POSTCRANIAL EVOLUTION IN HUMANS WITH RESPECT TO TRAIT COVARIANCE AND ECOGEOGRAPHY

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ABSTRACT

Human postcranial morphology varies with climate and geography (ecogeography), a pattern that has long been associated with thermoregulatory adaptation. The thermoregulatory imperative model of postcranial evolution suggests that groups living in colder climates have evolved stouter bodies to reduce their surface area/volume ratio, while the opposite is true for groups in the tropics. Recent applications of quantitative genetics methods to human postcranial evolution have allowed researchers to move beyond testing whether limb lengths and measures of body size adhere to ecogeographic expectations, and begin disentangling the natural selection from neutral evolutionary processes.

However, these have continued to model postcranial traits as if they were evolving independently. By examining human evolution on a trait-by-trait basis, researchers fail to account for evolution due to changes in correlated morphology. In addition, while these studies are able to identify the direction and magnitude of selective effects, they have yet to identify the source of that selective pressure, often relying on latitude as a problematic proxy for "climate." In this dissertation, I use quantitative genetic methods to elucidate the role of trait covariation in the evolution of the human postcranium, as well as explore the variables that drive directional selection. Using a large, globally-dispersed sample of human skeletal material, in addition to microsatellite and temperature data, I estimate the selection gradients driving among-group differentiation, compare indices of evolvability across regions, and examine the environmental variables influencing postcranial evolution.

Results indicate that 1. trait covariation plays an important role in shaping evolutionary response, 2. human groups may demonstrate emergent differentiation in evolvability across regions , and 3. the selective pressures acting on the postcranium are likely synergistic, complicating simplistic interpretations of the thermoregulatory imperative model. These findings have implications for our understanding of modern human variation, suggesting the need to develop multivariate models in which the reciprocal effects of multiple environmental variables can be examined on the covariance structure of multiple traits. Results also add to the growing evidence that population-specific trait covariance prevents evolutionary interpretations founded on modern humans to be meaningfully translated to ancient hominin lineages.

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CHAPTER I

INTRODUCTION, BACKGROUND, AND RESEARCH QUESTIONS

Introduction

Modern humans and their ancestors express variation in body form that corresponds with geography and climate (ecogeography) (Ruff 1994), but only in the last decade have studies used quantitative genetic methods to disentangle the evolutionary processes responsible for shaping this morphological variation (Madrigal & Willoughby 2010, Betti et al. 2013, Roseman & Auerbach 2015, Savell et al. 2016). In the foundational literature of ecogeographic variation in modern humans, natural selection via climactic adaptation has consistently been offered as the primary evolutionary factor underlying the observed patterns (Roberts 1953, Roberts 1978, Trinkaus 1981, Ruff 1994, Holliday 1997, Holliday & Ruff 2001). However, this interpretation is complicated by the high correspondence between patterns of climatic variation across geography and the pattern of human dispersals out of Africa (Roseman & Auerbach 2015). Quantitative genetic methods provide an avenue for distinguishing trait responses to natural selection from the effects of population history. Thus, the recent focus on identifying the evolutionary processes shaping phenotypic patterns using quantitative genetic methods marks an important shift in the study of human ecogeographic variation.

Despite the availability of this analytical approach, the vast majority of human body form and limb evolution research examines traits individually, failing to take trait covariation into consideration. By examining human postcranial variation on a trait-by-trait basis, researchers consistently (and implicitly) model evolutionary change as though each trait evolves independently of the rest of the organism. Yet, traits belonging to a single organism necessarily covary, and without explicitly examining the pattern and magnitude of this covariance, the amount of evolutionary independence in a trait cannot be assumed. Morphology is, instead, shaped by both the *direct* response of a trait to evolutionary forces, as well as by the *indirect* responses of correlated traits (Lande 1979, Lande & Arnold 1983, Arnold 1983).

In this dissertation, I therefore focus on understanding how variation in certain key elements of human body form – namely limb segment length and measures of body size – was shaped by evolutionary forces from within a larger framework of trait covariance. I examine which evolutionary processes have driven phenotypic change in body form across ecogeographic regions and explore the subsequent implications on our understanding of modern human and ancient hominin thermoregulation. Toward these general goals, I investigate three major questions:

1) How does covariance among traits affect morphological responses to evolutionary forces? (Chapter II)
2) How does population structure affect the ability of different human groups to respond to evolutionary forces? (Chapter III)
3) What role does temperature (as opposed to latitude) play in shaping evolutionary responses and variation in body shape and proportions? (Chapter IV)

These questions are addressed in the three subsequent chapters, which are manuscripts comprising the original research and analysis component of this dissertation. While these chapters provide enough background information to establish the context for each examined question, it is not possible to include a detailed review of the relevant research history for either the study of human ecogeographic variation or the theoretical framework of quantitative genetic and evolutionary modeling methods used in this dissertation. As such, a more comprehensive discussion of the relevant literature is provided here. In the remainder of this chapter, I briefly review the history of research on human body form variation with respect to ecogeographic models, thermoregulation, and the application of more recent quantitative genetic approaches. A preview of the methods used in this dissertation is provided at the end of the chapter.

Adaptationism

Before providing a detailed background on the ecogeographic distribution of biological variation and the quantitative genetic methods used to examine it, a brief note about adaptationism is required. Adaptation, as a process, is defined as the development of a certain phenotype or set of phenotypic characteristics, via natural selection, that improves the "fit" between an organism and its environment (see "Evolutionary Processes," below). Adaptationism, as defined by Gould and Lewontin (1979), is the tendency for evolutionary biologists and biological anthropologists to assume that phenotypic, behavioral, or genetic traits are the result of adaptive selection, to the exclusion of other evolutionary processes. As such, the neutral model of the adaptationist approach is that change results from environmental selective pressures motivating a given trait towards ever-improved adaptation, and that the only "brake upon perfection" are the "trade-offs among competing selective demands" (Gould & Lewontin 1979, p 147).

The adaptationist approach to the study of evolutionary trends is problematic because it ignores the nuanced interaction of microevolutionary forces that give rise to various phenotypic traits. Though adaptationist studies often acknowledge the presence of non-selective evolutionary processes, this is generally to either claim that the effects of other processes are not large enough to be influential, or to mention the possibility of alternate evolutionary influences without providing a direct exploration of those possibilities. Most importantly, adaptationism is not designed for true scientific hypothesis testing – proposed theories frequently are not or cannot be directly assessed. It is when new approaches to understanding the processes behind given patterns are utilized – as provided by quantitative genetic methods and the development of mathematical evolutionary models – that more scientific interpretations of biological observation can be evaluated.

Ecogeographic Rules

The relationship between ecogeography and morphological variation within and between taxa has been of interest for naturalists and evolutionary biologists for over 150 years.

Ecogeographic variation in body size and extremity length has traditionally been interpreted as evidence for climactic adaptation, following the respective observations that populations of the same endothermic species (or closely related species) demonstrate larger bodies and shorter appendages when living in colder environments than populations of the same species inhabiting warmer regions (Bergmann 1847, Allen 1877). Though Carl Bergmann (1847) and Joel Allen (1877) never attributed their observed patterns to evolutionary processes, this interpretation quickly became standard, especially by the mid-twentieth century. These patterns were codified as Bergmann's and Allen's ecogeographic rules by Mayr (1956) and have been supported across a variety of taxa (James 1970, Ashton et al. 2000, Meiri & Dayan 2003, Symonds & Tattersall 2010). Taken together, these ecogeographic rules, and the evolutionary expectations derived from them, form the historical framework within which this dissertation is conducted.

Bergmann's rule, as initially discussed in his 1847 work, states that endothermic vertebrates (organisms that maintain body temperature through the internal generation of heat) display a negative correlation between body size and latitude within their genus (Bergmann 1847, translated in James 1970). The thermoregulatory explanation of Bergmann's observation originates from the mathematical relationship between surface area and volume (Mayr 1956), a concept further developed by Ruff (1994; see "Human Ecogeographic Variation" below). Geometrically, as the volume of a three-dimensional object increases, the ratio of surface-area-to-volume decreases. In an endothermic organism, a disproportionate decrease in exposed surface area could allow for a significant reduction of heat loss – a potentially crucial trade-off with other factors (such as mechanical efficiency or metabolic cost) in colder climates (Schmidt-Nielsen 1984). In contrast, a decrease in body size would reverse this surface-area-to-volume relationship, allowing for greater heat diffusion. As a result, populations of endothermic species living in warmer climates (lower latitudes) are expected to display smaller bodies, since heat dissipation is of greater importance.

Similarly, Allen's rule states that endotherms display a negative correlation between climate and the ratio of extremity length (tails, limbs, beaks, etc.) to body size (Allen 1877, Mayr 1956).

Like Bergmann's rule, Allen's rule has been interpreted through the framework of thermoregulatory constraint, where disproportionally shorter extremities mitigate heat loss for organisms in colder climes and longer, thinner appendages aid in heat dissipation for individuals in warmer climes (Allen 1877). In this way, the extremities – which are generally less insulated than the body's core – act as "thermal windows," allowing refinement of the larger thermoregulatory patterns observed by Bergmann at a smaller scale (Phillips & Heath 1995).

Studies of body shape variation within and among closely-related species largely uphold the patterns proposed by Bergmann and Allen. In a large-scale review of studies investigating Bergmann's rule, Meiri and Dayan (2003) found that over 72% of birds (94 species) and 65% of mammals (149 species) adhered to established expectations. Rhesus macaques originating in cold, dry areas of China also demonstrate larger body mass, length, and height than those from the warmer Indian subcontinent (Clark & O'Neil 1999), and on a more geographically-reduced scale, gray mouse lemurs from the cooler, arid deciduous forests of northwest Madagascar display significantly higher body masses than those residing in the rainforests of the island's southern tip (Lahann et al. 2006). Although each of these studies supports the pattern of observations that underlie Bergmann's rule, evolutionary conclusions are drawn based on pattern adherence alone – none of these studies is designed to directly assess if thermoregulation is a driving factor of body size evolution. The ecogeographic literature also provides several examples of untested hypotheses, such as the observation that several species of South American subterranean rodents – mammalian endotherms – demonstrate nearly none of the expected body size patterns, despite a fairly wide geographic dispersal (Medina et al. 2007). Not to be stymied by a lack of adherence to expectation, the authors argue that because these organisms are presumably adapted for a well-insulated, temperature-consistent microclimate, the lack of relationship between climate and body size may actually support the thermoregulatory interpretation of Bergmann's rule (Medina et al. 2007).

Similar trends – both of morphological adherence and the subsequent adaptationist assumptions – are observed in the study of Allen's rule across taxa. In a classic example, Schmidt-Neilsen and colleagues (1965) observed that the ears of jack-rabbits appeared heavily

vascularized, and inferred a thermoregulatory relationship between ear length and heat dissipation. In a follow-up study, ear length was found to be positively correlated with temperature, appearing to provide support for both the explicit pattern and implicit process of Allen's rule (Griffing 1974). This interpretation, however, is complicated by alternate explanations for the same observation. While jack-rabbit ears are demonstrably longer in species that inhabit warmer environments (Stevenson 1986), issues of water-availability, rather than temperature, may place larger selective pressures on the species in question. Instead, it was postulated that the rabbits dissipate heat through their ears because of a lack of water to aid in evaporative thermoregulation, and as such, the xeric environment of the North American Southeast may be driving this adaptation at least as strongly as ambient temperature (Greenberg et al. 2012). While it could be argued that high temperatures and low water-availability are both elements of climate (although "climate" is almost always represented by latitude as a dubious proxy for temperature; see "Human Ecogeographic Variation" below), this kind of equivocation over the actual variables leading to evolutionary change marks adaptationist studies. This can also be seen in the failure to consider other possible explanations for the evolution of large ears in jack-rabbits, such as selection for improved hearing, the indirect evolution of large ears as a result of correlation with other traits under selection, or random genetic drift. In addition, while rabbit ear and tail length appear to adhere to the expectations derived from Allen's rule, the species investigated also demonstrate a negative correlation between temperature and foot length (Stevenson 1986).

In a large-scale interspecific analysis of Allen's rule, Nudds and Oswald (2007) examined lower limb lengths among seabirds. They found that exposed leg length was correlated with mean temperature measurements, rather than latitude (Nudds & Oswald 2007). Their findings support Allen's observed pattern, though again without directly testing for natural selection. Taking this research a step further, Symonds and Tattersall (2010) examined the bills of 214 species of birds from around the world and found strong evidence linking bill size to temperature (latitude was excluded, as per Nudds & Oswald 2007). The relationship between bird leg length and climate, while present, was notably weaker (Symonds & Tattersall 2010).

However, since birds have been observed dissipating 30-60% of their body heat through their bills (Tattersall et al. 2009), the authors argue that a lack of a strong ecogeographic pattern in the lower limbs of the birds could be interpreted as support for the argument that Allen's rule is thermoregulatory in origin (Symonds & Tattersall 2010). That the bill is known to dissipate the majority of heat in birds and that it also demonstrates a strong correlation with temperature (rather than latitude) is interpreted to support the idea that thermoregulatory constraints have influenced the evolution of bill size, though again without directly assessing any of the underlying evolutionary processes.

In addition, the adherence of species to ecogeographic expectations is only meaningful if the role of evolutionary processes assumed to drive phenotypic variation can be disentangled from changes due to developmental plasticity. For example, Burness and colleagues (2013) raised post-hatched Japanese quail in extreme temperatures and found that quails raised in colder environments demonstrated significantly shorter bills as adolescents than quails assigned to warmer environments. Following this, the adolescent quails were placed in a thermally common environment, where the short-billed quails displayed significant catch-up growth, eventually developing a bill similar in size to the quails raised in the warmer environment. Interestingly, while external bill morphology demonstrated reversible plasticity in adulthood (short-beaks grew to normal size), the density and location of the vascularization beneath the bill's surface – the actual mechanism of thermoregulation – did not change (Burness et al. 2013). These results demonstrate the degree of obscuration that the environment of development can have on the potential evolutionary processes underlying trait form and function. As is discussed below (see "Variation and Quantitative Methods"), the relationship traits have with each other (due to genetics, development, function, or an interaction of these and other factors), as well as the with the environment, are fundamental determinants of their eventual phenotype.

After 150 years of research into ecogeographic trends, thermoregulatory adaptation remains the most widely accepted interpretation of adherence to the morphological patterns predicted by Bergmann's and Allen's rules. The prevalence of this explanation grew following

an enthusiastic mid-20th century debate held between Mayr (1956) and Scholander (1955, 1956). In this discussion, Scholander (1955, 1956) argued that there was a lack of observational data to validate either Bergmann's or Allen's rules and that the physiology of soft-tissue thermoregulatory processes (insulating fat layers, arterio-venous countercurrent heat exchange, etc.) were not being given sufficient consideration. In contrast, Mayr (1956) claimed that the original intent of both Bergmann (1847) and Allen (1877) was to take note of statistically frequent, empirically observed patterns and make suggestions for possible mechanisms that could be driving these observations. Since the observed phenotypic pattern appears to align with the mathematical relationship between body size and some forms of endothermic thermoregulation, and provided with no alternate theories to explore, research on Bergmann's and Allen's rules have focused almost entirely on climactic adaptation as the source of ecogeographic variation.

The initial studies by biological anthropologists into the evidence for Bergmann's and Allen's rules in modern humans occurred roughly around the time of Mayr (1956) and Scholanders' (1955, 1956) debate (Ruff 1994). As one of the most widely-distributed species on the planet, modern humans can be found across nearly all climates and geographic regions. The ability of humans to regulate their own body temperature in response to changes in the environment is a key factor in the species' ability to inhabit this wide variety of climes. It also makes humans among the few taxa to potentially express *intraspecific* ecogeographic variation. While studies undertaken, especially after 1980, have considered morphological variation in body shape and size, it is important to review the physiological mechanisms that coexist with this variation to understand why morphology would be subject to evolutionary change with respect to ecogeographic factors.

Human Thermoregulation

As in other taxa, human biologists, biological anthropologists, and physiologists have focused on thermoregulation as the adaptive cause of variation when studying human morphology across ecogeographic regions. At its most basic level, thermoregulation in humans

occurs when body temperature rises above or drops below the range of comfort (the thermoneutral zone), to prevent tissue damage that occurs at more extreme temperatures. Thermoregulation mechanisms in response to excess heat or cold both function as negative feedback loops in which changes in internal or external temperature stimulate the proper response – heat dissipation or heat generation – until either a homeothermic balance is achieved or the system fails (ultimately resulting in death) (Boulant 2000, Charkoudian 2003).

Human core body temperature is maintained at the high end of the available range, which means the risk of overheating is far greater than that of overcooling (Ivanov 2006, Romanovsky 2007). While the average human internal temperature is often reported as a precise 37°C, the true average internal temperatures have been shown to vary by age and sex of a given subject, as well as by method used to collect the data (Sund-Levander et al. 2002). In a review of temperature data collected over the 20th century, Sund-Levander and colleagues (2002) found that adjusted oral temperature ranges in "normal" adult males and females were 35.7-37.7°C and 33.2-38.1°C respectively, while those collected rectally were 36.7-37.5°C and 36.8-37.1°C. These ranges are very close to the upper limits of survival for homeothermic animals. As Ivanov (2006) discussed, the rate of protein denaturation increases, and repair decreases as internal temperature rises. In addition, Dill and colleagues (2011) indicated that cell membranes of mesophiles (as opposed to extremophiles) begin suffering extreme heat damage and die if their immediate environment exceeds 50°C, and that an upward shift in temperature as slight as 4°C can induce heat shock. Cell death by hypothermia, however, does not occur in human cell colonies until around 10°C, a difference of approximately 25-27°C from normal averages rather than the 13-15°C found along the upper temperature limits. As such, the ability of the human body to maintain homeostasis within a comfortable homeoneutral range, especially in high temperatures, is critically important. The primary macroscopic mechanisms used in thermoregulation via heat dissipation in humans include sweating, vasodilation, and the arterio-venous countercurrent heat exchange.

Evaporative cooling or sweating is usually stimulated by warm-sensitive thermosensory neurons responding to hot environmental conditions (when the ambient temperature exceeds

skin temperature) (Romanovsky 2007), though it can also be the result of increased internal temperature caused by exercise or fever (Machado-Moreira et al. 2008). While nearly the entire body surface contributes to the production of thermal sweat, it has been demonstrated that the distribution of sweat flow is fairly uneven, varying both between and within segments of the body, though remaining relatively consistent across populations (Machado-Moreira et al. 2008, Smith et al. 2013). When sweat is produced, it is secreted onto the surface of the skin where the energy (heat) is used in evaporating the water components to vapor. As the water evaporates, skin and the superficial structures – such as cutaneous veins – are cooled, and that lower-temperature blood flows back into towards the heart, decreasing internal core temperature (Charkoudian 2003). The superficial venous blood cooled by sweating not only affects the temperature of the interior organs, but also immediately cools its surrounding structures.

The effectiveness of cooled venous blood in lowering internal temperature is significantly aided by an increase of skin blood flow during heat dissipation (Kellogg 2006). This increase can be dramatic: a resting skin blood flow of approximately 0.25 L/min in homeoneutral environments can intensify to 6 - 8 L/min in cases of extreme hyperthermia (Taylor et al. 1984, Charkodian 2003). Once a response is triggered, skin blood flow (vasodilation) and evaporative cooling increase proportionally to internal body temperature until either the heat dissipated equals or surpasses the heat created or the system reaches its maximum (Charkodian 2003). Heat dissipation through evaporative cooling is therefore dependent on the available skin surface area, and may be especially important in environments where the ambient temperature is at or above human internal temperature – as is predicted by the thermoregulatory explanation of ecogeographic rules.

Another important form of physiological thermoregulation in humans is the arterio-venous countercurrent heat exchange. The limbs, and to a greater degree the hands and fingers, function as countercurrent radiators for the dissipation of heat in human thermoregulation (Payne et al. 2018). As Bernard (1876) initially suggested, and Scholander (1955) further discussed, arteries passing deep to the skin's surface also transfer heat to the cooled blood of

their venae commitantes, lowering the temperature of the arterial blood and thus contributing to the overall lowering of body temperature. The countercurrent heat exchange is particularly significant in the extremities, and especially in the arterio-venous anastomoses of the feet, hands, and fingers (Hirata et al. 1993, Ferreira & Yanagihara et al. 2012). In fact, the rate of blood flow in the skin of the hands can fall near to zero in extremely cold environments and increase to almost sixty percent of cardiac output in cases of severe hyperthermia (Grahn et al. 2008 in Ferreira & Yanagihara et al. 2012).

Of course, the degree to which a body requires heat dissipation is largely a factor of the surrounding environment. Though temperature and humidity vary across Earth's climates, individual humans are able to improve their tolerance of high temperatures in new environments within a matter of days. Heat acclimation results in a lower resting core temperature, even in humid environments in which evaporative cooling is not as efficient (Mitchell et al. 1951, Garden et al. 1966, Buono et al. 1998). This seems to be partially the result of heat acclimation reducing the sensitivity of the thresholds leading to sweating and vasodilation (Roberts et al. 1977). In addition to a lowering core temperature and skin blood flow (higher thresholds), heat acclimation increases time to fatigue (Nielsen et al. 1993) and reduces heart rate (Roberts et al. 1997) when exercising in hot conditions. Acclimation to heat can occur from short- or long-term exposure to high ambient temperatures, or from the generation of a high internal temperature via several extended bouts of intense exercise.

Perhaps unsurprisingly, the human body's thermoregulatory adjustments for environments of extreme cold are functionally opposite to those employed during hyperthermia. As mentioned earlier, adult humans are in less immediate danger of overcooling than of overheating (Ivanov 2006, Romanovsky 2007). Unlike increases in internal body temperature, which can be caused by illness, exercise, metabolic, or hormonal changes, as well as ambient environment, decreases in the internal body temperature of endotherms are almost exclusively the result of external pressures.

In an examination of human internal body temperature in cold climates, Scholander (1955, p. 16) discusses the "critical temperature," defined as "the lowest air temperature at which the

animal can maintain a resting or basal metabolic rate, without losing body temperature." Research suggests that the body's ability to produce heat when subjected to temperatures below the human critical temperature is similar to, but somewhat less involved than, the processes of heat dissipation. However, the ethical limitations involved in examining long-term exposure to extreme cold have also contributed to a dearth of data on this topic (Xu et al. 2005). Much of the recorded experimental evidence for the effects of cold exposure on humans were obtained during times of war, either through military observation or unethical experimentation, such as studies performed by Nazi scientists (Berger 1990); the use of results from these studies continues to be the subject of ethical dilemmas.

The information that is available suggests that heat genesis via shivering in adult humans is a crucial element of thermoregulation. Xu and Werner (1997) devised a six-cylinder model of human temperature regulation and found it matched well against real-life data of heat stress, short-term cold stress, various exercise loads, and clothing arrangements. When used to predict long-term exposure to extreme cold, and when not accounting for muscle fatigue, the model suggested that homeostasis can be maintained indefinitely based on shivering (muscle vibration) alone (Xu & Werner 1997).

Although clearly capable of generating a considerable amount of heat, not all muscles are equally useful for warming core temperature. Because human tissues are not highly heat-conductive, heat produced by shivering in the limb muscles is unable to effectively radiate to the torso, where the most important survival organs are found (Xu et al. 2005). In addition, because of the same arterio-venous countercurrent exchange discussed previously, blood returning to the core from the shivering muscles in the extremities has been cooled by its proximity to the skin and thus the cold ambient environment (Bristow et al. 1994). Since an increase of warm core blood must be sent to the muscles to maintain the shivering – blood that then loses heat via radiation from the extremities – overall body temperature cools rapidly once muscles reach their fatigue point (Xu et al. 2005).

Vasoconstriction also occurs when cold-temperature thresholds are met, mitigating some of the issues associated with shivering-based heat generation (Charkoudian 2003). Most effective

in the limbs, vasoconstriction reduces blood flow to the skin and thus the potential for further heat radiation via blood cooling. In the distal anastomoses of the hands, vasoconstriction in cold environments can reduce skin blood flow to nearly nothing (Grahn et al. 2008 in Ferreira & Yanagihara et al. 2012). When blood flow to the peripheral tissues is reduced, the muscle, fat, and skin of the extremities acts as an insulating shell around the warm core of the body (Webb 1992) and in cases of extreme vasodilation, the insulating effect of these soft tissues can increase to more than 300% (Rintamäki 2007). While this extreme vasodilation can be harmful for the tissues of the limbs if maintained for an extensive amount of time, the resultant thermoregulatory safety mechanisms help maintain a safe internal temperature for the vital core organs.

Aside from shivering and vasoconstriction, additional physiological mechanisms vary among human populations, and research into identifying non-shivering thermogenesis in adults has become an area of increased interest over the past decade. It has long been recognized that human infants, unable to shiver, metabolize brown adipose tissue (a fat that produces heat to maintain homeostasis). Recently, however, studies have shown that brown adipose tissue is also present and has thermoregulatory relevance in the majority of human adults (van Marken Lichtenbelt et al. 2009, Virtanen et al. 2009, Hu et al. 2013). Van Marken Lichtenbelt and colleagues (2009) determined that brown adipose tissue was present in 96% of their subjects, and found it provided effective non-shivering thermogenesis in individuals of average weight or lower. Virtanen and colleagues (2009) also found evidence of brown adipose in adults and determined that if fully activated by a cold environment, brown adipose tissue could burn up to 4.1 kg of white adipose tissue a year based solely on glucose uptake (roughly two percent of the energy consumed). The role of brown adipose tissue in the study of human thermoregulation across ecogeographic regions may be crucial, as genes responsible for the differentiation of brown and “beige” (brown adipose cells found in white adipose tissue) adipocytes appear to be under strong selection in Greenlandic Inuit groups (Fumagalli et al. 2015, Racimo et al. 2016).

Brown adipose tissue may also contribute to acclimatization to extreme cold. In a ten-day examination of cold acclimation, van der Lans and colleagues (2013) found that brown adipose

tissue activity increased proportionally to non-shivering thermogenesis. This occurred in addition to other standard signs of cold acclimation: decreases in shivering and skin temperature, and subjects that self-report greater comfort in the cold environment (van der Lans et al. 2013). Interestingly, however, Castellani and colleagues (2001) also found that successful acclimation to cold environments can be seriously hampered by exhaustive exercise. Pushing their subjects to muscle fatigue for several days, the authors reported that although shivering still appeared to function as expected, individuals demonstrated much higher skin temperatures on the last day than at any point other point during the trial – an indication that fatigue resulted in a failure of vasoconstriction.

Although human bodies are equipped with a variety of physiological mechanisms for surviving extreme temperatures, it is clear that these systems are only able to respond within certain parameters. It is therefore argued that the evolution of postcranial morphology that provides any thermoregulatory advantage is necessary to augment the physiological processes of human thermoregulation. However, the sheer range of physiological mechanisms employed by the human body to maintain temperature homeostasis demonstrates that, as Scholander argued (1955, 1956), many variables beyond overall body morphology are likely under selection in humans inhabiting extreme climates. Indeed, Ruff (1994) made the same point nearly forty years later, suggesting that evolution of factors such as the type and thickness of subcutaneous fat could be more important in human climactic adaptation than changes in body size and shape. As he argued, however, biological anthropology is concerned with the evolution of all hominin linages, most of which are represented exclusively by fossil and skeletal remains (Ruff 1994). If the relationship between modern human morphological variation and climactic factors can be better understood, it will grant considerable insight into our evolutionary lineage.

Human Ecogeographic Variation

The Thermoregulatory Imperative and Human Variation

The earliest studies of modern human postcranial ecogeographic variation were generally supportive of the predictions of Bergmann's and Allen's rules, utilizing both among-group (Coon

et al. 1950, Schreider 1950, Roberts 1953) and within-group (Newman 1953, Hiernaux et al. 1975, Hiernaux & Froment 1976) comparisons. Though these studies provided evidence for the expectations established by ecogeographic rules, the majority of this early research was conceptually couched within the study of "races" and focused more on examining the morphological variation between populations of modern humans than investigating potential evolutionary relationships (Ruff 1994).

In addition, there has been some confusion over the manner in which predicted changes in morphology should be expected to manifest in humans. Bergmann's rule, for example, predicts that comparably smaller-bodied organisms will be found in tropical environments, but which specific variable(s) should anthropologists expect to best demonstrate this pattern? At various times, body mass and stature, both separately and together (Roberts 1953, Newman 1953), body mass/surface area (Schreider 1950), and head and face size (Newman 1953) were all used to verify the expected size relationship in human populations across ecogeographic regions. This range of potentially applicable variables – and their contradictory adaptive explanations – was a cause of concern. This is evidenced by Hiernaux's consternation when reporting that sub-Saharan African populations displayed significant variation in stature despite inhabiting the same climate (Hiernaux et al. 1975, Hiernaux & Froment 1976).

Invoking the now well-established "cylindrical model," Ruff (1991, 1994) provided an explanation for these discrepancies. Using this approach, the human form is reduced to a roughly cylindrical shape to allow for comparisons of volume and surface area/body size ratios for different variables between groups. Through this model, Ruff mathematically demonstrated that the width of the cylinder, rather than the height, determines variation in the surface area/body size ratio. By emphasizing the importance of the surface area/body size ratio in studying the postcranial ecogeographic variation of both modern humans and other hominins, Ruff (1991, 1994) provided a framework that explicitly connects thermoregulatory adaptation to the evolution of human body form. He referred to this as the "thermoregulatory imperative."

In his model, Ruff (1991, 1994) calculated the surface area/body size ratio and volume of various human groups by using bi-iliac breadth and stature as the diameter and height of his

anthropometric cylinder, respectively. From the cylindrical model, Ruff made body diameter, especially of the pelvis, a cornerstone of subsequent studies of human ecogeographic variation in body size and shape. Since the bi-iliac breadths of humans in sub-Saharan Africa are consistent across groups, the large variation in stature (height) observed among these groups does not actually contradict Bergmann's rule, as Hiernaux and colleagues had worried (Hiernaux et al. 1975, Ruff 1991). In fact, Ruff (1991, 1994) argued that the cylindrical model provides greater support for Bergmann's rule than previous anthropological research, as it reinforced that individuals in colder climates have wider bi-iliac breadths, and thus lower surface area/body size ratios, than those in warmer environments.

As this approach grew in popularity, bodFy breadth and appendage length (both absolute and relative) became codified as the variables of interest in examining postcranial ecogeographic patterns in human variation. Most studies have therefore focused on measures of limb length (humeral, radial, femur, and tibial length) as well as body size (bi-iliac breadth). Intra-limb indices (crural: tibial length/femoral length, and brachial: radial length/humeral length) have also been used to examine relative length of the limbs (Trinkaus 1981, Holliday 1997, Holliday 1999, see Hulsey 2016 for a review). As an additional measure of body size, estimations of body mass became important in the analysis of ecogeographic variation. To allow for the quantification of body mass from skeletal remains, Ruff and colleagues (1991, 1994) introduced the use of femoral head diameter as a proxy for body mass, founded in the the premise as the size of the hip joint is theorized to correspond with the biomechanical forces associated with humanity's upright bipedal posture.

Ruff (1994) further suggested that stature, while not affecting surface area/body size ratios when groups demonstrate similar body breadths, may instead be indicative of the "openness" of an environment rather than average temperature (or latitude). As discussed above, one form of thermoregulation for humans is the evaporation of sweat from exposed skin, and Ruff (1994) submitted the idea that in a hot, highly humid, closed-in environment such as the sub-Saharan tropical rainforest, the effectiveness of this evaporation may be limited. Instead, it is possible that groups in these environments may minimize heat loss by minimizing heat production; they

are constrained towards a smaller body mass. This is in contrast to other groups occupying the region, who have the same bi-iliac breadth but are significantly taller on average. Ruff (1994) suggested that the groups with larger stature tend to inhabit more open, savannah-like environments, allowing for considerably more effective sweat evaporation. It is therefore argued that all sub-Saharan groups are narrow in bi-iliac breadth as a result of their adaptation to high temperatures, but vary in stature as a result of the "openness" of the environment. It should be emphasized, however, that although Ruff's (1994) formalization of the association between ecogeographic patterns of postcranial variation and thermoregulation (the cylindrical model) allowed for hypothesis testing, the actual processes leading to the observed morphological changes are still not testable using this method.

In studying modern human adherence to Allen's rule specifically, Eveleth and Tanner (1976) found that limb lengths were significantly narrower and longer relative to body size for groups inhabiting tropical equatorial environments, and Stinson (1990) reported that the relative trunk length/limb length ratios among indigenous South Americans also met ecogeographic expectations. Caution should be exercised in light of single deterministic explanations (Auerbach 2012), however, as multiple other factors, including nutrition, metabolic stress, ranging distances, parasite loads, and population history could all also play roles in determining variation in stature and limb length (Auerbach 2010).

Various experimental and developmental studies also support human conformation to the ecogeographic expectations. In a more direct assessment of thermoregulatory processes, Tilkens and colleagues (2007), for example, found that individuals with longer limbs spent more energy maintaining their resting metabolic rate in cold environments than individuals with short limbs. Although the sample size was small, this study offers evidence linking the physiological underpinnings of ecogeographic research to morphological variation. Additional research has also indicated that morphological variation among humans is established early in ontogeny; a study of body proportions in juveniles from both living and archaeological populations revealed that the expected ecogeographic patterns of body breadth and limb lengths could be found in children aged as young as six years (Cowgill et al. 2012).

Applying the Thermoregulatory Imperative to Human Ancestors

There is also evidence that morphological trends adhering to Bergmann's and Allen's rules are not limited to modern humans. The majority of hominin fossils intact enough to compare also conform to the expectations established by Bergmann and Allen (Trinkaus 1981, Ruff & Walker 1993, Ruff 1994, Holliday 1997). One of the most cited examples of this relationship stems from Trinkaus' (1981) initial exploration of body size and limb proportions in European Neanderthals, who inhabited the glacial environment of the Late Pleistocene. As is predicted by certain interpretations of Allen's rule , European Neanderthals display significantly smaller brachial and crural indices than are found in modern humans. Trinkaus (1981) also devised regression equations to estimate mean annual temperatures from brachial and crural indices. When later adjusted and applied to western European Neanderthals, these equations predicted mean annual temperatures of approximately -2°C to 2.5°C (Holliday 1995). In addition, Holliday and Trinkaus (1991) determined that within Neanderthal populations, those in the glacial European climates appeared more "cold-adapted" with regard to limb length/trunk length than the West Asian Neanderthals inhabiting warmer environments. When compared to the global distribution of modern human body size and proportions, including various Aleut groups, European Neanderthals were found to fall at the extreme end of the range of human postcranial morphology, which was interpreted as strongly indicative of cold adaptation (Holliday 1997). Holliday (1997) determined that not only were European Neanderthals "hyperpolar" in body type, but also suggested they may have been displaying stronger morphological reactions to the cold as the result of less cultural buffering (e.g., efficient clothes and shelter).

Pre-Neanderthal hominin remains have also been interpreted within the thermoregulatory framework associated with ecogeographic trends in postcranial morphological variation. In his analysis of the proportions of sub-Saharan hominin fossils, Ruff (1994) examined an adult *Australopithecus afarensis* (AL 288-1, "Lucy"), a juvenile *Homo erectus* (KNM-WT 15000, "Nariokotome boy"), and an adult *Australopithecus africanus* specimen (STS 14) with regard to body form and ecogeography. He found that all three hominins demonstrated the bi-iliac

breadth expected of sub-Saharan Africa, though they varied widely in stature. In addition, Ruff & Walker (1993) applied corrected temperature-predicting regression equations devised by Trinkaus (1981) to the reconstructed brachial and crural indices of Nariokotome boy and concluded that these fossil remains appeared "well-adapted" for an environment around 30°C, a temperature similar to the current tropical climate of sub-Saharan Africa.

Studies of hominin postcranial morphology, whether of pre-modern or modern humans, have also been used to inform our understanding of migration and settlement patterns of the past. Some researchers, for example, have suggested that skeletal bi-iliac breadth is more evolutionarily conserved than stature or limb proportions (Tague 1989, Ruff 1994, Auerbach 2012). This interpretation is based on studies of New World morphology, as Native American groups tend to display significantly less variation in bi-iliac breadth than populations in Europe, Asia, or Africa (Ruff 1994, Auerbach 2010, Auerbach 2012). As Ruff (1994) discussed, the Pecos Pueblo Amerindian skeletal sample demonstrated bi-iliac breadths similar to those of the Aleut sample, despite a massive disparity in climate. In contrast, these groups are as different in their brachial and crural indices as would be expected given normal conformation to Allen's rule (Trinkaus 1981, Ruff 1994). Ruff (1994) therefore concluded that while the limb proportions of Native American groups reflect the expected ecogeographic patterning, bi-iliac breadth (which he suggested is a more genetically-conserved trait than limb length) still reflects the "cold-adapted" width of the Arctic migrants that initially populated the New World.

In an examination of postcranial morphological traits for five mostly complete North American Holocene males, Auerbach (2012) further supported this conclusion. Although Auerbach (2012) reported more variation in all traits than was expected based on Old World samples, he noted that the North American Holocene males trend towards wider bodies regardless of climate and suggested that this may be due to long-term high-latitude genetic isolation in their ancestors prior to the colonization of North America.

Critiquing the Adaptationism of the Thermoregulatory Imperative

These studies, however, highlight an important issue in the anthropological study of ecogeographic trends in postcranial morphology. When confronted with patterns of body form that do not adhere to the expectations established by Bergmann (1847) and Allen (1877), many researchers develop new, hypothetical adaptive hypotheses instead of looking to non-selective sources of evolutionary change. This can be seen in Ruff's (1994) appeal to the influence of "open" and "closed" environments to explain differences in stature among sub-Saharan African groups, as well as his discussion of why some Polynesian groups fail to conform to ecogeographic influences. Ruff (1994) argued that some Polynesian groups appear to be much stouter than would be anticipated such a warm climate, and that these groups may be adapted not to the actual ambient temperature of their islands of residence, but to the cold air immediately above the Pacific Ocean in which they, as sea-farers, spent most of their time. Such ad-hoc explanations are common in the ecogeographic literature, and it is in these equivocations that the weaknesses of the assumed link between thermoregulatory adaptation and adherence to Bergmann's and Allen's rules are demonstrated.

The over-reliance on thermoregulatory adaptation as the sole explanation for human ecogeographic variation is not only evidenced in Ruff's work (1991, 1994), but throughout the biological anthropology literature. In his examination of Upper Paleolithic modern humans, Holliday (1999) noted that the individuals in his sample display "cold-adapted" limb lengths, but "warm-adapted" intra-limb indices. He suggests that perhaps this group – assumed to be recent migrants from Africa into Paleolithic Europe (Trinkaus 1981, Holliday 1997, Holliday 1999) – demonstrate a half-way point in their adaptation to their new glacial climate. Clearly, Holliday, like many others, is focused only on explanations that fit a pre-conceived framework of adaptive change. In addition, although several researchers comment on the plastic response of limbs to extreme temperatures during development (Trinkaus 1981, Ruff 1994, Holliday 1997, Holliday & Ruff 2001, Higgins & Ruff 2011), the possible complicating factors of globalization and recent changes in nutrition (Katzmarzyk & Leonard 1998), and/or issues of allometry (Shea & Bailey 1996, Holliday & Ruff 2001) in the study of human ecogeographic variation, these

additional sources of variation are often merely mentioned, with primary conclusions hinging instead on adaptive, thermoregulatory explanations.

Recently, however, evidence of the role of population structure on skeletal morphological variation has emerged, resulting in a shift away from the exclusive reliance on adaptation in response to thermoregulation for the evolution of body form. Auerbach (2007, 2012) presaged this shift in explanations for morphological evolution through extensive equivocating about the evolutionary processes responsible for shaping human variation (noted in Roseman and Auerbach 2015). In his previously discussed study of Early Holocene North Americans, he argued that the presence of restricted morphological variation in some traits (body breadth) and not others (limb lengths) could have been a product of population history (as Native Americans represent descendants of a genetically bottlenecked population), directional selection, or a combination of both (Auerbach 2012).

Considerable research has demonstrated that a nested serial founder model originating in Africa can explain 75-85% of human genetic variation (Ramachandran et al. 2005, Liu et al. 2006, Hunley et al. 2009), as well as a significant portion of morphological variation in both the cranium (Roseman 2004, von Cramon-Taubadel & Lycett 2008, Betti et al. 2010), and postcranium (Betti et al. 2012, Betti et al. 2014) (see "Neutral Model of Human Variation," below). The influence of population structure on measurements traditionally associated with climate is not surprising, as latitude is often used as a proxy for climate (Ruff 1994, Holliday 1997, Auerbach 2012, Roseman & Auerbach 2015). If we accept that thermoregulation is the key factor driving variation in human body form across ecogeographic regions, the underlying cause of adaptive change would presumably be some measure of temperature. This is a crucial point, as the majority of ecogeographic studies rely on latitude, rather than temperature, as a proxy for "climate" (Trinkaus 1981, Ruff 1991, Ruff 1994, Holliday 1997, Holliday 1999, Holliday & Ruff 2001, Roseman & Auerbach 2015, Savell et al. 2016).

The use of latitude to represent climate when testing evolutionary models is problematic for a number of reasons. The supported model of human migration – a pattern of serial founder effects expanding outward from Africa – suggests that population structure tracks closely with

the same ecogeographic clines associated with Bergmann's & Allen's rules. This shared pattern of human movement likely conflates evidence of selection with that of population structure (Roseman 2004, von Cramon-Taubadel & Lycett 2008, Betti et al. 2009, Roseman & Auerbach 2015). Perhaps more importantly, locations across different latitudes do not differ only by temperature. Other possible factors that follow latitudinal clines, such as humidity, altitude, seasonality, and parasite load (Salkeld et al. 2008), could contribute unique, and potentially synergistic (see Chapters IV and V), selective pressures to the evolution of human body form, potentially complicating the thermoregulatory imperative model of ecogeographic variation (Katz et al. 2016).

Nevertheless, there is evidence that temperature may be an important force behind human postcranial evolution, as based on patterns of morphological variation and their association with and augmentation of physiological mechanisms for temperature homeostasis. Betti and colleagues (2012, 2015), for example, found that variation in limb lengths and intra-limb proportions appeared to be meaningfully affected by a temperature-related gradient (based on average minimum temperature), even when population structure was taken into consideration. This pattern has also been observed in human cranial morphology, as several studies have demonstrated a strong association between ecogeographic variation in cranial shape and mean minimum temperature after accounting for population history (Roseman 2004, Betti et al. 2010, von Cramon-Taubadel 2011). It should be noted that when the northern-most (highest latitude) groups are excluded from many of these analyses, the adherence of modern humans to ecogeographic expectations becomes considerably more muted. This has especially been the case in studies of cranial morphology (Roseman 2004, Harvati & Weaver 2006, Betti et al. 2010, Roseman 2016; though see Katz et al. 2016). Similar analyses of the disproportionate impact of extreme-cold groups on patterns of human variation are lacking in the postcranial literature, though the idea has been discussed by both Ruff (1994) and Auerbach (2007).

The serial founder model of human migration serves as a neutral model of human evolution (see "Neutral Model of Human Variation") and is currently being used to distinguish morphology under selective pressure from traits evolving as a result of population structure

(genetic drift and gene flow), stabilizing selection, and other neutral evolutionary processes. Betti and colleagues (2012), for example, found that the neutral model of human variation provided an excellent fit to most pelvic measurements while variation in limb lengths appeared to be better explained by average minimum temperature. Similarly, Betti and colleagues (2015) examined the role of Allen's rule in the hands and feet of human groups while also accounting for population structure. They found that even when accounting for population history, the first metacarpal is significantly shorter and more robust in colder climates than in warmer ones. When research accounts for the effects of neutral evolutionary processes, evidence that supports ecogeographic expectations can be interpreted as highlighting evolutionary processes rather than relying on pattern recognition alone.

Roseman and Auerbach (2015) further attempted to disentangle population structure from climactic effects by testing limb lengths and measures of body size for goodness- of-fit against models of latitude, population structure (as constructed from a globally distributed sample of genotypic microsatellites data – see "Materials Overview," below), and a combination of latitude and population structure. They found that the latitude-based model (assumed to represent climate) provided the worst fit for every trait, and that several traits (femoral head diameter, crural index, and proximal limb lengths) were as well fit by the model of population structure as by the combined model of population structure and latitude. Clearly, population structure must be taken into account when studying human morphological variation lest signals of human migration be misinterpreted as directional selection.

Taken together, such studies provide a solid foundation for the future of human ecogeographic variation research. It is increasingly obvious that establishing a meaningful interpretation of human postcranial evolution is reliant on our ability to distinguish observed adherence to ecogeographic expectations from the processes that cause them. After nearly 70 years of research, we can conclude that the pattern of ecogeographic variance in the human postcranium is broadly predictable, though not all of the traditionally used traits, especially intra-limb indices, are equally reliable (Holliday 1999, Sylvester 2008, Auerbach & Sylvester 2011). However, even in the more recent studies of ecogeographic variation, these traits have

been consistently treated as though they are independently evolving. This choice, implicit in common research design, limits our ability to understand the genetic, developmental, and functional relationships that may significantly affect the ability of these traits to respond to evolutionary forces.

Nearly all research on human limb evolution has modeled the relationships of limb length covariance and coevolution one of three ways: from within the upper or lower limb (humeral-radial or femoral-tibial comparisons); between homologous positions across the upper and lower limbs (humeral-femoral or radial-tibial comparisons); or as if each limb segment evolved independently. As reviewed above, previous research on human limb evolution has relied heavily on explaining the observed pattern of morphological traits with the untested hypothesis of thermoregulatory adaptation. However, over the past several decades, researchers have begun to apply quantitative genetic approaches to develop a more nuanced understanding of human body form evolution.

Evolutionary Processes

Quantitative genetics provides approaches for the study of continuous, generally pleiotropic traits rather than those that sort categorically into classic Mendelian ratios. As such, quantitative genetic methods are used to investigate population-level questions across generations. This is accomplished by exploring the influence of various evolutionary processes – primarily natural selection, genetic drift, gene flow, and mutation – on the evolution of organism form, function, development, and behavior (Falconer & Mackay 1996, Hansen & Houle 2011).

Natural selection refers to the change in allele frequencies that occurs between generations as a result of the differential success in reproduction of some phenotypes over others (Falconer & Mackay 1996). It is often understood as the process by which a population's fitness to their environment improves, as certain phenotypes demonstrate a higher chance of successfully navigating their environment and reproducing, thus contributing their genes to the next generation. While not incorrect, this definition can be limiting if not provided with additional

nuance. Many researchers have assumed that because the change in allele frequency resulting from natural selection results in a population that is better adapted ("more fit") for survival in its environment, selection must therefore act to progress a population towards some static, theoretical "optimum" of adaptation. This understanding of the process of selection fails to account for constant changes in the environment that are both caused by, and interact with, the organisms that inhabit it (Lewontin 2001). Rather than orchestrating a gradual march of increasingly "fit" generations towards some final, perfectly adapted form, adaptation to ongoing selective pressures instead allows populations to "keep up" with constantly a shifting environment (Red Queen hypothesis) (Van Valen 1973, Lewontin 2001).

The study of natural selection has been a major focus of biologists, geneticists, and anatomists since before the modern synthesis. Natural selection has long been viewed as the most important and influential of the evolutionary processes and became the default explanation for any observed traits or behaviors for several decades. This "adaptationist programme" was challenged most famously by Gould and Lewontin (1979), and (slowly) the biological sciences have responded. Rather than identifying traits and developing "just-so" stories to explain their adaptive significance, natural selection is now most commonly identified when deviations from a model of neutral evolutionary processes occur (Whitlock 1999, Weaver & Stringer 2015).

It should be noted that when discussing natural selection in an adaptive context (as well throughout this dissertation), researchers are often referring specifically to directional selection. Directional selection occurs when the phenotypic mean of a given trait in a population shifts in a new direction as a result of changes in allele frequency over many generations (the new mean representing a selective optimum, or better "fit") (Falconer & Mackay 1996). There are also other types of selection, such as disruptive selection, in which extreme forms of a phenotypic trait are favored over an intermediate (Falconer & Mackay 1996), and perhaps more importantly, stabilizing selection. Stabilizing selection occurs when selective pressures maintain a population phenotype around an optimum by reducing trait variance (Bulmer 1971, Bulmer 1976) and increasing the canalization of developmental

pathways involved in the manifestation of the trait (Waddington 1957). Stabilizing selection has long been argued to be a primary cause of phenotypic stasis in a population (Charlesworth et al. 1982, Lande 1985, Lande 1986), though the actual mechanisms by which this occurs remain vague (Hansen & Houle 2004). Because stabilizing selection keeps a phenotypic trait at its existing mean, making it more difficult for directional selection to shift that mean, it is notoriously difficult to disentangle from neutral evolutionary forces. As such, it will not play a large role in the analyses of this dissertation, but must be considered as a possible explanation for evidence supporting evolution through neutral processes.

Other than selection, the other primary forces of evolution are genetic drift, gene flow, and mutation. Genetic drift, until relatively recently, was one of the most underestimated in its impact on evolutionary change. Genetic drift is generally defined as the change in allele frequencies due to random sampling (Falconer & Mackay 1996). On its own, genetic drift reduces variation in the population – driving some alleles to fixation while eliminating others. Because this process is arbitrary, even non-lethal deleterious alleles can be driven to fixation by genetic drift. Genetic drift is particularly important in relatively isolated populations with a small effective population size (N_e). The effective population size is the subset of the overall population (census population size) that is actively breeding at a given time – the number of individuals actually contributing to the gene pool (Falconer & Mackay 1996). Small, isolated populations eventually end up with less genetic variation than larger populations because genetic drift can more quickly drive several alleles to fixation or elimination, causing potentially massive changes in phenotype. Until relatively recently, it was argued that the effects of genetic drift were much reduced in larger populations because the comparably higher degree of variation slowed the rate of fixation or elimination and provided stability against the changes seen in smaller populations (Lynch 2007).

As we have found, however, large populations are also meaningfully affected by genetic drift. In fact, it has been persuasively argued that that the influence of genetic drift on the evolutionary history of life has been grossly underestimated (Kimura 1968, Falconer & Mackay 1996, Lynch 2007). As these authors discuss, it is mathematically feasible, even likely, that

genetic drift and other neutral evolutionary forces (gene flow and mutation, see below) have played a far greater role in the evolution of life than natural selection. One of the key elements of this argument is that despite relative size differences between human populations, humanity averages such tiny *effective* populations sizes compared to other animals (prokaryotes, for example) that drift is capable of making enormous changes to allele frequency (Lynch 2007).

Enough research has now indicated the importance of genetic drift in shaping evolutionary history that it (along with gene flow and, to a lesser degree, mutation) has become established as part of the "neutral model" against which any studies of natural selection must be tested. We now know that major changes in phenotype do not necessarily indicate adaptation, but could be the result of other independent or interacting processes. On such example is the founder effect. In the founder effect, when a group of organisms leaves (or is separated) from their parental population, the founding group contains only a subset of the available genetic variation in the original population. As a result, the founder population contains a new set of allele frequencies with which evolutionary processes can interact, and the population may quickly become phenotypically distinct from their parental populations. A similar scenario also occurs in bottleneck effects, in which parental population size is reduced due to some environmental effect. As the population size is reduced, some variation in the population is lost due to random chance. Again, the allele frequencies of the remaining population are different from those of the parent population as a result (Falconer & Mackay 1996).

Interestingly, the effects of genetic drift can sometimes closely mimic those we would expect from natural selection. The phenomena of "allele surfing," for example, can leave a signature very similar to that of a selective sweep in the evolutionary record (Edmonds et al. 2004, Waters et al. 2013). A selective sweep occurs when selective pressure suddenly favors a given allele or new mutation that is able to respond through a rapid increase in frequency. As the allele proliferates in one area, it can sweep into neighboring regions in which the allele is also selectively advantageous (Maynard-Smith & Haigh 1974). "Allele surfing," in contrast, tends to occur along migratory routes as a result of the serial founder effect.

In a serial founder model, a small portion of a parental population moves to a new place, taking a subset of variation with it (Ramachandran et al. 2005, Liu et al. 2006). Once that new colony grows to a certain size, a new colonizing group separates, again representing a subset of the available variation, and the pattern repeats. This effect is marked most notably by decreasing heterozygosity in gene identity with increasing distance from the source population (Ramachandran et al. 2005, DeGeorgio et al. 2011). If an allele with low frequency in the initial population is highly represented in a colonizing population, it will exist at much higher frequencies in the new population. If this pattern continues due to random chance along a path of serial founder migration, the allele could "surf" the colonizing populations as they move into new areas and potentially leave a signature difficult to distinguish from that of a selective sweep (Edmonds et al. 2004, Waters et al. 2013). The role of genetic drift in the study of evolution is therefore vitally important, not only for establishing a neutral model against which to compare samples, grasping the importance of effective population size, and realizing the role of isolation, but also in helping scientists avoid our seemingly natural tendency to favor adaptive explanations for the appearance of various traits.

Gene flow is another important process of evolutionary change. It is understood to be the exchange of genetic variation between two populations that are not randomly mating, and in which the majority of breeding occurs within each population respectively (Falconer & Mackay 1996). Gene flow is an important means of adding variation to a population that is otherwise removed by genetic drift, and can also be used to explore patterns of migration and interaction between populations. Admixture – or the degree to which two or more populations have genetically mixed – can be used to assess the history of interactions between such populations (Hunley & Healy 2011) or distinguish the likelihood of population replacement against that of population diffusion in the archaeological record (Cabana et al. 2008). Perhaps most importantly, gene flow and genetic drift can be considered together as a force of "population history" or "population structure" which takes into consideration the random genetic effects of migration, colonization, diffusion, and the various likelihoods of local, regional, and global population interactions and relatedness. Developing a quantified measure of population

structure forms the foundation of the neutral model against which assessments of natural selection are tested and is crucial to our understanding of genetic relationships.

The last of the four major evolutionary processes is mutation. Mutation refers to the random alteration of one or more DNA base-pairs during the combination of chromosomes during reproduction (Falconer & Mackay 1996). It is often described as a copy error in DNA replication and is another way that variation is introduced into the population. The variation introduced due to mutation has generally been understood to counteract the variation removed through the process of genetic drift, a concept referred to as "mutation-drift equilibrium" (Falconer & Mackay 1996). Mutation-drift equilibrium has been used to explain why many populations display relatively stable variation due to neutral processes, and forms one of the key assumptions under which many theoretical studies of natural selection have been conducted (Crow & Kimura 1970, Lynch 2010, Schneider et al. 2016).

As a result of the complexities of organismal development and the random nature of mutation, the majority of mutations are a least slightly deleterious and many can be lethal. Mutations can occur both in the coding and non-coding regions of the DNA, with somewhat different results. Mutations that occur in coding regions – especially in areas that are highly constrained and vital to structuring development of the organism – are more likely to be lethal. However, it has been suggested that mutation on non-coding regions of DNA that interact with products of the coding regions (such as cis-regulatory processes) can provide the variation necessary for evolution in these constrained developmental systems without changing the highly-constrained coding elements (Towers & Tickle 2009).

Along with genetic drift and gene flow, estimations of mutation can be incorporated into a neutral model for investigating the role of natural selection. Weaver and Stringer (2015), for example, established a model based on an assumed mutation rate to determine a range for the split-times between humans and Neanderthals, as well as various chimpanzee populations. They argued that if the change in mutation rate between compared groups (humans and Neanderthals, for example) is the same as the change in mutation rate within each of the compared groups, the deviation between the two groups could result from neutral forces.

In terms of quantitative genetic methods and the creation of evolutionary models, these non-selective processes – genetic drift, gene flow, and mutation – provide the neutral model against which adaptive hypothesis are evaluated.

Neutral Model of Human Variation

On a global scale, the best description of the structure of modern human genetic variation appears to be that of a nested-region, serial founder model originating in East or Sub-Saharan Africa within a range of 37-135 thousand years ago (Prugnolle et al. 2005, Ramachandran et al. 2005, Liu et al. 2006, Henn et al. 2012, Reyes-Centeno et al. 2015). As discussed above, the serial founder model describes a pattern of migration in which a subset of individuals separates from their parental population to colonize a new location. Once the new colony has reached a certain population density, the pattern repeats, and a subset of the first colony migrates further to establish a second, and so on. Because each group of founders carries a subset of their population's overall genetic variance, the main predictions of the serial founder effect are a decrease in genetic heterozygosity, increase in linkage disequilibrium, and increase in derived alleles with increasing geographic (migratory) distance from the population of origin (Ramachandran 2005, DeGiorgio et al. 2011).

In the context of modern human genetic variation, "nested-regions" refers to the fact that the genetic diversity in a given region (Africa, Europe, the Americas, etc.) tends to be slightly more correlated within regions than between regions. This appears to be due to bottleneck effects that occurred at geographic choke-points as humans expanded via serial founder effect out of Africa (Hunley et al. 2009). These geographic choke-points include the relatively narrow area of the Levant, which connects North Africa to Eurasia, and the Bering Strait, which bridges East Asia and the Americas. If these small discontinuities in the otherwise linear pattern predicted by the serial founder effect are taken into account, a better fit is consistently provided for the genetic data than when the serial founder model is used alone (Hunley et al. 2009). Similarly, the nested-regions serial founder model fits the distribution of genetic diversity best when East or Sub-Saharan Africa is used as the point of origin (Prugnolle et al.

2005, Ramachandran et al. 2005, Liu et al. 2006, Henn et al. 2012), and retrospective coalescent studies have calculated the estimated time of out-of-Africa expansion to within a range of 37-135 thousand years ago – though back migration and gene flow can truncate the actual times of divergence (Liu et al. 2006, Henn et al. 2012, Reyes-Centeno et al. 2015).

Of course, the quantitative genetic approaches used in this dissertation only apply if the pattern of human phenotypic variation can be demonstrated to correspond with the genetic patterns of variation. The use of skeletal morphological characteristics for the study of human variation was made possible by Relethford and Blangero's (1990) adaptation of genetic distance equations (Wright's fixation index – F_{st}) to accommodate phenotypic data in both univariate and multivariate analyses. The authors demonstrated the power of their adapted approach by using morphological data to investigate local population history in Ireland and Nepal. They found that their phenotypic analysis of genetic distance was able to correctly predict a known history of out-of-region admixture or greater-than-average isolation based on morphological data alone (Relethford & Blangero 1990).

With the availability of this new analytical tool, biological anthropologists began to explore the relationship between the distribution of human genetic variation and the evolution of human skeletal morphology. One of the most important of these studies was Relethford's (2004) direct comparison of morphological and genetic data. Using large, globally-distributed datasets, Relethford (2004) compared patterns of variation between human blood types (as per Lewontin 1972), microsatellite information (STRs), and craniometric measurements to demonstrate that skeletal morphology could not only be used to examine questions about human variation, but could serve as an effective proxy for genetic data. Confirming this relationship was crucial, as many commonly measured skeletal morphological traits had long been assumed to result nearly-exclusively from the adaptive influence of natural selection. By demonstrating that variation in cranial data followed the same trajectory as that of microsatellite distribution, the incorporation of skeletal traits into a neutral evolutionary model became possible. Following these landmark applications of skeletal morphology to genetic

questions, such studies became much more common, traditionally dividing into those that focused on craniometrics and those that focused on postcranial traits.

Von Cramon-Taubadel and Lycett (2008), for example, used a globally-distributed dataset of craniometric characters to assess whether the serial founder model (Ramachandran et al. 2005) was a strong predictor of cranial morphological variation. They found that while the serial founder model was a good fit to their phenotypic data, the amount of morphological variation explained by this neutral model was significantly less than the amount of genetic variation attributed to it (~25% v. ~75%). This difference was credited to developmental and environmental influences that occur during genotype-to-phenotype mapping. Others, as a result, have attempted to disentangle the influences of neutral population history (serial founder model - SFE) from those of selection on the cranium (Betti et al. 2009, Relethford 2010, Betti et al. 2010).

Concerned by von Cramon-Taubadel and Lycett's (2008) attempt to remove climactic effects by standardizing their measurements by size, Betti et al. (2009) assessed a similar sample of craniometric measurements with a focus on the relationships between climate and the neutral model (SFE). They found that the variation of most cranial morphology, with the exception of nasal aperture breadth and cranial size, is best explained by the neutral model rather than by climactic effects (Betti et al. 2009). Indeed, climate fails to have a significant effect on cranial morphology even when population structure is taken into consideration (Betti et al. 2010). This relationship was further supported by the fact that the only populations that deviated significantly from the predictions of the neutral model in Relethford et al.'s (2010) analysis of craniometric data were those that lived in extremely cold climates (the Buriat and Greenland Inuit), or that appeared to have not yet reached migration-drift equilibrium (Peru).

In fact, the neutral model (SFE) has proven to be such a good predictor of human cranial morphological variation, that it may prevent us from being able to effectively compare human cranial traits across hominin or primate taxa. Biological anthropologists and primatologists have long attempted to correlate patterns of variation found in modern humans to those observed in other primates or previous human ancestors. However, homoplastic differences in morphology

have kept this from being a viable option (von Cramon-Taubadel 2014a). This has resulted in several hypotheses that attempt to make predictions about the mechanisms that underlie cranial morphological variation. If a mechanism can be identified that accurately predicts some element of cranial variation in modern humans, then that mechanism could be used to predict variation of the same trait in previous taxa. Three such mechanisms that have been hypothesized to predict cranial variation are biomechanical pressure, heritability, and functional complexity (von Cramon-Taubadel 2014a, 2014b). For each of these hypotheses, however, von Cramon-Taubadel (2014a, 2014b) demonstrates that although there may be some observable difference – food toughness can have a biomechanical impact on the robusticity of the masticatory apparatus, for example – such differences are not able to effectively predict cranial morphological variation. Because the neutral model that does accurately predict such variation is based on population history specific to modern humans, she asserts, human cranial variation cannot be effectively used to study other taxa (von Cramon-Taubadel 2014a).

The role of the neutral model in predicting postcranial skeletal variation is a little more mixed. As discussed above, body proportions have long been assumed to be under strong climactic influences. Bergmann's (1847) and Allen's (1847) ecogeographic rules predict that in populations of the same species, body sizes will be larger and appendages shorter in colder climates, while equatorial populations will be smaller, with longer relative limbs. These trends are generally attributed to thermoregulatory adaptation, as it is argued that shorter, wider bodies allow for less heat loss in colder climates while thinner bodies and longer limbs allow for greater heat dissipation. In addition to potential thermoregulatory pressures, the pelvis has also been argued to be not only under selective pressure from climactic effects, but from the biomechanics of bipedalism (selecting for a narrower pelvis) and obstetric requirements (selecting for a wider pelvis in females) (Washburn 1960, Betti et al. 2014, Mallard et al. 2017; but see Dunsworth 2016).

It is with such possible non-neutral influences in mind that researchers have approached the study of human morphological variation in the postcranium. Betti et al. (2012, 2014), for

example, found that while the variation in a globally-distributed dataset of pelvic measurements appeared to mostly align with the neutral model of population structure, there was some weak indication of climactic effects (as estimated by minimum average temperature) in pelvic breadth. This supports the theory that wider bodies may be selected for in colder climates (Bergmann 1847, Roseman & Auerbach 2015). The association between pelvic breadth and climate was not ubiquitous, however, and when populations with an average minimum temperature of -20°C were removed from the sample, the influence of climate disappeared (Betti et al. 2014). Variation in limb lengths, however, was consistently associated with minimum average temperature and the neutral model provided little, if any, explanatory power (Betti et al. 2012). These findings were nuanced, however, by the recent, model-based analyses of selection and neutral evolution in the limbs discussed above. In Roseman and Auerbachs' (2015) test of model-fit in limb lengths and measures of body size, they found that latitude alone did not explain the variation of any of these measurements. Instead, only the models that included (consisted exclusively of) population structure provided the best explanation for postcranial variation.

Though there are cranial and postcranial elements clearly affected by extreme climate, it can be argued that the patterns of human skeletal morphological variation correspond strongly with the neutral model of human genetic variation.

Variation and Quantitative Genetic Methods

For evolutionary processes to act on a population, and subsequently be estimated and quantified, both genotypic and phenotypic variation must be present (Lande & Arnold 1983, Arnold 1983, Cheverud 1984, Whitlock 1999, Lewontin 2001, Hallgrimmson et al. 2009, Hansen & Houle 2008, Hansen et al. 2011). This is especially true in the study of natural selection, as there can be no response to selective pressure if there is no variation for selection to act upon. Indeed, our conceptualization of quantitative genetic relationships is reliant on an understanding that variation is present and available within a population. As an interesting thought-exercise, Hallgrimmson and colleagues (2009) suggested that in a all-clone animal

sample (such as those often used with mice), natural selection – regardless of strength or direction – would have no influence on evolutionary change until mutation, gene flow, or epigenetic effects introduced genetic variation back into the population. Variation is critical, not only to our understanding of quantitative genetics as a whole, but to the ability of natural selection to act as a force of evolutionary change. In many ways, this dissertation is about the analyses of variance in a global distribution of modern humans. To this end, I review below the quantitative genetic methods for understanding how variance and covariance among traits within a species provide evidence for understanding the role of selection and neutral processes in shaping evolutionary history.

Variance and Heritability

In quantitative genetics, the study of a continuous trait is based in the examination of its variation. As defined by Falconer & Mackay (1996, p. 122), "variation is measured and expressed as variance: when values are expressed as deviations from the population mean the variance is simply the mean of the squared values." The total observed phenotypic variance (V_P) is considered the sum of the genotypic variance (V_G) and environmental variance (V_E), so that:

$$V_P = V_G + V_E$$
$$V_P = V_A + V_D + V_I + V_E$$

where V_A is the additive genetic variance, V_D the variance due to dominance, and V_I the variance due to epistatic interactions (the three components of V_G), and environmental variance (V_E) is all variance due to non-genetic effects (Falconer & Mackay 1996, Hansen et al. 2011). Of these, the additive genetic variance (V_A) is often considered the most important, as it quantifies the impact of inherited genes on phenotypic outcome – a contrast to the often-obscuring effects of dominance, epistasis, and the environment (Falconer & Mackay 1996, Lewontin 2001). Classically, the ratio of genetic variance over total phenotypic variance has been used to determine the degree to which a trait is determined by its underlying genotype

when the effects of environment are removed, especially in the context of breeding livestock. This measure is referred to as the narrow-sense heritability (h^2):

$$h^2 = \frac{R}{S}$$

where R is the change in observed phenotype, and S the selective differential (from the Breeder's equation, discussed below). This is mathematically equivalent to

$$h^2 = \frac{R}{S} = \frac{V_A}{V_P}$$

where V_A is the additive genetic variance as standardized by the total phenotypic variance of the trait in question.

Heritability is often presented as the "additive" aspect of additive genetic variance and has sometimes been naïvely interpreted as though it represents evolutionary determinism (Houle 1992, Hansen et al. 2011). As a result, some researchers have attempted to use heritability to distinguish how much of a measured phenotype is genetically-controlled, rather than developmentally plastic (Houle 1992, Hansen et al. 2011). By interpreting heritability in this way, researchers ignore the additional sources of genetic variance – the role of dominance and epistatic interactions on the overall genetic contribution to a phenotype. Both the external (nutrition, temperature, stress) and internal (epigenesis, epistasis, stochastic cellular processes) environments, as well as the interactions between these sources of variation, influence the developmental outcome of any phenotype. Instead, heritability is most meaningful not in predicting the influence of natural selection, but in breeding situations where selection and environment are fairly controlled (artificial selection) (Houle 1992, Hansen et al. 2011).

Heritability has also frequently been used to represent the ability of a trait (or traits) to respond to evolution (evolvability) (Houle 1992, Hansen & Houle 2008, Hansen et al. 2011). However, heritability is a notoriously poor predictor of evolvability because of the manner in

which these measures are scaled (Houle 1992, Hansen et al. 2011). As mentioned above, the most common calculation of heritability standardizes the additive genetic variance by the total phenotypic variance of the population. This is problematic, because the additive genetic variance of a trait will be contained within the total phenotypic variance. The standardization of the additive genetic variance by the phenotypic variance results in what Houle et al. (2011) and Hansen et al. (2011) refer to as the "rubber ruler effect," in which the scale shifts and stretches with the variables it intends to quantify because they are auto-correlated. As a result, attempts to use heritability to extrapolate the response of a trait or set of traits to evolution are mathematically flawed.

The failure of heritability to effectively predict evolvability is well demonstrated by Hansen et al.'s (2011) review of the use of heritability in evolutionary biology research. The authors assessed several decades' worth of studies by re-calculating nearly 1500 reported parameters with the scale-appropriate standardizations (mean or variation) to examine the correlations between heritability and evolvability when the metrics were properly scaled. Perhaps not surprisingly, Hansen et al. (2011) found a correlation between the two measures of almost zero. The failure of researchers to correctly scale their data, understand the statistical transformations they were using well enough to maintain meaningful relationships between measurements, and critically evaluate their analyses resulted in several decades' worth of incorrect conflation between the concepts of heritability and evolvability.

Evolvability and Evolvability Indices

In an effort to better understand and quantify evolvability, Hansen and Houle (2008) and Hansen et al. (2011) suggest an alternate, more specific definition: evolvability as the response of a trait or traits to selection per the strength of selection. The methodological approach used in this dissertation relies on this definition of evolvability, as well as the calculations of indices related to it (Hansen & Houle 2008).

When examining multivariate relationships, evolvability can be understood two ways: 1. as the relationship between a selection gradient (β) and the associated genotypic variance-

covariance matrix (*G*) (note that the selection gradient is used for standardization, rather than another measure of variance),

$$e(\beta) = \frac{\beta' G \beta}{|\beta|^2}$$

or 2. as the relationship between the mean change in phenotype(s) and the cosine of the angle between respondability and the selection gradient on a graph of phenotypic morphospace (see Figure 1):

$$e(\beta) = |\Delta \bar{z}| \cos(\theta)$$

In Figure 1 (adapted from Hansen & Houle 2008), evolvability is represented as the distance from the origin to where a line from the tip of the respondability vector (open orange circle) perpendicularly crosses the selection gradient (filled orange circle). Respondability [$r(\beta)$], or the ability of traits to respond in some way to natural selection, is not constrained to follow

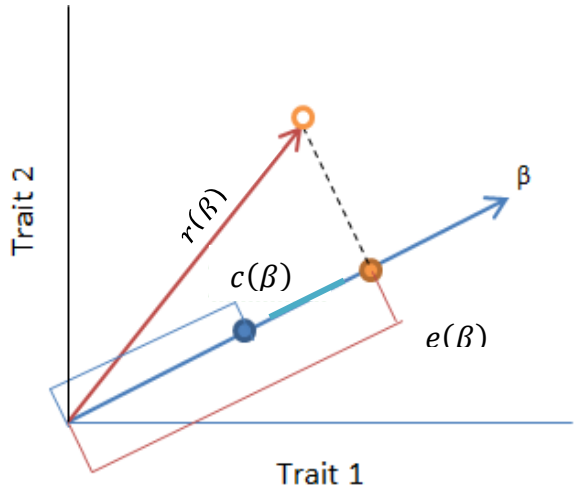

Figure 1. Evolvability [$e(\beta)$] is the distance from the origin to where a line from the tip (open orange cicle) of the respondability vector [$r(\beta)$] perpendicularly crosses the selection gradient (filled orange circle). Conditional evolvability [$c(\beta)$] is the distance from the origin to the dark blue circle, representing a fraction of overall evolvability remaining if the effects of correlation are removed.

the selection gradient, because of additional variation added by correlation between traits and other random effects. Respondability is generally measured as

$$r(\beta) = \frac{|\Delta \bar{z}|}{|\beta|}$$

where β, as in the preceding equation, is the vector of a selection gradient, and $\Delta \bar{z}$ is the average difference in a trait between generations (or groups).

Another important measure of evolvability is conditional evolvability [$c(\beta)$]. Conditional evolvability represents the amount of evolvability that occurs if stabilizing selection constrains the direction of evolvability to following the selection gradient. This can also be thought of as the change in trait one if stabilizing selection on trait two forces it to respond only along the direction of selective pressure (Figure 1). Conditional evolvability is demonstrated as the distance from the origin to the dark blue circle and represents only a fraction of overall evolvability if traits are allowed freedom of respondability. Conditional evolvability is calculated as

$$c(\beta) = (\beta' G^{-1} \beta)^{-1}$$

or as the multiplication of evolvability and autonomy $(a(\beta))$

$$c(\beta) = e(\beta) a(\beta)$$

where autonomy represents the fraction of evolvability that is due to variation in the trait alone, after the influence of correlated traits has been removed. Hansen and Houle (2008, p. 1207) define autonomy as

$$a(\beta) = 1 - i$$

where i stands for integration and refers to the loss of evolvability associated with trait covariance. Since conditional evolvability can be calculated as the autonomy multiplied against evolvability, conditional evolvability is also a measure of how much overall evolvability is explained when the effect of correlation has been removed. These metrics – evolvability, respondability, conditional evolvability, and autonomy – are much more effective at mapping and understanding the relationship between traits and their response to evolution than narrow-sense heritability, and as such will provide an important methodological approach for this dissertation.

Defining Selection on Traits

Like heritability, approaches for estimating the role of natural selection on a given trait have been founded in the relationship between genetic and environmental variance. Traditionally, and again similar to the estimation of heritability, the influence of selection has traditionally been calculated using the breeder's equation (Lande 1979, Hansen & Houle 2008, Rolian 2014),

$$R = h^2 S$$

in which R, the estimated phenotypic change between generations, is the product of heritability (assumed to represent additive genetic variance) and the selection differential (S) (Rolian 2014). The selection differential simply refers to the difference in the trait means between the selected (desired) individuals and the population total. This basic equation was adapted into a multivariate version by Lande (1979) to allow for the estimate of how a *set of correlated traits* responds to selective pressure:

$$\Delta \bar{z} = G P^{-1} S$$

In this equation, $\Delta \bar{z}$ indicates the observed change in phenotypes before and after selection, G is a matrix representing the genetic variance and covariance of traits (often substituted with the

proportional phenotypic variance and covariance matrix, or P-matrix, see below) and $P^{-1}S = \beta$, the selection gradient (discussed below). Though simple, this equation, and the multivariate analyses it allowed, was crucial to the furthering of quantitative genetic methods and forms the conceptual backbone of this dissertation.

Multivariate analyses, or the examination of how the interactions between multiple traits affect their ability to evolve together and independently, are mathematically founded in variance-covariance matrices. Variance-covariance matrices are commonly used in the study of evolutionary relationships in biology (Harmon & Gibson 2006, Kolbe et al. 2011, Pitchers et al. 2013, Houle & Fierst 2013) and biological anthropology (Gonzalez-Jose et al. 2004, Rolian 2009, Roseman et al. 2010, Roseman & Auerbach 2015, Savell et al. 2016; see Chapters II, III, and IV). These matrices capture both the variance within a given trait as well as the covariation of each trait with each other trait included in the analysis. Similarly, the directional selection gradient (β) is one of several ways to denote natural selection, and consists of a row vector of the partial regression coefficients of fitness on each trait for a series of characters. In other words, each element of the selection gradient represents the increase in fitness resulting from a per unit increase in a given trait, assuming all other traits are held constant (Lande & Arnold 1983, Arnold 1983, Hansen & Houle 2008). The selection gradient can therefore be interpreted as summarizing the magnitude and direction in which selection acts on each trait (Hansen & Houle 2008, Rolian 2014).

As many quantitative and population geneticists have discussed (Lande 1979, Lande & Arnold 1983, Arnold 1983, Lewontin 2001, Hansen & Houle 2008, Walsh & Blows 2009, Rolian 2014f), using a multivariate approach in the exploration of evolution is crucial to developing a more accurate understanding of observed and predicted changes, as covariance between traits prohibits one trait from changing without also affecting the traits with which it covaries. The ability of a single trait to respond to its specific selective pressure will therefore be constrained by the covariance structure it shares with other traits, which itself is the result of differing degrees of functional and developmental integration (Hallgrimmson et al. 2009).

Meaningful patterns of covariation between phenotypic traits – assumed to result from similar developmental processes, shared functional roles, and/or genetic interactions (i.e., *integrated* traits) – appear to occur in humans as a result of the highly correlated nature of our upper and lower limbs (Young et al. 2005, Hallgrimmson et al. 2009). Though not truly serially homologous according to the ancestral definition (in which similarities result from a morphological duplication event), the fore- and hindlimbs of tetrapods are be considered serial homologues in a developmental sense, meaning that they are the result of convergent transformations and therefore share a large proportion of their genetic network patterning (Sears et al. 2015). As a result, changes in the pattern of correlations between limbs and limb elements can be informative about evolutionary shifts in form and function.

A recent, demonstrative example of the application of these methodological approaches is found in the work of Rolian (2009) and Rolian et al. (2010). Rolian (2009) found that the highly divergent functionality of primate upper and lower limbs tended to be associated with markedly weaker correlations between individual limb segments. On an evolutionary scale, this weak correlation appears indicative of a greater ability for each limb type to respond to its own distinct evolutionary pressure (higher evolvability). Developmentally, the association between integration and evolvability underlies the concept of constraint, which refers to the inability of certain traits to respond to evolutionary pressures, such as directional selection, as a result of tight developmental and genetic associations they share with covarying traits.

In exploring the evolution of the human hand and foot, Rolian and colleagues (2010) further demonstrate how developmental constraints can influence evolutionary trends. Because human hands and feet are highly divergent in their biomechanical function, it had long been assumed that the morphology of these elements was the result of strong, independently acting selective pressures. Rolian et al. (2010) instead found that, despite their different functions, only foot morphology appeared to be under strong directional selection. The authors propose that directional selection leading to a stouter, more robust hallux and shorter toes (favorable traits for maximizing efficiency of the toe-off stage of human bipedalism) may have resulted in a similar shift in the hand, leading to the co-evolution of stouter, thicker thumbs and shorter

palms and fingers. It therefore appears likely that one of humanity's characteristic abilities – dexterous manual manipulation and our subsequent tool use – may not have stemmed from strong directional selection on these traits, but is instead a side effect of the covariance structure that exists between the human hand and foot (Rolian et al. 2010).

Such studies illustrate the degree to which patterns of covariation within and between limb segments may constrain and guide different paths of evolution through phenotypic space, as well as highlighting the how standard quantitative genetic approaches can be operationalized to explore these changes. Clearly, the manner in which forces of evolution act to effect change may not be as straightforward as has often been assumed. Until this dissertation, however, quantitative genetic methods have not been applied to the study of traditional ecogeographic measures of the modern human postcranium – long bone lengths and measures of body size.

Materials Overview

Prior to discussing the three research questions addressed in this dissertation, it is useful to briefly present an overview of the data used. Methods are all based on the general quantitative genetic approaches discussed above, and additional data sources (such as climatic data in Chapter IV) are explained in more detail for each particular study.

Phenotypic Data

To examine the influence of ecogeography on the evolution of human body form, a large, globally dispersed sample of human phenotypic variation is required. As such, my dissertation is based on the compiled osteometric data presented in four datasets: the Goldman Data Set (Auerbach & Ruff 2004); Americas Data Set (Auerbach 2012) and datasets generously shared by Trent Holliday and Chris Ruff (Roseman & Auerbach 2015, Savell et al. 2016). The inter-observer error calculated between the measurements of Auerbach and Holliday is less than one percent (Auerbach 2007). All data were combined, and remains with poor provenience, individuals of indeterminate sex, and duplicates between datasets were removed from the reconciled

dataset. The final compiled dataset consists of 3776 individuals (2187 males, 1589 females) representing 121 groups spanning Eurasia, Africa, Oceania, and the Americas.

Ecogeographic variation in the human postcranium has traditionally been investigated using six-dimensions representing limb lengths and body size: the maximum humeral, radial, femoral, and tibial lengths as well as femoral head diameter and bi-iliac breadth (Ruff 1991, Ruff 1994, Auerbach & Ruff 2004, Auerbach 2007, Roseman & Auerbach 2015, measurements originally defined by Martin 1928). These measurements were taken in millimeters from both the right and left sides, when available, and averaged to account for bilateral asymmetry (Auerbach & Ruff 2006, Roseman & Auerbach 2015).

Genetic Data

In addition to phenotypic data, genetic information is also required to address the third research question (Chapter IV). Because genetic markers are unavailable for the individuals that comprise the osteometric dataset, microsatellite molecular data from Pemberton and colleagues's (2013) aggregated dataset is used. It has been noted that higher-than-average allele similarity may be found in these data as a result of ascertainment bias (Eriksson & Manica 2011). However, as these data represent the widest global distribution of genetic data with the largest number of samples, they present the best fit for investigating ecogeographic questions in this context. These data were compiled from eight sets of human microsatellite variation at 645 loci from 5795 individuals comprising 267 globally distributed populations (Pemberton et al. 2013). Of these, 59 groups were chosen for their correspondence with the represented phenotypic populations (see Chapter IV).

Exact group matches were used when possible and linguistic relationships and geographic location were used when specific groups were not represented (Roseman & Auerbach 2015). Though this may introduce some error due to mismatch, all matches are local (no inter-regional mismatches have been made) so the effects of this bias should be diluted by the hierarchical structure of human genetic similarities among groups (Hunley et al. 2009, Long et al. 2009). Any effect should be minimized as long as the matched phenotypic and genetic data fall within the

correct local cluster (Roseman & Auerbach 2015). Similarly, in some cases (such as the Americas and a few populations in Europe), regional averages of among-group variation were used to match the phenotypic and genetic data. Unfortunately, this approach also introduces a bias into the analysis as it treats these groups as though they are evolutionarily independent of each other and share identical genetic differences with the rest of the groups included. As a result, if significant population structure differentiates the groups that are averaged to represent a single region, that population structure may be somewhat obscured throughout the analyses (Roseman & Auerbach 2015).

Research Questions

This dissertation will undertake three research directives. These directives broadly ask questions about the three topics introduced at the beginning of this chapter:

1. *Do the traits traditionally used to evaluate human body proportions (long bone lengths, measures of body size) evolve independently? In what ways does the covariation between these traits impact the effect of directional selection on human body form across ecogeographic regions?*

   I predict that long bone lengths and measures of body width do not evolve independently across ecogeographic regions in modern humans. Preliminary evidence indicates that strong trait covariation – especially between long bone lengths – can have a large effect on the response to directional selection (Savell et al. 2016).

2. *Do human groups across ecogeographic regions demonstrate comparable indices of evolvability? To what degree does population structure affect the ability of different human groups to respond to evolutionary forces?*

   As representatives of the same species, I predict that the examined human groups are so closely related that they will not meaningfully differ in predicted evolvability, respondability, conditional evolvability, or autonomy. It is also possible, however, that the

serial founder effects implicit in human population structure has resulted in decreased genetic variance as groups migrated away from Africa. This possibility could manifest in the decrease of indices of evolvability at higher latitudes.

3. *How large of a role does temperature (climate) play in the evolution of human body form across ecogeographic regions?*

I predict that temperature will account for most, if not all, of the selective pressure acting on long bones and measures of body size across ecogeographic regions. This will hold especially true for distal long bone lengths and measures of body size. If this prediction is correct, results will support the traditional narrative of thermoregulation as a primary cause of ecogeographic variation in human body form. If not, a new paradigm of ecogeographic selection will need to be explored.

Significance of Research

My dissertation provides informative models of postcranial trait coevolution across human evolutionary history, from ancient *Homo* to modern humans. Together, the whole of this research elucidates how variation in human limb bone morphology and overall body form – a foundational topic in our study of hominin evolution, thermoregulation, and locomotion – was shaped in response to evolutionary processes. My work provides evidence that trait differences among human populations may not directly reflect the forces of selection that influenced them, a concept counter-intuitive to how evolutionary studies in biological anthropology have traditionally been conducted. This research furthers the field by offering process-based evidence with regard to the theory of thermoregulatory adaptation, which has stood for over a hundred years on observational data alone. Overall, my dissertation results promote the use of a multivariate approach to modeling the evolution of traits, encouraging a nuanced, "whole-organism" perspective of human morphological evolution.

Transition from Chapter I to Chapter II

In Chapter I, we see that recent quantitative genetic analyses of postcranial diversity have supported many of the predictions associated with the thermoregulatory imperative model of human evolution (larger body size, shorter limb lengths at higher latitudes). The use of these methods marks an important shift in how ecogeographic variation is conceptualized, providing the ability to distinguish directional selection from neutral evolutionary processes, rather than simply quantifying the adherence of trait means to expected patterns. Like the pattern-based analyses conducted before, however, quantitative genetic studies of human postcranial variation are still being conducted on a trait-by-trait basis. By examining each trait individually, these studies implicitly assume that traits evolve only in response to their own (direct) selective pressures rather than a combination of direct selection and indirect selection stemming from the evolution of the traits with which they covary.

In Chapter II, we address this dissertation's first research question by evaluating the degree to which traits traditionally used to quantify human body proportions (long bone lengths, measures of body size) evolve independently. We then use quantitative genetic methods to test if these traits still support hypotheses of thermoregulatory adaptation once covariation is taken into consideration by estimating the direction and magnitude of selection needed to reflect observed differences between groups across ecogeographic regions. We also explore how the covariation between these traits influences the evolution of human body form by decomposing each trait's overall response to selection into direct and indirect responses.

CHAPTER II

CONSTRAINT, NATURAL SELECTION, AND THE EVOLUTION OF HUMAN BODY FORM

A version of this chapter was originally published by Kristen R. R. Savell, Benjamin M. Auerbach, and Charles C. Roseman as:

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This chapter is a research chapter. The text of this chapter regularly uses the pronouns "we" and "our" to reference the contributions of my coauthors, Drs. Benjamin M. Auerbach and Charles C. Roseman. It should be noted, however, that in addition to conducting the majority of the research and performing the analyses, I am the author in the ordinary sense.

Abstract

Variation in body form among human groups is structured by a blend of natural selection driven by local climatic conditions and random genetic drift. However, attempts to test ecogeographic hypotheses have not distinguished between adaptive traits (i.e. those that evolved as a result of selection) and those that evolved as a correlated response to selection on other traits (i.e. non-adaptive traits), complicating our understanding of the relationship between climate and morphological distinctions among populations. Here, we use evolutionary quantitative methods to test if traits previously identified as supporting ecogeographic hypotheses were actually adaptive by estimating the force of selection on individual traits needed to drive among-group differentiation. Our results show that not all associations between trait means and latitude were caused by selection acting directly on each individual trait. While radial and tibial length and bi-iliac and femoral head breadth show signs of responses to directional selection matching ecogeographic hypotheses, the femur was subject to little or no directional selection despite having shorter values by latitude. Additionally, in contradiction to ecogeographic hypotheses, the humerus was under directional selection for longer values by latitude. Responses to directional selection in the tibia and radius induced a non-adaptive correlated response in the humerus that overwhelmed its own trait-specific response to selection. This result emphasizes that mean differences between groups are not

good indicators of which traits are adaptations in the absence of information about covariation among characteristics.

Introduction

Among-group variation in human body form is the result of genetic drift, gene flow, and natural selection (Madrigal & Willoughby 2010, Bettie et al. 2012, Betti et al. 2015, Roseman & Auerbach 2015). Patterns of variation in human body shape appear to match ecogeographic expectations set out by Bergmann (1847) and Allen (1877). Comparisons of average body form among groups of humans living at different latitudes reflect these rules. Distal limb segments decrease relative to proximal limb segments, body mass increases, and the pelvis widens as latitude increases (Schreider 1950, Hiernaux & Froment 1976, Roberts 1978, Trinkaus 1981, Ruff 1994, Holliday 1997, Holliday & Ruff 2001, Temple et al. 2008, Auerbach 2010, Auerbach 2012). The prevailing explanation for these patterns is that among-group variation in body proportions was shaped by natural selection acting on thermoregulatory efficacy (Hiernaux & Froment 1976, Roberts 1978, Ruff 1994).

Two problems with this interpretation require further investigation. First, there is considerable overlap between the distribution of climate across latitude and the migratory routes of recent range expansions of humans from Africa into other parts of the world (Betti et al. 2012, Ingman et al. 2000, Ramachandran et al. 2005, Henn et al. 2012). Thus, patterns of body form variation among groups could reflect random genetic drift and gene flow and mimic the hypothesized effects of climate. Correspondingly, among-group differences in traits strongly associated with Bergmann's and Allen's rules – distal limb segment lengths and body breadth – best fit models that include both latitude and random genetic drift (Roseman & Auerbach 2015). In contrast, the among-group variation in proximal limb segment lengths and femoral head diameter (a proxy for body mass) were described best by population structure alone (Roseman & Auerbach 2015). A second, previously unexplored issue is that all studies of ecogeographic variation in body form to date have worked under the assumption that

morphological differences among populations are the result of natural selection, rather than having arisen due to a correlated response to selection on other traits.

The distinction between the action of selection on a trait (a trait's influence on fitness) and the evolutionary response of a trait to natural selection is a cornerstone of modern evolutionary theory (Fisher 1930). When natural selection is acting on a set of genetically covarying characteristics, individual responses to selection are a function of the relationship between that characteristic and fitness independent of all other traits, as well as the correlated responses imparted by directional selection acting on genetically covarying traits. Figure 2 (adapted from Figure 1 in Rolian 2014) shows this contrast graphically: if traits are uncorrelated, then they will respond to selection in the same direction as the force of selection irrespective of what direction in the morphospace selection is acting (Figure 2A). However, genetic correlations among traits may cause the response to selection not to match the direction of selection (β_2 and $\Delta\bar{z}_2$; Figure 2B), unless the response to selection closely parallels the main axis of variation (β_1 and $\Delta\bar{z}_1$; Figure 2B). Distinguishing between the action of selection (the estimated selective force) and the response to selection (the evolutionary change) is important because when there are strong genetic correlations among traits, as there are in those reflecting body form (Betti et al. 2015, Roseman & Auerbach 2015), the magnitude

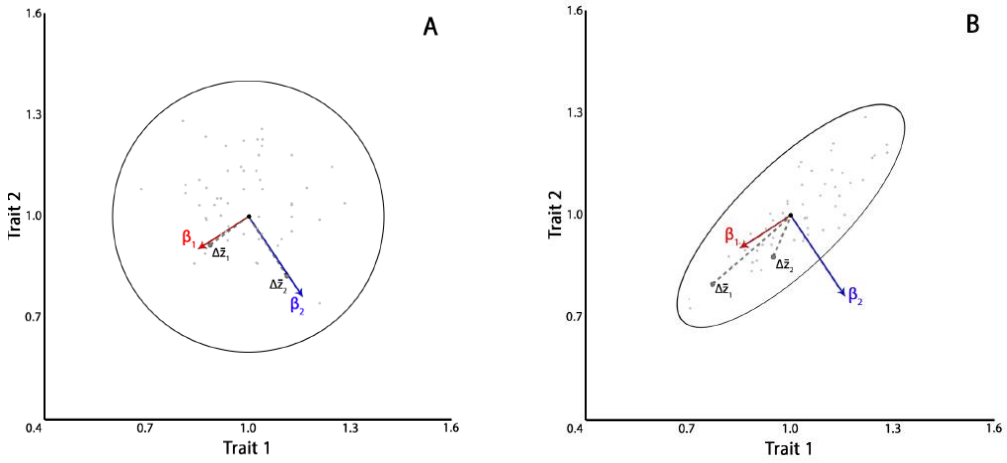

Figure 2. The differences between the force of directional selection (β) and responses to selection ($\Delta\bar{z}$) for two traits that are independent (A) or that strongly covary (B). Adapted from Rolian (2014).

of realized differences among groups may not reflect the strength and direction of natural selection. Adaptation will not be apparent from differences in means between groups. Similar studies have demonstrated that this is the case in cranial (Ackermann & Cheverud 2000, Ackermann & Cheverud 2004), pelvic (Grabowski 2013, Grabowski et al. 2011, Grabowski & Roseman 2015), and hand and foot bones (Rolian et al. 2010).

The standard ecogeographic model assumes the mean body form of groups migrating away from the tropics evolved from a tropically-adapted ancestral condition (Trinkaus 1981, Ruff 1994, Holliday 1997, Holliday & Ruff 2001, Temple et al. 2008, Auerbach 2010, Auerbach 2012). We take the average morphology of several groups from sub-Saharan Africa to represent the morphological range of variation for putatively tropically-adapted groups. We then used groups from regions of higher latitude (including North Africa, temperate Europe, and the circumpolar Arctic) to represent the range of variation in body form that resulted, in part, from climate mediated natural selection. Table 1 presents the sample sizes and measurement means for the groups used in this study.

To address these problems, we ask two questions: 1) Which characteristics of human body form (long bone lengths, femoral head breadth, and body breadth) were directly affected by directional selection? 2) Which traits evolved by correlated responses to directional selection acting on other traits? The traits we examine are all staples of the ecogeographic literature (Ruff 1994, Auerbach 2012, Holliday & Falsetti 1995): humeral, radial, femoral, and tibial maximum lengths; femoral head diameter; and bi-iliac breadth. Figure 3A presents the anticipated direction of natural selection on these traits when evolving from lower to higher latitudes based on ecogeographic expectations.

We use a model (Rolian et al. 2010, Lande & Arnold 1983, Arnold 1983, Phillips & Arnold 1983, Arnold & Wade 1984, Cheverud 1989, Roseman 2004) of retrospectively estimated selection gradients to identify those traits that were under directional selection for morphological evolution between different climate regions. These selection gradients are partial regression coefficients of relative fitness onto a characteristic holding the effects of other characteristics constant (Lande & Arnold 1983, Arnold 1983).

Table 1. Measurement means of study groups (males) – all dimensions in millimeters: HML, humerus maximum length; RML, radius maximum length; FML, femur maximum length; TML, tibia maximum length; FHD, femoral head diameter; BIB, bi-iliac breadth.

Geographic Region	Group	N	HML	RML	FML	TML	FHD	BIB
Sub-Saharan Africa	Uganda	12	333.6	265.6	474.0	407.7	42.5	241.2
	San	15	292.5	228.1	424.9	356.6	39.7	214.8
	West Africa	16	317.5	258.7	456.2	388.3	43.4	233.7
	Kikuyu	15	327.5	258.8	458.5	391.2	43.93	241.8
Northern Africa	Egypt	83	315.1	247.3	447.1	376.6	44.4	257.4
	Nubia	37	313.4	245.5	438.5	375.6	44.2	255.8
Temperate Europe	Ireland	20	329.3	243.3	457.8	368.0	47.6	271.7
	France	25	315.9	238.8	444.5	368.7	46.1	272.7
	Austria	48	317.1	244.4	442.9	3.67.2	45.8	272.8
	Bosnia	48	328.6	247.3	463.8	385.5	49.0	278.6
Circumpolar Arctic	NeoAleut	37	302.1	230.2	415.5	336.1	45.5	263.0
	Ikogmiut	29	313.1	233.8	425.2	348.4	45.7	264.8
	Kuskowagamiut	14	307.9	230.1	423.0	333.2	45.9	265.2
	Point Hope-Tigara	22	302.0	226.2	432.1	355.8	47.1	280.1

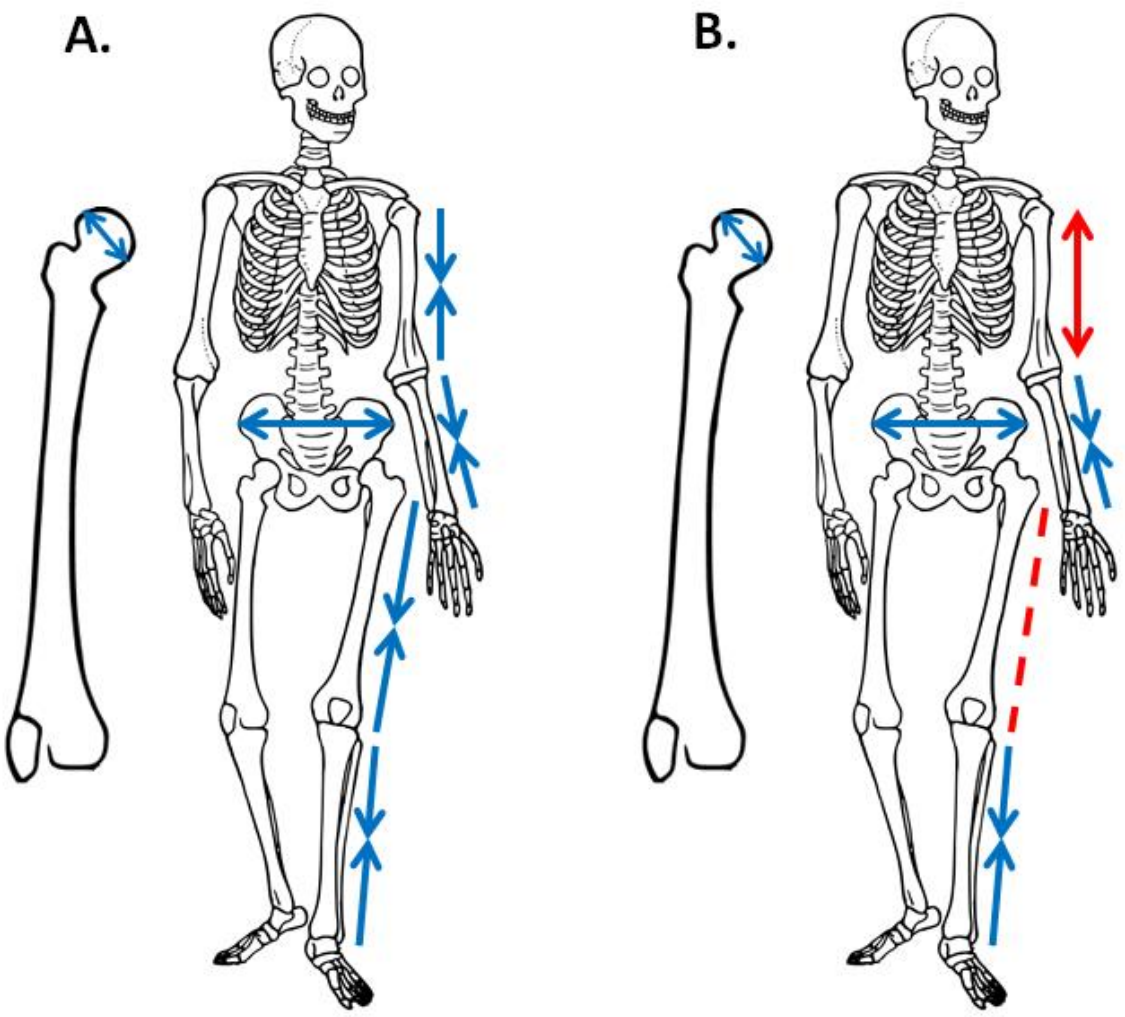

Figure 3. Directional selection pressures predicted by classic ecogeographic expectations (A) and the consensus pattern of directional selection from our analysis (B) for the six traits investigated in this study. Arrows indicate the direction of selection hypothesized (A) or estimated (B) to have led to trait differences between human groups in sub-Saharan Africa and higher latitudes. Inward-facing arrows indicate negative directional selection (the trait is predicted to shorten/narrow), whereas outward-facing arrows indicate positive directional selection (the trait is predicted to lengthen/widen). The dashed line indicates that estimates of directional selection were not distinct from zero in our consensus pattern. Red lines in B indicate differences between the classic ecogeographic expectations and the consensus pattern of directional selection from our analysis.

Selection gradients describe the direction and magnitude of selective pressures on individual traits. Positive selection gradients between groups at different latitudes indicate a net positive relationship with fitness (for long bones to lengthen, or bi-iliac breadth and femoral head diameter to broaden). Alternatively, negative selection gradients between groups at different latitudes indicate a net negative relationship with fitness. We also decompose separate components of the net response to selection into the response of each trait arising from selection acting directly on a trait and the response driven by selection acting on correlated traits (Rolian 2014, Ackerman & Cheverud 2000, Ackermann & Cheverud 2004, Grabowski 2013, Grabowski et al. 2011, Grabowski & Roseman 2015, Rolian et al. 2010).

To reemphasize, it is important to draw a distinction between the force of selection on a trait and the response to selection of that trait. If correlated responses to selection on other traits are larger than the independent response to selection on a characteristic, the sign of the response could be the opposite of the force of selection on that trait (see Figure 2).

Materials and Methods

We used a global distribution of phenotypic data provided by the Goldman Data Set (Auerbach & Ruff 2004), Americas Data Set (Auerbach 2012), and the generosity of Drs. Trent Holliday and Chris Ruff. When compiled, 2187 individuals from 121 groups were used. This is the dataset compiled and analyzed by Roseman and Auerbach (2015), and more information about it can be found in that publication. These data represent a wide latitudinal dispersion of human populations (Figure 4). The groups we chose have a representative range of the means for the six traits under investigation for each latitudinal group, based on the larger sampling of human groups in the data sets from which they were drawn. It is for this reason the San—who are not equatorial but are sub-Saharan – were included in the study; they have the smallest body size and limb dimensions of all of the sub-Saharan groups used by Roseman and Auerbach except the Biaka Pygmy (2015), which we excluded due to their very small sample size. We use the maximum lengths of the humerus (HML), radius (RML), femur (FML), and tibia (TML) as well as femoral head diameter (FHD), and bi-iliac breadth (BIB) to quantify body and limb form (all in

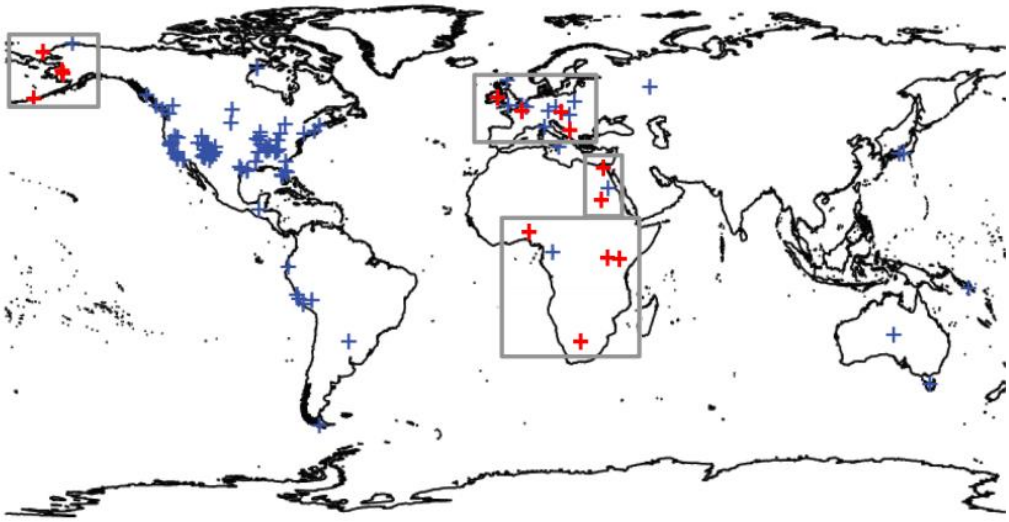

Figure 4. Plot of locations of all groups (crosses) sampled for trait data in the full data set. All groups were used in calculating the P-matrix. Groups used in pairwise comparisons for the calculation of selection gradients are denoted by red crosses. Regions for groups from distinct climates used in the calculation of selection gradients are indicated by the grey boxes (see Table 1).

millimeters). In an effort to maximize global representation and avoid issues of standardizing for sexual dimorphism, only males were used in this analysis (Roseman & Auerbach 2015).We used Lande's equation for multivariate response to selection (Lande & Arnold 1983, Lande 1979):

$$\Delta\bar{z} = G\beta$$

where $\Delta\bar{z}$ represents the change in mean phenotype values, G is the additive genetic variance-covariance matrix, and β is a vector of selection gradients, partial regression coefficients of relative fitness onto the traits. We conducted our analyses on the mean standardized scale (Houle et al. 2010). Since the phenotypic variance-covariance matrix (P-matrix) is proportional to the genetic variance-covariance matrix (G-matrix) in morphological characteristics (Ackermann & Cheverud 2000, Ackermann & Cheverud 2004, Cheverud 1988, Roff 1995), we follow standard practice and substitute the mean-standardized within-group

variance-covariance *P* matrix for the G matrix. This within-group *P* matrix was calculated using the full sample of 121 groups in Roseman and Auerbach (2015).

For the pairwise comparison of any two groups, the mean standardized difference between groups ($\Delta\bar{z}$) was determined using the equation:

$$\Delta\bar{z} = \frac{\bar{x}_1 - \bar{x}_2}{\bar{x}_1}$$

where $\bar{x}_1$ always refers to one of the four sub-Saharan African groups and $\bar{x}_2$ to one of the North African, temperate European, or circumpolar arctic groups. This difference in means was then multiplied against the inverse of the mean-standardized within-group variance-covariance matrix of phenotypes (*P*) to determine the selection gradients.

The change in mean phenotype values between groups ($\Delta\bar{z}$) and mean-standardized global variance-covariance matrix (*P*) was multiplied to estimate the selection gradients (β) (Hansen & Houle 2008):

$$\beta = P^{-1}\Delta\bar{z}$$

To examine relationships across climate regions, we conducted 40 pairwise comparisons between 14 globally distributed groups. We used the six traits above to estimate the directional selection that would have been necessary to evolve the group differences found between four sub-Saharan African groups (Uganda, Kikuyu, a combination of "Western African" groups, and the San) and groups from North Africa (Egypt, Nubia), temperate Europe (Ireland, France, Austria, Bosnia), and the circumpolar arctic (Neo-Aleut, Ikogmiut, Kuskowagamiut, Point Hope Tigara). Groups are listed in Table 1, and Figure 4 is a map of their regional distribution.

Confidence intervals were calculated using a bootstrap approach that resampled the two groups 1,000 times with replacement (as per their group-specific sample size) and determined the vectors of means for each group from the resampled iterations. These resampled means were then used to calculate the selection gradients that would have allowed the evolution of

the observed differences between group 1 and group 2. A 95% confidence interval was determined from these bootstrapped vectors of selection gradients.

Trait-specific responses to selection ($\Delta z_{element}$) sum to provide the net response to selection for a given characteristic ($\Delta\bar{z}$) (Lande & Arnold 1983, Arnold 1983). To further examine the relationship between changes in phenotype means between groups (*P*) and the net response to selection ($\Delta\bar{z}$), we therefore divided each trait's net response to selection into its component trait-specific responses to selection ($\Delta z_{element}$) (Tables 2a-c). These trait-specific responses to selection ($\Delta z_{element}$) consist of direct responses to selection (shaded values), which are calculated by multiplying the trait's selection gradient (β) against the pooled, mean-standardized variance, and indirect responses to selection (unshaded values), which are calculated by multiplying the trait's selection gradient (β) against the pooled, mean-standardized covariance with each other trait independently (Lande & Arnold 1983, Arnold 1983). These indirect responses to selection, therefore, provide information about how the genetic correlation between traits influences each traits' net response to selection ($\Delta\bar{z}$). All analyses were performed in the R statistical computing language (R Core Team 2013). Data and analysis code are available from the authors.

Results

Table 1 presents group means and Figures S1-S4 in Appendix I present group means and standard deviations of each of the six traits. The means among these regional groupings follow the general ecogeographic pattern of shorter distal limb segments relative to proximal limb segments, wider bi-iliac breadths, and wider femoral head diameters at increasing latitudes.

Figure 5 presents estimated selection gradients for each pairwise comparison between groups and their 95% confidence intervals (CI) generated using a non-parametric bootstrap (Efron & Tibshirani 1993). These selection gradients represent the independent action of directional selection on each trait. In these figures, each circle-and-whisker set represents the mean and 95% CI of a pairwise selection gradient estimation between one of four sub-Saharan groups and a group from the given region (see Table 1).

Table 2a-c. Examples of directional selection estimated between sub-Saharan African and non-sub-Saharan African groups: differences in trait means between groups, estimated selection gradients (β), net response to selection ($\Delta\bar{z}$), and correlated responses to selection on traits that combine to yield the net response ($\Delta z_{element}$). Within the Trait-Specific Responses to Selection matrix, direct responses to selection are shade and indirect (correlated) responses are not.

a. West Africa and Kuskowagamiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-9.6	**92.4 (67.2, 114.6)**	-0.03	0.20	-0.11	0.03	-0.31	0.07	0.08
RML	-28.6	**-54.7 (-80.2, -32.4)**	-0.12	0.18	-0.15	0.04	-0.35	0.07	0.08
FML	-33.2	18.5 (-25.5, 62.9)	-0.08	0.17	-0.10	0.04	-0.34	0.07	0.08
TML	-55.1	**-160.4 (-199.2, -121.8)**	-0.17	0.18	-0.12	0.04	-0.42	0.07	0.09
FHD	2.5	**46.3 (26.3, 66.9)**	0.05	0.14	-0.09	0.03	-0.25	0.13	0.10
BIB	31.5	**80.6 (56.7, 101.6)**	0.12	0.09	-0.05	0.02	-0.17	0.06	0.18

b. Uganda and Ireland (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-4.2	**61.2 (25.3, 95.5)**	-0.01	0.13	-0.13	0.04	-0.22	0.10	0.06
RML	-22.3	**-65.3 (-89.4, -40.1)**	-0.09	0.12	-0.18	0.04	-0.25	0.11	0.06
FML	-16.2	21.8 (-11.1, 54.7)	-0.04	0.11	-0.12	0.05	-0.25	0.11	0.06
TML	-39.7	**-115.7 (-157.5, -76.5)**	-0.11	0.12	-0.14	0.05	-0.30	0.11	0.06
FHD	5.1	**70.1 (56.7, 83.5)**	0.11	0.09	-0.10	0.03	-0.18	0.19	0.07
BIB	30.5	**60.1 (41.2, 78.5)**	0.11	0.06	-0.06	0.02	-0.12	0.08	0.13

c. West Africa and Egypt (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-2.4	**26.9 (8.1, 44.7)**	-0.01	0.06	-0.08	-0.03	-0.03	0.01	0.06
RML	-11.4	**-39.9 (-58.8, -19.3)**	-0.05	0.05	-0.11	-0.03	-0.03	0.01	0.06
FML	-9.1	-16.8 (-46.8, 12.8)	-0.02	0.05	-0.08	-0.04	-0.03	0.01	0.06
TML	-11.8	-13.3 (-38.8, 11.4)	-0.03	0.05	-0.09	-0.04	-0.03	0.01	0.06
FHD	1.0	9.2 (-9.3, 27.7)	0.02	0.04	-0.06	-0.03	-0.02	0.03	0.07
BIB	23.7	**57.0 (38.0, 73.5)**	0.09	0.03	-0.04	-0.02	-0.01	0.01	0.13

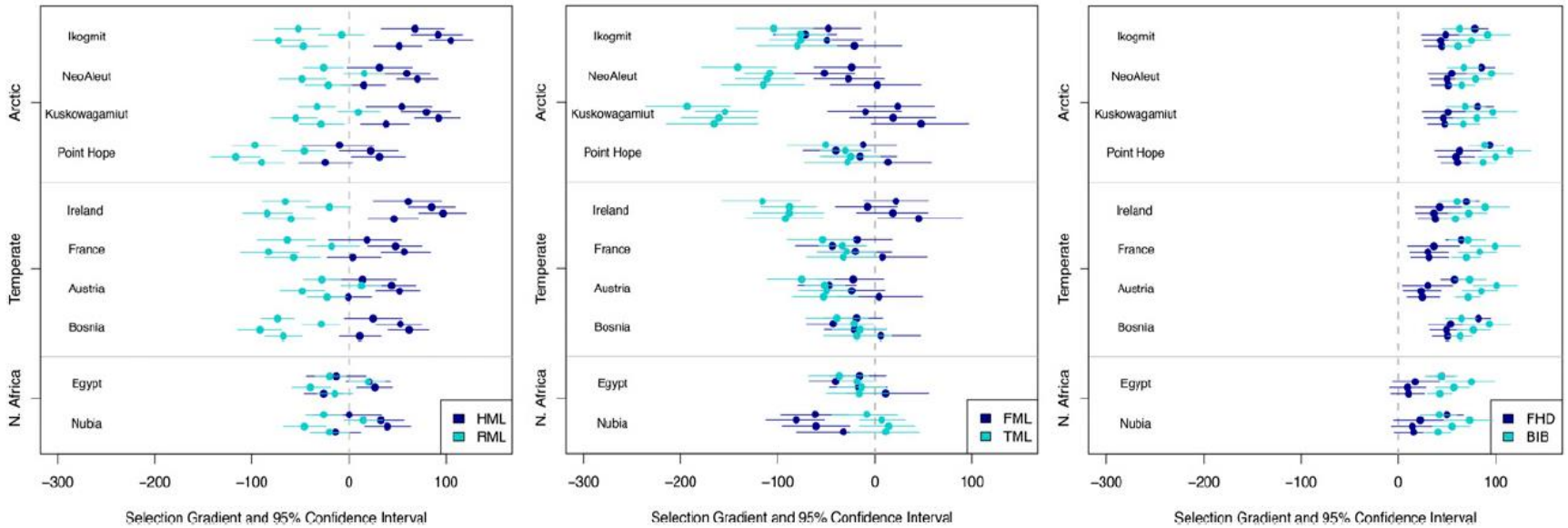

Figure 5. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of traits between sub-Saharan African groups and higher latitude groups. See legends in each figure for traits (Table 1). CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated). See Figures S5-S13 (Appendix I) for more detailed versions of these figures.

We interpret selection gradients whose 95% CIs do not encompass zero to show evidence of directional selection on a trait. Figures S5-S13 (Appendix I) present larger versions of Figure 5.

Humeral length tends to demonstrate positive selection gradients and radial length negative selection gradients in comparisons between the sub-Saharan groups and those of the temperate and circumpolar regions (Figure 5, left panel). The majority of CIs for femoral length overlap with zero regardless of interregional comparison, indicating little or no detectable directional selection (Figure 5, middle panel).

Tibial length displays negative selection gradients in among-group comparisons between the sub-Saharan groups and those of both the temperate and arctic regions (Figure 5, middle panel). Femoral head diameter and bi-iliac breadth generally show positive selection gradients across pairs of groups in different climate areas (Figure 5, right panel). Only the CIs for femoral head gradients estimated for groups in North Africa overlap with zero. The general trends are presented graphically in Figure 3b, which compares the consensus pattern of directional selection from our analysis against the ecogeographic predictions shown in Figure 3a.

Although the majority (27 of 40) of between-group comparisons show no directional selection in the femur, when directional selection for femoral length is estimated between groups, it is negative in all but one instance (12 of 13 gradients; see Figure 5). As noted above, more groups exhibit directional selection in humeral length, radial length, and tibial length from temperate to arctic ecogeographic regions. For example, four of eight comparisons between groups in sub-Saharan Africa and those in North Africa show directional selection in the humerus, while 10 of 16 comparisons between sub-Saharan and temperate groups and 12 of 16 sub-Saharan and arctic groups demonstrate directional selection in humeral lengths. This trend is not present in the two other dimensions (femoral head diameter and bi-iliac breadth).

Humeral length is shorter, on average, in groups from temperate and arctic regions than those in sub-Saharan Africa, but the selection gradients for humeral length are positive. Positive directional selection is opposite to ecogeographic expectations (Table 1; Ruff 1991, Holliday 1999). These results are illustrated in Tables 2a-c, which present examples of pairwise

comparisons between groups from sub-Saharan Africa and groups from each of the other regions. All pairwise comparisons between groups are reported in Tables S1a-nn (Appendix I).

The direction of net responses to selection generally matches the direction of differences in trait means between pairs of groups. Similar opposing gradients and responses in the femur are associated with selection gradients not statistically different from zero, so we do not offer an interpretation of them (Figure 5). An examination of the trait-specific contribution to the net response to selection in the humerus (Tables 2a-c: Δz_{HML}) shows that were humerus length independent of the other five traits, it would respond to selection by lengthening among groups from higher latitudes. However, this is clearly not the case.

The response to selection in the humerus is greatly attenuated by the correlated response to selection between the tibia and the radius with the humerus, respectively. The shared direction of the selection gradients, net response to selection, and direct response to selection for both the radius and tibia indicate a relationship between fitness and shorter distal limb segment lengths as latitude increases.

Discussion

We show strong evidence for directional selection on many of the traits, which are hypothesized to vary among humans as a result of climatic adaptation under the ecogeographic model. However, the magnitude and orientation of directional selection across the traits often does not match the pattern and magnitude of morphological change. Changes in trait means among regions (Table 1) do not mean selection was acting directly on those traits, or that the force of selection was the same as the direction of difference in means. This is especially apparent in the limb segment lengths, where genetic covariation among elements, especially with the tibia, diminishes the response to directional selection acting directly on those traits. Observed mean trait differences between groups may not be good indicators of what aspects of morphology most closely and directly covaried with fitness during the evolution of group differences (Ackermann & Cheverud 2000, Grabowski 2013, Rolian et al. 2010, Lande & Arnold

1983, Houle 1991, Arnold 1992, Hansen & Houle 2008). The evolution of morphology is a whole-organism problem (Houle et al. 2010).

The analysis of covariance among traits is the best predictor for how genetically complex traits have evolved. Limbs have a complex polygenic basis. They are found to be highly genetically correlated and exhibit strong pleiotropy when studied in a quantitative genetic framework (Rolian 2014, Leamy 1977, Leamy et al. 2002, Norgard et al. 2011). When sample sizes are sufficient to render precise estimates of genetic correlations for morphological characters, the genetic and phenotypic correlations are nearly identical, implying a high degree of proportionality between genetic and phenotypic covariance structures (Cheverud 1988, Hallgrimsson et al. 2009). Any pattern of covariation among traits can be caused by many different combinations of genetic variants acting through a variety of developmental processes (Hallgrimsson et al. 2009, Mitteroecker & Bookstein 2009). Over short evolutionary time scales, such as those over which recent human diversity evolved, an estimate of covariation gives us our best estimate of the tendency of traits to evolve together in response to processes of evolution and do not require a deep understanding of the developmental processes underlying limb development. This is not to downplay the important ways in which development and evolutionary forces conspire to change the presentation of covariation in populations over longer evolutionary time scales (Young et al. 2010).

Which Traits Were Directly Affected by Directional Selection?

Previous ecogeographic studies presumed that differences in trait means between groups reflected the direction of selection gradients. Both femoral head diameter and bi-iliac breadth are consistent with this assumption, having positive selection gradients and positive net responses to selection (Roseman & Auerbach 2015, Ruff 1994, Auerbach 2012). Ruff (1994) argued that pelvic breadth serves as a proxy dimension for surface area-to-volume ratios, and therefore is evolving in response to thermoregulatory requirements. Ecogeographic models also argue that larger body masses at increasing latitude are more fit (Ruff 1994), a trend our results support if femoral head size is a good proxy for body mass (Ruff et al. 1991, Auerbach &

Ruff 2004). We cannot test the mechanistic aspects of these models in our study, though our results support the argument that pelvic breadth and femoral head diameter were under and responded to natural selection, even in comparisons between groups from sub-Saharan Africa and North Africa.

In combination with the results of earlier studies, our findings generally show that three of the four limb segment lengths vary among humans in part because of directional natural selection (Roseman & Auerbach 2015, Ruff 1994, Holliday 1997, Holliday & Ruff 2001). The differences between group means, however, are not the same as what we would expect based on the selection gradients we calculate, especially in the humerus. These results show that while many of the traits we observe evolved by directional selection, the differences in trait means among groups are not proportional to the force of directional selection on each trait independently. Were it not for the covariance among traits, we might expect greater differences and different patterns of evolution in traits.

Which Traits Evolved by Correlated Responses to Directional Selection Acting on Other Traits?

Correlated responses to directional selection arising from covariance between the tibia and other limb elements dramatically affected responses of limb elements to directional selection. This relationship is particularly notable in the humerus. As shown in Tables 2a-c, directional selection on the tibia and radius, in combination with weak selection on the femur, cause a strong correlated negative response on the humerus. This overwhelms the response generated by the positive net relationship between fitness and humeral length. Specifically, selection on the distal traits counteracts the response of humeral length to the directional selection that is acting on it. The action and response to selection for the distal elements correspond with expectations from the ecogeographic literature (Figure 3).

Our findings highlight the ways in which evolutionary trajectories favored by natural selection can be constrained by covariation, even when all directions in a morphospace have some variation (Hansen & Houle 2004, Walsh & Blows 2009). Covariances among aspects of body form we include in this study do not covary so tightly that there are directions in their

morphospace with no variation (i.e. our covariance matrix is positive-definite), thus we are not presented with a hard variational constraint. Since the prevailing action of directional selection on the humerus (to lengthen) and the radius and tibia (to shorten) have opposite signs, the net response to selection for individual traits are constrained by the action of selection on other traits. Distal limb elements did not evolve as quickly as they might were they independent and the humerus evolved in a direction opposite to its contribution to increasing fitness.

An important point to recognize here is that we do not exhaustively cover all dimensions of body form, some of which might be more directly tied to fitness differences than the ones we do consider. It is entirely possible that the strong selection gradients that we estimate from comparisons of groups in sub-Saharan Africa and those in the arctic are driven by selection on some unmeasured aspect of body form (or physiology) genetically correlated with both humeral length and overall form. While this is certainly the case, our analyses cannot account for characteristics we did not measure. Nonetheless, our analyses considerably narrow the space of possible models that could be used (e.g., models that go beyond mean trait comparison) and gives a guide as to which traits we might consider in the future (Arnold 1983). Studies of humerus to body size allometry suggest a possible direction in which this study might be taken (Auerbach & Sylvester 2011).

Our study's results concerning directional selection for the humerus, femoral head, and femur differ in some respects from those reported by Roseman and Auerbach (2015). They showed equivalent performance for models including population structure on one hand, and both population structure and latitude on the other, as the explanation for among-group variance in the humerus. Their study (Roseman & Auerbach 2015) used the global sample of 121 groups, while we selected 14 groups from that sample for our study. The consistency of results among the many pairwise comparisons we made between sub-Saharan groups and those from other latitudes (Tables S1a-S2nn) argues against sampling bias. We attribute much of the discrepancy in results reported in this study with those in Roseman and Auerbach (2015) to differences between the univariate approach used by the latter, where each trait was examined in isolation, and the multivariate approach in this study. As we show, the covariation

of traits within an evolutionary framework affects the capacity of those traits to respond to directional selection. A multivariate approach avails us of the ability to apprehend otherwise cryptic evolutionary processes.

Conclusions

Directional selection has contributed to the differentiation of the tibia, radius, femoral head, and bi-iliac breadth among human groups from different ecogeographic contexts. In some respects, these results accord well with previous ecogeographic studies. More importantly, however, we show that differences in trait averages among groups are not good indicators of how traits responded to natural selection. Notably, because selection acted on correlated traits, the humerus shows an evolutionary response to directional selection opposite to its influence on fitness. Patterns of mean difference among groups are not necessarily an accurate reflection of the processes that created that variation.

The ecogeographic literature is silent when it comes to the fitness effects of humeral length, which are only apparent after taking into account covariance among traits. By focusing only on realized differences between groups, traditional adaptationist ways of studying ecogeographic variation have left the ways in which natural selection acted undescribed. Natural selection's effect on the humerus would not be apparent from a standard adaptationist perspective focused on explaining evolution using group differences on a trait-by-trait basis.

Transition from Chapter II to Chapter IIII

In the previous chapter (Chapter II), we demonstrate that covariation between postcranial traits has a substantial impact on how they response to directional selection. Although we show that certain traits are under directional selection that matches ecogeographic expectations (distal limb segments predicted to shorten at higher latitudes, and measures of body size to elongate), it appears the humerus is only shortening with increasing latitude as a result of its correlation with the distal limb lengths. When considered independently, the humerus is under directional selection to lengthen – a finding in direct opposition to expectations founded in the thermoregulatory model of human postcranial variation, and in contrast to the distribution of humeral length across ecogeographic regions. Similarly, the femur – also observed to shorten in higher latitude populations – does not appear to be under directional selection, and instead seems to vary with population structure alone. This study highlights the importance of assessing evolutionary trends within a multivariate framework that accounts for trait covariation, rather than relying on correlations between environmental variables and trait means.

The next chapter further explores the covariance structure between these traits by assessing the degree to which they vary across human groups. By comparing the variance-covariance matrices between human groups, we assume that these groups are equally evolvable. However, a decrease in additive genetic variance with increasing distance from Africa has been demonstrated as a product of the serial founder model of out-of-Africa migration attributed to ancient humans. In Chapter III, I therefore compare estimated indices of evolvability for 14 human groups across four ecogeographic regions against two contrasting hypotheses: 1. that humans will demonstrate equal evolvability across regions as a result of humanity's comparatively short evolutionary history, or 2. that human evolvability in these postcranial traits will decrease with latitude (migratory distance from Africa) as a result of a loss of genetic variance associated with migration and/or selective pressure.

CHAPTER III

EVOLVABILITY IN HUMAN POSTCRANIAL TRAITS ACROSS ECOGEOGRAPHIC REGIONS

Abstract

The diversity of modern human postcranial variation has long been attributed to thermoregulatory adaptation. Recent quantitative genetic research has demonstrated that directional selection appears to be acting on several of the traditional traits of interest (limb lengths and measures of body size) as expected, potentially supporting the thermoregulatory model of human evolution. However, such studies are founded on the assumption that all human groups are able to respond to selection equally, allowing for comparison between groups. However, differences in trait covariance structure due to ancient migration patterns, as well as the role of selection in decreasing additive genetic variance, may be limiting the evolvability of populations further from our African origins.

To explore this possibility, variance-covariance matrices were used to calculate the mean evolvability, respondability, conditional evolvability, and autonomy for four ecogeographic regions comprised of 14 groups. Using recently developed algorithms for determining the minimum sample sizes required for calculating indices of evolvability, it was determined that even relatively large individual groups (n = 151) provided only fair representation, and that accurate analyses of evolvability could only be conducted at the regional level. When compared between ecogeographic regions, humans do not demonstrate significant differences between indices of evolvability, possibly a result of modern humans' short evolutionary history; there simply hasn't been time for differentiation. There is evidence, however, of potentially emergent trends in evolvability across regions. Both mean evolvability and respondability show a strong negative correlation with latitude across regions, while mean autonomy is positively correlated with latitude. These patterns all correspond with a reduction in genetic variance potentially reflective of ancient human migration and/or the increased constraints associated with selective pressure.

Taken together, these findings confirm that human groups share a similar covariance structure, while also demonstrating possible emerging patterns that reinforce growing evidence of the role of selection on shaping human postcranial diversity at higher latitudes. In addition, these results argue for the importance of establishing patterns of evolvability in populations

before conducting further quantitative genetic analyses, as well as highlighting the influence of sample size on the accuracy of estimated indices of evolvability.

Introduction

Modern humans express variation in body form that corresponds with geography and climate (ecogeography) (Roberts 1978, Ruff 1994). With some exceptions (Hiernaux & Froment 1976, Holliday 1999, Auerbach 2012), human postcranial variation adheres to the expectations of Bergmann's (1847) and Allen's (1877) ecogeographic "rules"; these patterns have traditionally been explained as the result of thermoregulatory adaptation (Trinkaus 1981, Ruff 1991, Ruff 1994, Holliday 1997, Holliday 1999, Holliday & Ruff 2001, Auerbach 2012). This theory suggests that humans in warmer environments evolved narrower bodies and longer limbs to maximize surface area and allow for more efficient heat dissipation, while humans in colder climates evolved wider bodies and shorter extremities to decrease the surface area-to-body size ratio, minimizing heat loss (Scholander 1955, Ruff 1991, Ruff 1994). Traditionally, these studies relied on identifying correlations of human morphological variation with geography – namely latitude – and ascribed evolutionary causes (i.e., adaptation) to explain the eco-morphological relationship. More recently, research using quantitative genetic analytical methods has demonstrated that observed trait variation evolved in response to a combination of gene flow, genetic drift, and natural selection (Madrigal & Willoughby 2010, Betti et al. 2012, Betti et al. 2015, Roseman & Auerbach 2015, Savell et al. 2016). The current study builds on this literature to examine whether humans living across a global range of ecogeographic regions exhibit differences in the ability of body size and shape to respond to natural selection.

The study of ecogeographic variation in human body form has traditionally focused on limb segment lengths and measures of body breadth and body size (Trinkaus 1981, Ruff 1994, Holliday 1997). These traits are thought to reflect the ability of the body to dissipate heat though surface area (Ruff 1994) and have largely been examined individually (cf. Holliday 1999). However, recent studies have used multivariate approaches to explore how evolutionary covariance between traits affects the evolution of human postcranial variation (Savell et al.

2016, Chapter II). As has been frequently discussed in the evolutionary biology literature (Lande 1979, Lande & Arnold 1983, Arnold 1983, Hansen & Houle 2008, Walsh & Blows 2009, Rolian 2014), multivariate approaches allow for a more accurate understanding of evolutionary change, as individual traits are unable to evolve without affecting other associated traits in the same organism. The ability of a single trait to respond to its own specific selective pressure is constrained by the covariance structure it shares with other traits, the result of differing degrees of functional and developmental integration (Hallgrimmson et al. 2009, Rolian 2014). Trait covariance arising from these integrative mechanisms will ultimately constrain or promote the ability of other traits to respond to evolutionary forces (namely directional natural selection).

A recent study by Savell and colleagues (2016) provides an explicit analysis of these relationships by examining the effect of constraints imposed by trait covariance on trait evolution using a global sample of humans (Chapter II). This work contributes to a growing body of process-based research confirming that human postcranial variation is shaped both by selective pressures that differ across ecogeographic regions (Madrigal & Willoughby 2010, Betti et al. 2013, Roseman & Auerbach 2015), as well as by patterns of co-evolution between traits. Using a quantitative genetic approach, Savell and colleagues (2016) estimated the force of directional selection on the six traits most commonly used in the assessment of ecogeographic variation and thermoregulatory adaptation. They found that four of the six traits (radial maximum length, tibial maximum length, femoral head diameter, and bi-iliac breadth) demonstrated responses to directional selection across regions in accordance with ecogeographic expectations, while evolution in femoral length was best ascribed as a response to neutral processes (e.g., genetic drift, gene flow, and/or stabilizing selection).

Most unexpected, given observed patterns of morphological variation across geography, was their finding that humeral length was under directional selection to lengthen in human groups at increasing latitudes. This was unanticipated as observed humeral length displays an inverse relationship with latitude. Savell et al. (2016) concluded that constraints imposed by covariation with other traits under directional selection (namely the tibial and radial lengths)

were affecting the response of the humerus to selection. Thus, their study demonstrated how covariation between traits can considerably affect the ability of certain elements to evolve in response to their own, trait-specific selective pressures.

It should be noted, however, that by comparing multivariate responses to directional selection between human groups, we implicitly assume that the groups in question are identically evolvable. Evolvability is the response of a trait or traits to selection per the strength of selection (Hansen & Houle 2008, Hansen et al. 2011, Rolian 2014), or more simply, the ability of traits to change in the direction of selection (Bolstad et al. 2014). Human migration patterns, however, may complicate this assumption. The serial-founder expansion of humans out of Africa has been demonstrated to cause a decrease in overall genetic variance with increasing geographic (migratory) distance from Africa (Prugnolle et al. 2005, Ramachandran et al. 2005, Liu et al. 2006, Hunley et al. 2009, DeGiorgio et al. 2009). The population structure resulting from this pattern of migration tracks closely with the same ecogeographic clines associated with Bergmann's (1847) and Allen's (1877) rules (Roseman 2004, von Cramon-Taubadel & Lycett 2008, Betti et al. 2009, Roseman & Auerbach 2015). It is therefore possible that as humans expanded across the globe, the loss of genetic variance associated with numerous serial founder effects may have resulted in reduced evolvability in groups that settled further from our African origins. As is reviewed below, reductions in genetic variance within a population are likely to lead to reductions in morphological variation. This, in turn, could reduce the ability of traits to respond to selective pressures (Falconer and MacKay 1996), assuming the axis of the reduced variance does not lie in the same plane as the direction of selection toward an optimum (see Schluter 1996, Rolian 2014).

This study examines the hypothesis that humans at higher latitudes will express lower evolvability in the six traits examined in Savell et al. (2016): humerus, radius, femur, and tibia maximum lengths (extremity lengths); femoral head diameter (a proxy for body size; Ruff et al. 1991, Auerbach and Ruff 2004); and bi-iliac breadth (a measure of relative surface area; Ruff 1994). In addition to evolvability, I examine related indices: respondability, conditional evolvability, and autonomy.

Genetic Variance and Indices of Evolvability

The amount of genetic variance within a population is argued to correspond with the ability of that population to respond to novel environments and concomitant selection pressures (Falconer and MacKay 1996). Researchers are generally interested in the additive genetic variance within a population, which is either mean-scaled (e.g., Grabowski et al. 2011), or, more often, scaled against the population's total phenotypic variance; narrow sense heritability (h^2) is calculated as the additive genetic variance of traits divided by the total phenotypic variance. However, Hansen et al. (2011) demonstrated that narrow sense heritability of traits has no correlation with evolvability. That is, while the amount of total genetic variance in a population should predict the ability of traits to respond to selection, this relationship becomes evolutionarily meaningless if total genetic variance is scaled by total phenotypic variance. Phenotypic variance includes additional variance contributed by the environment and epistasis (among other factors) independent of the response of a trait to directional selection, meaning that phenotypic variance and heritability are poor measures of evolutionary potential (Hansen et al. 2011, see Chapter I: "*Variation and heritability*"). Thus, while modern humans have experienced multiple bottleneck events that have reduced genetic variation in some groups relative to others, it is possible that all human groups maintain similar trait evolvability.

This study examines four indices of evolvability. In addition to evolvability, which is defined above, the study also examines respondability, conditional evolvability, and autonomy. Respondability measures the ability of traits to change in response to selection; this effectively examines whether the orientation of greatest genetic variance within a population aligns with the direction selection is acting to drive traits toward an adaptive optimum. Conditional evolvability measures the ability of traits to change in the direction of selection when stabilizing selection restricts change in other directions. Autonomy – the proportion of evolvability that remains on a single trait when conditioning on other traits is taken into consideration – is effectively a measure of constraint (Hansen & Houle 2008, Marriog et al. 2009, Bolstad et al. 2014, Rolian 2014).

Indices of evolvability are usually estimated in the exploration of underlying diversity in trait covariation between taxa (Marriog et al. 2009, Grabowski et al. 2011, Young et al. 2010, Rolian et al. 2009), but are also appropriate for examining differences in the variance-covariance structures between groups within a species (Rolian 2014). The short evolutionary history of modern humans and particular pattern of global dispersion leads to at least two possible patterns of postcranial evolvability across groups:

1. Human groups across ecogeographic regions may have similar indices simply because not enough time has passed to differentiate within-group evolutionary potential. Relative to the total evolutionary history of *Homo*, anatomically modern humans have existed for an incredibly short period of time, which may mean that all humans – regardless of migration patterns or recent ancestry – are so closely related that all indices of evolvability will be fundamentally identical across groups and regions.
2. Human groups across ecogeographic regions may demonstrate reduced measures of evolvability with increased distance from Africa as a result of decreased genetic variance associated with migratory patterns.

Given the short evolutionary history of *Homo sapiens*, as well as continued gene flow among groups (which increases genetic variance), it is anticipated that evolvability indices will not be statistically different among human groups from different ecogeographic regions, despite lower genetic variance with distance from the equator.

Material and Methods

Materials

To estimate indices of evolvability for human groups spanning four broad ecogeographic regions (as defined in Savell et al. 2016)— Sub-Saharan Africa, North Africa, Temperate Europe, Circumpolar Arctic—a large, globally-dispersed sample of human phenotypic variation is

required. To this end, osteometric data was compiled from the Goldman Data Set (Auerbach & Ruff 2004), the Americas Data Set (Auerbach 2012), and datasets generously provided by Drs. Trent Holliday and Chris Ruff (Roseman & Auerbach 2015, Savell et al. 2016). When combined, individuals with indeterminate sex, poor provenience, and duplicated entries were removed (Roseman & Auerbach 2015). The dataset used here consists of 875 individuals (522 males, 353 females) representing 14 groups from four ecogeographic regions (Table 3; Figure 6). With one exception, these are the same 14 groups used by Savell et al. (2016) (Chapter II), and were selected to represent the full range of latitudes settled by humans, while matching the distribution of latitudes often studied in the ecogeographic literature. The only exception is Bavarian Germany, which was chosen to replace Ireland because of the larger sample size. Each ecogeographic region is represented by a clustered subset of these 14 groups (Figure 6), providing a range of means for each trait of interest (Table 3).

Since patterns of ecogeographic variation have traditionally been examined using various measures of limb segment length and body size (Trinkaus 1981, Ruff 1991, Ruff 1994, Auerbach & Ruff 2004, Auerbach 2007), the six dimensions used in this study are the maximum humeral, radial, femoral, and tibial lengths, as well as femoral head diameter and bi-iliac breadth (Ruff et al. 1991, Ruff 1994, Auerbach & Ruff 2004). Using these measurements not only allows for comparison with the foundational literature of human ecogeographic variation, but permits interpretation within the covariation framework established by Savell et al. (2016). All dimensions were measured in millimeters and limb lengths have been averaged to minimize the potential noise of bilateral asymmetry (Auerbach & Ruff 2006, Roseman & Auerbach 2015). Inter-observer error between measurements was assessed at less than one percent (Auerbach 2007).

Methods – Indices of Evolvability and Confidence Intervals

Indices of evolvability are estimated from phenotypic covariation among multiple correlated traits. Variance-covariance matrices quantify this covariation and are commonly used in the study of evolutionary relationships in biology (Harmon & Gibson 2006, Kolbe et al. 2011,

Table 3. Groups and region names, latitude, sample size (N), and number of non-singular variance-covariance matrices used to calculate 95% confidence intervals (out of 1000 resampling attempts)

Region	Mean Lat.	N Region	CI Sample	Group	Latitude	N Group	CI Sample
Sub-Saharan Africa	-4.49	104	1000	San	-27.22	37	26*
				Kikuyu	0.00	30	1000
				Uganda	0.31	16	995
				West African	8.96	21	1000
North Africa	26.40	206	1000	Nubia	22.79	55	1000
				Egypt	30.01	151	1000
Temperate Europe	47.19	338	1000	Bosnia	42.71	79	1000
				Austria	48.37	77	1000
				Germany	48.82	145	1000
				France	48.86	37	924
Circumpolar Arctic	60.42	227	1000	NeoAleut	51.50	60	1000
				Kuskowagamiut	60.28	28	1000
				Ikogmiut	61.57	60	1000
				Point Hope	68.34	79	1000

*The San are not included in discussions of between-group confidence due to poor resampling

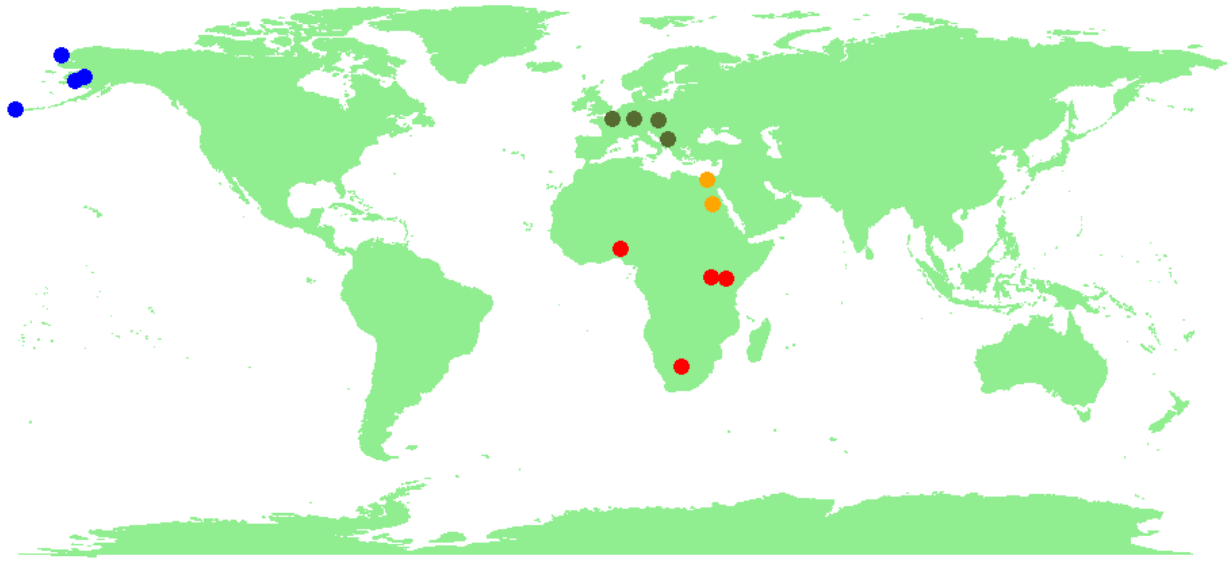

Figure 6. Plot of locations of all groups sampled for trait data. Indices of evolvability were calculated for each of the 14 groups represented (dot), as well as the 4 regions distinguished by color (red: sub-Saharan Africa, yellow: North Africa, green: Temperate Europe, blue: Circumpolar Arctic).

Pitchers et al. 2013, Houle & Fierst 2013) and biological anthropology (Gonzalez-Jose et al. 2004, Rolian 2009, Roseman et al. 2010, Roseman & Auerbach 2015, Savell et al. 2016).These matrices capture both the variance within a given trait, as well as the covariation of a given trait with each other trait included in the analysis.

Genotypic variance-covariance matrices are notoriously difficult to determine and phenotypic variance-covariance matrices, which are understood to be proportional to genotypic variance-covariance matrices, are often used in their place (Cheverud 1988, Roff 1995, Ackermann & Cheverud 2000, Marriog & Cheverud 2001, Ackermann & Cheverud 2004, Sodini et al. 2018). As such, this study calculates mean-standardized phenotypic variance-covariance matrices for each individual group (n = 14) and ecogeographic region (n = 4) to estimate indices of evolvability. Differences due to sex were controlled by applying a multivariate analysis of variance (MANOVA) to each group or regional variance-covariance matrix.

Evolvability measures were estimated following the equations set out by Hansen and Houle (2008). Their methods are derived from Lande's equation for multivariate response to selection ($\Delta\bar{z} = G\beta$) (Lande 1979, Lande & Arnold 1983), where $\Delta\bar{z}$ represents the change in mean phenotype values, *G* the additive genetic variance-covariance matrix, and β a vector of selection gradients. Using Hansen and Houle's (2008) approach, multivariate evolvability is estimated along selection gradients (Figure 1). Directional selection gradients (β) provide one of several ways to denote natural selection, and consist of a row vector of partial regression coefficients of fitness on each trait in a multivariate system. In other words, each element of the selection gradient represents the increase in fitness resulting from a per unit increase in a given trait, assuming all other traits are held constant (Lande & Arnold 1983, Arnold 1983, Hansen & Houle 2008). The selection gradient can therefore be interpreted as summarizing the magnitude and direction in which selection acts on each trait (Hansen & Houle 2008, Rolian 2009). To determine average evolvability, a range of possible selection gradients for a trait must be used. These are obtained by subjecting the phenotypic variance-covariance matrices to 1,000 symmetrically distributed, randomly generated selection gradients, each element of

which was independently sampled from a univariate Gaussian distribution with a mean of zero and unit variance. Each selection gradient was then normalized by unit length (Bolstad et al. 2014). Indices of evolvability were calculated following Hansen and Houle (2008), using the R package "evolvability" (Table 4) (Bolstad et al. 2014). Since latitude is commonly used as proxy for climactic differences in ecogeographic studies, and as it parallels human patterns of migration out of sub-Saharan Africa for this sample, correlations were determined between latitude and mean evolvability, respondability, conditional evolvability, and autonomy for each individual group and region.

Table 4. Equations to calculate evolvability measures (Hansen & Houle 2008, Bolstad et al. 2014)

Index of Evolvability	Symbol	Equation
Mean evolvability	*e(β)*	$\mathrm{E}[\beta' \mathrm{P} \beta]$
Mean respondability	*r(β)*	$\mathrm{E}[\sqrt{(\beta' \mathrm{P}^2 \beta)}]$
Mean conditional evolvability	*c(β)*	$\mathrm{E}[(\beta' \mathrm{P}^{-1} \beta)^{-1}]$
Mean autonomy	*a(β)*	$\mathrm{E}[c/e]$

To examine results between groups and across ecogeographic regions, 95% confidence intervals (CI) were calculated by resampling the data for each group or region 1,000 times with replacement and estimating indices of evolvability for each resampled iteration. Due to missing data, the variance-covariance matrices of some resampled iterations were essentially singular and were unable to be used in establishing confidence intervals (see Table 3 for the number of iterations used to determine confidence intervals for each group and region). The San, whose considerable missing data resulted in only 26 non-singular variance-covariance matrices out of the 1,000 resampled, are not included in the discussion of between-group differences.

Methods – Sample Size and Inaccuracy

As Grabowski and Porto (2017) have demonstrated, sample size is crucial when estimating indices of evolvability. They determined that the minimum sample size required to accurately calculate indices of evolvability vary based on the number of traits used and the population-specific level of integration (r^2) between traits. In the current study, minimum suggested sample sizes for each group and region were estimated using the equations and R code provided by Grabowski and Porto (2017).

This method of sample size estimation relies on known population integration and trait number. To develop a range of potential suggested sample sizes, four estimates were produced. These four minimum sample sizes were estimated based on the highest (San, r^2 = 0.584) and lowest (West African, r^2 = 0.378) levels of integration across groups and regions, for both n = 6 and n = 10 traits (Table 5a). Although this study only includes six traits, Grabowski and Porto (2017) recommend against using their method for less than 10 or more than 90 traits. To be as conservative as possible in comparing differences between evolvability indices, both trait numbers were included in determining minimum sample size. Groups and regions were then assessed on their adherence to these suggested sample sizes. A group or regions' sample size was considered "good" if it surpassed the highest of the four minimum sample size recommendations, "fair" if its sample size fell within the range of the lowest and highest of the suggested sample sizes, and "poor" if its sample size was below the lowest of the suggested sample sizes.

In addition, the expected degree of inaccuracy for each evolvability index was also estimated. Grabowski and Porto (2017) define inaccuracy as the mean squared distance of an estimate of evolvability from the parameter, and argue that the inaccuracy measure incorporates both bias and imprecision due to the effects of sample size and number of traits. Inaccuracy was estimated for the mean evolvability, respondability, and conditional evolvability of each group and region for both six and ten traits, as standardized by each group or regions' respective measure of integration (r^2, see Table 5b). All analyses were performed using the R statistical computing software (https://cran.r-project.org).

Table 5a-b. A range of minimum required sample sizes were estimated using highest and lowest level of integration (r^2) across groups and regions (bolded, asterisk) for both six and ten traits (the number used in the study, and the minimum suggested by Grabowski & Porto 2017). Green indicates a sample size surpassing the highest of the four minimum sample sizes estimated ("good"), yellow indicates a sample size between recommended sample sizes ("fair"), and red indicates sample sizes below the lowest of the estimated sample sizes ("poor").

a.

Integration (r^2)	6 traits	10 traits
0.378, West Africa	77	69
0.584, San	176	139

b.

Region	N Region	r^2 Region	Group	N Group	r^2 Group
Sub-Saharan Africa	104	0.564	San	37	***0.584***
			Kikuyu	30	0.564
			Uganda	16	0.484
			West African	21	***0.378***
North Africa	206	0.420	Nubia	55	0.418
			Egypt	151	0.426
Temperate Europe	338	0.460	Bosnia	79	0.456
			Austria	77	0.485
			Germany	145	0.465
			France	37	0.394
Circumpolar Arctic	227	0.407	NeoAleut	60	0.539
			Kuskowagamiut	28	0.421
			Ikogmiut	60	0.423
			Point Hope	79	0.403

Results

Indices of Evolvability and Confidence Intervals

When examined by group, mean evolvabilities ranged from the lowest, 0.0021 with a 95% confidence interval of 0.0012-0.0026 (Kuskowagamiut), to the highest, 0.0038 with a confidence interval spanning 0.0023 to 0.0058 (Nubia) (Table 6, Figure 7a). There was no correlation between group mean evolvabilities and latitude (r = 0.196, see Table 7). A similar pattern is noted for respondability, as the Kuskowagamiut again demonstrate the lowest mean respondability (0.0032, 95% CI: 0.0018, 0.0044) and the NeoAleut the highest (0.0060, 95% CI: 0.00327, 0.0087), with no correlation between latitude and mean respondability (r = 0.124) (Figure 7b). Mean conditional evolvability and autonomy displayed a higher correlation with latitude (r = 0.447, r = 0.488 respectively), and in both indices the San measured the lowest (*c* = 0.00013, 95% CI: 0.00009, 0.00012; *a* = 0.0864, 95% CI: 0.0606, 0.0926) and Egypt the highest (*c* = 0.00095, 95% CI: 0.00072, 0.00105; *a* = 0.0864, 95% CI: 0.0606, 0.0926) (Table 6, Figures 7c-20d). For estimates of conditional evolvability, several groups demonstrate confidence intervals that fail to contain the mean (Figure 7c), a phenomenon that Grabowski and Porto (2017) associate with bias due to small sample sizes. Indeed, all of the groups displaying this trend had "poor" sample sizes that fell below the lowest of the estimated minimums (Table 5b). Across all group-based indices of evolvability, confidence intervals overlapped substantially, indicating no meaningful differences between groups.

When these indices of evolvability are viewed across ecogeographic regions – sub-Saharan Africa, North Africa, Temperate Europe, and Circumpolar Arctic – a clearer pattern emerges. There are strong negative correlations between latitude and mean evolvability (r = -0.961) and mean respondability (r = - 0.957) (Table 7), as well as a positive relationship between latitude and mean autonomy (r = 0.872) and a weaker negative correlation between latitude and mean conditional evolvability (r = -0.656). For mean evolvability and respondability, the largest measures were found in sub-Saharan Africa (*e* = 0.0044, 95% CI: 0.0033, 0.0054; *r* = 0.0074, 95% CI: 0.0053, 0.0095) while the smallest were found in the circumpolar arctic (*e* = 0.0029, 95% CI: 0.0024, 0.0035; *r* = 0.0045, 95% CI: 0.0036, 0.0056) (Table 6, Figure 8a-b).

Table 6. Mean evolvability, respondability, conditional evolvability, and autonomy by group and region with 95% confidence intervals

Group	***e* (95% CI)**	***r* (95% CI)**	***c* (95% CI)**	***a* (95% CI)**
San	0.00224 (0.00157, 0.00262)	0.00382 (0.00253, 0.00475)	0.000133 (0.000090, 0.000121)	0.0864 (0.0606, 0.0926)
Kikuyu	0.00331 (0.00194, 0.00453)	0.00559 (0.00295, 0.00814)	0.000704 (0.000375, 0.000686)	0.3258 (0.1895, 0.3771)
Uganda	0.00227 (0.00114, 0.00287)	0.00361 (0.00164, 0.00501)	0.000414 (0.000015, 0.000401)	0.2422 (0.0111, 0.2699)
West African	0.00241 (0.00113, 0.00311)	0.00353 (0.00160, 0.00502)	0.000690 (0.000135, 0.000624)	0.3346 (0.0813, 0.3775)
Nubia	0.00381 (0.00227, 0.00578)	0.00589 (0.00330, 0.01003)	0.000809 (0.000533, 0.000836)	0.2722 (0.1779, 0.3455)
Egypt	0.00342 (0.00268, 0.00403)	0.00536 (0.00401, 0.00663)	0.000951 (0.000724, 0.001047)	0.3641 (0.2855, 0.4110)
Bosnia	0.00273 (0.00196, 0.00336)	0.00428 (0.00288, 0.00559)	0.000726 (0.000554, 0.000748)	0.3501 (0.2718, 0.3969)
Austria	0.00319 (0.00243, 0.00387)	0.00508 (0.00364, 0.00650)	0.000754 (0.000536, 0.000809)	0.3201 (0.2351, 0.3633)
Bavarian Germany	0.00357 (0.00287, 0.00415)	0.00562 (0.00433, 0.00683)	0.000864 (0.000705, 0.000932)	0.3210 (0.2628, 0.3651)
France	0.00324 (0.00166, 0.00458)	0.00494 (0.00241, 0.00777)	0.000530 (0.000027, 0.000508)	0.1967 (0.0124, 0.2409)
NeoAleut	0.00346 (0.00201, 0.00479)	0.00596 (0.00327, 0.00870)	0.000597 (0.000356, 0.000596)	0.2727 (0.1759, 0.3117)
Kuskowagamiut	0.00206 (0.00124, 0.00263)	0.00317 (0.00176, 0.00440)	0.000376 (0.000171, 0.000362)	0.2288 (0.1155, 0.2703)
Ikogmiut	0.00283 (0.00192, 0.00366)	0.00442 (0.00282, 0.00612)	0.000682 (0.000468, 0.000706)	0.3115 (0.2182, 0.3507)
Point Hope	0.00259 (0.00181, 0.00335)	0.00403 (0.00262, 0.00555)	0.000833 (0.000593, 0.000877)	0.4225 (0.3225, 0.4603)

Region	***e* (95% CI)**	***r* (95% CI)**	***c* (95% CI)**	***a* (95% CI))**
SubSaharan Africa	0.00440 (0.00329, 0.00541)	0.00742 (0.00529, 0.00952)	0.000925 (0.000710, 0.000965)	0.316 (0.2467, 0.3529)
North Africa	0.00355 (0.00288, 0.00436)	0.00553 (0.00431, 0.00715)	0.000957 (0.000776, 0.001050)	0.349 (0.2828, 0.3962)
Temperate Europe	0.00350 (0.00306, 0.00392)	0.00550 (0.00469, 0.00630)	0.000903 (0.000806, 0.000957)	0.341 (0.3065, 0.3711)
Circumpolar Arctic	0.00293 (0.00242, 0.00347)	0.00454 (0.00359, 0.00560)	0.000870 (0.000749, 0.000930)	0.383 (0.3285, 0.4193)

Table 7. Correlations between latitude and mean indices of evolvability by group and region

	Index of Evolvability	Corr. with Latitude
By Group	Mean evolvability	0.196
	Mean respondability	0.124
	Mean conditional evolvability	0.447
	Mean autonomy	0.488
By Region	Mean evolvability	**-0.961**
	Mean respondability	**-0.957**
	Mean conditional evolvability	-0.656
	Mean autonomy	**0.872**

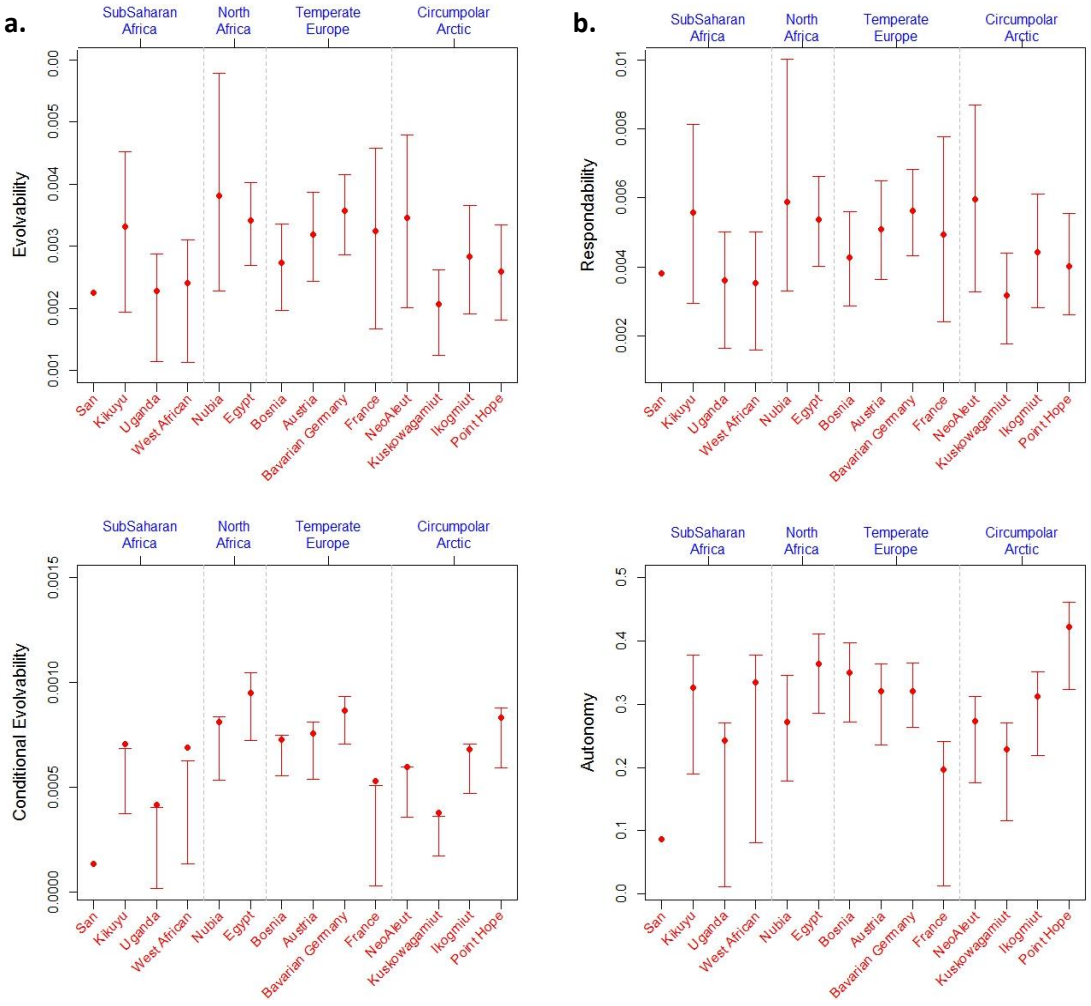

Figure 7a-d. Indices of evolvability by group (dots) with 95% confidence intervals (whiskers). Group names listed in red, region names in blue. 95% CI not displayed for San due to poor replication.

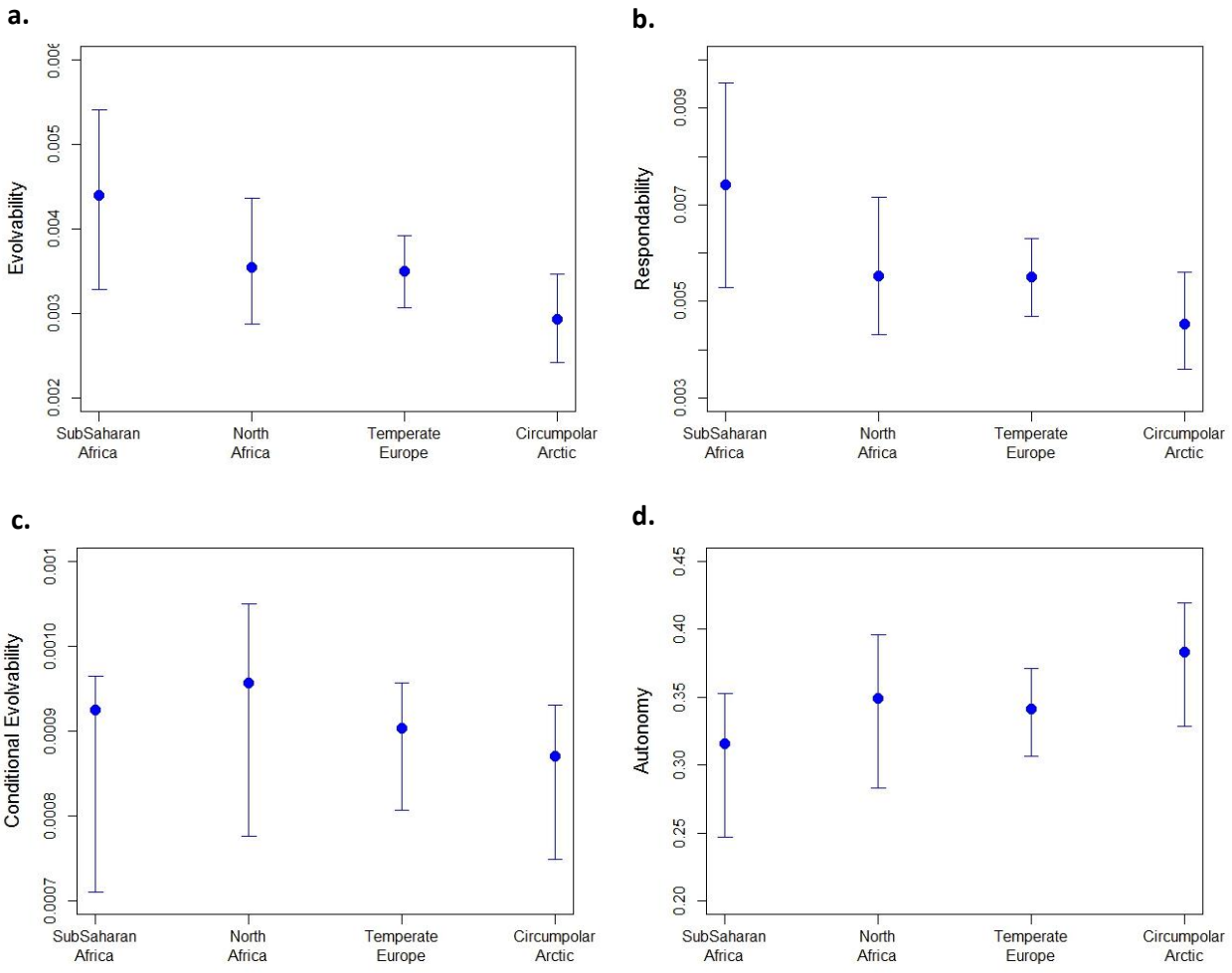

Figure 8a-d. Indices of evolvability by region (dots) with 95% confidence intervals (whiskers).

Despite displaying a strong negative correlation, there is a slight overlap between the confidence intervals of these most extreme areas for both evolvability and respondability.

This was also the case with mean autonomy across regions, which was found to be lowest in sub-Saharan Africa (0.316, 95% CI: 0.247, 0.353) and highest in the circumpolar arctic (0.383, 95% CI: 0.329, 0.419) (Figure 8d). Mean conditional evolvabilities demonstrated the weakest correlation with latitude, as well as significant overlap of confidence intervals. North Africa was found to have the highest mean conditional evolvability at 0.00096, with 95% confidence intervals spanning 0.00071 to 0.00097, and the Circumpolar Arctic had the lowest at 0.00087, with 95% confidence intervals spanning 0.00075 to 0.00093 (Table 6, Figure 8c).

Sample Size and Inaccuracy

Using the lowest morphological integration across groups and regions (West African, r^2 = 0.378) the minimum suggested sample size was 77 for six traits (the number used in the study) and 69 for ten traits (the minimum number Grabowski and Porto suggest). At the largest integration (San, r^2 = 0.584), suggested sample sizes ranged from 176 for six traits to 139 for ten traits (Table 5a).

Groups and regions were defined as having "poor" sample sizes if they had less than the smallest of the suggested sample sizes (n = 69). Nine of the fourteen groups – the San, Kikuyu, Uganda, West African, Nubia, France, NeoAleut, Kuskowagamiut, and Ikogmiut – were found to have poor sample sizes (Table 5b). However, none of the regionally aggregated groups have "poor" sample sizes. "Fair" sample sizes were those that fell between the smallest (n = 69) and largest (n = 176) minimum suggested sample sizes, and included the groups of Egypt, Bosnia, Austria, Germany, and Point Hope, as well as the region of sub-Saharan Africa. The three remaining regions – North Africa, Temperate Europe, and Circumpolar Arctic – all had "good" sample sizes, in that they surpassed the largest of the minimum suggested sample sizes (n = 176). When viewed broadly, the majority of groups had unsatisfactory sample sizes to estimate indices of evolvability for either number of traits, and the highest sample size for groups was n = 151 (Egypt), which still did not meet the most conservative minimum suggested sample size

(n = 176). In contrast, three of the four tested regions did surpass this largest of the minimum suggested sample sizes, with only sub-Saharan Africa having a “fair” sample size of 104 (Table 5b).

As was expected based on differences in sample size, estimated inaccuracies were significantly higher for groups than for regions across all indices of evolvability (Figure 9). Generally speaking, groups with the smallest sample sizes, such as those comprising sub-Saharan Africa, demonstrated higher inaccuracies across evolvability indices regardless of whether six or ten traits were used in the estimation. All regional estimations of indices of evolvability fell well below an inaccuracy of 0.05, excepting the estimation of inaccuracy associated with respondability measures in sub-Saharan Africa (Figure 10). This was true when inaccuracies were measured with either six or ten traits. The number of traits used for estimation did not seem to substantially affect inaccuracy in evolvability, respondability, and conditional evolvability across regions (Figure 10).

Discussion

In addition to exploring the ability of traditional limb length and body size measures to respond to directional selection, this study provides insight into the distribution of postcranial variance across human ecogeographic regions. Results indicate that when sample sizes are satisfactory, humans do not demonstrate significantly different indices of evolvability across regions. However, there do appear to be meaningful trends in the relationship between latitude (averaged within regions) and evolvability, respondability, and autonomy that deserve closer inspection. These trends indicate that patterns of postcranial variance and measures of evolvability do not neatly adhere to either of the suggested hypotheses, but may instead be influenced by a combination of factors, especially migration, gene flow, natural selection, and trait covariation.

To unpack these results, it is helpful to revisit each of the two proposed hypotheses in turn. The first hypothesis stated that humanity’s short evolutionary history, as well as the fact that phenotypic variance is an imperfect (and at times incongruous) measure of additive genetic

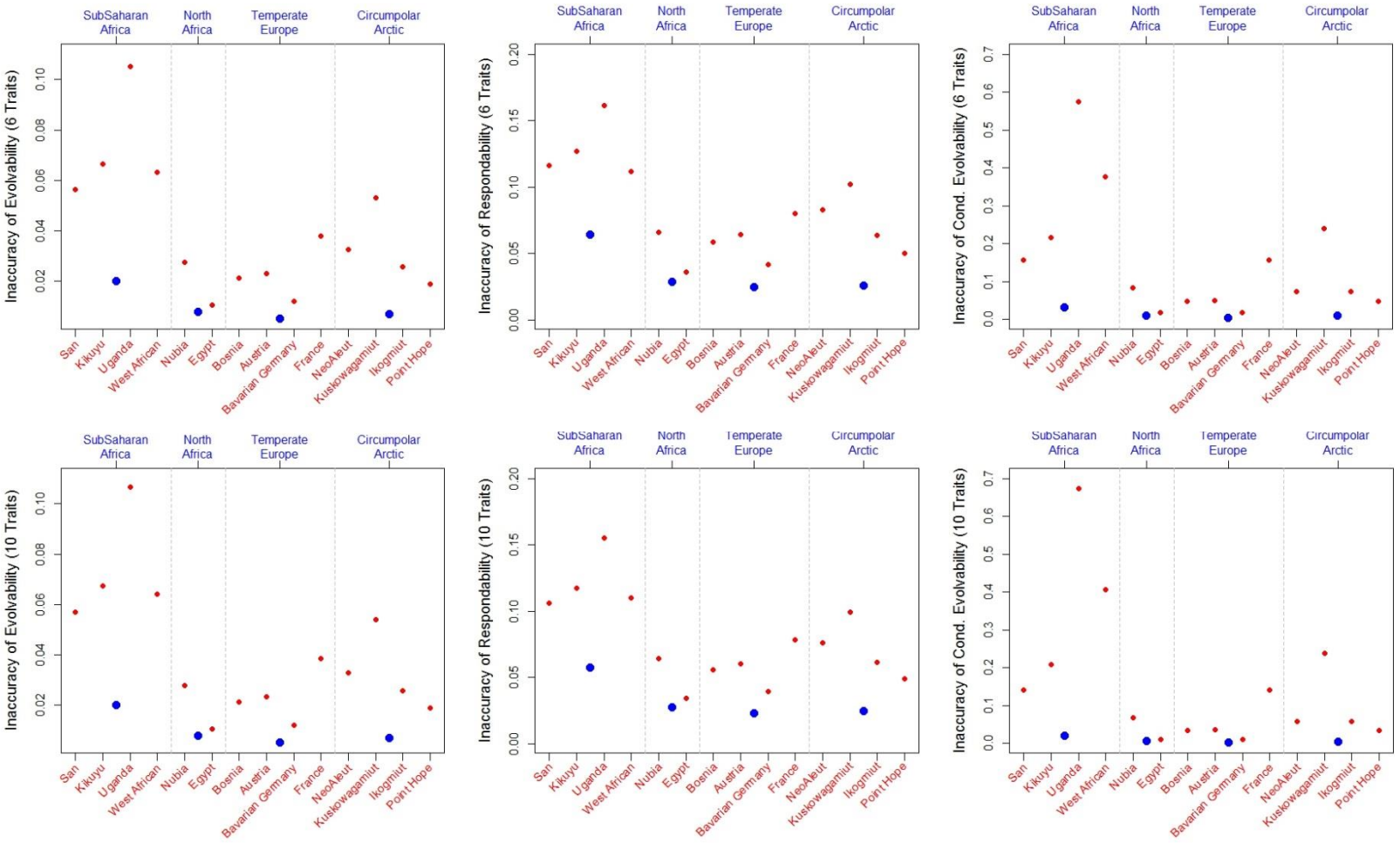

Figure 9. Measures of inaccuracy for mean evolvability, respondability, and conditional evolvability for six and ten traits across groups (red dots), and regions (blue dots).

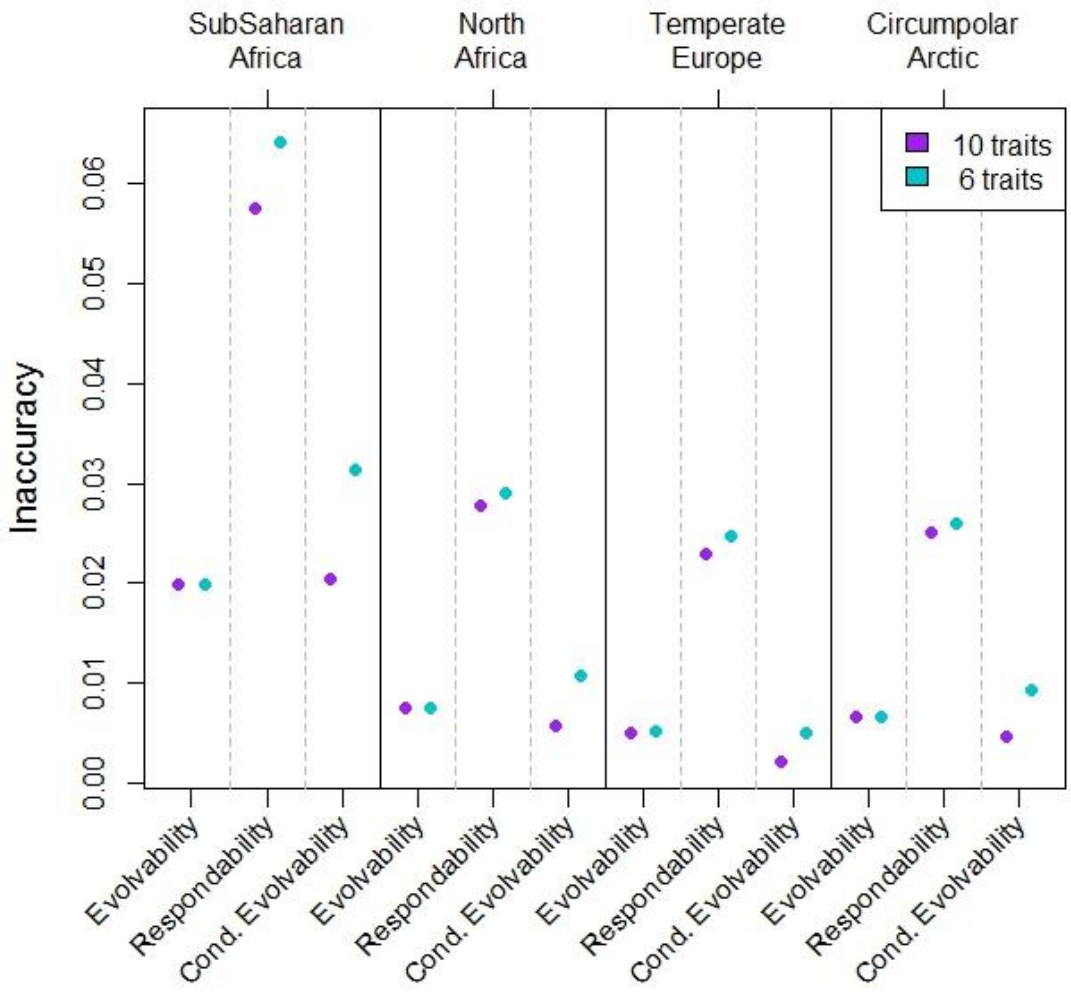

Figure 10. Estimates of inaccuracy for evolvability, respondability, and conditional evolvability for six (teal) and ten (purple) traits across regions.

variance (the real variable of interest) (Hansen et al. 2011), would result in similar trait evolvabilities across ecogeographic regions. This hypothesis is supported, as even the regions with the most extreme differences in latitude, climate, and geographic distances (sub-Saharan Africa and circumpolar Arctic) demonstrate overlap in the 95% confidence intervals for each index of evolvability – they are not significantly different from each other. It is therefore possible that, despite the observed decrease in overall variation associated with a serial founder pattern of migration out of Africa (Prugnolle et al. 2005, Ramachandran et al. 2005, Liu et al. 2006, Hunley et al. 2009, DeGiorgio et al. 2009), changes in the phenotypic variance of the traits in this study resulted not from a concordant decrease in their associated additive genetic variance, but from a decrease in the variance due to environmental, epistatic, and other effects (Houle 1992, Hansen & Houle 2004, Hansen et al. 2011).

Strong similarities in evolvability could be maintained across regions if the additive genetic variance associated with linear measures of long bone length, femoral head diameter, and bi-iliac breadth was also similar, regardless of observed changes in the total phenotypic variance (Hansen et al. 2011). As noted previously, this could be a result of the short evolutionary history of modern humans; perhaps there simply hasn't been enough time for the evolvability of these traits to substantially diverge between regions. It is also possible that indices of evolvability are similar across regions because the variance that was removed due to serial founder effects was replaced by variance-adding mechanisms such as gene flow and mutation (see Chapter I, "Evolutionary Processes"). However, gene flow tends to occur between local groups (Relethford 1994) that would have been similarly affected by serial founder effects, and the variance contributed by mutation is generally understood to be countered by the effects of selection and random genetic drift (Falconer & Mackay 1996).

The second hypothesis of this study proposed that measures of evolvability may be reduced across ecogeographic regions as a result of the decreased genetic variance associated with human patterns of migration. Although the overlap between 95% confidence intervals of the most extreme regions prohibits a claim of statistical significance, the strong correlations between latitude and the means of evolvability, respondability, and autonomy are worth

further exploration (Figure 8a-d). Namely, there is a distinct decrease in evolvability and respondability in traits concordant with regions of increased latitude. Though not indicative of a strong signal of heterogeneity in humans, these observed trends suggest that decreasing genetic variation resulting from human migratory patterns may have influenced the ability of groups in different regions to evolve in response to selective pressures.

It is also possible that the selective pressures themselves play an active role in the observed relationship between measures of evolvability and latitude. Given recent research demonstrating the directional selection to which many of these traits have been subjected (Roseman & Auerbach 2015, Savell et al. 2016), it is likely that these trends partly reflect a reduction in additive genetic variance due to selective pressure (Falconer & Mackay 1996). Measures of limb length (excepting the femur) and body size appear to have adapted, either directly or indirectly, in a manner that matches ecogeographic expectations associated with thermoregulation and latitude (Roseman & Auerbach 2015, Savell et al. 2016). As these traits evolved in response to selective pressures, non-adaptive genetic variance will have been reduced. Savell et al. (2016) demonstrated that estimated selective pressures on these traits were strongest in the circumpolar Arctic region, the same region driving the strong correlations observed in the current study.

As selective pressures push multiple traits towards an adaptive peak, the relationship between these traits can also change, potentially leading to an increase in trait covariation. As discussed above, the strong negative correlation between latitude and mean evolvability/respondability is likely due to human migration and directional selection reducing additive genetic variance. The positive relationship between latitude and mean autonomy is also enlightening. Autonomy effectively functions as a measure of constraint (Hansen & Houle 2008, Marriog et al. 2009, Bolstad et al. 2014, Rolian 2014), and the large positive correlation in constraint across ecogeographic regions suggest that groups in the Arctic, which have undergone the largest directional selective pressures (Savell et al. 2016), also display larger constraints between these traits (Figure 8d).

For traits to be evolvable, two elements must be in place: the existence of additive genetic variance, the various interpretations of which are discussed above; and selection must act along an axis in morphospace that is not constrained, or where the orientation of trait covariance morphospace is able to rotate toward an optimum (Hansen & Houle 2008, Walsh & Blows 2009). When traits do not covary, responses to selective pressure are essentially able to directly follow the path of selection (Box 1; Figure 1 in Rolian 2014, Figure 1 in Savell et al. 2016). Covariation between traits, however, channels response to selective pressure along the major axis of variation. Selection gradients that are perpendicular to the major axis will result in little to no evolution in the covaried traits, whereas selection gradients that parallel the major axis will see significant, large-scale shifts in the direction of selection. Because the limb lengths and body size of groups from the Arctic evolved under the strongest directional selection of the examined regions (Savell et al. 2016), these groups experienced a reduction in additive genetic variance that likely resulted a more constrained covariance structure (shorter minor axes) that is unable to easily shift towards new adaptive peaks. This increase in constraint is reflected in the high mean autonomy (Figure 8d), and low mean evolvability and mean respondability (Figure 8a, b) found in this study. Of the 1,000 randomly-generated selection gradients used to mimic evolution for the regional variance-covariance matrices, the Arctic groups would only be capable of evolving along those gradients that happened to fall in that narrow window, limiting their overall evolvability and respondability.

Unlike the other three indices, conditional evolvability demonstrates no correlation with latitude and the confidence intervals share considerable overlap (Figure 8c). Conditional evolvability reflects the ability of traits to evolve in the direction of selection when stabilizing selection restricts change in every direction orthogonal to the selection gradient (Bolstad et al. 2014). The lack of correlation between latitude and conditional evolvability is perhaps unsurprising, therefore, as groups in all regions share the same pattern (if not strength) of multivariate constraints between these six traits.

Finally, this study supports Grabowski and Portos' (2017) assessment of how sample size influences inaccuracy in estimating indices of evolvability. When viewed across groups within

regions, small sample sizes introduced considerable inaccuracy to the analyses – particularly in estimations of conditional evolvability – limiting interpretation of evolvability indices and latitudinal trends (Table 5, Figure 9). Had this study examined human patterns of evolvability across groups alone, not only would estimations have been highly inaccurate, but the meaningful latitudinal relationships between evolvability, respondability, conditional evolvability, and autonomy found across regions would have been obscured. When groups were merged into representative regions, increased sample sizes met or surpassed Grabowski and Portos' (2017) suggested minimums, and inaccuracies were below 0.5 in all but one case (sub-Saharan African respondability).

Again, it must be emphasized that the observed differences in the indices of evolvability found here represent what is likely an emergent trend in the global dispersal of additive genetic variance and evolvability, but not statistically significant heterogeneity between groups within the four regions. This study uncovered strong correlations between latitude and evolvability, respondability, and autonomy that may be related to the decrease in additive genetic variation. These findings argue for including the estimation and verification of indices of evolvability into future studies comparing evolution across ecogeographic regions. In addition, this research reinforces previous findings that Arctic groups have a disproportionate effect on driving our evolutionary models (discussed in Ruff 1994 and Auerbach 2007). In the context of global variation, Arctic groups may lie at the fringe of human variation and evolutionary response. Results also highlight the influence of sample size on inaccuracy in estimations of evolvability measures, further supporting the need to ascertain a study-specific minimum sample size prior to analyzing indices of evolvability within or between taxa.

Transition from Chapter III to Chapter IV

While Chapter II demonstrates that the structure of covariance between limb segment lengths and measures of body size is crucial to our understanding of how these traits respond to directional selection, it does not evaluate the environmental variable or variables that are driving that selection. Since ecogeographic expectations are founded in a framework of thermoregulatory adaptation, it is assumed that the primary forces of selection will originate from some measure of temperature. It is therefore problematic that the majority of ecogeographic studies have used latitude as a proxy for "climate," as there are many variables that covary with latitude that are not encompassed by, and may not covary with, temperature.

Since Chapter III showed that human groups display equal evolvability across latitudes, we use quantitative genetic mixed-effect models to disentangle the influence of latitude and temperature as sources of the directional selection shown to be acting on human postcranial variation (Chapter II). If thermoregulatory adaptation does provide the major impetus of selection shaping the human postcranium, the temperature models should account for most, if not all, of the selective pressure acting on limb segment lengths and measures of body size. If, on the other hand, the directional selection influencing these traits is attributed more strongly to latitude than temperature, this will have implications for the traditional narrative of the thermoregulatory imperative model of human evolution.

CHAPTER IV

MIXED MODELS FOR THE RELATIONSHIP BETWEEN LATITUDE, TEMPERATURE, AND HUMAN POSTCRANIAL EVOLUTION

A version of this chapter is being prepared for publication by Kristen R. R. Savell, David C. Katz, Benjamin M. Auerbach, and Timothy D. Weaver as:

> Savell KRR, Katz DC, Auerbach BM, Weaver TD (2018) Mixed models for the relationship between latitude, temperature, and human postcranial evolution. *In preparation.*

This chapter is a research chapter. The text of this chapter regularly uses the pronouns "we" and "our" to reference the contributions of my coauthors, Drs. David C. Katz, Benjamin M. Auerbach, and Timothy D. Weaver. It should be noted, however, that in addition to conducting the majority of the research and performing the analyses, I am the author in the ordinary sense.

Abstract

The adherence of modern human body proportions to ecogeographic rules is argued to be the result of thermoregulatory adaptation to climate. However, much of the history of human migration follows the same latitudinal clines associated with variation in body form, and latitude is used as a common proxy for climate in ecogeographic studies. As such, relationships between body form and latitude are interpreted to indicate temperature-based adaptation, despite the numerous other variables that also vary with latitude.

We investigated the relationship between latitude, temperature, and post-cranial form in modern humans, with the goal of distinguishing the strength and source of selective pressure from population structure. Using multivariate quantitative genetics mixed models, we estimated morphological effects associated with latitude, minimum temperature, and maximum temperature for long bone lengths and body size using osteometric data from 71 globally-distributed groups and geographically matched genetic data representing 59 groups.

We found that among-group variation was tightly correlated within, but not between, limb lengths and body size measures. In the latitude model, only measures of body size demonstrate a directional effect when population history was taken into consideration. Interestingly, bi-iliac breadth did not show a directional effect in either temperature model, though femoral head

diameter was under selective pressure from both minimum temperature and latitude. This may indicate that the soft-tissue elements of body mass (represented by femoral head diameter) are under more thermoregulatory selection than body breadth, which appears evolve in response to non-temperature variable(s) within latitude. In the limbs, directional trends skew positive for humeral length and negative for distal limb lengths, supporting previous research. The effects of minimum and maximum temperature, however, appear to act in opposition. The femur, appearing neutral in most latitude-based studies, was strongly affected by both temperature models, but in opposite directions. The femur's apparent neutrality may result from synergistic effects between measures of temperature within latitude.

This study highlights the importance of considering multiple potential sources of selection within a multivariate evolutionary model, demonstrating the possible synergistic effects of selective pressures. As such, these results complicate the classic thermoregulatory model of human postcranial evolution.

Introduction

Humans exhibit a well-established global pattern of postcranial morphological variation argued to have been shaped in response to climate factors. This ecogeographic pattern of variation corresponds with predictions for larger body sizes and shorter appendage lengths for groups occupying colder climates, and narrower bodies with longer extremities for groups inhabiting warmer climates, trends first predicted by Bergmann (1847) and Allen (1877). Defined as rules by Mayr (1956), anthropologists have sought and generally found these trends to be well-supported among modern humans (Roberts 1953, Trinkaus 1981, Ruff 1994, Holliday 1997, Holliday & Ruff 2001) with some exceptions (Hiernaux & Froment 1976, Holliday 1999, Auerbach 2012). These patterns are established early in human childhood development (Cowgill et al. 2012), and appear to be maintained between generations even after migrations to new climates (Auerbach 2010).

The primary interpretation of this pattern has been that humans adapted to their climactic environments through the evolution of more geometrically efficient thermoregulation

(Bergmann 1947, Mayr 1956, Trinkaus 1981, Ruff 1991, Ruff 1994, Betti et al. 2015, Savell et al. 2016, though see Scholander 1955, 1956). For biological anthropologists, the understanding of ecogeographic variation via Ruff's (1991, 1994) "thermoregulatory imperative" and cylindrical model is a frequently cited interpretation of human postcranial evolution, arguing that arctic populations have evolved body forms that minimize their surface-area-to-volume ratios to mitigate heat loss, with the opposite holding true for tropical populations. Although support for the thermoregulatory imperative has long been inferred from the continued verification of human adherence to expected morphological patterns, such evidence is unable to address the role of either directional selection or temperature on human postcranial evolution.

In a series of recent experimental physiology and quantitative genetic studies, researchers have provided evidence that temperature has likely been a motivating factor in ecogeographic variation in human body form. For example, Tilkens et al. (2007) demonstrated that shorter limbs reduce the energetic cost of maintaining body temperature, while longer limbs allow for greater heat dissipation, as expected. Similarly, hand breadth and finger length appear to play a role in real-time heat dissipation, as hands with lower surface-area-to-volume ratios lose less heat when immersed in a cold-water bath relative to hands with higher surface-area-to-volume ratios (Payne et al. 2018). A series of quantitative genetic papers by Betti, von Cramon-Taubadel, and colleagues (Betti et al. 2012, Betti et al. 2014, Betti et al. 2015, von Cramon-Taubadel et al. 2013) demonstrated that, when population structure is accounted for, postcranial morphological trends appear to be driven by average minimal temperature (more so than by overall average or average maximum temperatures). These studies rely on examining deviance from a neutral model of human evolution to highlight traits that may have been influenced by directional selection. Other quantitative genetics studies have also indicated that selection does appear to be acting on human postcranial traits, with several suggesting that measures of body size and distal limb lengths maybe responding to the strongest selective pressures (Roseman & Auerbach 2015, Savell et al. 2016).

Combining the evidence from observational patterns, physiological studies, and quantitative evolutionary research, we conclude that ecogeographic trends in human postcranial evolution

are influenced by directional natural selection, and it appears likely that the commonly-assumed thermoregulatory imperative could be a major selective force. A caveat to this conclusion, however, is drawn from the fact that the vast majority of ecogeographic studies rely on latitude as a proxy for "climate." Following the logic of the thermoregulatory imperative, some measure(s) of temperature should be the primary factor underlying the aforementioned morphological trends, and latitude – while a good proxy for climate (Ruff 1994; Auerbach 2007) – covaries with a number of factors other than temperature (Auerbach 2007, 2011, 2012; Katz et al. 2016). Reasons for using latitude as a proxy may have been because the majority of the foundational analyses of human postcranial variation were conducted with the intent to elucidate hominin evolution and the reconstruction of extinct climates is notoriously difficult (Trinkaus 1981, Ruff 1994, Holliday 1997), or because latitude can potentially capture (if not distinguish between) various climactic factors such as temperature, humidity, and seasonality (Hiernaux et al. 1975, Hiernaux & Froment 1976, Ruff 1994).

Relying on latitude in ecogeographic studies introduces several complicating factors, however (Roseman & Auerbach 2015). One such issue is the conflation between the distribution of ecogeographic regions and the patterns of human migration. On a global scale, the most widely-accepted explanation for the pattern of human genetic variation is that of a nested-region serial founder model originating in East or Sub-Saharan Africa approximately 37-135 thousand years ago (Ramachandran et al. 2005, Liu et al. 2006, DeGiorgio et al. 2011, Reyes-Centeno et al. 2015). A northward migration into Eurasia out of tropical Africa progresses along the same latitudinal ranges used to study ecogeographic variation, potentially confounding population structure with evidence of directional selection (Roseman & Auerbach 2015). Although, as discussed above, some research has taken population structure into account when investigating postcranial evolutionary trends (Betti et al. 2012, Betti et al. 2014, Betti et al. 2015, von Cramon-Taubadel et al. 2013), these relationships are just beginning to be teased apart (Roseman & Auerbach 2015).

Additional factors may covary with latitude, as well as with climate. Auerbach (2007), for example, showed that subsistence variance and climatic variance are inexorably linked, such

that broad continental and regional analyses of morphological variation among humans in the Americas in relation to these three variables yielded similar results. Yet, in most studies, relationships between ecogeographic trends in postcranial traits and latitude are often interpreted to be indicative of *temperature-based* selective pressure (supporting the thermoregulatory imperative), rather than selection in response to the multiple variables associated with latitude. This is despite the fact that humidity, altitude, precipitation, seasonality, nutrient availability, electric fields, parasite load, and many variables beyond temperature also vary with latitude (Mendillo et al. 1992, Schoech & Hahn 2007, Salkeld et al. 2008). It is therefore likely that variables beyond temperature (or in addition to/interacting with temperature) are affecting human postcranial evolution.

This study will begin to disentangle the relationship between latitude and temperature in human postcranial evolution by comparing mixed-effects models of latitude and temperature to determine whether evolution in postcranial traits was shaped by selection in response to variables associated with latitude, or a narrower set of variables associated with temperature. As reviewed in Katz, Grote, and Weaver (2016), mixed-effects models based on the structure of Lynch's (1991) equations provide means to quantify effect sizes and confidence intervals of factors on morphology – such as amount of expected change in limb bone lengths per degree decrease in average minimum temperature – within a phylogenetic framework. These methods show the expected effects of directional selection given the population structure within a regional or global sample. To apply this method, Katz, Grote, and Weaver adapted the Bayesian sparse factor model developed by Runcie and Mukherjee (2013) to take high-dimensional trait covariance matrices (**G**) and use a sparse analysis, as those traits are thought to correspond with few integrated sets (e.g., modules), improving model fits while reducing computational burdens. Previous studies (Savell et al. 2016; Chapter II) demonstrate that long bone lengths and dimensions associated with body size and breadth form separate integrated sets, and so we would expect these two modules to exhibit independent relationships with both responses to selection in climate or latitude as well as population structure.

Given the evidence supporting the thermoregulatory imperative, reviewed above, we predict temperature will account for most, if not all, of the selective pressure acting on limb segment lengths and measures of body width across ecogeographic regions. This is likely to hold especially true for distal long bone lengths and measures of body size and breadth (Savell et al. 2016). If this prediction is correct, results will support the traditional narrative of thermoregulation as a primary cause of ecogeographic variation in human body form. If not, a new paradigm of ecogeographic selection apart from the effects of temperature will need to be explored, focusing on the additional factors associated with latitude outlined above.

Materials

Phenotypic and Geographic Data

The six dimensions traditionally used in the analyses of human ecogeographic variation are measures of limb length (maximum humeral, radial, femoral, and tibial lengths) and body size (femoral head diameter and bi-iliac breadth) (Auerbach & Ruff 2004, Auerbach 2007, Roseman & Auerbach 2015; measures defined by Martin 1928). Our sample includes 2611 individuals (1518 males, 1093 females) representing 71 groups included in the combined the Goldman Data Set (Auerbach & Ruff 2004), Americans Data Set (Auerbach 2012), and datasets shared by Trent Holliday and Christopher Ruff (Roseman & Auerbach 2015, Savell et al. 2016). The 71 phenotypic groups are globally distributed, spanning six continents (Figure 11, Table S2 in Appendix II). When available, these measurements (taken in millimeters) were collected from both the right and left sides and averaged to mitigate the effect of asymmetry (Auerbach & Ruff 2006).

The geographic location of each group was designated either as the location of burial (in the majority of samples, which are archaeological), the recorded location for remains obtained from living groups (based on accession records at institutions), or (in a minority of cases) as a geographic mean for the range occupied for living groups based on ethnographic records. While these locations are imperfect, any inaccuracies in pinpointing the locations in which groups of

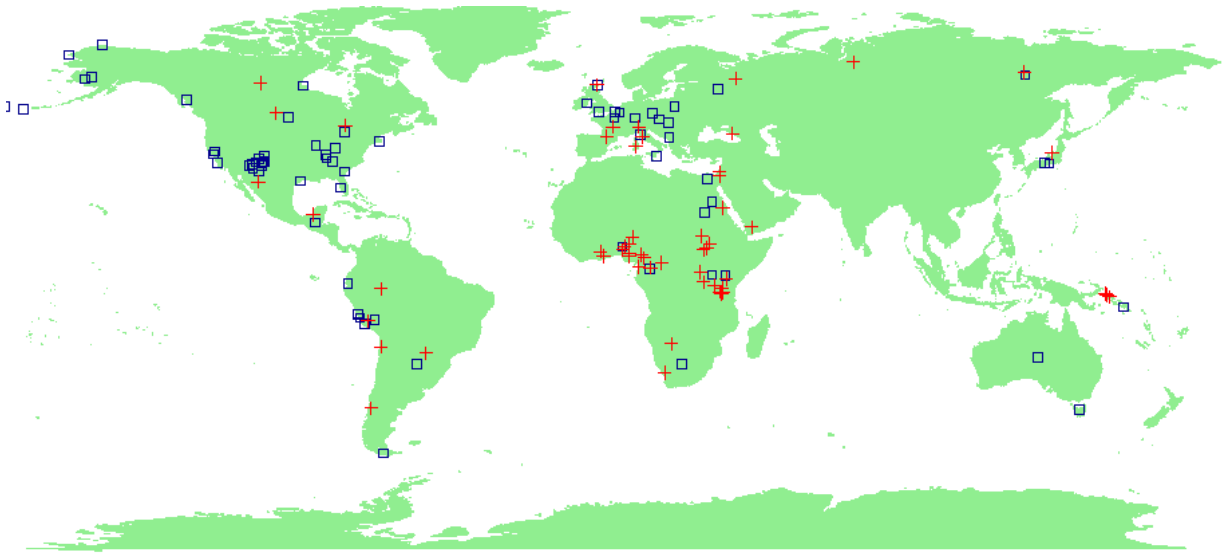

Figure 11. Map of geographic locations of sampled groups used in this study. Open squares (blue) indicate phenotypic sample. Crosses (red) indicate sites used from the microsatellite data set (Pemberton et al. 2013).

individuals lived are thought to be minimal on a global scale. Latitudes and longitudes for each group are presented in Table S2.

Temperature Data

The long-term averages for the mean temperature of the coldest and warmest months of the year were determined from weather stations at the nearest location to each group represented in our phenotypic sample. The latitude and longitude coordinates associated with each group were used to determine the nearest Global Historical Climatology Network (GHCN) weather station, from which temperature data was collected (online GHCN database, version 3, available at: ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/). These measures were chosen to represent the long-term temperature extremes of a given location, since thermoregulation is commonly considered the primary impetus for the evolution of ecogeographic variation. In an effort to mitigate the recent, considerable rise in average global temperatures, no data after 1989 was included in the calculation of minimum or maximum temperature (Auerbach 2007,

Cowgill et al. 2012). GHCN station identifications and temperature data for each group used in this study are provided in Table S2.

Genotypic Data

As there is no genotypic data directly associated with the individuals measured for skeletal morphology, we used human microsatellite molecular data from the Rosenberg laboratory website (http://www.stanford.edu/group/rosenberglab/data/), as compiled by Pemberton et al. (2013) (Roseman & Auerbach 2015). Pemberton and colleagues' (2013) dataset includes human microsatellite variation at 645 loci from 5795 individuals representing a global distribution of 267 groups. From this dataset, 59 "genotypic" groups were matched to the 71 "phenotypic" groups represented in the morphological sample (Table S3 in Appendix II).

As per Roseman and Auerbach (2015), linguistic and geographic relationships were used when specific groups were not represented. Since any potential mismatch occurs at the local, rather than inter-regional level, the effects of a matching error should be minimal when considered on a global scale (Hunley et al. 2009, Long et al. 2009). In addition, for some regions, among-group averages of variation were used to match the genotypic and morphological data, which treats groups as though they are equally genetically similar (Roseman & Auerbach 2015) (Table S3 in Appendix II). It should therefore be noted that if a region that is represented by among-group averages is defined by strong within-region population structure, this pattern maybe obscured in the analyses (Roseman & Auerbach 2015).

Methods

To examine the role of temperature in the evolution of modern human ecogeographic variation, we apply a quantitative genetics mixed-effects model that has adapted to allow for within-species multivariate analyses (Lynch 1991, Hadfield & Nakagawa 2010, Runcie & Mukherjee 2013, Katz et al. 2016, Katz et al. 2017). Mixed-effects models were designed specifically to account for interactions within structured samples (Hadfield & Nakagawa 2009) and were adapted to an evolutionary framework based on the idea that statistically,

phylogenies provide analogous information to pedigrees (Lynch 1991). Following the work of Katz and colleagues (2016), our mixed model for the matrix of observations **Y**,

$$\boldsymbol{Y} = \boldsymbol{XB} + \boldsymbol{ZU} + \boldsymbol{E}$$

contains *p* = 6 measurements on *n* = 2611 individuals. In this model, **B** is 3*6 matrix of the intercept, sex effect coefficient, and fixed effect coefficient for each of the six traits. **X** and **Z** are known design matrices for **B** and **U**, and **E** is a 2611*6 (number of individuals*number traits) error matrix.

U is a 29*6 (number of collapsed genotypic groups, see Table S3 *number of traits) matrix of structured random effects for each sampled population, and **U = H⊗A** (where ⊗ is the Kronecker product). In this equation, matrix **A** (a 29*29 population relationship matrix) encodes the population structure derived from the microsatellites, and matrix **H** (a 6*6 dispersion matrix for traits) can be understood as an estimate of among-group variance and covariance if the populations had evolved completely independently from a common ancestor. Matrix **A** is populated directly by calculating the delta-mu squared microsatellite distance measure from the genetic dataset. For populations *i* and *j* having a delta-mu squared distance D_{ij}, the correlation due to structure is

$$A_{ij} = \frac{D_{max} - D_{ij}}{D_{max}}$$

where D_{max} is the maximum delta-mu squared between sampled pairs. Each of these elements (A_{ij}) estimates a pair's shared evolutionary history (Katz et al. 2016, Katz et al. 2017).

With these equations, parameters were estimated for three models: one with structured random effects and fixed effects for sex and latitude (latitude model), and two that substitute minimum and maximum temperature as fixed effects in place of latitude (minimum and maximum temperature models, respectively). Parameters were estimated using the Bayesian sparse factor model (BSFG), which uses an adaptive Gibbs sampler to estimate posterior

densities of model parameters. This approach eliminates the need for an *a priori* decision about the factors that need to be included in a given model. Instead, the model only uses factors that explain more than a prescribed percentage of variance (traditionally set at 1%) (Runcie & Mukherjee 2013, Katz et al. 2016). Because the BSFG approach limits both the number of factors and the number of traits that can load on a given factor, BSFG factors can be interpreted as estimates of co-varying groups of traits (modules). For this project, the BSFG was used to estimate 1,000 posterior samples for our two models, generated from a single Markov Chain using a 1,000,000 iteration burn in and thinning at a rate of 1,000.

Mean climate coefficients and 95% posterior credibility intervals were produced for each trait within the model, and to allow comparison across models these measures were standardized by their respective average pairwise differences. For example, the standardized latitude model was calculated by dividing each of the six climate coefficients and 95% posterior credibility intervals by the mean difference in latitude between all possible pairings of the 71 groups represented in the phenotypic data set, and the same is true for the minimum and maximum temperature models. It should be noted that the standardized measures are only used to compare the relative magnitude of mean climate coefficients and credibility intervals in one figure. All other figures show non-standardized model results.

The BSFG was computed in Matlab (Mathworks), and all other analyses were performed using the R statistical computing software (https://cran.r-project.org). Data and analyses are available from the authors.

Results

Pearson's correlation coefficients (r) were determined, and both latitude and maximum temperature (r = -0.69) as well as latitude and minimum temperature (r = -0.83) demonstrated fairly strong correlations (Figure 12a-b). Correlations for latitude and temperature above the Tropic of Cancer (latitude: 23°26' north) were also calculated, as maximum temperatures can vary considerably in the tropics, potentially weakening the overall correlation. Indeed, while the correlation between minimum temperature and latitude remains similar for latitudes above the

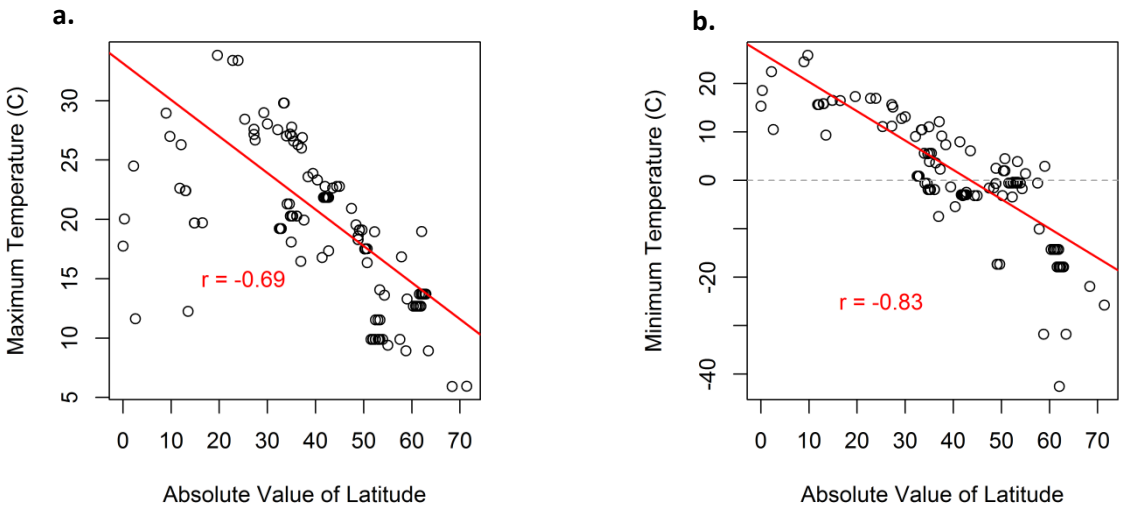

Figure 12a-b. Pearson's correlation coefficient (*r*) between the absolute value of latitude with the long-term averages of the A. warmest (maximum) and B. coldest (minimum) months of the year.

Tropic of Cancer (*r* = -0.79), the correlation between latitude and maximum temperature increases considerably (*r* = -0.89) (Figure 13a-b). The strong negative correlations between latitude and temperature allows for comparison between the results of the latitude and temperature mixed models, as we are assured that differences will address the role of latitude as a proxy for temperature and not reflect the distinct patterns of uncorrelated variables

Trait-specific regression coefficients were estimated by the model for each of the three fixed-effect predictors (latitude, minimum temperature, and maximum temperature). The coefficient mean and 95% posterior credibility intervals were calculated for each trait within each of the three models (Table 8). It should be noted that because the results of all three models are based on a low-to-high gradient, the results of the two temperature models have been reversed around zero so as to be comparable with the results of the latitude model (when traveling from the tropics to the arctic, latitude increases and temperature decreases) (Figure 14a-c).

As such, positive coefficients will indicate larger-than-expected trait values in groups that are closer to the arctic (Katz et al. 2016, Katz et al. 2017).

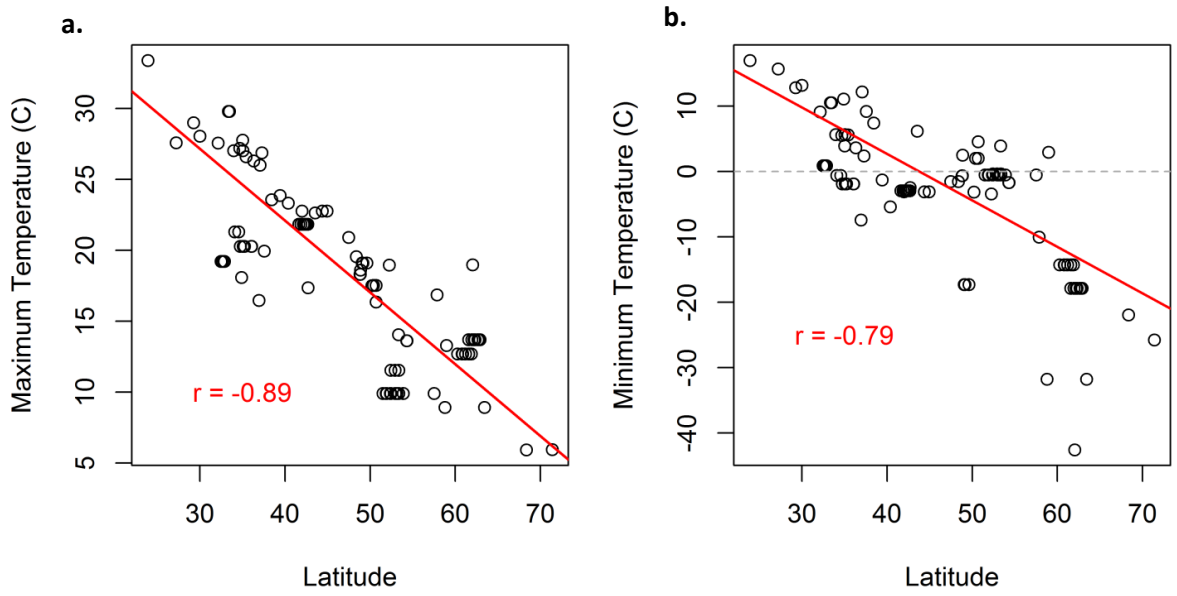

Figure 13a-b. Pearson's correlation coefficient (*r*) between latitudes above the Tropic of Cancer with the long-term averages of the A. coldest (minimum) and B. warmest (maximum) months of the year.

Table 8. Coefficients for each fixed-effect predictor (95% credibility intervals), untransformed (top), and standardized by the average of the pairwise differences across groups (bottom).

	Latitude	Max. Temp.	Min. Temp.
IB	0.1930 (0.0697, 0.3092)	0.1589 (-0.1884, 0.5036)	0.1007 (-0.0931, 0.2882)
HML	0.0551 (-0.0712, 0.1745)	-0.2648 (-0.6477, 0.1090)	0.2586 (0.0875, 0.4378)
FHD	0.0346 (0.0190, 0.0504)	-0.0084 (-0.0601, 0.0446)	0.0435 (0.0177, 0.0696)
FML	0.0281 (-0.1736, 0.2080)	-0.5934 (-1.1233, -0.0380)	0.4500 (0.1934, 0.7077)
RML	-0.0606 (-0.1662, 0.0372)	-0.3400 (-0.6531, -0.0232)	0.0588 (-0.0980, 0.2168)
TML	-0.1217 (-0.3087, 0.0485)	-0.7181 (-1.2277, -0.2011)	0.1497 (-0.0968, 0.3915)
	Latitude (std)	**Max. Temp. (std)**	**Min. Temp. (std)**
BIB	0.0068 (0.0025, 0.0109)	0.0224 (-0.0265, 0.0709)	0.0077 (-0.0071, 0.0220)
HML	0.0019 (-0.0025, 0.0061)	-0.0373 (-0.0912, 0.0154)	0.0198 (0.0067, 0.0335)
FHD	0.0012 (0.0007, 0.0018)	-0.0012 (-0.0085, 0.0063)	0.0033 (0.0014, 0.0053)
FML	0.0010 (-0.0061, 0.0073)	-0.0836 (-0.1582, -0.0053)	0.0344 (0.0148, 0.0541)
RML	-0.0021 (-0.0059, 0.0013)	-0.0479 (-0.0920, -0.0033)	0.0045 (-0.0075, 0.0166)
TML	-0.0043 (-0.0109, 0.0017)	-0.1011 (-0.1729, -0.0283)	0.0114 (-0.0074, 0.0299)

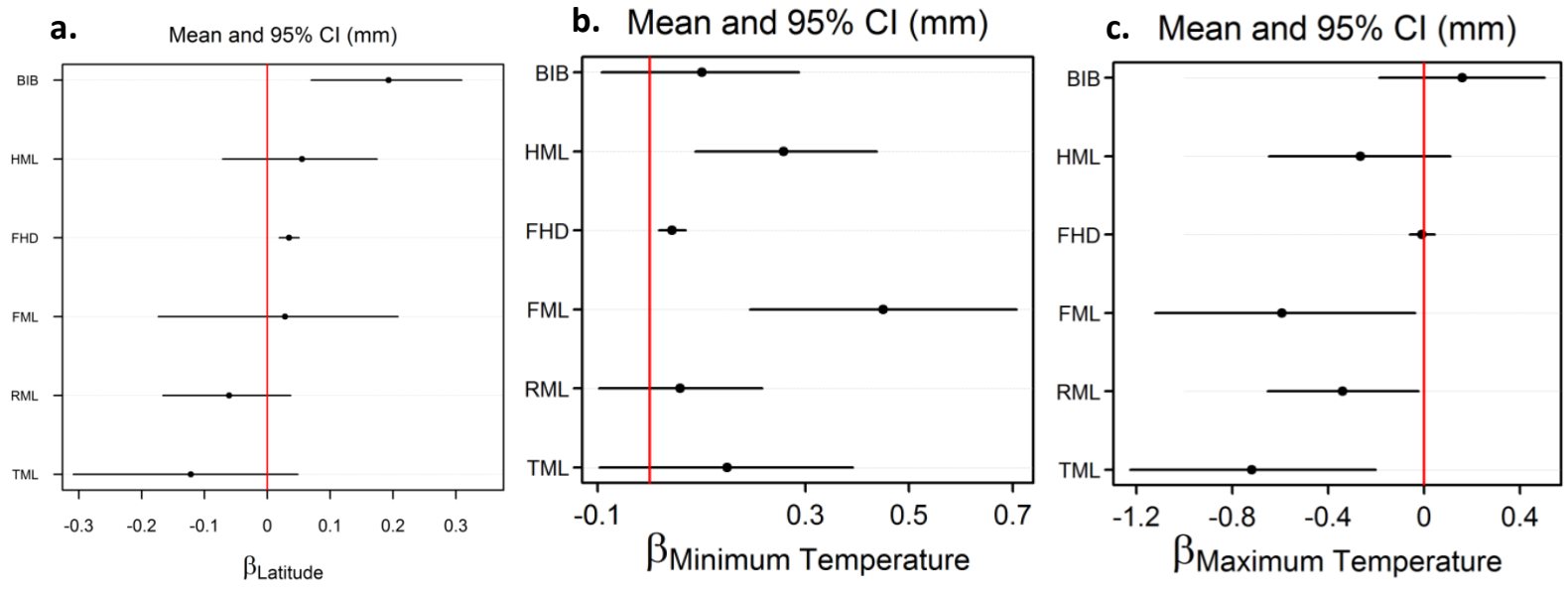

Figure 14a-c. Unstandardized mixed-model results of the latitude, minimum temperature, and maximum temperature models, with mean climate coefficients (dots) and 95% credibility intervals (whiskers). Credibility intervals that cross the red line are considered "non-zero" results and are statistically indistinguishable from population structure. Climate coefficients and credibility intervals for the temperature models have been reversed around zero so as to allow for direct comparison with the results of the latitude model - therefore all positive trends can be interpreted as indicating selective pressure to lengthen at higher latitudes, while negatively skewing traits are under pressure to shorten. For ease of comparison across models, traits have been listed in the largest-to-smallest order determined by the latitude model.

Heat maps of the **H** matrix (an estimate of among-group trait variance and covariance assuming independent evolution among groups) for the six traits are presented in Figures 15a-c for the latitude, climate, and sex effect models, respectively (see Katz et al. 2016 for further detail about these maps). From these heat maps it is evident that the limb lengths are largely independent of the body size and breadth traits. Limb lengths are highly covariant. For this reason, body size dimensions (femoral head diameter and bi-iliac breadth) and limb lengths may be considered separately.

Body Size

In measures of body size, the mean coefficient for bi-iliac breadth (BIB) is both positive and nonzero. The 95% CI for BIB in both of the temperature models, however, does overlap with zero (Figure 14b-c). This suggests that BIB varies in response to directional selection forces associated latitude as predicted (Savell et al. 2016). However, selection is linked to a variable that covaries with latitude but not with either the maximum or minimum long-term mean temperature. The coefficient for femoral head diameter (FHD), however, is positive and nonzero in both the latitude and minimum temperature models (Figure 14a, 14c).

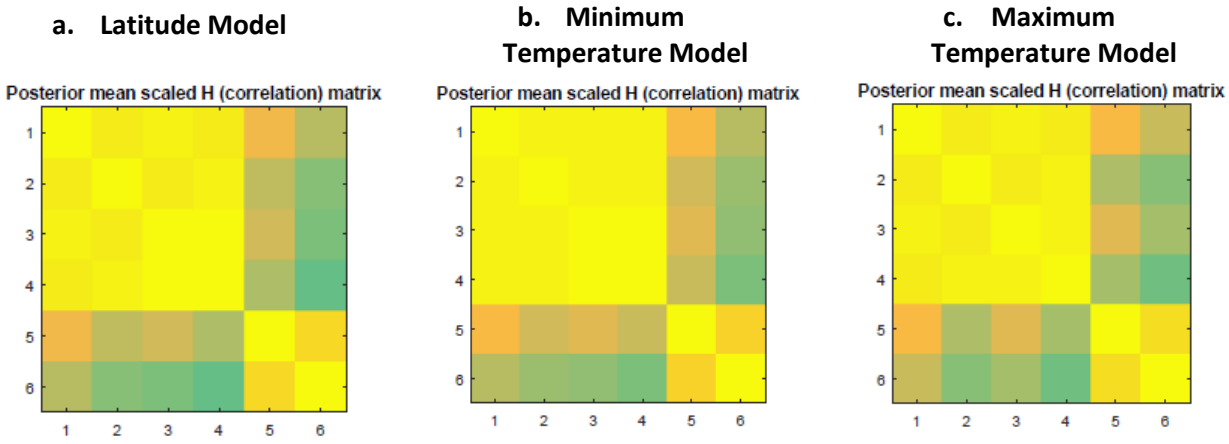

Figure 15a-c. Heat maps of the H matrix for each model respectively. Across models, the modularity of limbs lengths (traits 1-4) and measures of body size (traits 5-6) are distinct.

This indicates that FHD (a proxy for body mass, rather than body breadth) increases in response to selection associated with colder minimum temperatures, as expected in the thermoregulatory interpretation of ecogeographic variation. FHD does not appear to be distinguishable from population structure when maximum temperature is the fixed-effect predictor (mean = -0.0084, 95% CI = -0.0601, 0.0446) (Table 8).

Limb Length

The magnitude and directionality of the latitude model coefficients suggest morphological evolutionary trends consistent with previous research on ecogeographic limb variation (Roseman & Auerbach 2015, Savell et al. 2016). Distal elements are under pressure to shorten in higher latitudes, while the lengths of proximal elements are either responding positively to increasing latitude (the humerus), or are not showing an association with latitude once taking population structure into account (the femur) (Figure 14a). However, the credibility intervals for all of the limb segment length coefficients cross zero, indicating that population structure and/or residual uncertainty clouds the signal of selection driven by latitude in these measures (Katz et al. 2016).

Interestingly, the effects of minimum and maximum temperature appear to be in opposition with each other. In the minimum temperature model, all of the limb length coefficients are positive (lengthening), while they are all negative (shortening) when maximum temperature is the fixed-effect predictor (Table 8, Figures 14b-c). Distal limb elements (RML, TML) cross zero in the minimum temperature model, suggesting that the effects of minimum temperature are not strong enough to be distinguished from the effects of population structure on these traits. In the maximum temperature model, however, RML and TML are both nonzero and strongly negative, indicating that the observed relationship between shortened distal limb segments and cold climates in modern human populations may be the result of maximum, rather than minimum temperature (von Cramon-Taubadel et al. 2013, Roseman & Auerbach 2015, Savell et al. 2016) (Figure 14c).

A similar, if opposite, pattern is observed in the humerus (HML). HML appears to lengthen in response to minimum temperature (positive coefficient, nonzero) while maximum temperature does not appear to have a strong enough effect to distinguish observed change from population structure. The effect of the temperature on the femur length (FML) coefficients highlights the pattern of opposition between the minimum and maximum temperature models (Figures 14b-c). When sex and population structure are controlled, FML appears to be under selection to lengthen due to minimum temperature and to shorten as a result of maximum temperature. The contrast between these effects may suggest that the seeming stability in FML at higher latitudes is not explained by population as previously discussed (Roseman & Auerbach 2015, Savell et al. 2016), but by the opposite selective effects of minimum and maximum temperature neutralizing each other.

Comparing Credibility Intervals

Although the pattern of positive, negative, and neutral coefficients can be interpreted by comparing the results of the three models, significant differences in the magnitude of credibility intervals also exist depending on which climactic variable is used as the fixed-effect predictor. When the estimated climate coefficients and credibility intervals are standardized by their respective average pairwise differences between the 71 phenotypic groups, these differences in magnitude become obvious (Figure 16).

Credibility intervals compared among the models differ by magnitudes (Table 8). Latitude demonstrates the smallest credibility intervals of all three models, perhaps indicating that inclusion of all the latent variables associated with latitude allows for greater precision, while isolating the two temperature measures results in a loss of these non-temperature variables, increasing uncertainty. In comparing the standardized model results, the maximum temperature model clearly displays coefficients of much larger magnitude and as well as considerably larger credibility intervals.

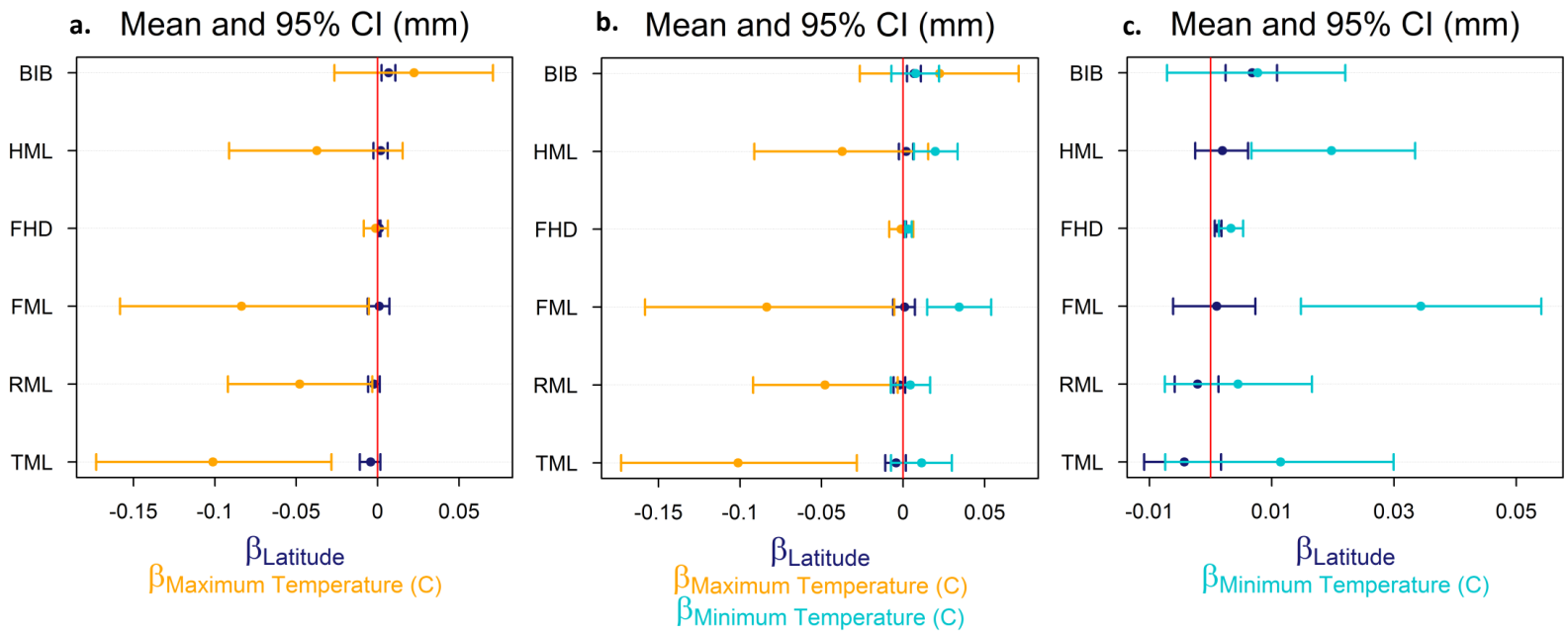

Figure 16a-c. *Standardized* mixed-model results of the latitude, minimum temperature, and maximum temperature models, with mean climate coefficients (dots) and 95% credibility intervals (whiskers). All climate coefficients and credibility intervals for each model have been standardized by the average pairwise distance of the fixed-effect predictor used in that model (see "Methods" above). Credibility intervals that cross the red line are considered "non-zero" results and are statistically indistinguishable from population structure. Climate coefficients and credibility intervals for the temperature models have been reversed around zero so as to allow for direct comparison with the results of the latitude model - therefore all positive trends can be interpreted as indicating selective pressure to lengthen at higher latitudes, while negatively skewing traits are under pressure to shorten. For ease of comparison across models, traits have been listed in the largest-to-smallest order determined by the latitude model.

While the large credibility intervals may indicate significant noise complicating the effects of maximum temperature, it has the same number of nonzero trait coefficients (3 of 6) as the minimum temperature model, and more than the latitude model (2 of 6), further lending support that the strength of the effect of maximum temperature on the observed traits is high (Figure 14c).

Discussion

The results of the mixed-effects models both corroborate previous findings as well as contribute information and nuance to understanding the evolution of limb lengths and body size among modern humans. All three mixed-effects models indicate that directional natural selection was responsible for some trait evolution, a result that supports the findings of multiple other studies that have used different evolutionary models to arrive at the same conclusion (Betti et al. 2012, Roseman and Auerbach 2015, Savell et al. 2016, Chapter II). By approaching the evolutionary model with fixed effects of latitude and temperature variables, however, this study shows that selection is driven unequally by latitude and temperature across traits, and at times results in combinatory effects of those fixed effects.

Evolutionary Covariance Among Postcranial Traits

As implicated in other studies of the six traits considered in this analysis (Roseman and Auerbach 2015, Savell et al. 2016), traits associated with body size are largely independent of limb length traits, and so form separate integrated sets (Figure 15). This result has implications for how we interpret Bergmann's and Allen's rules in humans; the influence of evolutionary forces on body size and on extremity size will be independent. Selection on body mass, for example, does not incur correlated responses in the lengths of limbs. This may help explain some of the apparent asynchronistic variation in limb segment lengths and body size reported for anatomically modern humans in Europe (Holliday 1997), Japan (Temple et al. 2008), and the Americas (Auerbach 2007, 2012).

Additionally, such findings lend corroboration of the geometric argument made by Ruff (1994) in developing the cylindrical model through multivariate evolutionary evidence; Ruff showed that body breadth is the trait that dictates surface area-to-volume ratio variation, and that the length of the cylinder (i.e., stature) has no mathematical influence. The ratio of surface area to mass is under selection, which our model suggests, but a caveat to Ruff's cylindrical argument is that body mass is responding to selection motivated by minimum temperature and by latitude, but body breadth, which covaries with but does not determine body mass (Ruff et al. 1997, Auerbach and Ruff 2004), is responding to selection associated with latitude, but *not* temperature.

Implications for the Thermoregulatory Imperative

This study, as discussed in the Introduction, was prompted by disentangling the effects of latitude from those of temperature on the evolution of human body size and limb proportions under the thermoregulatory imperative model (Ruff 1994). Recent quantitative genetic studies (Roseman & Auerbach 2015, Savell et al. 2016) provide support for distal limb lengths and body size as evolving in response to directional selection, though the global variation in these traits reflects a combination of the effects of selection and population structure (cf. Betti et al. 2012). As latitude and temperature are significantly correlated (Figure 2), especially at mid- and high-latitudes, both also share latent variables (e.g., subsistence effects, pathogen loads, and seasonality). Thus, the interpretation of model results for latitude versus temperature requires subtlety.

Body mass, for which femoral head size is a proxy, has evolved in modern humans in response to selection. Both the latitude and minimum temperature models predict that, when accounting for population structure, femoral head size (and thus body mass) increases as latitude increases and minimum temperature decreases. This result supports the conclusions of Savell et al. (2016), wherein selection gradients were estimated by simulating evolution between living human groups at different latitudes, but it adds to those results by indicating that selection is driven, at least in part, by temperature. Additional latent variables shared

between latitude and minimum temperature are undoubtedly influencing body mass as well, but this result is novel in that it is the first to support the evolution of body mass through natural selection in response to temperature within a multivariate model. Our results contrast with Roseman and Auerbach (2015), whose model supported evolution of the femoral head in response to population structure, though their model examined evolution in traits independently.

As noted above, and in contrast to femoral head diameter, bi-iliac breadth is the only trait in this study that, accounting for the effects of population structure and sex differences, is expected to increase with latitude but *not* temperature; selective pressure from some non-temperature variable that correlates with latitude appears to be acting on bi-iliac breadth. That bi-iliac breadth is responding to directional selection is a result of latitude, but not minimum or maximum temperature, complicates the cylindrical model and the thermoregulatory imperative. Instead of indicating selective pressure for wider bodies that lower the surface area-to-body volume ratio and allow for greater heat conservation, we interpret this result to be related to soft-tissue physiology. Wider body breadths are associated with increased body size, though the model we use accounts for this evolutionary covariance. Yet body breadth also permits greater overall support for soft tissue (see Ruff's 1994 arguments concerning Polynesians, for example), which may in turn make a case for increased adiposity in higher-latitude groups. The importance of soft tissue to physiology—wider bodies may provide for more caloric storage in harsh environments—instead of the geometric arguments made in the thermoregulatory imperative may therefore be at work to explain selection on body breadth in association with latitude but not temperature. Future studies that explore the effects of body breadth on overall physiology will be necessary to test this hypothesis.

The interpretation of limb length evolution from the model requires examining the results of all three mixed-effects models together. The results of the latitude fixed-effect model demonstrate the same pattern as shown in Savell et al. (2016), predicting a shortening of the distal elements in response to selection, femoral length evolving through neutral processes, and selection driving a lengthening of the humerus at increasing latitudes. All of limb

confidence intervals overlap with zero (Figure 14a), however, so these evolutionary changes cannot be distinguished from the effects of population structure. In contrast, regardless of whether they overlap with zero, all of the temperature model coefficients for limb lengths are positive (lengthening) in response to minimum temperature and negative (shortening) in response to maximum temperature. Examining the confidence intervals reveals a complex relationship between selection in response to temperatures and limb length evolution.

Among the three models, distal limb elements appear to be under selection in response to average maximum temperature; this matches the observed pattern, where increased tibial and radial lengths are associated with warmer climates. Humeral length is under selection in response to minimum temperatures, though as shown in Savell et al. (2016), the observed pattern among humans is that humerus length *decreases* with minimum temperature. Savell and colleagues (2016) also demonstrated that the response of the humerus to selection is attenuated by its covariance with tibial and radial lengths, and so while the length of the humerus may be expected to increase in response to selection from minimum temperature, this evolutionary covariance overrides the independent response of the humerus. Finally, femur length is expected to have opposite responses to selection from both maximum and minimum temperature. We interpret these effects as cancelling each other out, so that it appears that the length of the femur is not under selection and instead evolves in response to neutral processes. This result reconciles conflicting findings among Betti et al. (2012), Roseman and Auerbach (2015), and Savell et al. (2016), which argued alternatively for femur length to have evolved in response to neutral processes or in response to a combination of neutral processes and directional selection.

Toward a New Model for Human Postcranial Evolution

Taken together, these results modify our current understanding of the relationship between postcranial trait variation among modern humans and the evolutionary processes that shaped that variation. Before the application of quantitative genetic methods to explore the evolutionary processes that shaped the body, researchers found patterns of variation that

correlated well with latitude as a proxy for climate, which they interpreted to support the effects of natural selection due to thermoregulatory requirements (e.g., Trinkaus 1981, Ruff 1994, Holiday 1997). Climatic variables have only been used in these pattern-based studies in rare instances (e.g., Stock 2002, Auerbach 2007, Cowgill et al. 2012). The application of quantitative genetics has been mostly focused on distinguishing the effects of population structure, and therefore neutral evolutionary forces, from directional selection as being the process that shaped postcranial variation. Yet, as explained in the Introduction, the majority of these studies have used latitude instead of climatic variables to test these models.

The results of this study therefore present an opportunity to build a new model for human postcranial evolution in response to population structure, directional selection resulting from thermoregulatory pressures (or other variables associated with temperature), and selection arising from factors associated with latitude to the exclusion of temperature. The thermoregulatory imperative is supported for evolution of femoral head size (and therefore body mass) and distal element lengths; these three traits have responded to directional selection imposed by temperature. The length of the humerus is also expected to respond to directional selection in response to temperature, but previous analyses (Savell et al. 2016) indicate correlated responses to selection in the distal limb elements override the independent response in the humerus. Unexpectedly, bi-iliac breadth does not correspond with the thermoregulatory imperative. Instead, other factors associated with latitude are likely driving the directional selection to which this trait is responding. In addition, our study is the first to show that conflicting selection forces might be nullifying each other, as in the case of femoral length, leaving this trait to appear to evolve in response to neutral processes.

That minimum and maximum temperature, but not latitude, predicts changes in the limbs requires further exploration. Given the high correlation between temperature and latitude, selection in response to temperatures should be reflected by latitude. We explain this by noting that maximum and minimum temperatures have opposite effects on limb lengths (though some of these predicted changes are not statistically distinct from from zero change), which means that responses to the selective effects of temperature are synergistic. Because latitude is

equally correlated with both temperature variables, if decreasing *minimum* temperature predicts shorter limb lengths but decreasing *maximum* temperature predicts longer limb lengths, the net effect will appear to be no predicted change when examining latitude alone. Therefore, we conclude that latitude is at best an imperfect factor for measuring the selection effects of climate, and more likely obscures the effects of selection of individual climate variables.

Limitations and Future Directions

This study in many ways resolves questions that have lingered as researchers sought to better understand postcranial evolution in humans, first through pattern analysis and then through various quantitative genetic approaches. We support many of the findings of these prior studies, especially recent quantitative genetic studies, and our results lend additional weight to this growing evidence, as our analysis incorporates the assessment of multiple climactic variables. For example, Savell et al. (2016) estimated selection gradients through pairwise comparisons of contemporaneous groups that would never, in actuality, "evolve" into each other. Our latitude fixed-effect model results, though, match the general results found in that previous study, which effectively corroborates their conclusions. Furthermore, the results of our study strongly point toward the importance of using not only evolutionary models that include multiple traits, but the potential importance of developing evolutionary models that explore the effects of multiple hypothesized selection factors simultaneously.

Our approach allows for multiple fixed-effect factors to be examined together in the same model, but model behavior (and thus interpretation) is complicated by the high correlations among the three factors, latitude and the two temperature measures. Under such circumstances, the interpretation of results from these multiple fixed-effects models is difficult, and so we elected to present the three models separately in this study. Nevertheless, this is a less vigorous research design than a methodology in which models include both latitude and minimum temperature, for example. Future studies will need to examine multiple traits as well

as multiple potential selection factors simultaneously within the same model, and will need to develop methods for accounting for predicted effects when those factors are covariant.

As noted in the Methods, the latitude and temperature data used in this study are imperfect. Though the global scale of this study minimizes the effects of local inaccuracies, such local effects nonetheless will introduce unknown error into the models. This is apparent when comparing the confidence intervals of the latitude model against the two temperature models (Figure 16). Alternatively, because of the noisiness of the temperature data, results that show predicted change with confidence intervals that do not overlap with zero (Figures 14b-c) are deemed to be especially reliable.

Finally, a limitation to this study is the inability to identify, quantify, and assess all of the factors that likely covary with latitude. Because the thermoregulatory imperative has been the primary hypothesis for explaining human postcranial form variation for more than a half century, we chose to focus on testing this theory. Yet temperature is only one factor associated with latitude (Ruff 1994). For example, pathogen and parasite loads covary with latitude (Salkeld et al. 2008), but their effects on body size, for example, are not established. Yet, without establishing the physiological effects of these multiple factors on body form, developing hypotheses to test, and applying approaches like BSFG method used here, remain out of reach. Identification of additional potential factors and measurement of their variation should be a goal for researchers, so that we may develop a holistic model for the evolution of human postcranial evolution. The thermoregulatory imperative is an incomplete model.

Conclusions

This study demonstrates the importance of examining multiple potential selection factors against trait variation within a multivariate quantitative genetic model. Taken together, our results demonstrate the potential combinatory or synergistic effects of different selective pressures. Latitude and minimum temperature work together to influence body mass, while body breadth may be reflecting selection in response to latitude-related factors independent of temperature. The opposite effects of the minimum and maximum temperature models on the

limbs appear to result in some latitudinal effects that look neutral. We have improved our abilities to examine several traits using a multivariate approach, and highlight the importance of improving the estimation of the multivariate interactions of several factors within evolutionary models.

CHAPTER V

DISCUSSION, LIMITATIONS, AND FUTURE RESEARCH

In this dissertation, I used quantitative genetic methods to explore how patterns of variation in modern human limb segment lengths and measures of body size were shaped by trait covariation and evolutionary forces. Bringing the results of these studies together to address the three major questions raised in the Introduction (p. 45, Chapter I), three key points emerge that address our understanding of human postcranial evolution:

1. Trait covariation plays an important role in shaping how traits respond to selective pressure.
2. Modern human groups share comparable measures of evolvability, though decreased genetic variance due to human migration and/or selection may be driving emergent patterns across regions.
3. The adaptive forces underlying observed directional selection are likely synergistic, complicating simplistic interpretations of the thermoregulatory imperative model for postcranial shape and body size variation.

These major findings are explored in detail below, in addition to their broader implications for the evolution of human morphological variation. This synthesis is followed by a discussion of study limitations and avenues for future research.

Trait Covariation in the Human Postcranium

In the analyses of covariance among postcranial traits, the six dimensions considered throughout this dissertation (humeral, radial, femoral, and tibial maximum lengths; femoral head diameter; and bi-iliac breadth) have not evolved independently across ecogeographic regions in modern humans. This research provides evidence that differences in trait means cannot be interpreted as signals of trait adaptation because those mean differences arose from

a combination of direct and correlated responses to evolutionary forces. Strong between-trait covariation – especially between long bone lengths – substantially affects responses to directional selection. Indeed, in the case of the humerus, patterns of trait covariation resulted in responses to selection that differed not only from what was predicted by Allen's rule, but also from the trait's own estimated directional selection (Figure 3, Figure 5).

The distal limb segment lengths (radius, tibia) significantly affect the ability of other bones (especially the humerus) to respond to trait-specific estimated selective pressures (Table 2). Given the commonly-used thermoregulatory interpretation of Allen's rule (Trinkaus 1981, Ruff 1991, Ruff 1994, Holliday 1997, Holliday 1999, Holliday & Ruff 2001, Auerbach 2012, Betti et al. 2015, Payne et al. 2018), expectations suggest that long bone lengths should shorten at higher latitudes as an adaptation to ambient temperature. However, the directional selection acting on the humerus was positive – indicating selective pressure for longer humerii at higher latitudes. This *directly contradicts* both ecogeographic expectations and the observed differences in global skeletal means. In a deconstruction of the response to selection, the pattern of covariation between the humerus and distal limb bones was so strong that the humerii not only failed to lengthen at higher latitudes (as would be expected given the estimated directional selection), but are observed to shorten (Table 2); arctic groups have demonstrably shorter humerii than equatorial groups (Table 1). As such, the shortening of humeral length appears to be a direct result of covariance with the radius and tibia, which are under strong negative selective pressure to shorten.

In contrast to this unexpected finding, the selective pressures acting on distal limb lengths (RML, TML) and body size (FHD, BIB) conform to expectations based on a thermoregulatory interpretation of the ecogeographic rules. Radial and tibial lengths appear to be under directional selection to shorten at higher latitudes while measures of body size are subjected to positive selective pressure (widening in dimension) – trends that align with observed patterns of morphology (Table 1, Figure 5). Femoral length, however, does not appear to be subject to selective pressures strong enough to distinguish from population history (Figure 5), a result that deviates from both ecogeographic expectations and the pattern of the mean change in femoral

length observed across groups included in this sample (although see the discussion of factors driving selection below).

These results demonstrate that the morphological pattern associated with Bergmann's (1847) and Allen's (1877) rules – which is well supported when comparing trait means across ecogeographic regions (Hiernaux & Froment 1976, Roberts 1978, Trinkaus 1981, Ruff 1991, Ruff 1994, Holliday 1997, Holliday 1999, Holliday & Ruff 2001) – is not the result of an unambiguous relationship between adaptive pressure and trait response. Instead, the pattern of human postcranial evolution associated with ecogeographic rules is the outcome of a complex interaction between selective force and trait covariation. As a result of the covariation between characters, evolutionary trajectories that might be favored by selection (i.e., an adaptation that would increase fitness) may not only be reduced in strength, but potentially reversed – as seen in the pattern of selection and response displayed in humeral length. Similarly, although the length of the distal limb elements conforms to ecogeographic expectations of how selection should act in relation to latitude (as a proxy for temperature), it is likely these traits are unable to evolve as quickly as they could were they unhindered by the opposing selective pressures acting on the humerus, with which they covary. As noted above, covariation between traits prevents a direct association between differences in morphological means across latitude and the evolutionary processes that create that variation.

Trait covariation not only substantially affects evolutionary responses to selective pressures, as seen here, but selection and environment also affect the evolution of the genetic variance-covariance matrix (*G*) underlying morphological trait covariation (Pigliucci 2005, Wood & Brodie 2015). Although traditional evolutionary processes (selection, genetic drift, gene flow, and mutation) can gradually alter a *G*-matrix (Arnold et al. 2008), it has been demonstrated that a population's genetic variance-covariance matrix can be significantly and rapidly altered in direction, magnitude, and geometry as a result of exposure to new environments (Wood & Brodie 2015, as discussed in Sneigula et al. 2018). Changes in environment can unlock genetic variation that had been suppressed (McGuigan & Sgro 2009), which can then be further shaped by selective pressures (Schroeder & Ackermann 2017). Indeed, patterns of covariation

(measured as integration) have been demonstrated to differ between closely related primate species (Rolian 2009, Young et al. 2010), and in a recent application of quantitative genetic methods, Schroeder & Ackermann (2017) found that although much of the cranial diversity across hominin lineages was shaped by neutral processes, the first *Homo* migration out of Africa was marked by an adaptive response to the new environment, altering the observed morphology as well as the associated trait covariance structure.

The potentially rapid evolution of the *G*-matrix, as well as the effect trait covariation can have on postcranial evolution, as demonstrated here, has serious implications for anthropologists applying the thermoregulatory interpretation of ecogeographic morphology derived from modern humans to ancient hominin lineages. This throws a great amount of caution on the use of the cylindrical model (Ruff 1991, Ruff 1994) and the trait-based temperature-estimating equations discussed in Chapter I, which comprise a cornerstone of modern ecogeographic models for human evolution and were precisely designed to allow researchers to apply the understanding of the relationship of body shape and size with ecogeography to human ancestors (Trinkaus 1981, Ruff & Walker 1993, Holliday 1995). Ruff (1994) specifically argued that because the soft-tissue is not available when investigating hominin fossils, skeletal traits can serve as a reasonable proxy. The results of the dissertation, however, support the growing evidence that not only do differences in trait means fail to predict selection – which is how the majority of fossil measures are analyzed when attempting to reconstruct postcranial evolution – but that researchers cannot expect patterns of trait covariation to remain the same between populations within a species, let alone across species with large differences in environment and evolutionary time.

Postcranial Variance across Ecogeographic Regions

The role of trait covariation in human postcranial evolution was further explored by assessing indices of evolvability for groups across ecogeographic regions. This study was constructed with two potential outcomes in mind. In one outcome, human groups would demonstrate similar indices of evolvability across regions due to maintenance of trait variation,

likely resulting from humanity's short evolutionary history (see above). In the alternative outcome, different indices of evolvability across regions occur because of reduced variance, potentially associated with human patterns of migration and serial founder effects. As explored in Chapter III, the results of the analysis point toward a middle ground between these two outcomes. While humans have not differentiated enough in trait variance to affect the evolvability of traits, there is enough structure provided through evolutionary history to produce trends in evolvability indices that coincide with latitude and migratory history.

The results of this study highlight the importance of sample size when comparing indices of evolvability (as per Grabowski & Porto 2017), as well as demonstrating that when sample sizes are large enough to allow for meaningful interpretation, human groups do not differ significantly in estimated evolvability, respondability, conditional evolvability, or autonomy (Figure 8). Broadly, the results of this study therefore support the first expected outcome, in which human groups display similar indices of evolvability across regions. The lack of differentiation in measures of evolvability between even the most extreme ecogeographic regions (sub-Saharan Africa and the circumpolar arctic, Figure 8) is likely due to the maintenance of additive genetic variance in these six traits (and the various multivariate combinations of these traits) across human groups, despite observed phenotypic differences (Hansen et al. 2011). Additive genetic variance is the primary material upon which evolutionary forces act (Falconer & Mackay 1996, Hansen et al. 2011) and it is likely that this variance is maintained in populations that demonstrate disparate observed phenotypic variation as a result of modern humanity's short evolutionary history, or possibly, as a result of gene flow and mutation adding back variance lost to the serial founder effect (although see Relethford 1994, Chapter III).

However, despite the lack of significant differentiation between groups across regions, this research also exposed potentially emergent trends in the patterns of human postcranial variance. Estimations of mean evolvability and respondability, for example, demonstrated a negative correlation with latitude, while mean autonomy increased in colder climates (Figure 8) Though these regions are, again, not distinctly heterogeneous (95% standard deviations

overlap), the observed trends may indicate a nascent negative relationship between additive genetic variance and latitude/ecogeographic regions with regard to postcranial traits. This pattern was predicted by the second outcome proposed by this study, which holds that additive genetic variance would decrease as a result of the out-of-Africa serial founder model of human migration, the strength of selective forces acting on these traits (individually and in correlation with each other), and the resultant increase in the strength of covariation between the traits.

The out-of-Africa serial founder model of neutral evolution is associated with a decrease in overall genetic variance with increasing geographic distance from Africa (Prugnolle et al. 2005, Ramachandran et al. 2005, Liu et al. 2006, Hunley et al. 2009, DeGiorgio et al. 2009). Since the regions represented in this study (sub-Saharan Africa, North Africa, Temperate Europe, and Circumpolar arctic) differ not only in increasing latitude, but in distance from sub-Saharan Africa, the resultant trends may therefore represent the loss in total genetic variance associated with ancient human migration. It is also possible that the selection observed to drive phenotypic variance in these traits (Roseman & Auerbach 2015, Savell et al. 2016, see Chapter II), is reducing genetic variation as well, and is impacting the ability of traits in arctic populations to respond to evolutionary pressures, as selection is known to remove non-adaptive genetic variance (Falconer & Mackay 1996).

When taken in consideration with the positive relationship between latitude and autonomy (a measure of trait constraint) (Figure 8), this research may indicate a consequent increase in the strength of trait covariation in arctic groups, likely stemming from the reduction in genetic variation associated with migration and selective pressures. Stronger trait covariation would restrict avenues of evolution to a narrower range of phenotypic space, reducing evolvability and respondability for selection gradients that do not align precisely with the traits' major axis (Rolian 2014, Savell et al. 2016). This is unlike conditional evolvability, which does not correlate with latitude and can instead be interpreted to indicate that the *pattern* of trait covariation in these traits is nearly identical across human groups, even if the *strength* of that covariation changes in response to decreasing genetic variance.

While it is important to reiterate that the trends discussed above are patterns within a statistically homogenous comparison of evolvability across ecogeographic regions, these emergent trends illuminate trait respondability to evolutionary pressures is shaped by the relationship between population structure, trait covariation, and evolutionary history. They also provide further evidence against using an interpretation of modern human postcranial evolution to better understanding the evolution of ancient hominins. The results of this study indicate increasing regional differentiation in the covariance structure of these six postcranial traits, a trend that would have emerged in the conservative 37-135 thousand years since the initiation of humanity's out-of-Africa migration (Liu et al. 2006, Henn et al. 2012, Reyes-Centeno et al. 2015). In contrast, the earliest line of *Homo* known to have migrated out of Africa (*H. erectus* from Dminisi, Georgia) is estimated to be 1.8 million years old (Ferring et al. 2011, Schroeder & Ackermann 2017). Modern humans have therefore been interacting with and adapting to their non-African environments for <0.1% of the time as the Dminisi hominins and their decedents.

If unique patterns of evolvability and additive genetic covariance are becoming distinguished among human populations over the course of as few as 135 thousand years, how then could the postcranial trait evolution found in modern humans be meaningfully translated to early *Homo*, or further back to *Australopithecus afarensis* or *A. africanus* (Ruff 1994)? Any observed similarity between how modern human and ancient hominin morphology vary with climate cannot be assumed to indicate presence of identical adaptive pressures (or other evolutionary causes) until a concordant similarity in genetic and environmental structure for the traits of interest is also established.

The Thermoregulatory Imperative and Synergistic Selective Effects

The large impact of covariance structure on the ability of some traits to respond to selective pressures, as well as the associated effect of trait covariation on evolvability and additive genetic variance across groups, demonstrate the importance of investigating evolutionary trends within a multivariate context. Rarely, however, are the multivariate interactions of the

selective pressures themselves considered. While the findings of this dissertation generally support the evolutionary expectations set forth by the thermoregulatory imperative in modern humans, they also illuminate the complexity of the interactions between potentially synergistic selective pressures that can lead to (in concert with underlying trait covariance) the patterns of postcranial morphology established by Bergmann (1847) and Allen (1877). The cause(s) of selection will first be analyzed for measures of body size (FHD, BIB) and then for the limbs (HML, RML, FML, TML).

Regarding body size and body breadth, this research demonstrates femoral head diameter and bi-iliac breadth are under (positive) selective pressure to increase at higher latitudes (Chapter II, Chapter IV), as would be expected given the thermoregulatory imperative model (Ruff 1994). When considered within the entire suite of traits, femoral head diameter and bi-iliac breadth demonstrate modularity only with each other (Figure 15) and are moderately covariant, with a weaker covariance than is found between limb lengths (Table 2). However, when the effects of population size and trait covariation are accounted for, only femoral head diameter appears to be responding to selective pressure driven by temperature (Figure 14). The directional selection pushing femoral head diameter to increase, and thus higher body masses, at higher latitudes is best predicted by a model in which minimum temperature is the fixed effect predictor, seemingly supporting the theory that larger femoral head diameters are adaptive for modern humans living in environments that are extremely cold. In contrast, while bi-iliac breadth is under similar directional selection to broaden at higher latitudes, its adaptive pressure is not associated with either minimum or maximum temperature (Figure 14). This not only undermines the thermoregulatory interpretation of bi-iliac breadth variation across ecogeographic regions, it further complicates Ruff's (1994) cylindrical model, in which diameter (bi-iliac breadth) is claimed to be the most important measure for comparing evolutionary trends in human and hominin postcranial morphology.

As femoral head diameter and bi-iliac breadth are both measures of body size, the discrepancy in the origin of directional selective pressure for each trait may offer insight into a larger pattern of adaptation. While bi-iliac breadth provides a straightforward measure of pelvic

(body) breadth, femoral head diameter is technically an estimate of body *mass* (Ruff 1991, Ruff 1994, Auerbach & Ruff 2004). It is possible that femoral head diameter is responding not to an adaptive push towards decreased surface area/volume ratio in northern climes (mitigating heat dissipation in humans), but is instead demonstrating a response to selection for increasing body mass – and potentially a thicker shell of insulating tissue (see "Human Thermoregulation," Chapter I) – at higher latitudes and in colder environments. Similarly, the increase of bi-iliac breadth with latitude (but not temperature) might serve to support increased adiposity, providing additional caloric storage in a notoriously nutrient-scarce environment. It should be emphasized that while these suggested interpretations cannot be proven definitively by the findings reported here, they both provides a testable hypotheses derived from a quantitative approach that accounts for population structure, trait covariance, and multiple climactic variables.

In contrast to femoral head diameter, bi-iliac breadth's directional selection is associated exclusively with latitude when controlling for the effects of population structure and trait covariation. This suggests that the adaptive forces shaping bi-iliac breadth originate from a variable or variables associated with latitude that *are not temperature*. The failure of bi-iliac breadth to demonstrate selective pressure associated with temperature also relates to the soft-tissue interpretation of femoral head evolution discussed above. When decoupled from the general category of "body size," it becomes clear that these two traits are likely following distinct evolutionary paths. While femoral head diameter supports expectations that track with an increase in the insulating and heat generating soft-tissue associated with higher latitudes, morphological variance in bi-iliac breadth appears to be driven by adaptive pressures that are not thermoregulatory in nature and instead originate with some untested variable or variables, such subsistence (nutrient scarcity, caloric storage).

Like femoral head diameter and bi-iliac breadth, long bone lengths have more complicated evolutionary responses to thermoregulation than is commonly assumed under preexisting models. Although the results of the first study (Chapter II) demonstrated that the distal limb segments (RML, TML) were, as expected, under directional selection to shorten at increased

latitudes, the adaptive cause of that pressure is more difficult to parse. The same negative selection (pressure to shorten) was observed to be acting on the distal limb segments in the latitude model in Chapter IV, which controls for trait covariation and population history, though this relationship could not be differentiated from changes in dimensions due to population structure (Figure 14). Interestingly, the model that appeared to best describe the primary adaptive force behind distal limb shortening was the maximum temperature model, rather than minimum temperature model (Figure 14). This may suggest that, unlike femoral head diameter – which appears to respond to exposure to extreme cold (minimum temperature) – the distal limb segments may instead be driven by the fact that the arctic groups comprising this sample are never exposed to natural environmental temperatures above 15°C (59°F) (though this study cannot account for examples of cultural buffering such as clothing, fire, or protective constructions, Holliday 1997). The differences between these variables may therefore represent the difference between adaptations that protect the body from extreme, acute cold exposure (minimum temperature; FHD, HML, FML) and adaptations that protect against the heat lost to a constant, low-level thermoregulatory expense associated with maximum temperature (FML, RML, TML).

In fact, the selective pressures imposed by minimum and maximum temperature appear to be acting in opposition across all six traits when population structure and trait covariation are taken into account (Figure 14). For example, the first study demonstrated that the humerus was under selection to lengthen with latitude despite the fact that humeral length is observed to shorten in colder climates, a result of the strong covariance between limb lengths (Chapter II). This finding is supported by the third study, which demonstrates that minimum temperature (which is associated with zero-or-positive selection pressure on all of the examined traits) is the primary source of directional selection influencing the humerus (Chapter IV) (Figure 14). In the latitude and maximum temperature models, selective pressures are indistinguishable from neutral processes. Indeed, it is possible that the directional selection on the humerus in response to factors associated with latitude are so close to zero because the negative directional selection imposed by maximum temperature and the positive directional selection

imposed by minimum temperature are mitigating each other when combined within a variable that includes both temperature measures (that is, latitude) (Figure 14).

This interpretation is further supported by the role of selection on the femur. The femur is under significant (non-zero) directional selection to shorten in response to decreasing maximum temperature, while also being subjected to significant (non-zero) directional selection to length driven by increasing minimum temperature (Figure 14). As a result, latitude appears to have a purely neutral effect on femoral evolution (as was estimated in Chapter II and found previously by Roseman and Auerbach, 2015) (Figure 5). Because the study described in Chapter II relied exclusively on latitude as an indicator of climactic differences, the lack of any estimated selection was interpreted to mean that changes in femoral length were driven primarily by population history and trait covariation (Savell et al. 2016). Instead, it appears that the strong, synergistic effects of maximum and minimum temperature, couched within the higher-order variable of latitude, sent a false signal that femoral length is under no directional selection.

This unexpected result further demonstrates that not only do differences in trait means fail to predict the presence of adaptation, but that estimations of selective pressure can be misleading if the correct variable or variables are not identified. In many ways, this finding reflects the critique of the ecogeographic literature upon which this dissertation is based: interpretations stemming from analyses that fail to account for the covariation of traits are inherently flawed. Similarly, it appears that analyses attempting to distinguish selective pressures from evolutionary processes can be likewise flawed if they fail to account for the synergistic interactions between the variables that could be driving adaptation. Instead, deciding which potential sources of selective pressure are going to be included in a given analysis should be subject to careful consideration, and potential interactions between sources of selection (such as the hierarchical relationship between measures of temperature and latitude) should be identified *a priori*.

Implications for Future Ecogeographic Studies

The findings of this dissertation have serious implications for the study of ecogeographic variation in modern humans and ancient hominins. This research demonstrates that the covariance structure underlying human limb lengths and measures of body size substantially affects how these traits respond to selective pressure. The effects of trait covariation, as demonstrated here, render attempts to examine the distribution of trait means, or their correlations with environmental variables, meaningless with regard to actual evolutionary processes. In addition, this dissertation shows that the evolution of phenotypic traits is likely to be driven not by a single environmental variable, but by the actions and interactions of multiple covarying sources of selective pressure. Disentangling these multi-variable, multi-trait interactions, while also accounting for the influence of neutral evolutionary processes, can only be done using quantitative genetics methods and large, globally-representative samples.

Unfortunately, these requirements also severely limit the degree to which the evolutionary processes acting on modern humans can be translated to the fossil record. As the second study of this dissertation demonstrates, there is evidence for emergent differentiation between human groups across ecogeographic regions. If that degree of difference is obvious in modern humans after only 37-135 thousand years of evolution, how could findings derived from modern humans be meaningfully translated to hominin lineages that lived 1.8 million years ago? Ancient humans groups had their own distinct population histories, selective pressures, and patterns of trait covariance. As such, the results of modern human quantitative genetics research cannot be applied to our hominin ancestors.

Limitations of Study

The results of these analyses are, necessarily, limited by the available data. Despite being the largest, most globally-dispersed dataset of postcranial skeletal measurements available, the combined Goldman and Americas datasets (with generous contributions from Holliday and Ruff), do not provide perfect representation of human phenotypic variation. Groups from western Africa, eastern South America, Central America, Central Asia, East Asia, the Indian

subcontinent, and Pacific Islands are particularly poorly represented (Figure 4), potentially obfuscating important patterns of trait covariation, among-group evolvability, and climactic response. In addition, while there was fairly even representation of both males and females in the overall phenotypic sample (2187 males/3776 individuals = 58% male, 42% female), some groups were represented entirely by males. Although differences due to sex and size were accounted for in the analyses presented herein, additional female representation across all groups would allow for a more nuanced investigation of sex-based differences in human ecogeographic evolution.

Another issue with the data in this dissertation is that these analyses rely on only six postcranial traits. While these traits were chosen due to their ubiquitous use in the human ecogeographic literature and correspond with the morphology specifically predicted to vary with climate by Bergmann (1847) and Allen (1877) (Trinkaus 1981, Ruff 1991, Ruff 1994, Holliday 1997, Holliday 1999, defined in Martin 1928), they comprise a small portion of the possible postcranial characteristics that are likely to correlate and coevolve in modern humans; for example, see the more traits considered by Auerbach (2007) or Betti et al. (2012). It is therefore possible that the inclusion of other traits could introduce new patterns of covariation that would alter the pattern of the results found in this study, or that the patterns uncovered in these studies could be reflecting the effects of selection on some unobserved trait. The addition of postcranial measurements such as articular topography, long bone robusticity, or soft tissue characteristics such as body composition and insulation, could potentially allow for a more complete investigation of trait covariation with regard to our understanding of functional and thermoregulatory trends in human evolution.

In addition, as discussed in detail in Chapter IV, “Materials and Methods,” the microsatellite variant data use to represent the global distribution of human variation had to be matched to the phenotypic dataset by region as they were not collected from the same individuals. Ideally, the morphological and genetic data would originate from the same individuals, allowing for a more direct analysis of the genotype-to-phenotype relationship and some understanding of the amount of variance introduced by development, epistatic interactions, and other

environmental factors. However, as there is no large-scale dataset consisting of both the postcranial measures of interest and genetic data (either microsatellite or single-nucleotide polymorphisms), this study relies on the veracity of the matches made between phenotypic and genomic datasets. As discussed in Chapter IV, "Materials and Methods," biases resulting from any mismatches are local, and are likely to be obscured in the overall pattern of genetic variation.

Future Research

This dissertation lends itself to several potential avenues for future research. On a practical level, as discussed above, there are many regions that are poorly represented in the large phenotypic data set and collecting osteometric data to fill those gaps would improve future quantitative genetic studies of human ecogeographic variation.

There is also growing evidence that the northern-most (highest latitude) groups may be driving a disproportionate amount of observed variation (Roseman 2004, Harvati & Weaver 2006, Betti et al. 2010, Roseman 2016; though see Katz et al. 2016), though the majority of this work has been done on cranial morphology. I would therefore be interested in examining which (if any) populations may be influencing these evolutionary trends. Using genome-wide association studies (GWAS), Berg and Coop (2014) developed an approach for detecting strong correlations between environmental variables and genetic data, which they use to identify groups that have a disproportionate effect on overall gene dispersal. An application of this method to GWAS data associated with limb bone lengths and body breadths could be enlightening about the role of extreme-environment groups in driving patterns of human evolution.

In addition, I am currently coauthoring a grant application for a project that will more directly examine the connection between thermoregulation and the evolution of body geometry and composition. This will be my first foray into studying the physiology associated with human body form evolution, and I am excited to explore new lines of evidence that will complement the quantitative genetics methods used thus far.

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APPENDICES

Appendix I: Supplementary Tables and Figures, Chapter II

Table S1a-nn. Examples of directional selection estimated between sub-Saharan African and non-sub-Saharan African groups: differences in trait means between groups, estimated selection gradients (β), net response to selection ($\Delta\bar{z}$), and correlated responses to selection on traits that combine to yield the net response ($\Delta z_{element}$). Within the Trait-Specific Responses to Selection matrix, direct responses to selection are shade and indirect (correlated) responses are not.

a. Kikuyu and Point Hope - Tigara (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-25.5	-24.5 (-51.7, 4.0)	-0.08	-0.05	-0.18	0.03	-0.05	0.09	0.08
RML	-32.6	**-90.0 (-113.3, -66.2)**	-0.14	-0.05	-0.24	0.03	-0.06	0.10	0.09
FML	-26.4	13.6 (-32.2, 57.9)	-0.06	-0.05	-0.17	0.03	-0.06	0.10	0.09
TML	-35.4	-28.3 (-72.2, 8.5)	-0.10	-0.05	-0.19	0.03	-0.07	0.09	0.09
FHD	3.2	**60.4 (43.5, 78.3)**	0.07	-0.04	-0.14	0.02	-0.04	0.17	0.10
BIB	38.3	**87.2 (73.8, 101.4)**	0.14	-0.02	-0.09	0.01	-0.03	0.07	0.19

b. West Africa and Point Hope - Tigara (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-15.5	**31.2 (3.0, 58.3)**	-0.05	0.07	-0.23	-0.03	-0.05	0.09	0.10
RML	-32.5	**-116.3 (-142.8, -91.6)**	-0.14	0.06	-0.31	-0.03	-0.05	0.09	0.10
FML	-24.1	-15.5 (-54.0, 22.5)	-0.06	0.06	-0.22	-0.03	-0.05	0.10	0.10
TML	-32.6	-24.6 (-56.7, 5.7)	-0.09	0.06	-0.25	-0.03	-0.06	0.09	0.11
FHD	3.7	**59.2 (40.4, 78.0)**	0.08	0.05	-0.19	-0.02	-0.04	0.16	0.12
BIB	46.4	**100.0 (81.0, 117.7)**	0.17	0.03	-0.11	-0.02	-0.03	0.07	0.22

c. San and Point Hope - Tigara (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	9.5	22.7 (-9.8, 50.4)	0.03	0.05	-0.09	-0.07	-0.06	0.09	0.11
RML	-1.9	**-45.8 (-69.1, -24.5)**	-0.01	0.04	-0.12	-0.08	-0.07	0.10	0.11
FML	7.2	**-40.0 (-73.8, -5.5)**	0.02	0.04	-0.09	-0.09	-0.07	0.10	0.12
TML	-0.9	**-30.4 (-56.3, -3.6)**	<0.01	0.04	-0.10	-0.09	-0.08	0.10	0.12
FHD	7.4	**62.8 (37.4, 88.5)**	0.16	0.03	-0.07	-0.06	-0.05	0.17	0.14
BIB	65.3	**114.8 (86.1, 136.5)**	0.23	0.02	-0.04	-0.04	-0.03	0.07	0.25

d. Uganda and Point Hope - Tigara (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-31.6	-9.7 (-47.8, 25.8)	-0.10	-0.02	-0.19	-0.02	-0.10	0.14	0.09
RML	-39.4	**-96.7 (-119.4, -74.3)**	-0.18	-0.02	-0.26	-0.02	-0.11	0.15	0.09
FML	-41.9	-12.1 (-49.2, 22.0)	-0.10	-0.02	-0.18	-0.03	-0.11	0.15	0.09
TML	-51.9	**-50.8 (-89.9, -13.7)**	-0.15	-0.02	-0.21	-0.03	-0.13	0.14	0.09
FHD	4.6	**93.7 (80.9, 108.0)**	0.10	-0.01	-0.15	-0.02	-0.08	0.26	0.11
BIB	38.9	**88.9 (72.8, 107.1)**	0.14	-0.01	-0.09	-0.01	-0.05	0.11	0.20

e. Kikuyu and Kuskowagamiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-19.6	**38.2 (12.0, 62.1**)	-0.06	0.08	-0.06	0.09	-0.31	0.07	0.06
RML	-28.6	**-28.5 (-50.6, -5.2)**	-0.12	0.07	-0.08	0.09	-0.36	0.08	0.07
FML	-35.5	47.7 (-3.6, 96.9)	-0.09	0.07	-0.05	0.11	-0.35	0.08	0.07
TML	-57.9	**-165.1 (-214.7, -120.4)**	-0.17	0.07	-0.06	0.10	-0.43	0.07	0.07
FHD	2.0	**47.6 (29.7, 67.5)**	0.04	0.06	-0.05	0.08	-0.25	0.13	0.08
BIB	23.3	**66.7 (47.9, 84.2)**	0.09	0.04	-0.03	0.05	-0.17	0.06	0.15

f. West Africa and Kuskowagamiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-9.6	**92.4 (67.2, 114.6)**	-0.03	0.20	-0.11	0.03	-0.31	0.07	0.08
RML	-28.6	**-54.7 (-80.2, -32.4)**	-0.12	0.18	-0.15	0.04	-0.35	0.07	0.08
FML	-33.2	18.5 (-25.5, 62.9)	-0.08	0.17	-0.10	0.04	-0.34	0.07	0.08
TML	-55.1	**-160.4 (-199.2, -121.8)**	-0.17	0.18	-0.12	0.04	-0.42	0.07	0.09
FHD	2.5	**46.3 (26.3, 66.9)**	0.05	0.14	-0.09	0.03	-0.25	0.13	0.10
BIB	31.5	**80.6 (56.7, 101.6)**	0.12	0.09	-0.05	0.02	-0.17	0.06	0.18

g. San and Kuskowagamiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	15.4	**79.7 (53.5, 104.3)**	0.05	0.17	0.02	-0.02	-0.29	0.08	0.09
RML	2.1	9.7 (-11.0, 31.7)	0.01	0.16	0.03	-0.02	-0.33	0.08	0.10
FML	-1.9	-9.7 (-49.0, 27.8)	<0.01	0.15	0.02	-0.02	-0.33	0.08	0.10
TML	-23.4	**-154.3 (-184.5, -120.5)**	-0.07	0.15	0.02	-0.02	-0.40	0.08	0.10
FHD	6.2	**51.3 (24.4, 76.4)**	0.14	0.12	0.02	-0.02	-0.24	0.14	0.12
BIB	50.4	**96.8 (69.8, 122.4)**	0.19	0.08	0.01	-0.01	-0.16	0.06	0.21

h. Uganda and Kuskowagamiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-25.7	**54.5 (17.2, 85.0)**	-0.08	0.12	-0.06	0.04	-0.37	0.12	0.07
RML	-35.5	**-32.8 (-52.5, -13.7)**	-0.16	0.11	-0.09	0.05	-0.42	0.13	0.07
FML	-51.0	23.7 (-18.2, 61.6)	-0.12	0.10	-0.06	0.05	-0.41	0.13	0.07
TML	-74.5	**-193.4 (-235.5, -148.7)**	-0.22	0.10	-0.07	0.05	-0.51	0.13	0.07
FHD	3.4	**81.3 (65.4, 97.4)**	0.07	0.08	-0.05	0.04	-0.30	0.22	0.08
BIB	23.9	**68.7 (49.6, 89.2)**	0.09	0.05	-0.03	0.02	-0.20	0.10	0.15

i. Kikuyu and NeoAleut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-25.3	15.3 (-7.1, 38.1)	-0.08	0.03	-0.04	<0.01	-0.22	0.08	0.06
RML	-28.6	-21.5 (-45.2, 3.1)	-0.12	0.03	-0.06	<0.01	-0.25	0.08	0.06
FML	-43.0	2.3 (-45.3, 47.7)	-0.10	0.03	-0.04	0.01	-0.25	0.08	0.07
TML	-55.1	**-114.9 (-158.0, -72.8)**	-0.16	0.03	-0.05	0.01	-0.30	0.08	0.07
FHD	1.5	**51.4 (34.3, 68.6)**	0.03	0.02	-0.03	<0.01	-0.18	0.14	0.08
BIB	21.2	**65.2 (52.1, 78.6)**	0.08	0.01	-0.02	<0.01	-0.12	0.06	0.14

j. West Africa and NeoAleut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-15.4	**70.6 (48.9, 92.0)**	-0.05	0.15	-0.09	-0.05	-0.21	0.07	0.08
RML	-28.6	**-48.1 (-72.6, -23.5)**	-0.12	0.14	-0.13	-0.05	-0.24	0.08	0.08
FML	-40.7	-27.0 (-62.2, 10.1)	-0.10	0.13	-0.09	-0.06	-0.24	0.08	0.08
TML	-52.3	**-110.6 (-143.6, -81.6)**	-0.16	0.13	-0.10	-0.06	-0.29	0.08	0.08
FHD	2.0	**50.1 (32.7, 67.4)**	0.04	0.10	-0.08	-0.04	-0.17	0.14	0.09
BIB	29.4	**79.1 (58.5, 95.7)**	0.11	0.07	-0.05	-0.03	-0.12	0.06	0.18

k. San and NeoAleut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	9.7	**59.8 (36.1, 83.3)**	0.03	0.13	0.03	-0.10	-0.21	0.08	0.09
RML	2.1	15.8 (-5.1, 37.3)	0.01	0.12	0.04	-0.10	-0.23	0.09	0.09
FML	-9.4	**-52.1 (-83.9, -20.8)**	-0.02	0.11	0.03	-0.12	-0.23	0.09	0.10
TML	-20.6	**-108.1 (-133.8, -83.8)**	-0.06	0.11	0.03	-0.11	-0.28	0.08	0.10
FHD	5.8	**54.9 (30.4, 79.4)**	0.13	0.09	0.03	-0.08	-0.17	0.15	0.11
BIB	48.3	**95.5 (70.5, 118.1)**	0.18	0.06	0.02	-0.05	-0.11	0.07	0.21

l. Uganda and NeoAleut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-31.4	31.3 (-2.4, 64.9)	-0.10	0.07	-0.05	-0.04	-0.27	0.13	0.07
RML	-35.5	**-25.9 (-46.5, -5.9)**	-0.16	0.06	-0.07	-0.05	-0.30	0.14	0.07
FML	-58.5	-23.7 (-62.1, 6.5)	-0.14	0.06	-0.05	-0.05	-0.30	0.14	0.07
TML	-71.6	**-141.3 (-178.2, -101.7)**	-0.21	0.06	-0.06	-0.05	-0.37	0.13	0.07
FHD	2.9	**85.6 (72.6, 98.6)**	0.06	0.05	-0.04	-0.04	-0.22	0.24	0.08
BIB	21.8	**67.1 (50.9, 85.7)**	0.08	0.03	-0.03	-0.02	-0.15	0.10	0.15

m. Kikuyu and Ikogmiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-14.3	**51.7 (25.6, 75.3)**	-0.05	0.11	-0.09	-0.04	-0.15	0.07	0.06
RML	-24.9	**-46.7 (-71.2, -22.2)**	-0.11	0.10	-0.13	-0.04	-0.17	0.07	0.06
FML	-33.3	-21.0 (-69.2, 28.1)	-0.08	0.10	-0.09	-0.05	-0.17	0.07	0.06
TML	-42.8	**-79.9 (-122.0, -39.3)**	-0.12	0.10	-0.10	-0.04	-0.21	0.07	0.06
FHD	1.8	**44.5 (26.3, 60.7)**	0.04	0.08	-0.07	-0.03	-0.12	0.12	0.07
BIB	23.0	**61.0 (45.5, 75.0)**	0.09	0.05	-0.05	-0.02	-0.08	0.05	0.14

n. West Africa and Ikogmiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-4.4	**104.9 (82.2, 127.9)**	-0.01	0.23	-0.14	-0.09	-0.14	0.06	0.07
RML	-24.9	**-72.4 (-98.3, -46.0)**	-0.11	0.21	-0.20	-0.09	-0.16	0.07	0.07
FML	-31.0	**-49.2 (-86.9, -12.6)**	-0.07	0.19	-0.14	-0.11	-0.16	0.07	0.08
TML	-40.0	**-75.9 (-108.6, -44.5)**	-0.11	0.20	-0.16	-0.11	-0.20	0.07	0.08
FHD	2.3	**43.2 (24.3, 61.9)**	0.05	0.15	-0.12	-0.08	-0.12	0.12	0.09
BIB	31.1	**75.0 (52.3, 95.2)**	0.12	0.10	-0.07	-0.05	-0.08	0.05	0.17

o. San and Ikogmiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	20.7	**91.6 (64.1, 116.7)**	0.07	0.20	-0.01	-0.13	-0.15	0.07	0.09
RML	5.7	-7.5 (-31.1, 15.1)	0.03	0.18	-0.02	-0.14	-0.16	0.08	0.09
FML	0.3	**-71.7 (-104.8, -39.2)**	<0.01	0.17	-0.01	-0.16	-0.16	0.08	0.09
TML	-8.3	**-76.4 (-102.0, -49.6)**	-0.02	0.17	-0.02	-0.15	-0.20	0.07	0.10
FHD	6.0	**48.5 (23.7, 73.6)**	0.13	0.13	-0.01	-0.12	-0.12	0.13	0.11
BIB	50.0	**91.7 (62.4, 114.6)**	0.19	0.09	-0.01	-0.07	-0.08	0.06	0.20

p. Uganda and Ikogmiut (sub-Saharan Africa to Arctic)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-20.4	**67.9 (32.9, 98.1)**	-0.07	0.15	-0.10	-0.09	-0.20	0.11	0.06
RML	-31.8	**-52.0 (-76.9, -29.0)**	-0.14	0.13	-0.14	-0.09	-0.22	0.13	0.06
FML	-48.9	**-47.7 (-87.9, -14.8)**	-0.11	0.13	-0.10	-0.11	-0.22	0.13	0.06
TML	-59.4	**-104.2 (-142.9, -63.3)**	-0.17	0.13	-0.11	-0.10	-0.27	0.12	0.07
FHD	3.2	**78.3 (64.7, 92.0)**	0.07	0.10	-0.08	-0.08	-0.16	0.22	0.07
BIB	23.6	**62.7 (44.3, 81.3)**	0.09	0.07	-0.05	-0.05	-0.11	0.09	0.14

q. Kikuyu and Bosnia (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	1.2	11.0 (-9.6, 32.8)	<0.01	0.02	-0.13	0.01	-0.04	0.07	0.06
RML	-11.5	**-67.7 (-86.3, -47.9)**	-0.05	0.02	-0.18	0.01	-0.04	0.08	0.06
FML	5.3	6.2 (-35.0, 47.2)	0.01	0.02	-0.13	0.01	-0.04	0.08	0.06
TML	-5.7	-18.7 (-52.8, 17.1)	-0.02	0.02	-0.15	0.01	-0.05	0.08	0.07
FHD	5.1	**50.6 (35.1, 65.8)**	0.10	0.02	-0.11	0.01	-0.03	0.14	0.08
BIB	36.7	**63.5 (50.6, 75.9)**	0.13	0.01	-0.07	0.01	-0.02	0.06	0.14

r. West Africa and Bosnia (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	11.1	**61.9 (40.5, 82.1)**	0.03	0.13	-0.18	-0.04	-0.03	0.07	0.07
RML	-11.5	**-91.9 (-114.6, -69.4)**	-0.05	0.12	-0.25	-0.04	-0.03	0.08	0.08
FML	7.6	-20.6 (-52.1, 11.9)	0.02	0.11	-0.18	-0.05	-0.03	0.08	0.08
TML	-2.8	-15.6 (-43.3, 11.6)	-0.01	0.12	-0.20	-0.04	-0.04	0.08	0.08
FHD	5.6	**49.3 (32.9, 66.8)**	0.11	0.09	-0.15	-0.03	-0.02	0.14	0.09
BIB	44.9	**76.9 (60.0, 94.2)**	0.16	0.06	-0.09	-0.02	-0.02	0.06	0.17

s. San and Bosnia (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	36.2	**52.9 (27.7, 75.1)**	0.11	0.11	-0.06	-0.08	-0.04	0.08	0.09
RML	19.2	**-28.3 (-48.1, -9.5)**	0.08	0.10	-0.08	-0.08	-0.05	0.09	0.09
FML	38.9	**-42.5 (-70.3, -13.9)**	0.08	0.10	-0.05	-0.10	-0.05	0.09	0.10
TML	28.9	**-21.3 (-40.3, -1.0)**	0.07	0.10	-0.06	-0.09	-0.06	0.08	0.10
FHD	9.3	**53.8 (31.1, 77.7)**	0.19	0.08	-0.05	-0.07	-0.03	0.15	0.11
BIB	63.8	**93.3 (67.1, 114.9)**	0.23	0.05	-0.03	-0.04	-0.02	0.06	0.21

t. Uganda and Bosnia (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-4.9	24.9 (-5.0, 55.2)	-0.02	0.05	-0.14	-0.03	-0.07	0.12	0.06
RML	-18.4	**-73.8 (-90.7, -56.7)**	-0.08	0.05	-0.20	-0.04	-0.08	0.13	0.06
FML	-10.2	-18.8 (-52.4, 8.4)	-0.02	0.05	-0.14	-0.04	-0.08	0.13	0.07
TML	-22.2	**-39.1 (-71.2, -6.8)**	-0.06	0.05	-0.16	-0.04	-0.10	0.13	0.07
FHD	6.5	**82.2 (70.0, 94.6)**	0.13	0.04	-0.12	-0.03	-0.06	0.23	0.08
BIB	37.3	**65.0 (48.0, 80.2)**	0.13	0.02	-0.07	-0.02	-0.04	0.10	0.14

u. Kikuyu and Austria (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-10.4	-0.6 (-25.0, 23.5)	-0.03	<0.01	-0.04	0.01	-0.10	0.04	0.07
RML	-14.4	**-22.7 (-42.9, -1.9)**	-0.06	<0.01	-0.06	0.01	-0.11	0.04	0.07
FML	-15.6	4.2 (-39.0, 49.3)	-0.04	<0.01	-0.04	0.01	-0.11	0.04	0.07
TML	-24.0	**-53.0 (-84.9, -17.5)**	-0.07	<0.01	-0.05	0.01	-0.14	0.04	0.08
FHD	1.9	**24.3 (8.7, 42.3)**	0.04	<0.01	-0.04	0.01	-0.08	0.07	0.09
BIB	30.9	**71.7 (58.2, 84.4)**	0.11	<0.01	-0.02	<0.01	-0.06	0.03	0.16

v. West Africa and Austria (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-0.4	**52.2 (27.5, 73.6)**	<0.01	0.11	-0.09	-0.04	-0.09	0.03	0.08
RML	-14.3	**-47.9 (-71.3, -24.9)**	-0.06	0.10	-0.13	-0.05	-0.11	0.04	0.08
FML	-13.3	-23.6 (-56.8, 10.6)	-0.03	0.10	-0.09	-0.05	-0.11	0.04	0.09
TML	-21.2	**-49.5 (-77.9, -21.8)**	-0.06	0.10	-0.10	-0.05	-0.13	0.04	0.09
FHD	2.4	**23.3 (5.0, 43.5)**	0.05	0.08	-0.08	-0.04	-0.08	0.06	0.10
BIB	39.1	**85.2 (65.3, 102.8)**	0.14	0.05	-0.05	-0.02	-0.05	0.03	0.19

w. San and Austria (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	24.6	**44.0 (18.1, 68.5)**	0.08	0.10	0.02	-0.09	-0.10	0.04	0.10
RML	16.3	12.7 (-8.2, 32.8)	0.07	0.09	0.03	-0.09	-0.11	0.05	0.10
FML	18.0	**-46.9 (-78.8, -19.2)**	0.04	0.08	0.02	-0.11	-0.11	0.05	0.10
TML	10.5	**-51.8 (-72.0, -31.1)**	0.03	0.08	0.03	-0.10	-0.14	0.05	0.11
FHD	6.1	**30.3 (4.2, 55.8)**	0.13	0.06	0.02	-0.08	-0.08	0.08	0.12
BIB	58.0	**101.0 (76.7, 122.2)**	0.21	0.04	0.01	-0.05	-0.05	0.04	0.22

x. Uganda and Austria (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-16.4	13.7 (-20.5, 48.5)	-0.05	0.03	-0.05	-0.04	-0.14	0.08	0.07
RML	-21.2	**-27.7 (-46.5, -8.0)**	-0.09	0.03	-0.08	-0.04	-0.16	0.09	0.07
FML	-31.1	-22.1 (-58.6, 9.5)	-0.07	0.03	-0.05	-0.05	-0.16	0.09	0.07
TML	-40.5	**-75.1 (-110.9, -41.9)**	-0.11	0.03	-0.06	-0.05	-0.20	0.09	0.08
FHD	3.3	**57.7 (43.3, 71.9)**	0.07	0.02	-0.04	-0.04	-0.12	0.16	0.09
BIB	31.5	**73.2 (57.2, 90.3)**	0.11	0.01	-0.03	-0.02	-0.08	0.07	0.16

y. Kikuyu and France (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-11.5	4.1 (-22.5, 32.5)	-0.04	0.01	-0.11	0.01	-0.06	0.05	0.07
RML	-20.0	**-57.3 (-86.7, -29.5)**	-0.08	0.01	-0.15	0.01	-0.07	0.05	0.07
FML	-14.0	7.8 (-36.3, 53.6)	-0.03	0.01	-0.11	0.02	-0.07	0.05	0.07
TML	-22.5	-32.4 (-70.6, 3.4)	-0.06	0.01	-0.12	0.02	-0.08	0.05	0.07
FHD	2.1	**31.4 (12.3, 51.8)**	0.05	0.01	-0.09	0.01	-0.05	0.09	0.08
BIB	30.8	**70.0 (54.8, 85.1)**	0.11	<0.00	-0.06	0.01	-0.03	0.04	0.15

z. West Africa and France (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-1.6	**57.0 (32.8, 83.7)**	<0.00	0.12	-0.16	-0.04	-0.06	0.04	0.08
RML	-19.9	**-82.5 (-112.0, -50.9)**	-0.08	0.11	-0.22	-0.04	-0.06	0.05	0.08
FML	-11.7	-20.1 (-59.0, 17.2)	-0.03	0.11	-0.16	-0.05	-0.06	0.05	0.08
TML	-19.7	-29.0 (-59.2, 0.9)	-0.05	0.11	-0.18	-0.04	-0.08	0.05	0.09
FHD	2.6	**30.3 (11.4, 51.6)**	0.06	0.08	-0.13	-0.03	-0.04	0.08	0.10
BIB	39.0	**83.4 (61.2, 101.7)**	0.14	0.06	-0.08	-0.02	-0.03	0.04	0.18

aa. San and France (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	23.5	**47.8 (19.8, 75.3)**	0.07	0.10	-0.03	-0.08	-0.06	0.05	0.10
RML	10.7	-17.9 (-43.2, 10.9)	0.05	0.09	-0.05	-0.08	-0.07	0.06	0.10
FML	19.5	**-43.5 (-81.8, -9.2)**	0.04	0.09	-0.03	-0.10	-0.07	0.06	0.10
TML	12.0	**-33.6 (-57.5, -8.1)**	0.03	0.09	-0.04	-0.09	-0.09	0.06	0.11
FHD	6.4	**36.5 (9.1, 62.5)**	0.14	0.07	-0.03	-0.07	-0.05	0.10	0.12
BIB	57.9	**99.4 (73.7, 125.5)**	0.21	0.05	-0.02	-0.04	-0.04	0.04	0.22

bb. Uganda and France (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-17.6	18.5 (-21.3, 54.2)	-0.06	0.04	-0.12	-0.03	-0.10	0.09	0.07
RML	-26.8	**-63.3 (-94.3, -35.0)**	-0.11	0.04	-0.17	-0.04	-0.12	0.10	0.07
FML	-29.6	-18.4 (-55.3, 17.6)	-0.07	0.03	-0.12	-0.04	-0.12	0.10	0.07
TML	-39.0	**-53.9 (-90.0, -20.1)**	-0.11	0.04	-0.14	-0.04	-0.14	0.10	0.08
FHD	3.5	**64.7 (49.2, 81.4)**	0.08	0.03	-0.10	-0.03	-0.08	0.18	0.09
BIB	31.4	**71.4 (52.4, 89.6)**	0.12	0.02	-0.06	-0.02	-0.06	0.08	0.16

cc. Kikuyu and Ireland (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	1.9	**46.3 (20.3, 71.7)**	0.01	0.10	-0.12	0.08	-0.18	0.06	0.06
RML	-15.5	**-59.7 (-83.9, -35.6)**	-0.06	0.09	-0.16	0.09	-0.20	0.06	0.06
FML	-0.7	**45.4 (2.7, 89.6)**	<0.00	0.09	-0.11	0.10	-0.20	0.06	0.06
TML	-23.1	**-92.0 (-132.1, -52.8)**	-0.06	0.09	-0.13	0.10	-0.24	0.06	0.06
FHD	3.7	**38.0 (20.3, 54.8)**	0.08	0.07	-0.10	0.07	-0.14	0.10	0.07
BIB	29.9	**58.6 (41.0, 74.3)**	0.11	0.05	-0.06	0.05	-0.10	0.05	0.13

dd. West Africa and Ireland (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	11.8	**96.9 (72.1, 120.3)**	0.04	0.21	-0.16	0.03	-0.17	0.05	0.07
RML	-15.4	**-84.1 (-109.6, -58.1)**	-0.06	0.19	-0.23	0.03	-0.19	0.06	0.07
FML	1.6	18.3 (-19.0, 54.3)	<0.00	0.18	-0.16	0.04	-0.19	0.06	0.07
TML	-20.3	**-88.2 (-125.2, -53.0)**	-0.06	0.18	-0.18	0.04	-0.23	0.06	0.08
FHD	4.2	**36.7 (17.8, 54.5)**	0.09	0.14	-0.13	0.03	-0.14	0.10	0.09
BIB	38.0	**72.3 (51.8, 91.2)**	0.14	0.09	-0.08	0.02	-0.09	0.04	0.16

ee. San and Ireland (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	36.9	**84.8 (61.2, 109.7)**	0.11	0.18	-0.04	-0.01	-0.17	0.06	0.09
RML	15.2	-20.4 (-44.2, 2.5)	0.06	0.17	-0.06	-0.01	-0.19	0.07	0.09
FML	32.9	-7.3 (-40.3, 23.2)	0.07	0.16	-0.04	-0.02	-0.19	0.07	0.09
TML	11.4	**-88.1 (-117.5, -59.6)**	0.03	0.16	-0.04	-0.02	-0.23	0.07	0.09
FHD	7.9	**42.3 (17.7, 65.1)**	0.17	0.12	-0.03	-0.01	-0.14	0.12	0.11
BIB	57.0	**89.2 (64.5, 113.8)**	0.21	0.08	-0.02	-0.01	-0.09	0.05	0.20

ff. Uganda and Ireland (sub-Saharan Africa to Temperate Europe)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-4.2	**61.2 (25.3, 95.5)**	-0.01	0.13	-0.13	0.04	-0.22	0.10	0.06
RML	-22.3	**-65.3 (-89.4, -40.1)**	-0.09	0.12	-0.18	0.04	-0.25	0.11	0.06
FML	-16.2	21.8 (-11.1, 54.7)	-0.04	0.11	-0.12	0.05	-0.25	0.11	0.06
TML	-39.7	**-115.7 (-157.5, -76.5)**	-0.11	0.12	-0.14	0.05	-0.30	0.11	0.06
FHD	5.1	**70.1 (56.7, 83.5)**	0.11	0.09	-0.10	0.03	-0.18	0.19	0.07
BIB	30.5	**60.1 (41.2, 78.5)**	0.11	0.06	-0.06	0.02	-0.12	0.08	0.13

gg. Kikuyu and Nubia (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-14.1	-13.6 (-39.9, 11.8)	-0.04	-0.03	-0.04	-0.06	0.02	0.02	0.04
RML	-13.3	**-20.3 (-39.9, -0.1)**	-0.05	-0.03	-0.05	-0.06	0.02	0.02	0.04
FML	-20.0	-32.3 (-80.2, 15.4)	-0.05	-0.03	-0.04	-0.07	0.02	0.03	0.04
TML	-15.6	11.4 (-25.2, 46.0)	-0.04	-0.03	-0.04	-0.07	0.03	0.02	0.04
FHD	0.2	15.6 (-3.8, 34.3)	<0.00	-0.02	-0.03	-0.05	0.02	0.04	0.05
BIB	14.0	**40.6 (25.4, 54.0)**	0.05	-0.01	-0.02	-0.03	0.01	0.02	0.09

hh. West Africa and Nubia (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-4.2	**39.6 (15.8, 63.6)**	-0.01	0.09	-0.09	-0.11	0.03	0.02	0.05
RML	-13.2	**-45.7 (-66.9, -23.7)**	-0.05	0.08	-0.12	-0.12	0.03	0.02	0.05
FML	-17.7	**-60.2 (-95.0, -25.4)**	-0.04	0.07	-0.09	-0.14	0.03	0.02	0.06
TML	-12.7	14.2 (-16.0, 40.8)	-0.03	0.08	-0.10	-0.13	0.04	0.02	0.06
FHD	0.7	14.4 (-7.6, 34.8)	0.02	0.06	-0.07	-0.10	0.02	0.04	0.07
BIB	22.1	**55.3 (35.4, 73.5)**	0.09	0.04	-0.04	-0.06	0.02	0.02	0.12

ii. San and Nubia (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	20.9	**32.6 (5.4, 56.9)**	0.07	0.07	0.03	-0.15	0.01	0.03	0.07
RML	17.4	14.5 (-5.1, 34.6)	0.07	0.06	0.04	-0.15	0.02	0.04	0.07
FML	13.6	**-80.9 (-111.9, -52.1)**	0.03	0.06	0.03	-0.18	0.02	0.04	0.07
TML	19.0	7.1 (-16.0, 31.4)	0.05	0.06	0.03	-0.17	0.02	0.03	0.08
FHD	4.4	22.3 (-4.8, 45.9)	0.10	0.05	0.02	-0.13	0.01	0.06	0.09
BIB	41.0	**73.4 (47.2, 96.8)**	0.16	0.03	0.01	-0.08	0.01	0.03	0.16

jj. Uganda and Nubia (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-20.2	0.3 (-38.1, 33.2)	-0.06	<0.00	-0.05	-0.11	-0.02	0.07	0.04
RML	-20.1	**-25.9 (-44.4, -7.0)**	-0.08	<0.00	-0.07	-0.12	-0.02	0.08	0.04
FML	-35.5	**-61.2 (-96.4, -27.6)**	-0.08	<0.00	-0.05	-0.14	-0.02	0.08	0.04
TML	-32.1	-8.1 (-43.9, 23.7)	-0.09	<0.00	-0.06	-0.13	-0.02	0.08	0.04
FHD	1.6	**49.9 (33.6, 67.2)**	0.04	<0.00	-0.04	-0.10	-0.01	0.14	0.05
BIB	14.6	**41.9 (22.4, 59.4)**	0.06	<0.00	-0.03	-0.06	-0.01	0.06	0.09

kk. Kikuyu and Egypt (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-12.3	**-26.1 (-45.9, -5.6)**	-0.04	-0.06	-0.03	0.02	-0.03	0.02	0.04
RML	-11.5	-14.7 (-32.6, 4.5)	-0.05	-0.05	-0.04	0.02	-0.04	0.02	0.04
FML	-11.4	11.3 (-29.4, 55.0)	-0.03	-0.05	-0.03	0.03	-0.03	0.02	0.04
TML	-14.6	-16.4 (-50.3, 14.2)	-0.04	-0.05	-0.03	0.02	-0.04	0.02	0.04
FHD	0.5	10.4 (-8.1, 26.3)	0.01	-0.04	-0.02	0.02	-0.03	0.03	0.05
BIB	15.6	**42.4 (29.1, 55.1)**	0.06	-0.03	-0.01	0.01	-0.02	0.01	0.09

ll. West Africa and Egypt (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-2.4	**26.9 (8.1, 44.7)**	-0.01	0.06	-0.08	-0.03	-0.03	0.01	0.06
RML	-11.4	**-39.9 (-58.8, -19.3)**	-0.05	0.05	-0.11	-0.03	-0.03	0.01	0.06
FML	-9.1	-16.8 (-46.8, 12.8)	-0.02	0.05	-0.08	-0.04	-0.03	0.01	0.06
TML	-11.8	-13.3 (-38.8, 11.4)	-0.03	0.05	-0.09	-0.04	-0.03	0.01	0.06
FHD	1.0	9.2 (-9.3, 27.7)	0.02	0.04	-0.06	-0.03	-0.02	0.03	0.07
BIB	23.7	**57.0 (38.0, 73.5)**	0.09	0.03	-0.04	-0.02	-0.01	0.01	0.13

mm. San and Egypt (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	22.7	20.9 (-3.3, 42.9)	0.07	0.05	0.04	-0.07	-0.04	0.03	0.07
RML	19.2	19.4 (-0.2, 37.4)	0.08	0.04	0.05	-0.08	-0.04	0.03	0.07
FML	22.2	**-40.3 (-67.8, -15.0)**	0.05	0.04	0.04	-0.09	-0.04	0.03	0.08
TML	19.9	-18.4 (-37.3, 1.5)	0.05	0.04	0.04	-0.09	-0.05	0.03	0.08
FHD	4.7	17.5 (-6.4, 42.2)	0.11	0.03	0.03	-0.06	-0.03	0.05	0.09
BIB	42.6	**75.0 (47.9, 98.3)**	0.17	0.02	0.02	-0.04	-0.02	0.02	0.17

nn. Uganda and Egypt (sub-Saharan Africa to North Africa)

Trait	Groups Mean Difference (mm)	Selection Gradients (β) & 95% CI	Net Response to Selection ($\Delta\bar{z}$)	Trait-Specific Responses to Selection					
				Δz_{HML}	Δz_{RML}	Δz_{FML}	Δz_{TML}	Δz_{FHD}	Δz_{BIB}
HML	-18.4	-12.7 (-43.7, 17.5)	-0.06	-0.03	-0.04	-0.03	-0.07	0.07	0.04
RML	-18.3	**-20.0 (-35.5, -3.4)**	-0.07	-0.02	-0.05	-0.03	-0.08	0.07	0.04
FML	-26.9	-16.0 (-46.8, 11.6)	-0.06	-0.02	-0.04	-0.04	-0.08	0.07	0.04
TML	-31.2	**-36.7 (-68.6, -6.2)**	-0.08	-0.02	-0.04	-0.03	-0.10	0.07	0.05
FHD	1.8	**44.3 (31.6, 56.7)**	0.04	-0.02	-0.03	-0.03	-0.06	0.12	0.05
BIB	16.2	**43.7 (27.1, 60.0)**	0.06	-0.01	-0.02	-0.02	-0.04	0.05	0.10

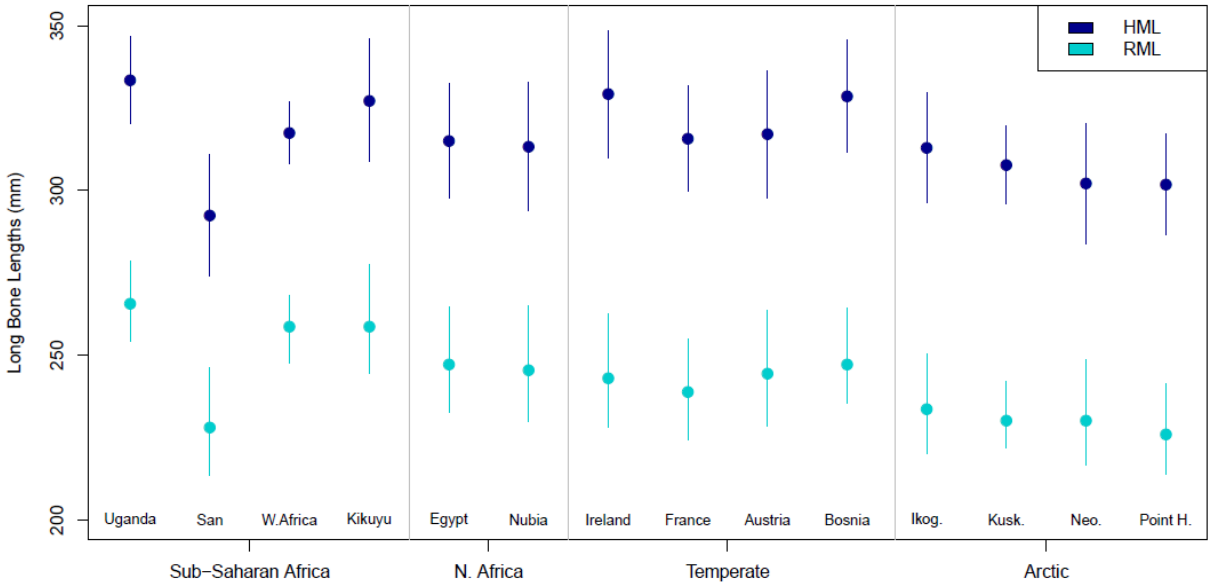

Figure S1. Trait means of measured traits (all measured in millimeters) and standard deviations for each sampled group, organized by ecogeographic group (see Table 1): humeral maximum length (HML), purple dots, radial maximum length (RML), teal dots.

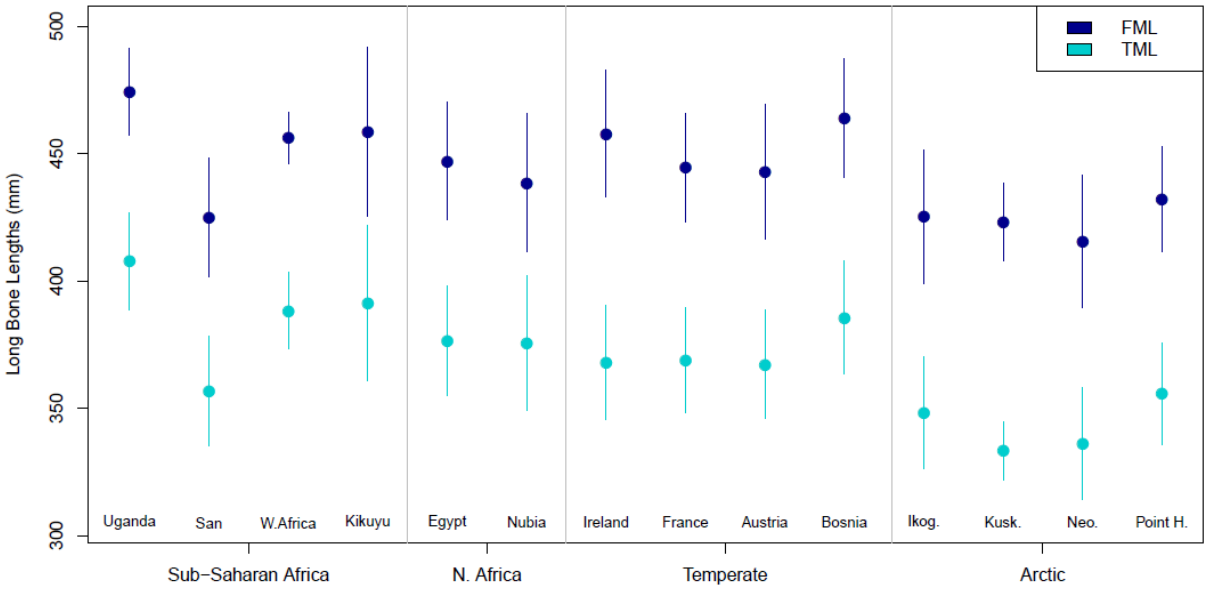

Figure S2. Trait means of measured traits (all measured in millimeters) and standard deviations for each sampled group, organized by ecogeographic group (see Table 1): femoral maximum length (FML), purple dots, tibial maximum length (TML), teal dots.

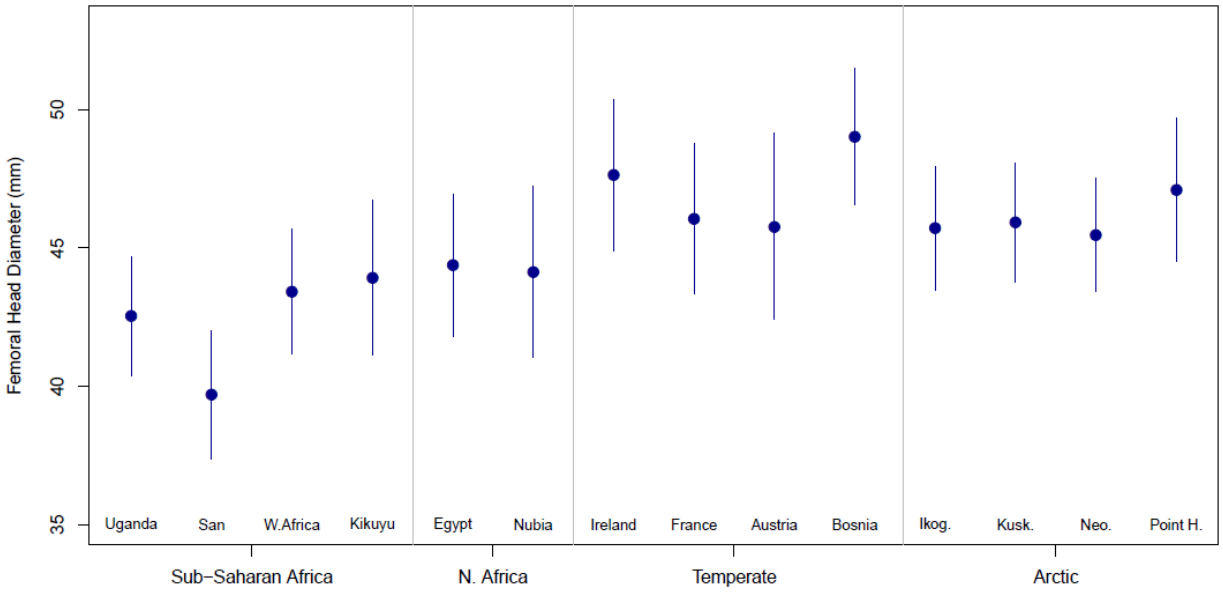

Figure S3. Trait means of femoral head diameter (measured in millimeters) and standard deviations for each sampled group, organized by ecogeographic group (see Table 1).

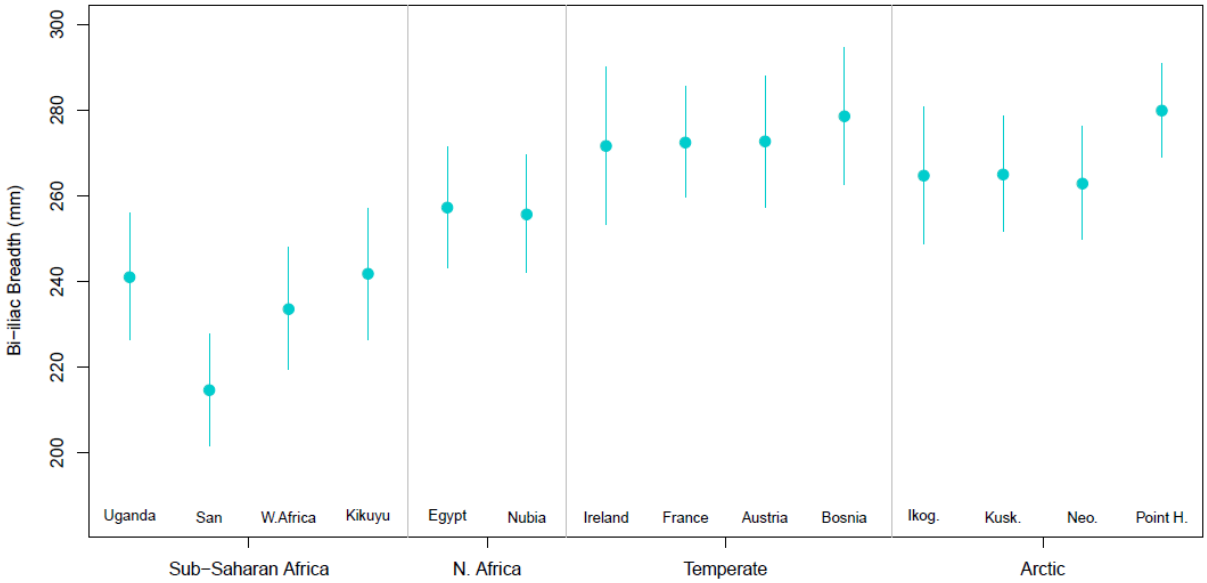

Figure S4. Trait means of bi-iliac breadth (measured in millimeters) and standard deviations for each sampled group, organized by ecogeographic group (see Table 1).

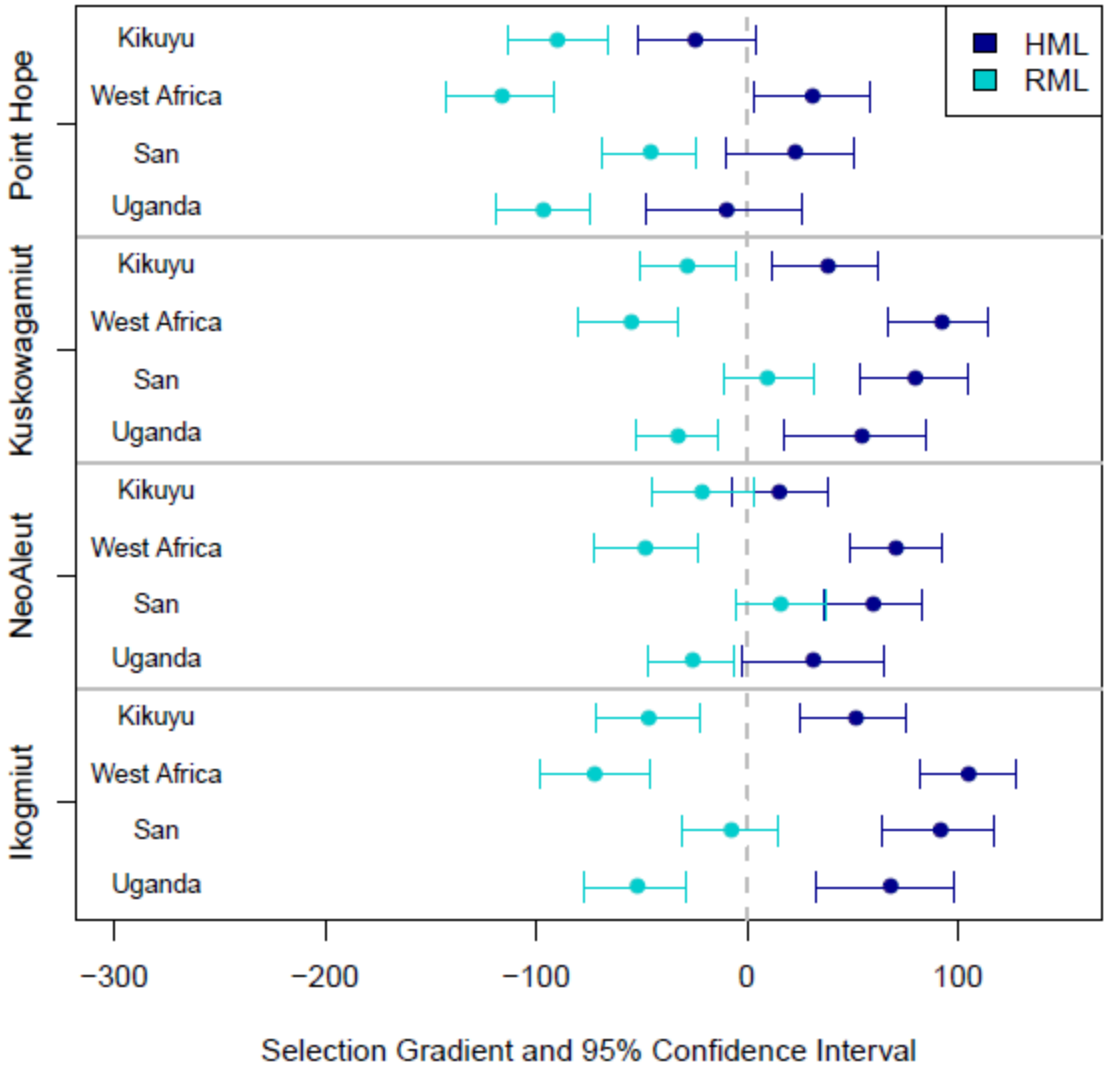

Figure S5. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of humerus maximum length (HML) (purple dots and whiskers) and radius maximum length (RML) (teal dots and whiskers) between sub-Saharan African Groups and arctic groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

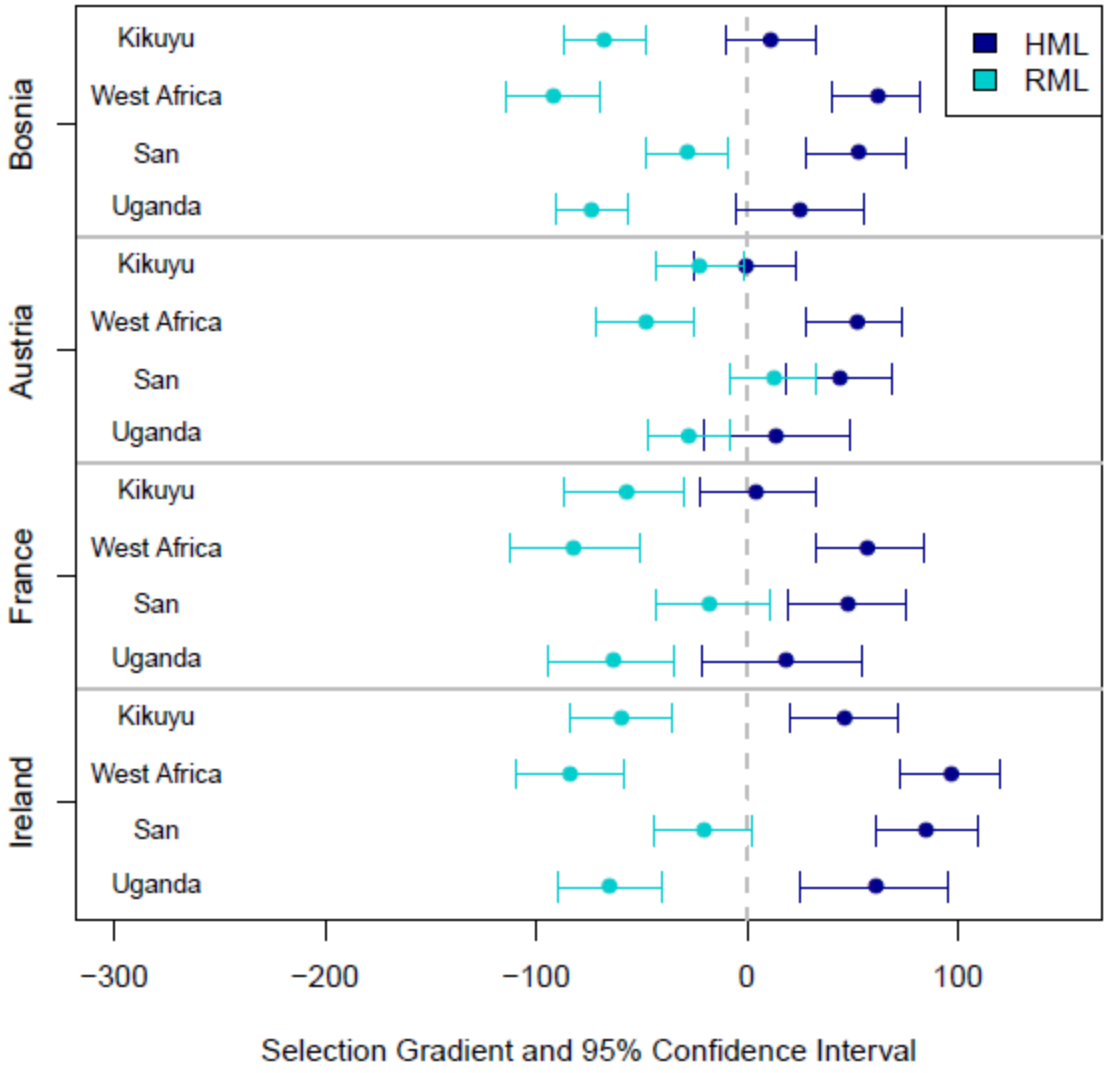

Figure S6. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of humerus maximum length (HML) (purple dots and whiskers) and radius maximum length (RML) (teal dots and whiskers) between sub-Saharan African Groups and temperate groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

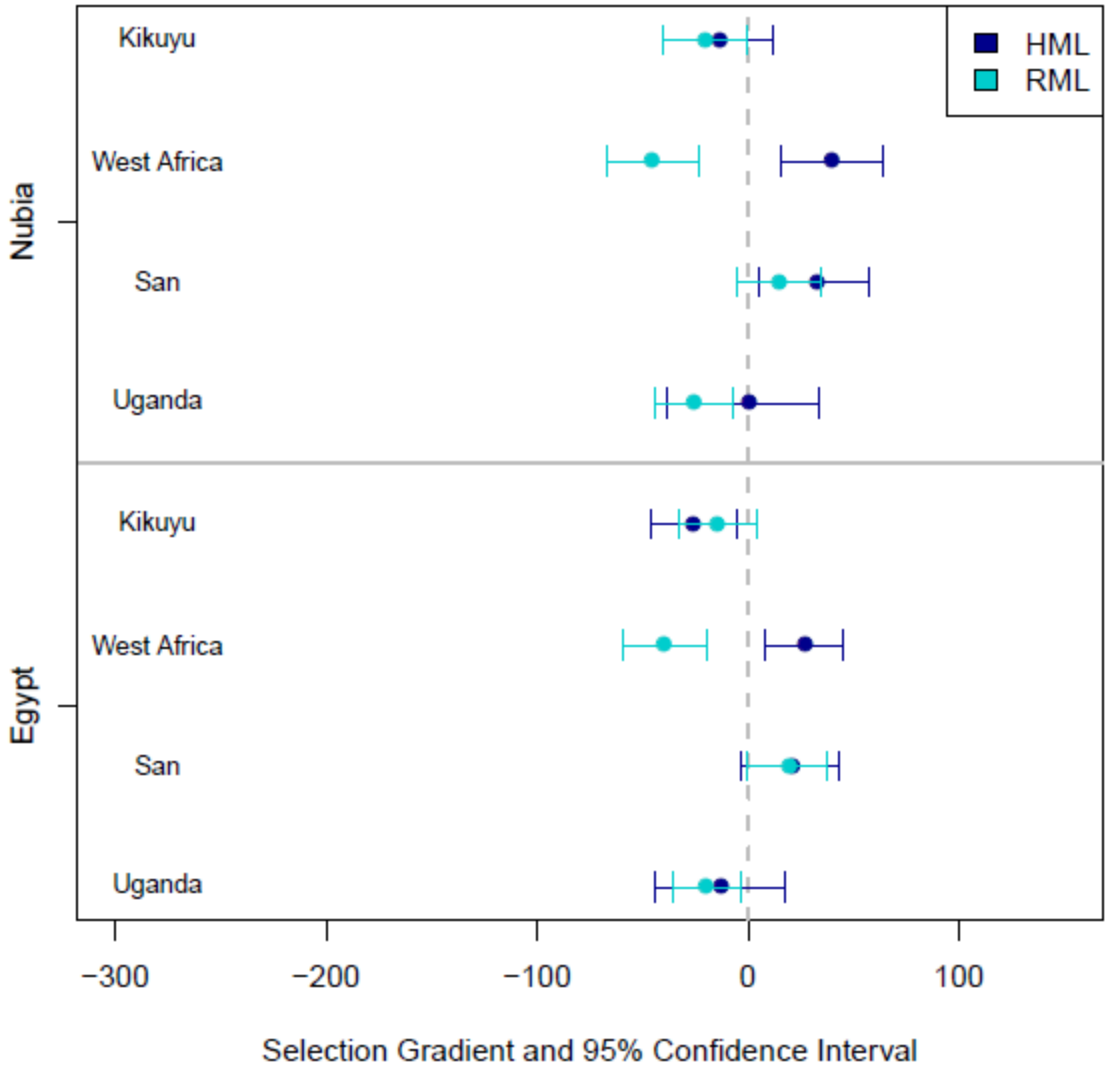

Figure S7. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of humerus maximum length (HML) (purple dots and whiskers) and radius maximum length (RML) (teal dots and whiskers) between sub-Saharan African Groups and North African groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

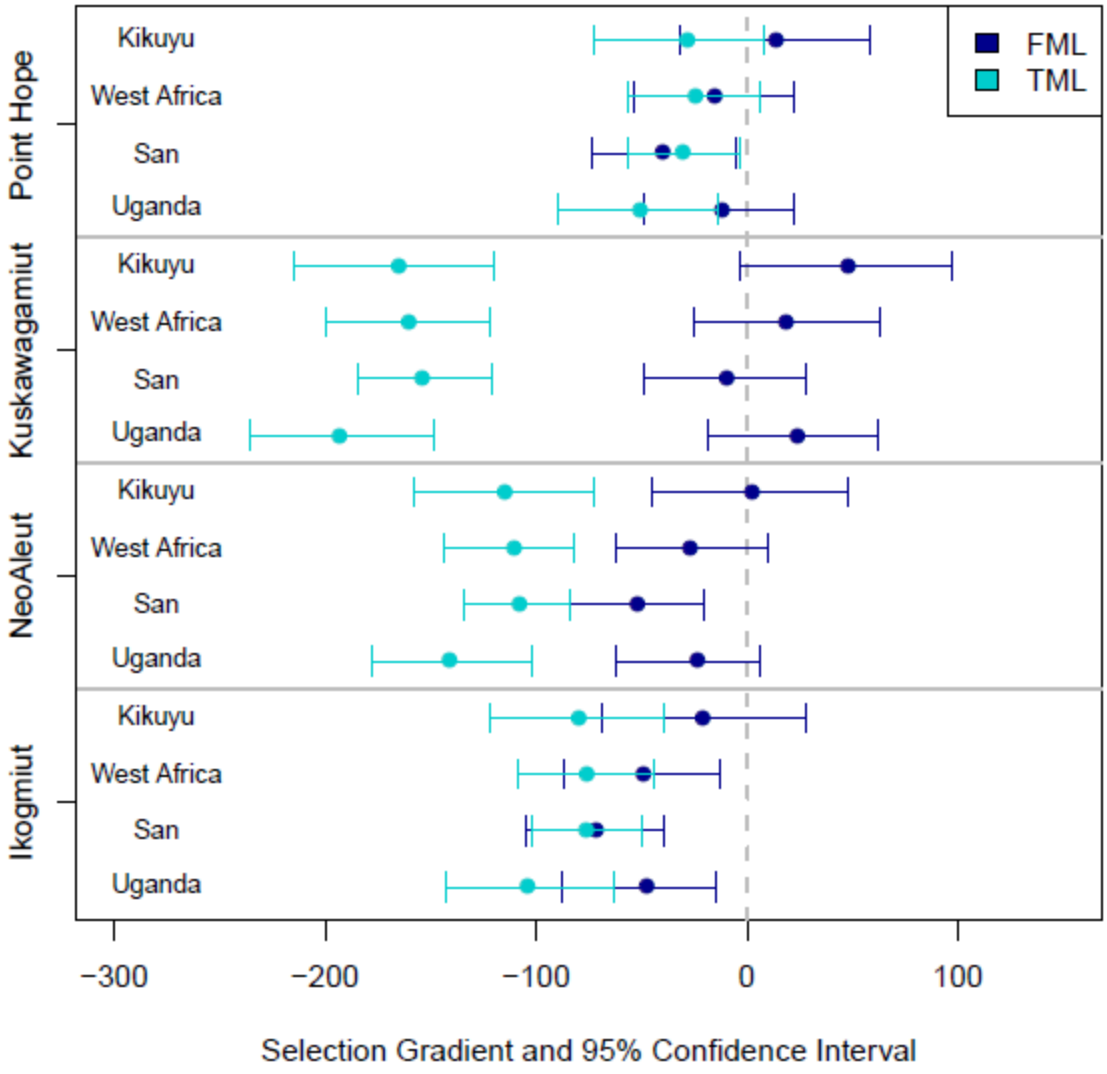

Figure S8. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of femoral maximum length (FML) (purple dots and whiskers) and tibial maximum length (TML) (teal dots and whiskers) between sub-Saharan African Groups and arctic groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

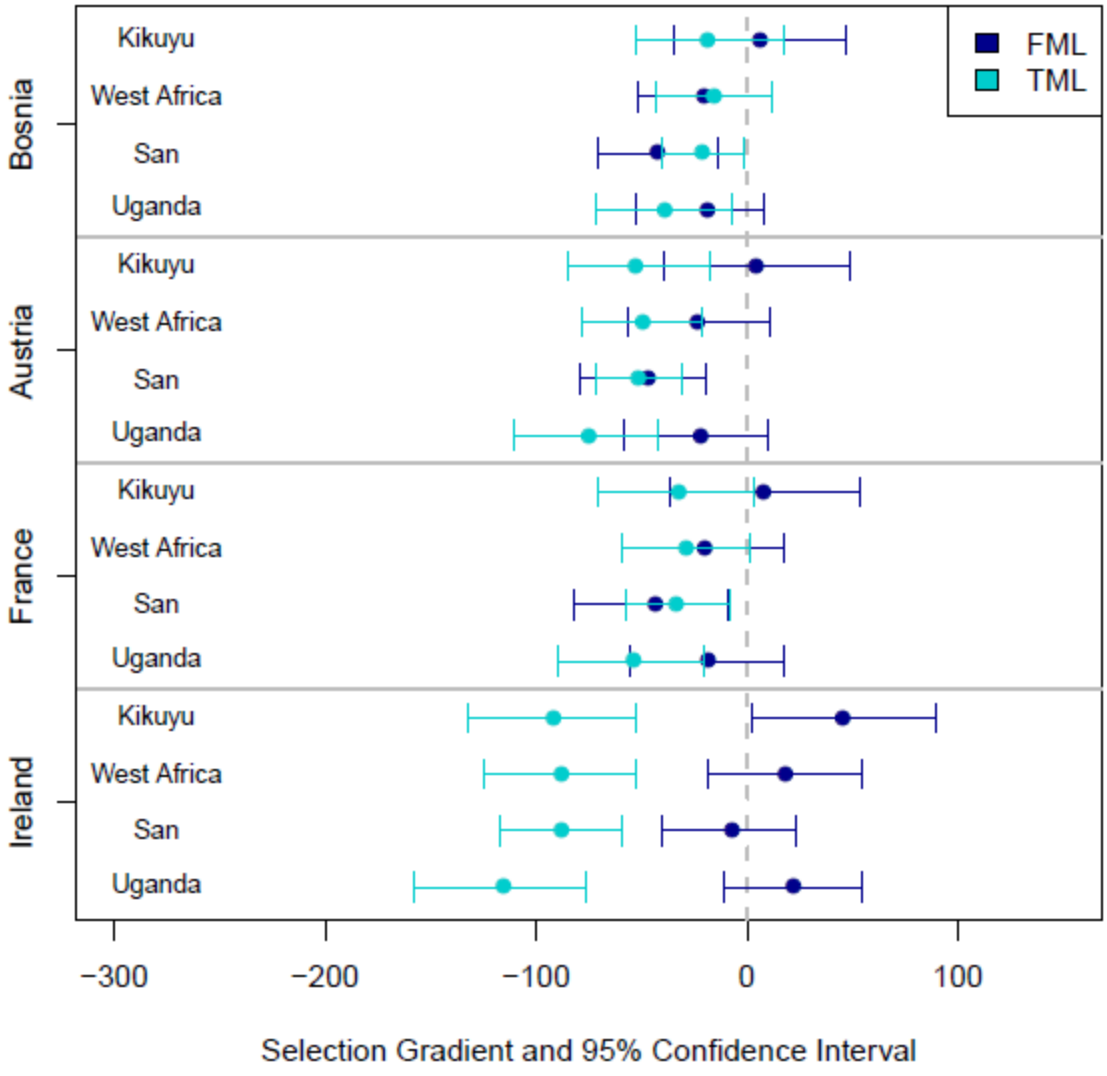

Figure S9. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of femoral maximum length (FML) (purple dots and whiskers) and tibial maximum length (TML) (teal dots and whiskers) between sub-Saharan African Groups and temperate groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

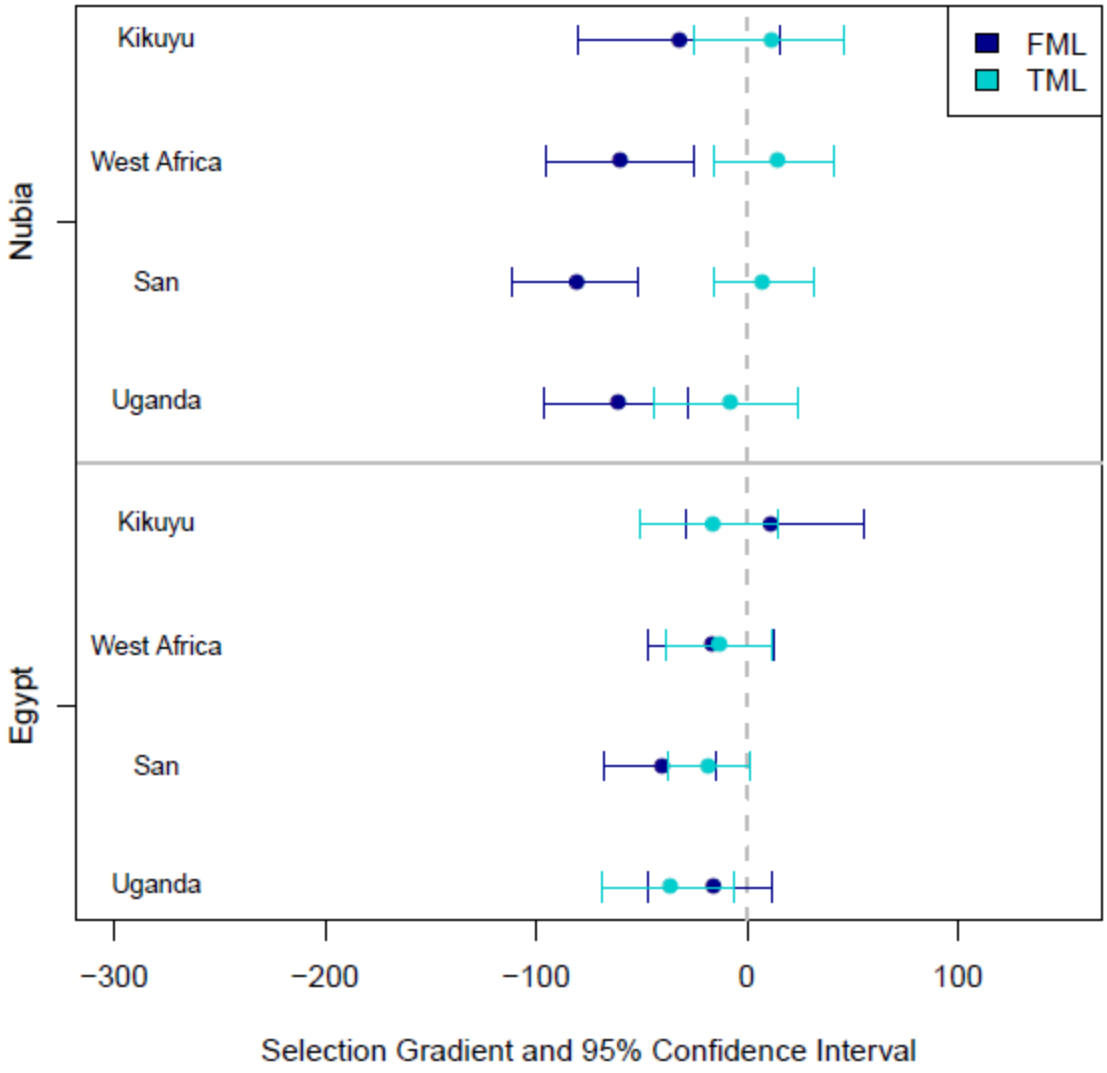

Figure S10. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of femoral maximum length (FML) (purple dots and whiskers) and tibial maximum length (TML) (teal dots and whiskers) between sub-Saharan African Groups and North African groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

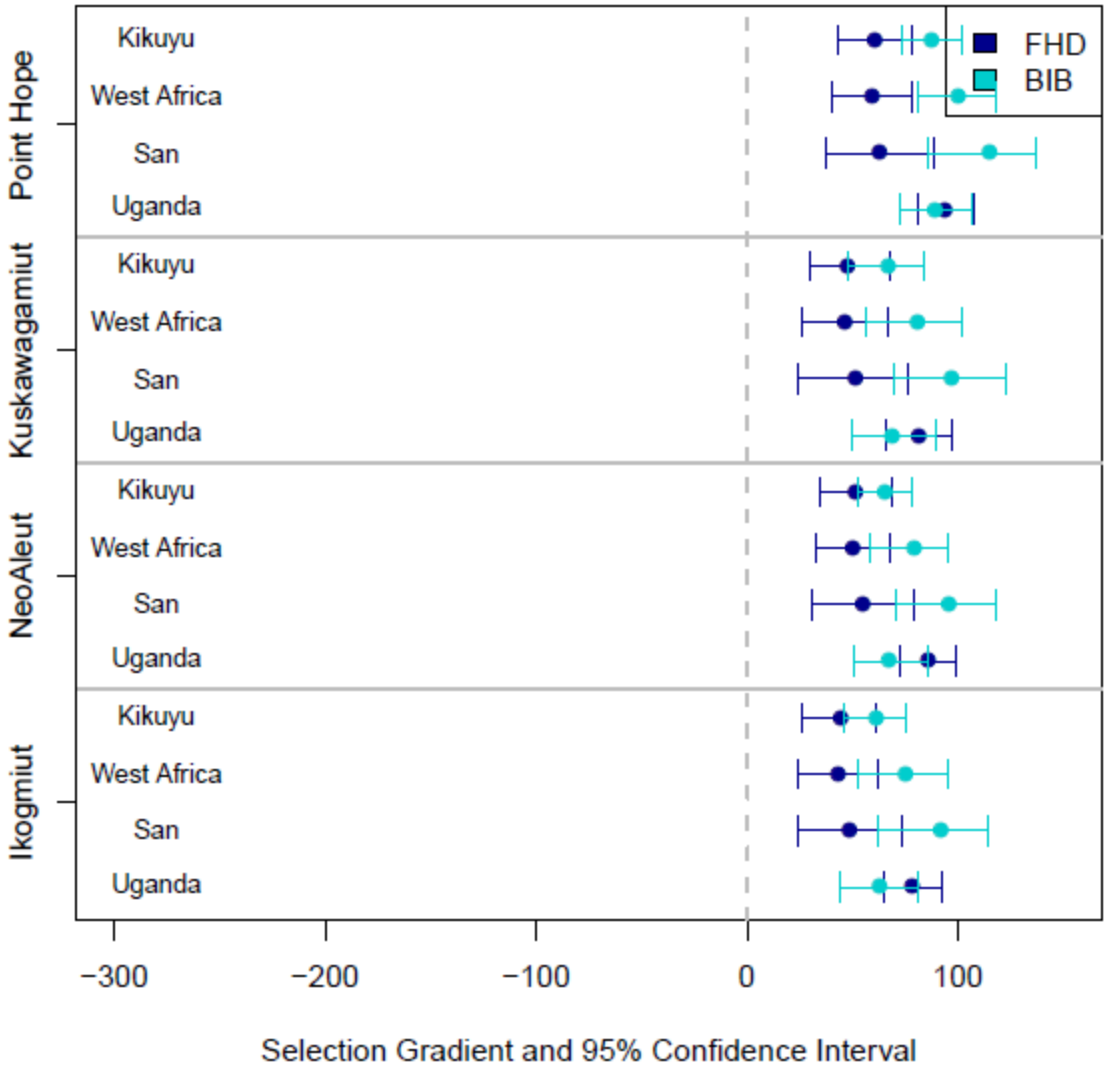

Figure S11. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of femoral head diameter (FHD) (purple dots and whiskers) and bi-iliac breadth (BIB) (teal dots and whiskers) between sub-Saharan African Groups and arctic groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

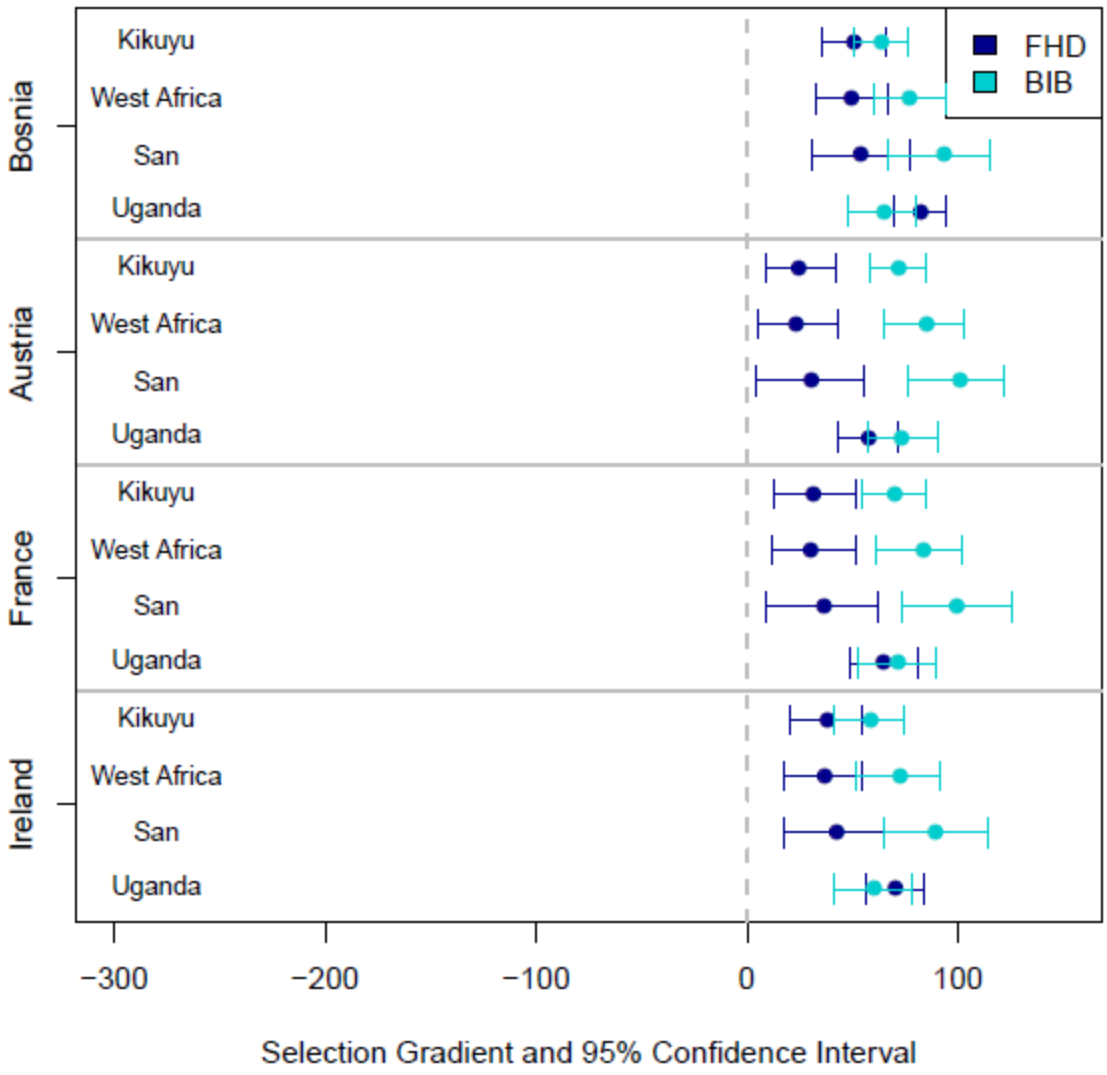

Figure S12. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of femoral head diameter (FHD) (purple dots and whiskers) and bi-iliac breadth (BIB) (teal dots and whiskers) between sub-Saharan African Groups and temperate groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

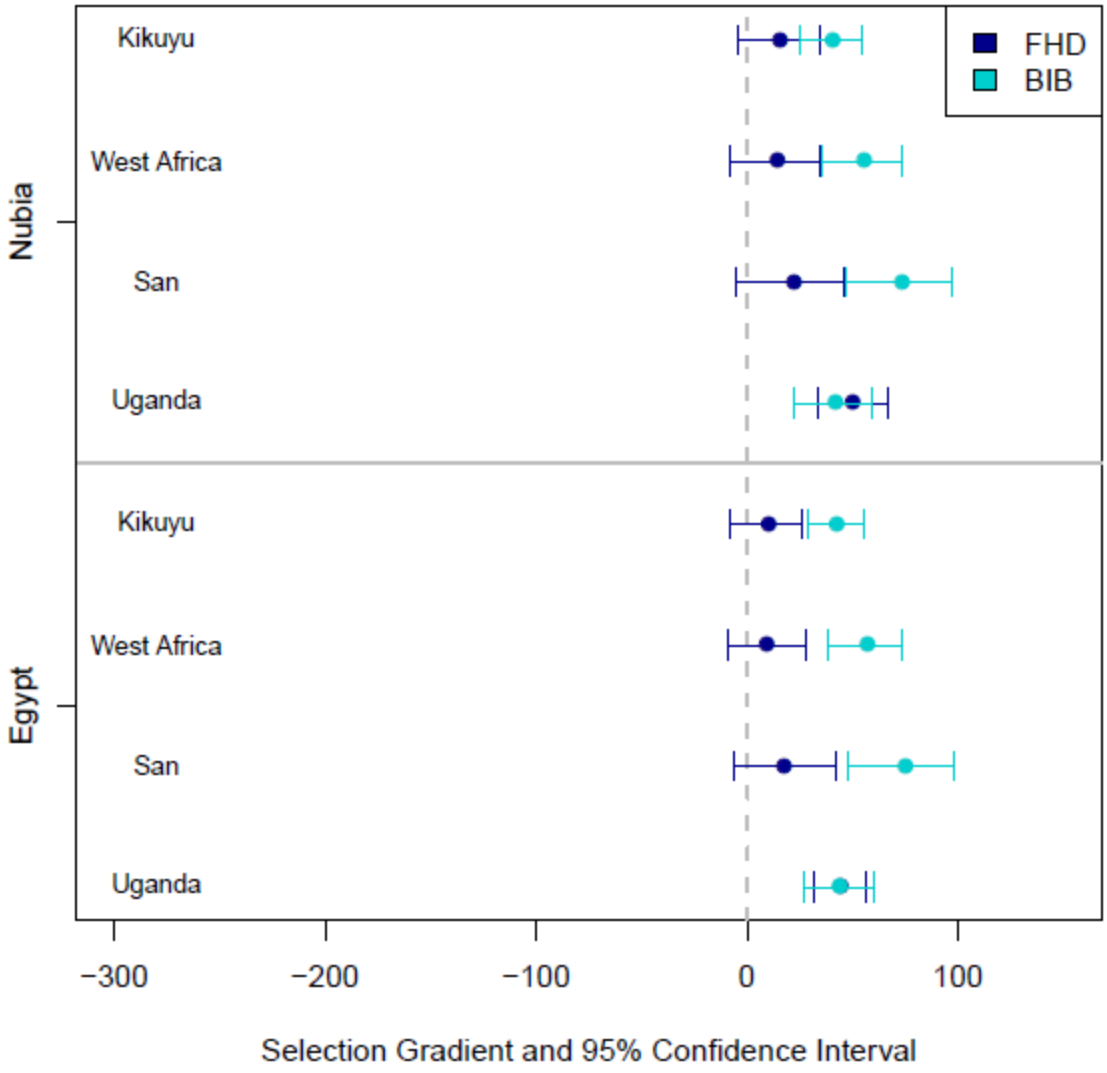

Figure S13. Selection gradients (dots) and 95% CIs (whiskers) for pairwise comparisons of femoral head diameter (FHD) (purple dots and whiskers) and bi-iliac breadth (BIB) (teal dots and whiskers) between sub-Saharan African Groups and North African groups. CIs that overlap with zero indicate a selection gradient not discernable from zero (i.e., no directional selection is estimated).

Appendix II: Supplementary Tables and Figures, Chapter IV

Table S2. Measurement means of phenotypic study groups – all dimensions in millimeters: HML, humerus maximum length; RML, radius maximum length; FML, femur maximum length; TML, tibia maximum length; FHD, femoral head diameter; BIB, bi-iliac breadth. Latitude (LAT) and longitude (LONG) for each group are also reported, as well as the GHCN station identifications (STAT) and the long term averages for the mean temperature of the coldest (MIN) and warmest (MAX) months of the year (in °C).

Group Name	N	HML	RML	FML	TML	FHD	LAT	LONG	STAT	MIN	MAX
Alayan	9	289.8	226.3	403.4	341.4	40.7	-2.6	-80.2	84226	10.5	11.6
Ancon	51	287.9	223.7	401.2	341.7	43.8	-11.8	-77.2	84628	15.7	22.6
Antler Plain	21	318.8	252.8	450.9	377.8	46.3	49.1	-98.8	71148	-17.3	19.1
Aramburu	7	292.5	226.1	388.4	324.5	41.2	-12.1	-77.1	84628	15.7	26.3
Australian	27	315.8	245.7	442.4	373.9	42.3	-25.3	133.8	94466	11.1	28.4
Austria	77	309.4	237.1	433.1	359.5	44.0	48.4	16.3	11035	-1.5	19.6
Averbuch	55	313.9	242.2	437.6	363.6	43.5	36.3	-86.8	72327	3.6	26.3
Bavarian Germany	145	320.8	242.6	451.1	370.1	45.7	48.8	8.7	10739	-0.7	18.3
Belgium	41	310.0	232.7	431.4	355.9	44.8	50.4	4.0	7015	2.0	17.5
Biaka	12	274.3	216.4	372.5	318.5	36.8	2.2	13.3	64460	22.5	24.5
Bohemia	39	315.9	236.2	441.0	362.9	45.6	50.2	14.2	11518	-3.2	17.5
Bosnia	79	317.2	237.3	447.2	371.0	46.5	42.7	19.4	13363	-2.5	17.4
Canete Valley	14	277.8	222.5	396.3	331.3	41.9	-13.0	-76.4	84691	15.8	22.4
Carter Ranch	16	295.6	230.1	407.9	345.2	40.9	34.5	-109.9	72374	-0.6	21.3
Chaco Canyon	25	297.0	230.2	420.0	352.4	39.6	36.1	-108.0	72365	-1.9	20.3
Chamisal	12	298.7	231.3	407.6	337.6	40.7	35.1	-106.7	72365	-1.9	20.3
Cuzco	14	296.9	228.7	407.1	341.9	42.1	-13.5	-72.0	84686	9.3	12.3
Dickson Mounds	53	317.1	244.3	440.3	368.8	43.7	40.4	-90.1	72532	-5.4	23.3

Table S2 Continued

Group Name	N	HML	RML	FML	TML	FHD	LAT	LONG	STAT	MIN	MAX
Donaldson Site	10	336.8	260.6	470.7	396.3	45.5	44.4	-81.3	72524	-3.1	22.8
Egypt	151	303.9	237.0	432.5	363.7	42.1	30.0	31.2	62378	13.2	28.1
England Iron Age	50	307.8	229.8	428.7	347.9	44.0	50.7	2.5	7015	2.0	17.5
England Medieval	22	309.3	234.0	428.2	352.0	44.5	50.7	-2.5	3862	4.5	16.4
Fort Ancient	62	310.2	242.3	437.5	365.1	44.7	39.4	-84.1	72421	-1.3	23.9
France	37	309.1	231.3	433.5	359.3	44.3	48.9	2.4	7150	2.5	18.6
Gallina Springs	12	302.4	233.8	417.0	352.2	41.2	34.0	-107.1	72271	5.6	27.0
Georgia	32	311.2	238.0	432.0	361.5	41.4	32.1	-81.2	72207	9.1	27.6
Grasshopper	48	303.7	236.0	420.6	358.0	41.5	34.1	-110.7	72374	-0.6	21.3
Hawikuh	74	292.8	226.2	409.6	342.6	39.8	35.1	-108.8	72271	5.6	27.0
Hiwassee Island	40	312.7	240.7	431.2	357.4	42.8	35.4	-85.0	72324	5.6	26.6
Hungary	26	322.1	238.6	442.6	357.7	46.7	47.5	19.1	12843	-1.6	20.9
Ikogmiut	60	299.7	221.4	412.0	333.3	43.5	61.6	-159.8	70232	-17.9	13.7
Indian Knoll	61	307.5	234.0	422.1	352.6	40.5	37.3	-87.0	72423	2.3	26.9
Ireland	23	325.7	240.1	453.1	364.1	46.9	53.3	-6.3	3969	3.9	14.1
Italy Iron Age	20	308.7	229.7	429.7	354.8	44.3	43.5	10.3	16158	6.1	22.7
Japan	51	287.2	218.7	403.0	325.3	43.4	35.0	135.8	47759	3.9	27.8
Jomon	43	275.6	221.5	397.4	332.8	41.7	34.7	137.3	47653	5.5	27.2
Kerma	57	312.2	244.8	448.2	378.5	41.9	19.6	30.4	62650	17.3	33.8
Kikuyu	30	311.0	244.2	438.1	373.7	41.2	0.0	36.8	63686	15.3	17.8
Kuskowagamiut	28	299.0	220.8	411.3	326.5	43.7	60.8	-161.8	70219	-14.3	12.7
Masachusetts Bay	25	315.0	245.1	444.7	372.2	42.9	41.6	-70.4	72509	-3.0	21.8
Mimbres	14	307.5	239.8	426.8	362.1	42.5	32.5	-108.0	74732	0.9	19.2
Mitchell Ridge	27	309.1	243.4	436.0	367.4	42.6	29.2	-94.9	72242	12.8	29.0

Table S2 Continued

Group Name	N	HML	RML	FML	TML	FHD	LAT	LONG	STAT	MIN	MAX
Nazca Valley	19	294.9	229.2	406.8	350.0	42.7	-14.8	-75.0	84673	16.6	19.7
NeoAleut	60	294.9	222.9	404.7	327.5	44.0	51.5	-180.9	70454	-0.5	9.9
Nubia	55	305.5	238.2	429.6	366.8	42.3	22.8	32.7	62600	17.0	33.4
Orkney	31	309.1	236.5	433.9	349.5	44.0	59.0	-3.0	3091	2.9	13.3
Paa-Ko	28	300.9	228.8	413.2	347.2	41.0	35.2	-106.2	72365	-1.9	20.3
PaleoAleut	29	292.7	222.4	404.4	329.8	43.7	52.4	-186.4	70482	-0.4	11.5
Palmer	52	306.3	233.2	430.4	359.8	43.0	27.2	-82.5	72210	15.7	27.6
Peten	14	306.2	233.6	420.9	358.5	43.0	16.5	-90.5	78640	16.5	19.7
Point Barrow	23	299.6	225.0	423.0	342.8	44.9	71.4	-156.5	70026	-25.8	6.0
Point Hope	79	293.3	216.7	409.4	333.2	44.3	68.3	-166.8	25399	-21.9	5.9
Point of Pines TC	18	298.4	232.1	412.2	352.3	40.9	33.4	-109.7	72274	10.5	29.8
Point Sal	22	307.6	235.6	415.2	355.1	42.7	34.9	-120.7	72394	11.1	18.1
Poland	24	330.6	245.6	455.5	366.4	48.5	52.2	21.0	12375	-3.4	19.0
Pottery Mound	41	296.0	230.2	412.2	347.9	40.8	34.7	-106.9	72365	-1.9	20.3
Prince Rupert Harbor	61	302.3	232.2	410.9	337.2	45.1	54.3	-130.3	71898	-1.7	13.6
Puye	40	291.1	223.5	404.6	338.8	39.0	36.9	-106.2	72462	-7.4	16.5
Russia	28	323.2	238.2	439.7	358.0	47.0	57.8	34.4	26298	-10.1	16.9
Ryan Mound	79	302.3	232.5	422.3	352.2	42.5	37.6	-122.0	74509	9.2	19.9
Sacramento Valley	26	303.3	234.1	427.9	357.9	43.4	38.4	-121.5	72483	7.4	23.6
San	37	277.3	213.7	405.3	338.8	38.2	-27.2	23.2	68328	11.2	27.2
Sicily	31	302.7	226.9	421.7	352.4	43.3	37.1	15.3	16480	12.2	26.0
Solomon Islander	4	317.2	251.9	438.3	378.1	40.1	-9.7	160.1	91520	25.9	27.0
Tasmania	1	283.3	230.3	421.5	349.3	38.8	-41.4	146.6	95960	8.0	16.8
Tierra del Fuego	21	300.1	234.2	415.3	343.7	43.3	-55.0	-69.2	87938	1.4	9.4

Table S2 Continued

Group Name	N	HML	RML	FML	TML	FHD	LAT	LONG	STAT	MIN	MAX
Toba	21	312.4	246.8	438.3	367.1	45.0	-27.4	-59.0	87166	15.2	26.7
Uganda	16	333.1	265.6	473.0	406.2	42.0	0.3	32.6	63674	18.6	20.0
West African	21	312.7	253.7	448.9	382.6	42.6	9.0	4.8	65101	24.5	28.9
Western Hudson Bay	22	298.7	218.0	428.5	346.0	46.5	58.8	-94.2	71083	-31.8	8.9
Yakut	8	302.2	231.5	416.5	334.9	44.2	62.0	129.7	24959	-42.6	19.0

Table S3. The 29 groups used to populate the population structure matrix (A) consists of various combinations of phenotypic groups (n = 71) matched with genetic groups (n = 59) to assure the most accurate possible representation given the data.

Matched Set	Phenotypic Groups	Genetic Groups
Alayan	TicunaArara, TicunaTarapaca	Alayan
AntlerPlainCree	Antler Plain	Cree
Arctic	Ikogmiut, Kuskowagamiut, NeoAleut, PaleoAleut, Point Barrow, Point Hope, Western Hudson Bay	TundraNentsi
AustraliaTasmania	Australian, Tasmania	Australian
Biaka	Biaka	MbutiPygmy, Bedzan, Bakola, Baka, BiakaPygmy
Chile	Aramburu, Canete Valley, Nazca Valley	Aymara
DonaldsonOjibwa	Donaldson Site	Ojibwa
Egypt	Egypt	Palestinian, Temani, Bedouin
Europe	Austria, Bavarian Germany, Belgium, Bohemia, Bosnia, England Iron Age, England Medieval, Hungary, Ireland, Poland	Italian, Russian, Orcadian, French, Adygei, Basque, Tuscan, Sardinian
France	France	French
Italy Iron Age	Italy Iron Age	Tuscan
JapanJomon	Japan, Jomon	Japanese
Kerma	Kerma	Beja, Banuamir
Kikuyu	Kikuyu	Kikuyu, Mbugwe, Turu, Sandawe, Burunge, Rangi
NorthAmerica	Averbuch, Dickson Mounds, Fort Ancient, Georgia, Hiwassee Island, Indian Knoll, Masachusetts Bay, Mitchell Ridge, Palmer, Point Sal, Prince Rupert, Harbor, Ryan Mound, Sacramento Valley	Chipewyan, Cree, Ojibwa
Nubia	Nubia	Shilook, Nyimang, Nuer, Dinka
Orkney	Orkney	Orcadian
Peru	Ancon, Cuzco	Quechua
PetenMaya	Peten	Maya
RussiaWest	Russia - West	Russian
San	San	San, !XunKxoe
Sicily	Sicily	Italian
SolomonIsland	Solomon Islander	Saposa, Teop, Aita, Nasioi

Table S3 Continued

Matched Set	Phenotypic Groups	Genetic Groups
SWNorthAmerica	Carter Ranch, Chaco Canyon, Chamisal, Gallina Springs, Grasshopper, Hawikuh, Mimbres, Paa-Ko, Point of Pines TC, Pottery Mound, Puye	Pima
TierradelFuego	Tierra del Fuego	Huilliche
TobaAche	Toba	Ache
Uganda	Uganda	Sukuma, TutsiHutu
West African	West African	Wimbum, Hausa-Nigeria, Bassange, Brong, Ashanti, Igala, Igbo, Yoruba, Yoruba, Gwari
Yakut	Yakut	Yakut

VITA

Kristen Renée Rectenwald Savell was born into a family in the United States Air Force, to parents Robert and Sharon Rectenwald. She attended Ramstein American High School in Germany (2001-2004), eventually graduating from John Jay Science and Engineering Academy in San Antonio, Texas in 2005. She received her B.A. in religious studies with minors in biology and anthropology from Elon University in Elon, North Carolina in 2009. She then began her graduate work in biological anthropology, earning a M.A. in anthropology from North Carolina State University in Raleigh, North Carolina in 2012, eventually pursuing a doctorate at the University of Tennessee, Knoxville. During her time at the University of Tennessee, Kristen served as the laboratory manager and head teaching assistant for anatomy courses at both the undergraduate and graduate levels. She earned her Ph.D. from the University of Tennessee in August 2018, and is about to begin her career as a tenure-track assistant professor in the biology department at Sacred Heart University, in Fairfield, Connecticut.