averaged data (**Table 1B**).

Ln Subscapular skinfold was negatively associated with average precipitation in cold settings in females (ß = -0.031, CI -0.058, -0.003) but not males (ß = -0.003, CI -0.019, 0.012), but positively associated with average precipitation in hot settings in both sexes (Males: ß = 0.008, CI 0.003, 0.014; Females: ß = 0.009, CI 0.000, 0.017) (**Figure 6, Table 1A**). Conversely, Ln Subscapular skinfold was positively associated with temperature volatility in hot settings (Males: ß = 0.076, CI 0.020, 0.132; Females: ß =0.117, 0.020, 0.214), and also in cold settings though in males the relationship was weaker (Males: ß = 0.045, CI -0.008, 0.098; Females: ß =0.116, 0.046, 0.185). These findings were similar when the analysis was restricted to location-averaged data, though some of the correlations and interactions were weaker (**Table 1B**).

Taking advantage of the large sample size for males in hot settings, we illustrate the contrasts between Hypotheses 1 and 2 in **Figure 7** by plotting standardised data for both BMI-residual and triceps against the two climate predictors. BMI residual increased with average precipitation, whereas triceps showed no significant association (*p* for interaction = 0.06). Likewise, BMI-residual decreased in association with temperature volatility, whereas triceps skinfold increased (*p* for interaction = 0.001).

Hypothesis 3: sex differences

We tested formally for sex differences in the associations of climate predictors with body composition outcomes.

Using all available data, the association of annual average precipitation with lean mass differed significantly between the sexes in cold settings (interaction coefficient -0.217, 95%CI -0.400, 0.034, *p*=0.021) but not in hot settings (interaction coefficient 0.022, 95%CI -0.034, 0.78, *p*=0.4). The association of annual average precipitation with triceps and subscapular skinfolds likewise differed significantly between the sexes in cold settings (Ln triceps: interaction coefficient 0.042, 95%CI 0.013, 0.071, *p*=0.006; Ln Subscapular: interaction coefficient 0.028, 95%CI 0.001, 0.055, *p*=0.044) but not in hot settings (Ln triceps: interaction coefficient 0.007, 95%CI -0.003, 0.018, *p*=0.16; Ln Subscapular: interaction coefficient 0.001, 95%CI -0.009, 0.010, *p*=0.8). When restricted to the populations where matching data were available for both sexes, the interaction in cold settings was similar in magnitude for lean mass (interaction coefficient -0.217, 95%CI -0.400, 0.034), but reduced in magnitude for both Ln triceps (interaction coefficient 0.023, 95%CI -0.001, 0.056) and Ln subscapular (interaction coefficient 0.024, 95%CI -0.006, 0.054) and none of these interactions remained significant.

Using all available data, the association of temperature volatility with lean mass did not differ by sex in either setting (*p>0.5*). For triceps skinfold, there was weak evidence of a sex-difference for Ln triceps in both settings (cold: interaction coefficient -0.091, 95%CI -0.201, 0.019, *p*=0.102; hot: interaction coefficient -0.092, 95%CI -0.095, 0.011, *p*=0.081); equivalent coefficients for Ln subscapular were smaller and *p*>0.15. Again, however, these interactions for skinfolds were weaker in magnitude and non-significant when restricted to the populations where matching data were available for both sexes.

Discussion

Eco-geographical associations of different components of human morphology with annual average temperature were first reported in the 1950s (Roberts, 1953; Schreider, 1950), and have been replicated subsequently (Crognier, 1981; Hiernaux & Froment 1976), though they are starting to weaken under the stress of global nutrition transition (Katzmarzyk & Leonard, 1998). These relationships are then widely used to interpret morphological variability among fossil hominins (Ruff, 2002; Weaver, 2009). To break new ground, we have diverged from a purely thermodynamic approach to develop a more comprehensive bio-energetic framework, which can be linked with evolutionary life history theory (Hill, 1993). This allows us to address several new questions: whether human body composition varies in association with markers of ecological productivity such as annual average precipitation, and furthermore whether lean mass and adiposity have adapted as forms of 'risk management', responding to components of climate that are not stable.

Our study produced several key findings. Most broadly, independent of annual average temperature, we found that both mean precipitation and temperature volatility explain variability in male and female body composition, highlighting the importance of climatic factors other than stable thermal conditions, the primary focus of previous analyses. However, consistent with our hypotheses, these associations varied between cold versus hot settings, differed between proxies for fat and lean mass, and showed some differences between the sexes.

We found that BMI increased in association with precipitation in hot settings, but not in cold settings. This indicates that greater precipitation may translate into greater availability of food in hot settings, allowing more tissue accretion. In cold settings, in contrast, BMI increased in association with greater temperature volatility, suggesting that in such environments tissue accretion represents more of a defence against uncertainty.

Looking in more detail, in hot settings both sexes accreted both lean and fat tissue in association with greater precipitation, indicating that given more resources, energy was invested both in costly functional tissues and also in protective energy reserves. A surprising result was that the association of precipitation with triceps skinfold was not significant in females, despite peripheral adiposity being important for funding reproduction. However, it is important to note that the primary maternal tissue associated with offspring birth weight is in fact lean mass, not adipose tissue, which is associated more strongly with lactation (Wells 2018). The findings for temperature volatility were broadly as predicted in hot settings: both sexes had greater adiposity in more volatile environments, while males had lower levels of costly lean mass, though this was not replicated in females.

In cold settings, the primary association of temperature volatility was with skinfolds, indicating greater energy reserves in more volatile environments. It is less clear why BMI-residual also increased with temperature volatility in both sexes in this setting. The precipitation associations were also less easy to interpret: increasing precipitation was not significantly associated with lean mass in either sex, and was inversely associated with skinfolds in females but not males. Thus, there was little indication that precipitation was a predictor of resource availability in cold settings.

Overall, therefore, our hypotheses (1) that lean tissue is expensive and increases when ecological resources permit, and (2) that fat represents insurance against volatile environments but can also be gained in resource-rich settings, were supported in hot settings, but the only prediction supported in cold settings was the association of adiposity with temperature volatility. We were able to demonstrate most clearly the contrasting associations of lean and fat tissue with both climate predictors in males in hot settings, while may partly reflect the large sample size available for males.

Our third hypothesis, that associations of body composition traits and climate would differ between the sexes, also received weak support. Surprisingly, the sex differences were primarily detected in cold settings, and were largely driven by females showing stronger associations with climate predictors than males. However, only the sex-difference in the association of average precipitation and BMI-residual showed a similar magnitude of effect when analysis was restricted to the populations with data from both sexes, and none of the interactions remained significant in the reduced sample. This may reflect both lower statistical power, but also a reduced range of geographical representation. Further work on larger sample sizes from a wider geographical range is therefore needed to confirm or refute these sex differences.

Geographical variability in average precipitation is well-established, and our finding that it predicts variability in human morphology is consistent with recent work on non-human species, indicating that precipitation drives global variation in natural selection (Siepielski et al., 2017). However, there is also increasing interest in the implications of climate volatility as a selective pressure. Temperature volatility can be attributed to several climate cycles that affect different geographical regions. The best-known, the El Niño Southern Oscillation (ENSO) cycle, is associated with extreme droughts or floods, with antagonistic effects across different regions (Couper-Johnston, 2000). These stresses are irregular and unpredictable, but nevertheless occur sufficiently frequently to represent a major selective pressure for many organisms (Couper-Johnston, 2000). Other cycles include the Indian Ocean Dipole (Saji & Yamagata, 2003) and Atlantic and Pacific Decadal Oscillations (Meehl et al., 2009). Collectively, such cycles influence many species through perturbations of population dynamics, geographic distribution, food supply, predator-prey dynamics and disease exposures (Couper-Johnston, 2000; Ottersen et al., 2001).

Our analyses suggest that such selective pressures may extend to humans, and our findings have relevance to contemporary concerns over climate change, which may impact plastic components of body composition in similar ways. For example, short-term shocks such as droughts reduce child growth in sub-Saharan Africa (Hoddinott & Kinsey, 2001), while children born around the time of ENSO floods in northwest Peru had reduced height and lean mass compared to unexposed peers, but similar fat mass (Danysh et al., 2014). In less extreme circumstances, however, precipitation before and after birth was positively associated with childhood growth in Uganda and Nepal (Shively, 2017). Given these short-term responses, it is very plausible that persistent geographical variability in climate might have driven genetic adaptation in human body composition.

Substantial work has linked climatic volatility with infectious disease epidemics (Rogers 1925), often due to changes in the viable geographic range of disease vectors such as insects or rodents (World Health Organization, 2005). Beyond its sensitivity to food supply, adipose tissue is predicted to respond to the burden of infections as it provides both energy and metabolic precursors for immune function (Demas et al., 2003; Lord, 2002). This may explain the association of both skinfolds with temperature volatility in both sexes in both settings.

Extrapolation to past populations

Our findings relate to populations investigated within the last half-century, and we must consider the extent to which earlier human populations might have demonstrated similar associations. The Holocene climate of the last 10,000 years has been relatively stable (Richerson et al., 2001), and major climate change within large geographical regions is unlikely, though the ecosystems of areas such as the north of Africa have changed markedly within the last few thousand years. Prior to the Holocene, glaciation cycles are known to have generated larger-scale climate change, though again major regional contrasts appear to have persisted over these time-frames (Bartlein et al., 2011; Brown et al., 2018). Therefore, it is reasonable to assume that climate stresses have played an important role in shaping contemporary geographic variability in human morphology, though whether through genetic adaptation or plastic responses remains unclear. Moreover, any association between past climate and body composition may have been rendered less visible by subsequent migration patterns.

However, despite our focus on small-scale societies, the more northern populations in our sample may have benefited from long-term cultural or technological means for the mitigation of climate stress. More generally, by compiling our database from heterogeneous publications, we were unable to address systematically factors such as illness or mortality risk, reproductive patterns, exposure to famine or the influence of market economies, or other stresses that might contribute to variability in body size and composition. Nor could we address genetic variability in our outcomes that might have emerged under selective pressures unrelated to climate. Given the unique cultural capabilities that characterise modern humans, the associations we have described between climate and body composition may not generalise to non-human species.

Strengths and limitations

Our analyses have several strengths. We tested two components of climate that traditionally have received negligible attention in eco-geographical analysis of human morphology. This includes a novel index of inter-annual temperature volatility that allowed us to explore ecological instability. This allowed us to extend the theoretical framework beyond stable thermal stresses, the dominant paradigm in earlier research. We also stratified our analyses between hot and cold settings, to address the possibility that exposures such as average precipitation might not have similar associations with human phenotype in all thermal conditions. Finally, our database covered a wide range of geographical locations in each sex.

However, our analyses also had some limitation. First, our skinfold data were obtained from the upper body, and therefore do not incorporate information on subcutaneous fat depots from the gluteofemoral region, which is particularly important for reproduction in females (Rebuffe-Scrive et al., 1985). Second, our climate variables are modelled for the period 1901-2013, whereas our human data were collected over the period 1969 to 2010. However, any climate change over the last century is unlikely to have introduced bias into our analyses, and we controlled where appropriate for variability in the date of the individual studies. Due to the relatively small sample size and its patchy geographical distribution, we did not control for shared ancestry, which is likely to contribute to these eco-geographical associations. Further work on a larger sample size could address this issue. Third, we assumed that greater rainfall would broadly increase ecological productivity, and hence increase the supply of food, thus allowing greater accretion of lean tissue. However, there are other possible effects of greater rainfall, including an increased prevalence of parasites and pathogens (Couper-Johnston et al., 2000), or an increased level of local competition among humans due to the greater resource availability. Therefore even if climate has tracked over long periods, the association of climate with human body composition might have changed over time.

Nevertheless, while the magnitudes of effect that we report here may be unique to contemporary ecological and societal conditions, the directions of effect are likely to have broader relevance beyond contemporary humans, and are consistent with the predictions of life history theory. Moreover, as discussed in the introduction, many ecological factors may best be considered as mediating the associations of climate with human phenotype. For example, a recent report of a thrifty gene in Polynesian populations (Minster et al., 2016) may ultimately indicate adaptation to of ecological volatility in their environment, though it might alternatively relate to human-generated stresses associated with regular migrations between islands.

Conclusions

Our observations that human body composition variability is associated with markers of ecological productivity and volatility are broadly consistent with life history predictions, though more so in hot than cold settings. Considering lean mass as an 'expensive' tissue, we found in hot settings that it increases in association with a marker of overall food supply, and decreases in association with a proxy for food insecurity. Conversely, levels of body fat increase in association with temperature volatility, an established driver of infectious disease risk. However, in cold settings, equivalent associations were only partially consistent with our hypotheses, and they also showed weak evidence of differences between the sexes. Collectively, our results suggest that associations between human body composition and climate are more complex than those predicted by Bergmann's rule. Under contemporary nutrition transition, these population differences in body composition have importance for differential susceptibility to chronic non-communicable diseases such as stroke, diabetes and cardiovascular disease (Dulloo et al., 2010; Wells, 2016).

Authors' contributions

The study was conceived and directed by JCW and MAS. The database was compiled by JCW and MKS. The climate index data and all publication quality manuscript figures were generated by MAS and ASL. The statistical analysis was conducted by JCW and MCB. JCW wrote the first manuscript draft. All authors contributed to revising the manuscript.

Competing interests

We declare that we have no competing interests.

Funding

The study received funding from the UCL Grand Challenges programme. This research benefited from funding awarded to the NIHR Great Ormond Street Hospital Biomedical Research Centre. The UCL Institute of Child Health receives a proportion of funding from the Department of Health's National Institute for Health Research Biomedical Research Centre funding scheme. Any views expressed are those of the authors and not necessarily those of the funders.

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Table 1. Strength and significance of correlations between climate indices and body composition measures in each sex, stratified by hot and cold settings.

	Males					Females				
	Below 20°C (*n*=38)		Above 20°C (*n*=95)		*P* for interaction	Below 20°C (*n*=24)		Above 20°C (*n*=81)		*P* for interaction
	r	*p*	*r*	*p*		*r*	*p*	*r*	*p*	
(A) ALL LOCATIONS										
BMI										
Average annual precipitation (mm)	-0.17	0.3	0.59	<0.0001	0.001	-0.14	0.5	0.33	0.003	0.044
Temperature volatility residual (°C)	0.57	<0.0001	-0.03	0.7	0.033	0.69	<0.0001	0.21	0.063	0.4
BMI-residual										
Average annual precipitation (mm)	-0.16	0.3	0.51	<0.0001	0.020	0.21	0.3	0.30	0.009	0.6
Temperature volatility residual (°C)	0.48	0.003	-0.22	0.035	0.001	0.31	0.1	-0.04	0.7	0.2
Triceps										
Average annual precipitation (mm)	-0.16	0.3	0.03	0.7	0.2	-0.49	0.025	-0.08	0.5	0.031
Temperature volatility residual (°C)	0.40	0.015	0.41	<0.0001	0.3	0.72	<0.0001	0.48	<0.0001	0.3
Subscapular										
Average annual precipitation (mm)	-0.07	0.6	0.29	0.005	0.049	-0.47	0.031	0.23	0.045	0.027
Temperature volatility residual (°C)	0.28	0.09	0.28	0.008	0.4	0.61	0.002	0.26	0.018	0.8
(B) LOCATION-AVERAGED										
BMI										
Average annual precipitation (mm)	0.19	0.4	0.57	<0.0001	0.2	-0.17	0.5	0.30	0.032	0.047
Temperature volatility residual (°C)	0.43	0.044	-0.04	0.7	0.2	0.63	0.005	0.28	0.041	0.9
BMI-residual										
Average annual precipitation (mm)	0.07	0.7	0.44	0.001	0.6	0.23	0.3	0.20	0.1	0.4
Temperature volatility residual (°C)	0.31	0.16	-0.17	0.2	0.1	0.18	0.4	0.06	0.6	0.8
Triceps										
Average annual precipitation (mm)	-0.03	0.8	0.04	0.7	0.7	-0.53	0.027	0.03	0.8	0.018
Temperature volatility residual (°C)	0.44	0.04	0.31	0.021	0.9	0.73	0.001	0.45	0.001	0.6

Legends for illustration

Figure 1. Schematic diagram illustrating the associations tested in this analysis. We explored potential associations of four markers of body composition with two markers of climate, adjusting for average population age and study date. (a) Initial analyses tested for crude associations in each sex, stratified by hot or cold setting. (b) Within each sex, we then tested for interactions of such associations with hot/cold setting, while within each setting, we then tested for interactions of such associations with sex.

Figure 2. Global maps displaying ***(a)*** annual average temperature, ***(b)*** annual average precipitation, ***(c)*** inter-annual temperature volatility, and ***(d)*** the location of the human samples.

Figure 3. Associations of BMI with annual average precipitation and with inter-annual temperature volatility stratified by hot (red) and cold (blue) population settings. ***(a)*** BMI versus annual average precipitation for males; ***(b)*** BMI versus annual average precipitation for females; ***(c)*** BMI versus inter-annual temperature volatility for males; ***(d)*** BMI versus inter-annual temperature volatility for females.

Figure 4. Associations of BMI-residual with annual average precipitation and with inter-annual temperature volatility stratified by hot (red) and cold (blue) population settings. ***(a)*** BMI-residual versus annual average precipitation for males; ***(b)*** BMI-residual versus annual average precipitation for females; ***(c)*** BMI-residual versus inter-annual temperature volatility for males; ***(d)*** BMI-residual versus inter-annual temperature volatility for females.

Figure 5. Associations of Triceps skinfold with annual average precipitation and with inter-annual temperature volatility stratified by hot (red) and cold (blue) population settings. ***(a)*** Triceps skinfold versus annual average precipitation for males; ***(b)*** Triceps skinfold versus annual average precipitation for females; ***(c)*** Triceps skinfold versus inter-annual temperature volatility for males; ***(d)*** Triceps skinfold versus inter-annual temperature volatility for females.

Figure 6. Associations of Subscapular skinfold with annual average precipitation and with inter-annual temperature volatility stratified by hot (red) and cold (blue) population settings. ***(a)*** Subscapular skinfold versus annual average precipitation for males; ***(b)*** Subscapular skinfold versus annual average

precipitation for females; ***(c)*** Subscapular skinfold versus inter-annual temperature volatility for males; ***(d)*** Subscapular skinfold versus inter-annual temperature volatility for females.

Figure 7. Associations of BMI-residual (green circles) and sample-standardised Triceps z-score (blue circles) with ***(a)*** annual average precipitation and ***(b)*** inter-annual temperature volatility in the sample of males in hot settings. The two tissues show different slopes in association with precipitation (p=0.06) and temperature volatility (p=0.001).

Figure 1

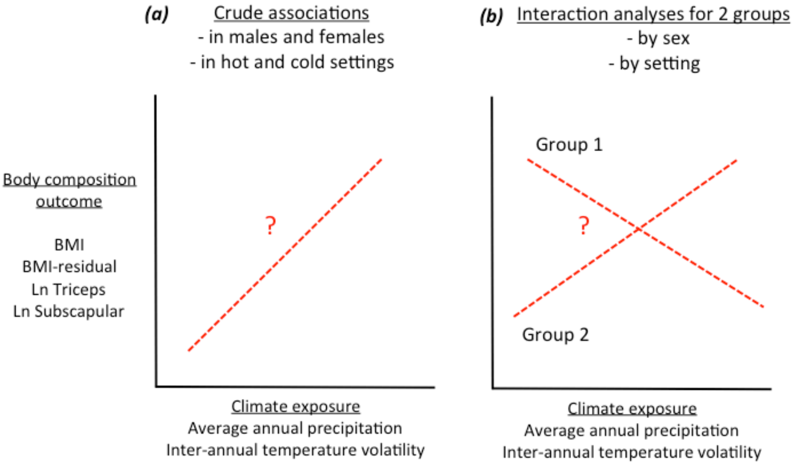
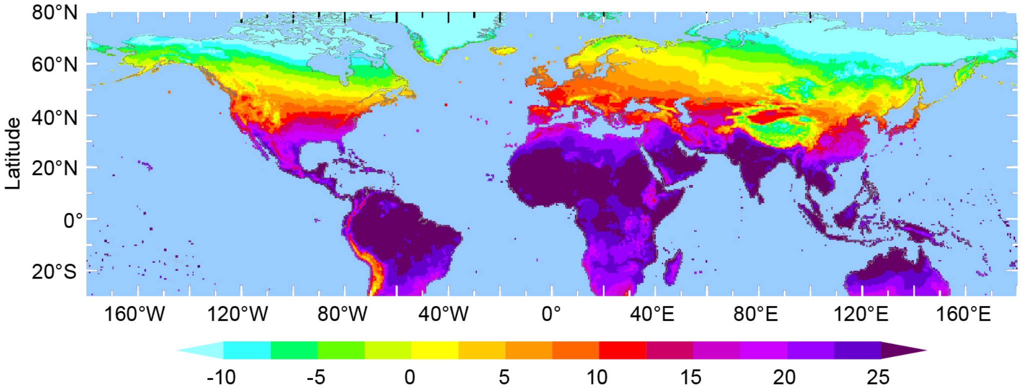
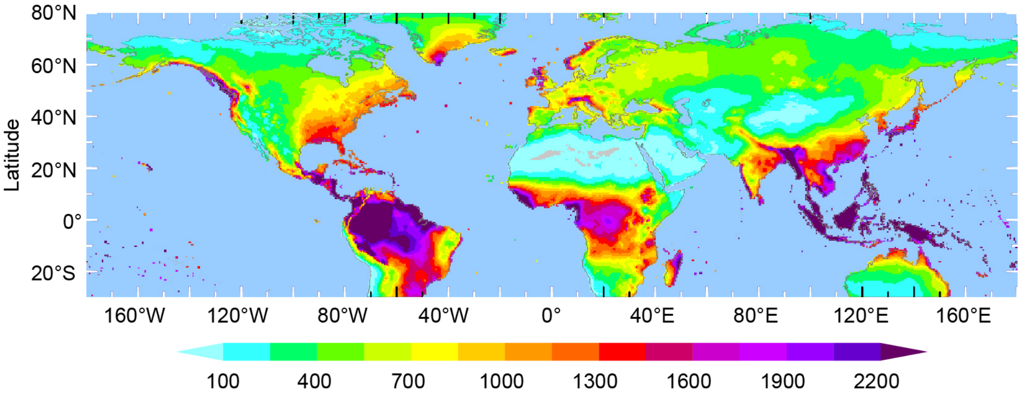

(a)
Crude associations
- in males and females
- in hot and cold settings
(b)
Interaction analyses for 2 groups
- by sex
- by setting
Body composition outcome
BMI
BMI-residual
Ln Triceps
Ln Subscapular
?
Group 1
?
Group 2
Climate exposure
Average annual precipitation
Inter-annual temperature volatility
Climate exposure
Average annual precipitation
Inter-annual temperature volatility

Figure 2

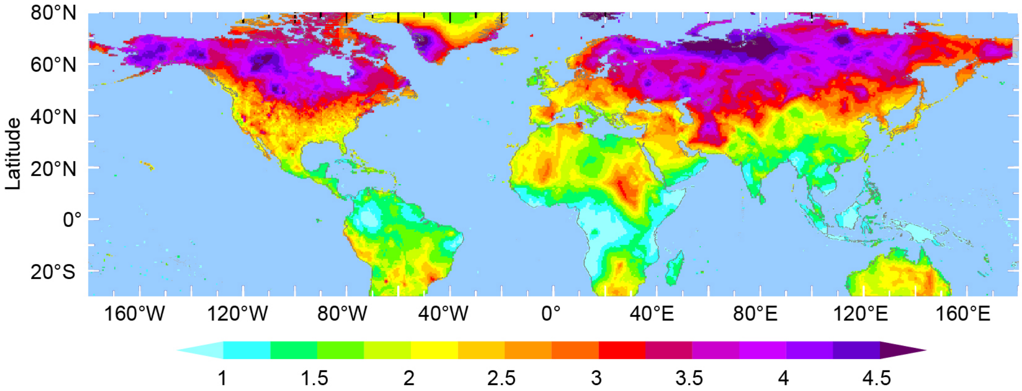
(a) **Annual average temperature (°C)**



(b) **Annual average precipitation (mm)**



(c) **Annual temperature 95th - 5th percentile (°C)**



(d) **Population locations**

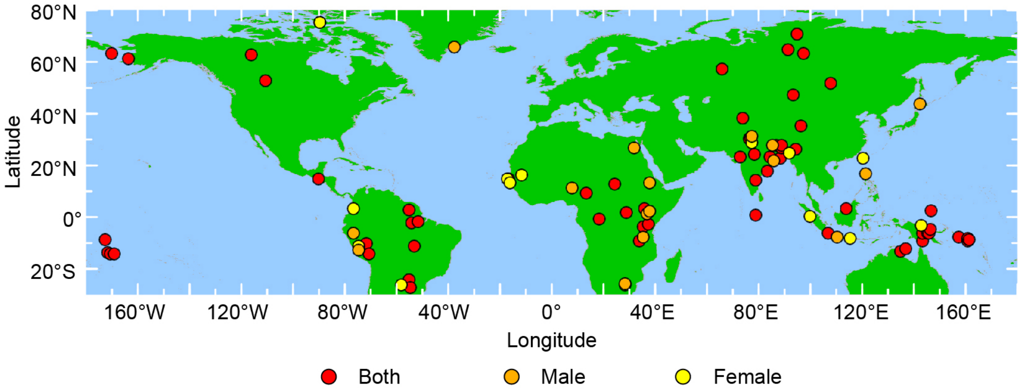


Figure 3

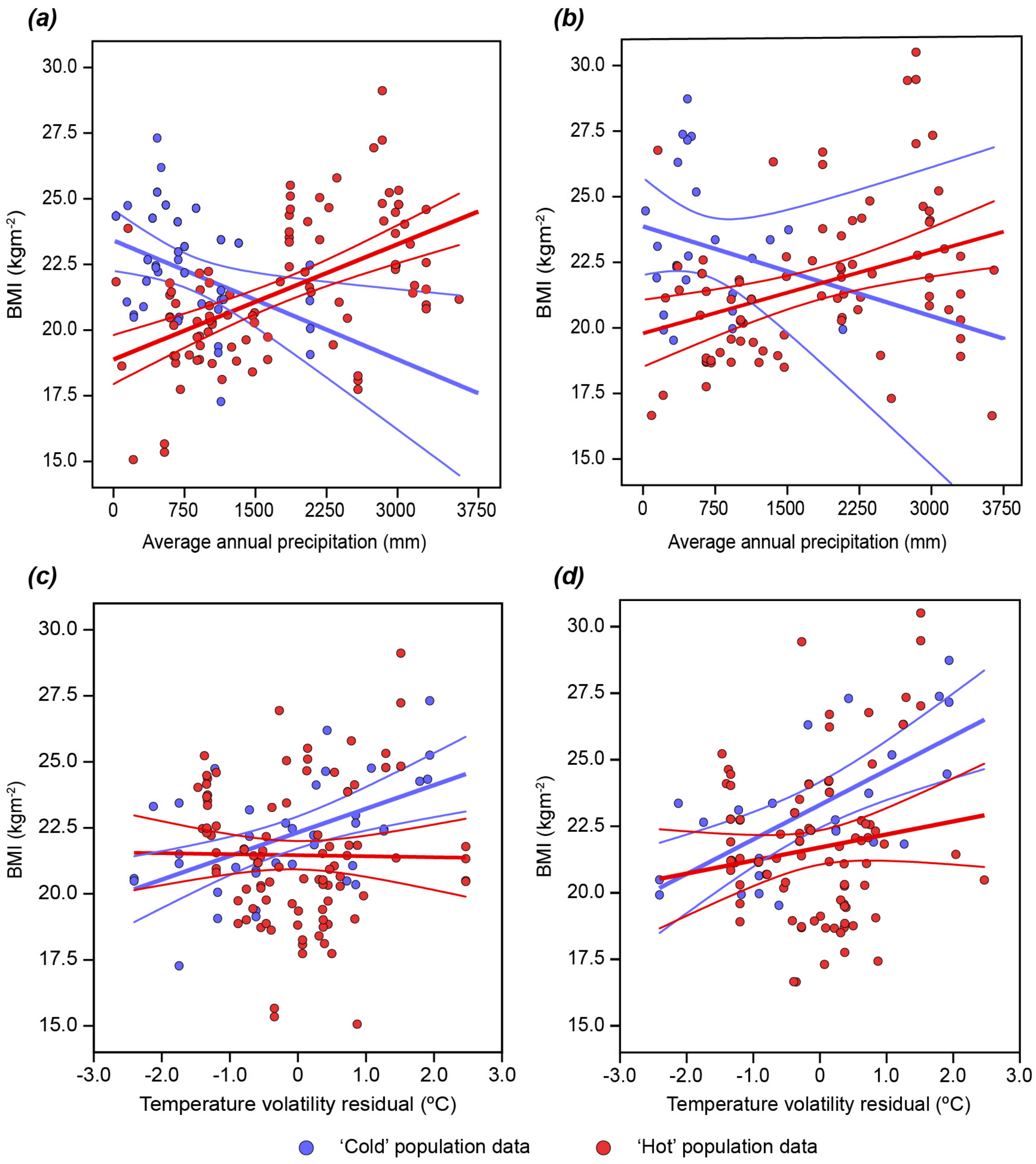

(a)
(b)
(c)
(d)
BMI (kgm^{-2})
30.0
27.5
25.0
22.5
20.0
17.5
15.0
0
750
1500
2250
3000
3750
Average annual precipitation (mm)
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
Temperature volatility residual (ºC)
‘Cold’ population data
‘Hot’ population data

Figure 4

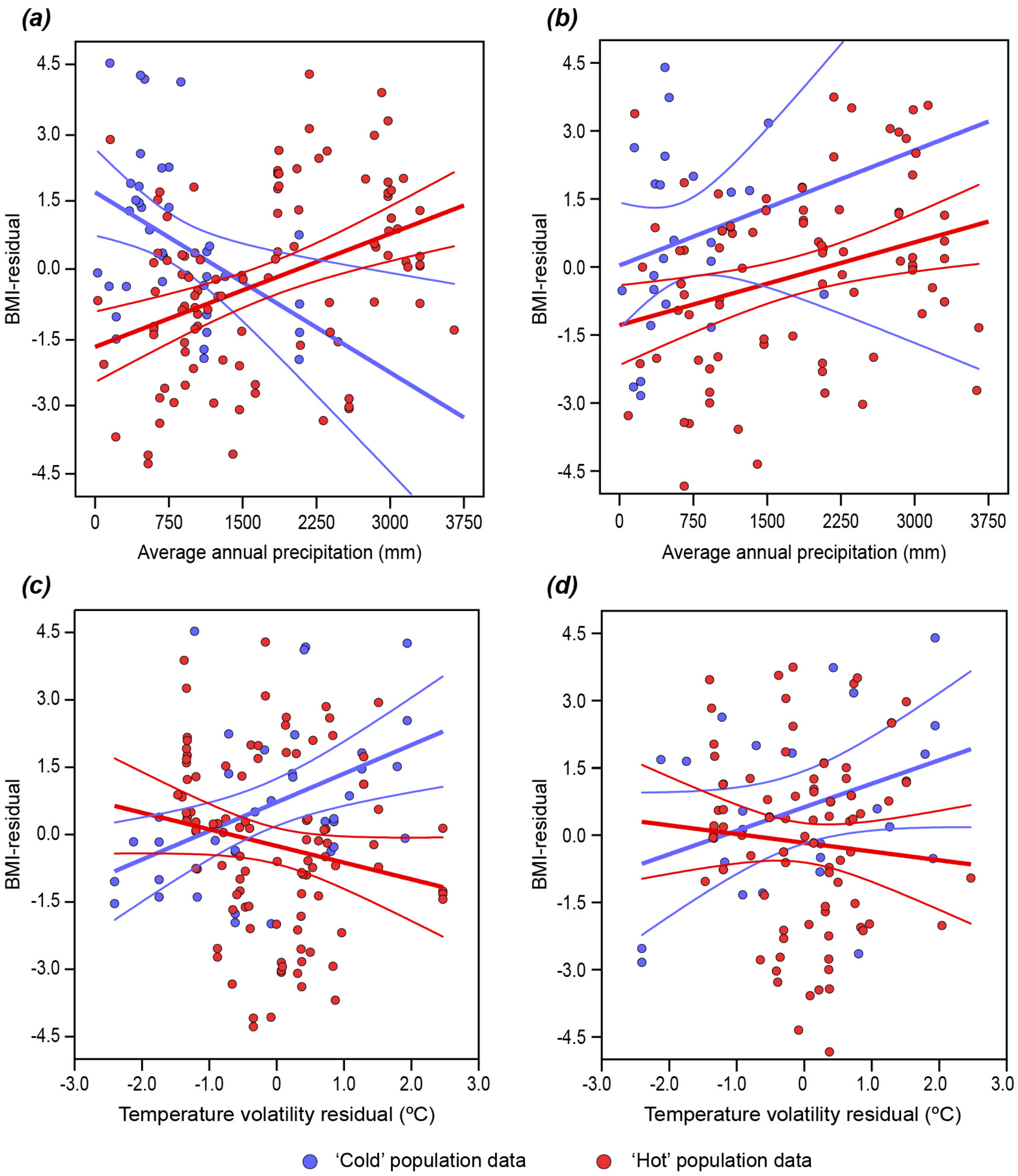

(a)
(b)
(c)
(d)
BMI-residual
4.5
3.0
1.5
0.0
-1.5
-3.0
-4.5
0
750
1500
2250
3000
3750
Average annual precipitation (mm)
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
Temperature volatility residual (°C)
● 'Cold' population data
● 'Hot' population data

Figure 5

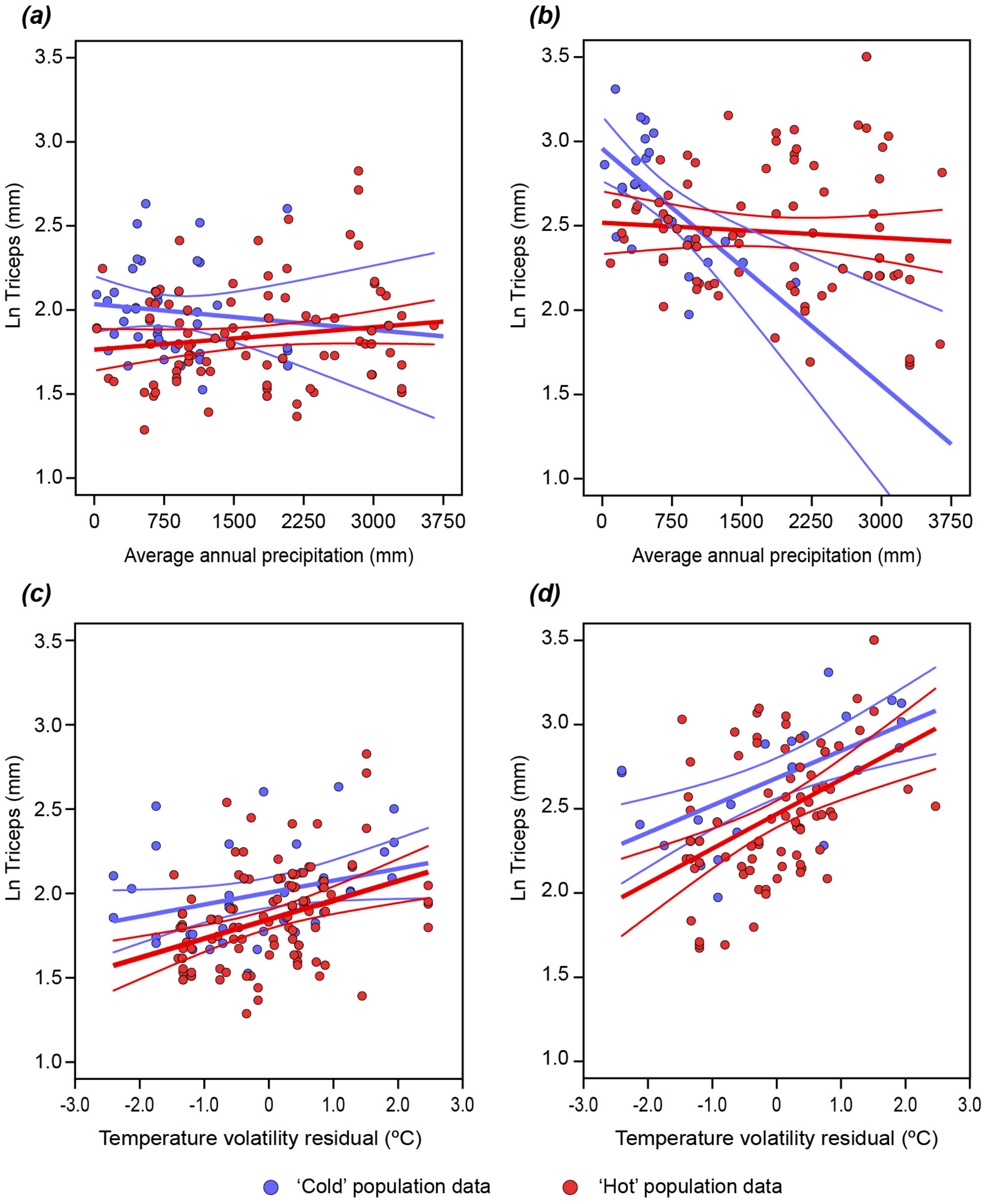

(a)
(b)
(c)
(d)
Ln Triceps (mm)
3.5
3.0
2.5
2.0
1.5
1.0
0
750
1500
2250
3000
3750
Average annual precipitation (mm)
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
Temperature volatility residual (ºC)
● 'Cold' population data
● 'Hot' population data

Figure 6

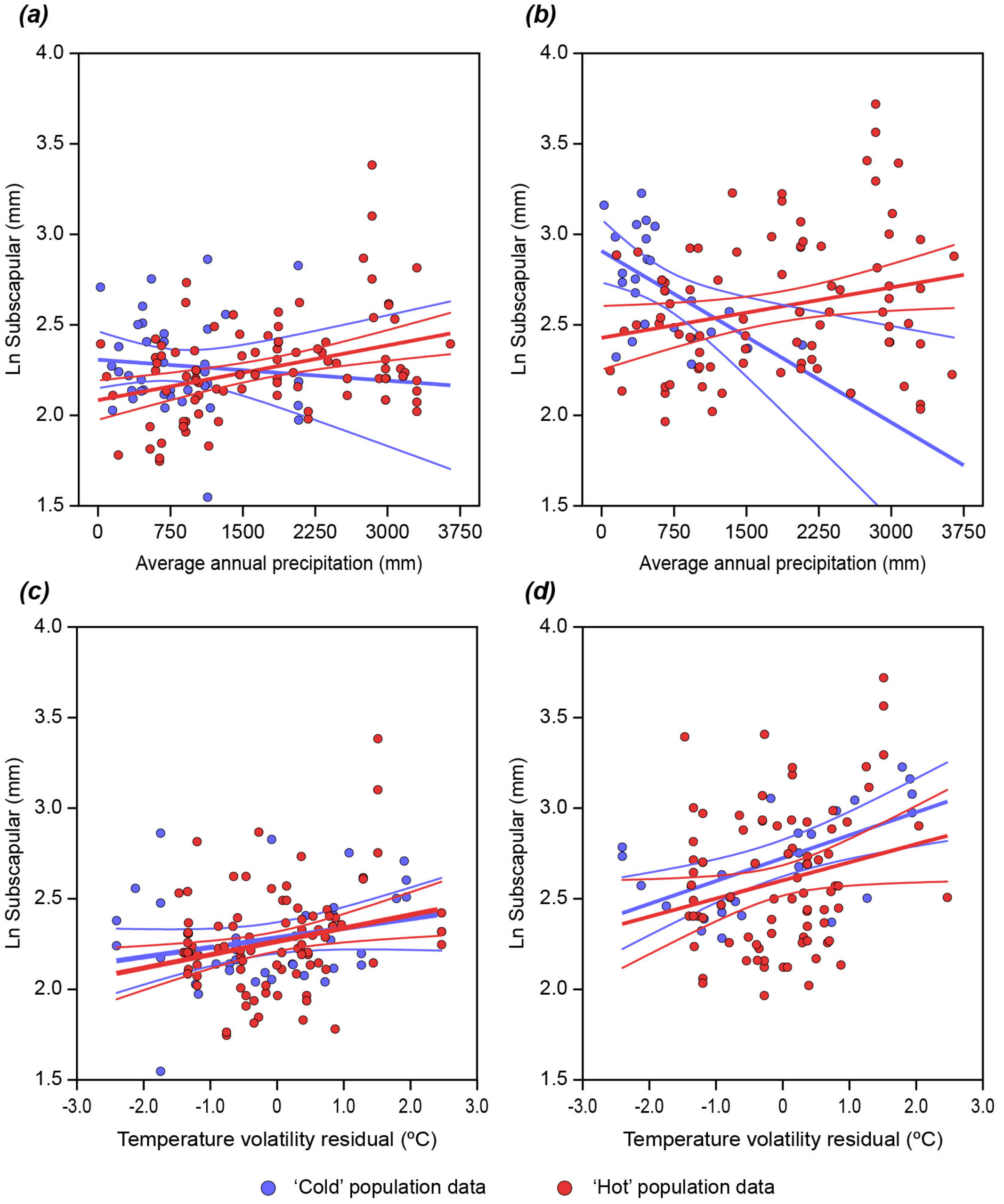
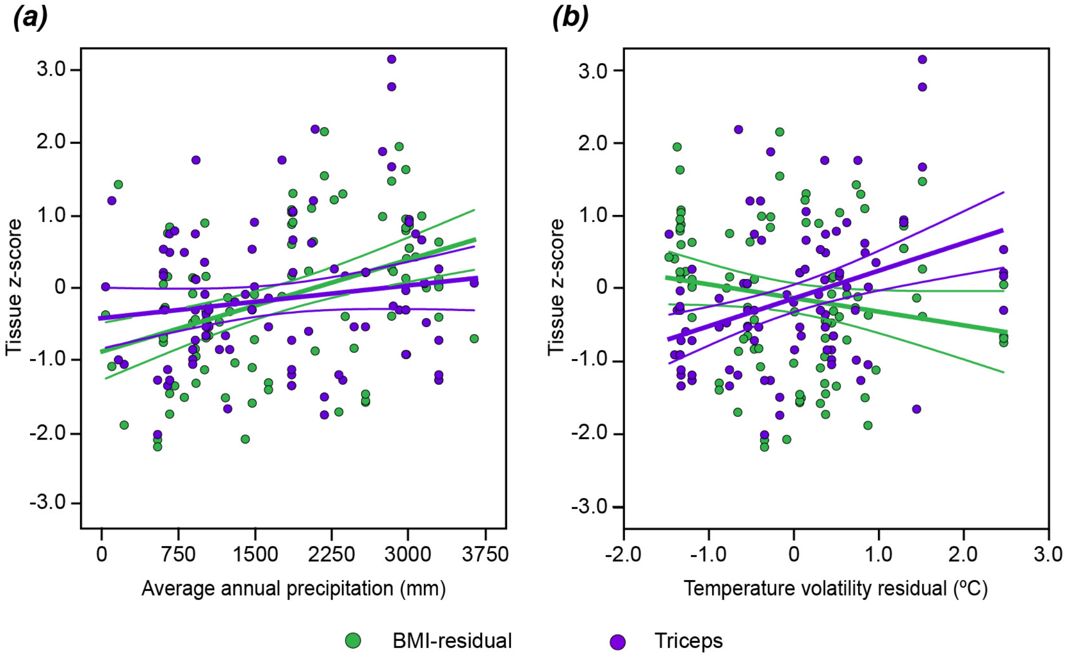

(a)
(b)
(c)
(d)
Ln Subscapular (mm)
4.0
3.5
3.0
2.5
2.0
1.5
0
750
1500
2250
3000
3750
Average annual precipitation (mm)
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
Temperature volatility residual (ºC)
'Cold' population data
'Hot' population data

Figure 7


(a)
(b)
3.0
2.0
1.0
0
-1.0
-2.0
-3.0
Tissue z-score
0
750
1500
2250
3000
3750
Average annual precipitation (mm)
-2.0
-1.0
0
1.0
2.0
3.0
Temperature volatility residual (ºC)
BMI-residual
Triceps