X-chromosomal diversity may reflect climate (when considering human expansion from Africa)

Zarus Cenac
Independent Researcher
Email: zarus.cenac@city.ac.uk

Abstract

A decreasing of diversity with increasing distance from Africa has been interpreted as a signal of modern humans having expanded (across the globe) from Africa. Research is consistent with a climatic signal being present in mitochondrial diversity, but not in other genetic diversities (e.g., X-chromosomal) or cranial diversity. Some of that research involved adjusting diversity for distance from Africa, and seeing whether this adjusted diversity is associated with climate. The choice of African location which the distance from Africa is measured from may affect whether adjusted diversity appears to be related to climate. To bypass this potential effect of location, some analyses in the present study featured only populations outside of Africa. Other analyses included African populations. The present study used diversities, distances, and minimum temperatures from beforehand. Autosomal, X-chromosomal, and cranial diversities were adjusted for distance from Africa. Y-chromosomal diversity was adjusted for distance from Asia because previous research suggested that Y-chromosomal microsatellite heterozygosity offers more support to expansion from Asia (than Africa). Whether populations were worldwide or only outside of Africa, adjusted X-chromosomal diversity increased with minimum temperature. Other adjusted diversities were not related to minimum temperature. Perhaps previous research found no indication of a climatic signal in X-chromosomal diversity because of two populations, one of which likely had an atypical adjusted diversity for their minimum temperature. These populations may have led to heteroscedasticity and the climatic signal being obscured.

Introduction

Global expansion

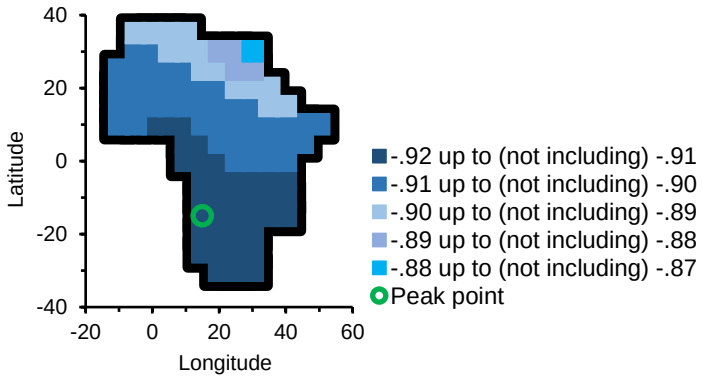
Diversities can decline for populations as geographical distance from Africa rises (Betti et al., 2012; Prugnolle et al., 2005; von Cramon-Taubadel & Lycett, 2008). Such diversities include the heterozygosity of autosomal single nucleotide polymorphism (SNP) haplotypes (Balloux et al., 2009; Li et al., 2008), X-chromosomal microsatellite heterozygosity (Balloux et al., 2009), and cranial form diversity (Betti et al., 2009). A decline of diversity appears to signal the expansion of modern humans from Africa which reached across the world (e.g., von Cramon-Taubadel & Lycett, 2008) (see Figure 1). A decrease is in tune with bottlenecks being a part of global expansion (Ramachandran et al., 2005; von Cramon-Taubadel & Lycett, 2008).

Climate

Diversity does not only seem to reflect expansion (Balloux et al., 2009; Betti et al., 2012). Research has asked if climate is related to biological diversity (Balloux et al., 2009; Betti et al., 2009, 2012; Manica et al., 2007). For instance, in Balloux et al. (2009), climate (minimum temperature) exhibited an association with mitochondrial diversity. Moreover, this association with climate was also apparent when mitochondrial diversity was adjusted for *linear* distance from Africa (Balloux et al., 2009);[1] no such association was apparent for adjusted autosomal, X-, or Y-chromosomal diversities (Balloux et al., 2009). The autosomal diversities were microsatellite heterozygosity and SNP haplotype heterozygosity, and, for the X and Y chromosomes, diversities were microsatellite heterozygosity (Balloux et al., 2009). As for the skeleton, minimum temperature is related to the shape diversity of the femur and tibia (Betti et al., 2012), whilst a relationship with climate fails to be supported for cranial form diversity (Betti et al., 2009)[2] and pelvic shape diversity (Betti et al., 2012). Therefore, research seems in line with a climatic signal in some diversities (Balloux et al., 2009; Betti et al., 2012) but not in others (Balloux et al., 2009; Betti et al., 2009, 2012).

Figure 1

X-Chromosomal Diversity and the African Origin of Global Expansion



Note. To indicate where expansion started, various locations can be used (one at a time) as if each was where the expansion originated, and it can be seen how well distance from that location is related to diversity (e.g., Manica et al., 2007). Support for some location being the origin of expansion is indicated by the (relative) extent to which diversity declines as distance from a location increases – a stronger decline (and therefore a stronger expansion signal) suggests the origin of expansion (e.g., Ramachandran et al., 2005; von Cramon-Taubadel & Lycett, 2008). The location where the decline is at its most negative can be called the peak point (e.g., Cenac, 2022). Like has been done with correlation coefficients for relationships between genetic diversity and distance from Africa (Luca et al., 2011; Ramachandran et al., 2005), Figure 1 presents correlation coefficients (*r* – blue areas) regarding X-chromosomal microsatellite heterozygosity and distance from Africa (coefficients are from Cenac, 2023a, who used diversities from Balloux et al., 2009, and distances in Cenac, 2022). The peak point is the location giving the lowermost correlation coefficient (Cenac, 2022) (green circle). Figure 1 adjusts Figure 4 in Cenac (2023b) which employed coordinates (in Africa) that are contained in a figure by Betti et al. (2013) (Figure 4 in Cenac, 2023b, did not feature correlation coefficients, and it had some basis on Cenac, 2022).

Diversity adjusted for distance

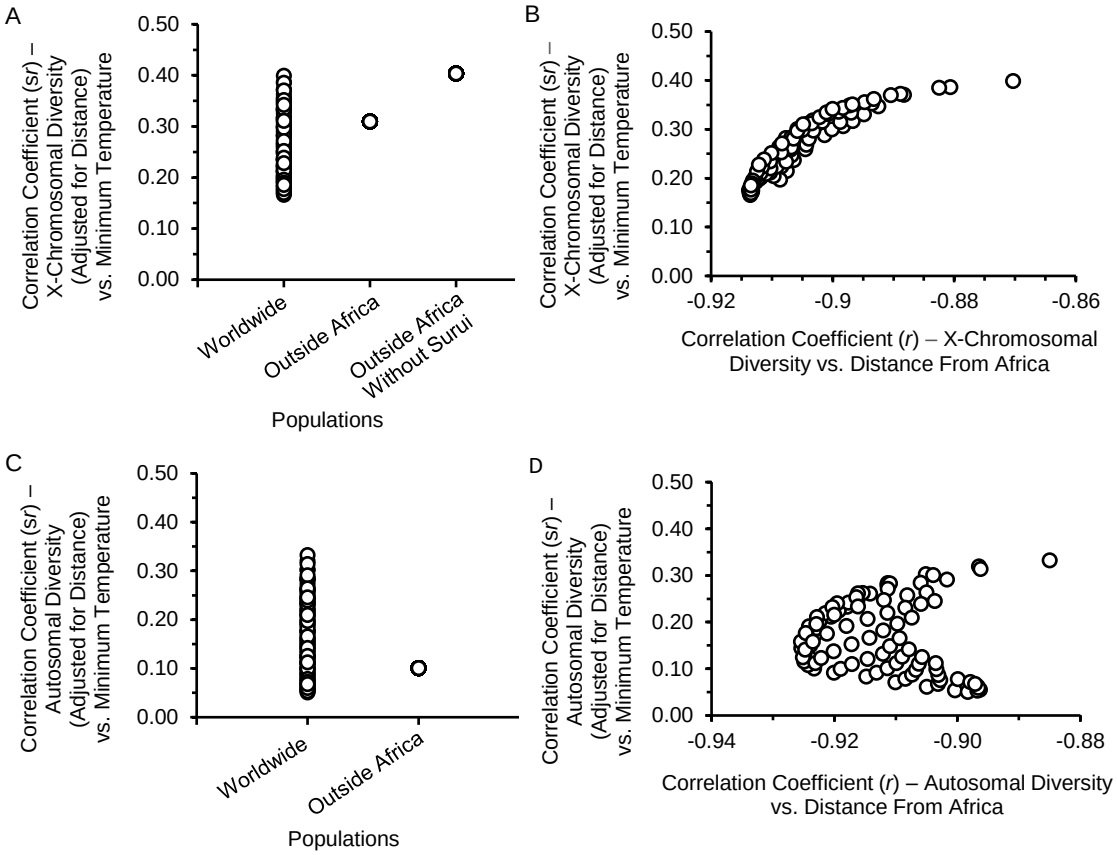
If one is interested in seeing if diversity is reflective of climate, an approach can involve adjusting diversity for distance from Africa, and then seeing if this adjusted diversity is related to climate (Balloux et al., 2009). However, when using populations worldwide, the relationship between diversity (adjusted for linear distance) and climate can be affected by which location in Africa distances are measured from (Figure 2A and 2C). Therefore, a supposed lack of relationship with climate (e.g., for adjusted X-chromosomal diversity in Balloux et al., 2009) could be due to research having employed distance from somewhere which just so happens to lead to a weaker correlation coefficient.

Distances from *which* location should be used to adjust diversity? The location whose distances give the fall of diversity at its strongest (or predicted it best) (e.g., Betti et al., 2013; Ramachandran et al., 2005) has been called the peak point (Cenac, 2022). The extent of decline indicates how strong the signal of expansion is (Ramachandran et al., 2005; von Cramon-Taubadel & Lycett, 2008), therefore, in order to remove the influence of expansion on diversity, it would make sense generally to adjust diversity for distance from the peak point. However, different diversities can have different peak points (Cenac, 2022); did Balloux et al. (2009) use distance from diversity-specific peak points to adjust diversities? Balloux et al. (2009) used distance from a location (in Africa) from Manica et al. (2007). From reading Balloux et al. and Manica et al., this location was arrived at from autosomal microsatellite heterozygosity and cranial form diversity. That location would seem to be reasonably similar to the peak points for mitochondrial diversity and X-chromosomal diversity (in Cenac, 2022), less so for the peak point (linear trend) for autosomal microsatellite heterozygosity (in Ramachandran et al., 2005), even less so for autosomal SNP haplotype heterozygosity, but markedly different for Y-chromosomal microsatellite heterozygosity (in Cenac, 2022). Indeed, peak points for autosomal, mitochondrial, and X-chromosomal diversity are in Africa (Cenac, 2022; Ramachandran et al., 2005), unlike Y-chromosomal microsatellite heterozygosity (Cenac, 2022).

Whilst Y-chromosomal microsatellite heterozygosity does linearly decrease with the increasing of distance from Africa (Balloux et al., 2009), the strongest decline is not from Africa – Y-chromosomal microsatellite heterozygosity does not appear to portray expansion worldwide from Africa, but could be representing a movement from Asia, with the peak point seeming to be in the Asian continent (Cenac, 2022). Therefore, if one is to see if Y-chromosomal microsatellite heterozygosity is associated with climate, rather than adjusting diversity for distance from Africa (Balloux et al., 2009), it may make more sense to adjust diversity for distance from Asia. Hence, Y-chromosomal microsatellite heterozygosity aside, Balloux et al. (2009) are likely to have greatly adjusted for an expansion signal.

Figure 2

Diversity, Climate, and Distance from Africa



Note. Distances from 99 locations in Africa (Cenac, 2022), X-chromosomal microsatellite heterozygosities, autosomal SNP haplotype heterozygosities, and minimum temperatures (Balloux et al., 2009) were used in Figure 2. Figure 2A and 2B are with respect to X-chromosomal diversity, whilst Figure 2C and 2D are regarding autosomal diversity. In some instances, like in Balloux et al. (2009), diversity was adjusted for linear distance from Africa (see the *y*-axes of 2A, 2B, 2C, and 2D). With respect to minimum temperature (Balloux et al., 2009) and adjusted diversity, semi-partial Pearson correlation coefficients were calculated (*y*-axes). This procedure was done with and without populations in Africa. For X-chromosomal diversity, in the absence of the populations in Africa (Figure 2A), there was an atypical datapoint – this datapoint was for the population referred to as Surui in Balloux et al. (2009). Regarding populations worldwide, Balloux et al. used distance from a particular location in Africa – the present study observed quite similar R^2s (compared to Balloux et al.) when using distances in the vicinity of that particular location – the corresponding s*r*s are generally amongst the lowest for populations worldwide in Figure 2A and 2C. For Figure 2B and 2D, populations worldwide were used – a significance test was not run as there would likely be nonindependence (see Judd et al., 2009, regarding nonindependence), but patterns do seem to clearly be indicated visually. For some diversities, a weaker correlation coefficient may indicate that the signal of expansion from Africa has been controlled for better – regarding X-chromosomal diversity, it appears that correlation coefficients may become weaker as more of the expansion signal is removed (Figure 2B). However, this is likely not the case for all diversities – it seems not to be for autosomal SNP haplotype heterozygosity (Figure 2D).

Nonetheless, regarding populations worldwide, peak points (when they are in Africa) seem like they may be greatly determined by African populations, and few African populations *may* feature in data when finding peak points (e.g., seven African populations regarding X-chromosomal and autosomal haplotype diversity) (Cenac, 2022). And so, it seems unclear if it is wise to simply use the peak point when adjusting diversity for distance.

Therefore, when adjusting diversity, there is ambiguity concerning which location distances should be from. An alternative could be to only use populations outside of Africa – when only those populations are used, the correlation coefficient does not vary according to the location in Africa used as the origin (Figure 2A and 2C). However, to comprehensively understand if there is a climatic signal in diversity, it would not be desirable to exclude an entire continent.

Cranial form diversity

Betti et al. (2009) explored climate and diversity in a different way to Balloux et al. (2009). Betti et al. used coordinates across the Earth like each was an origin. For each origin, they started with a model for predicting cranial form diversity, using distance (to populations) terms and climatic terms. For each origin, Betti et al. (2009) found the most effective model for predicting diversity. Out of all the origins, the origin which had a model that best predicted diversity was in Africa, and it only featured distance, and not climate (Betti et al., 2009). This happened with respect to male crania, and female crania too (Betti et al., 2009). However, as mentioned above, the peak point may particularly lean towards being influenced by African populations (Cenac, 2022), which could be worth considering in the event that models using other *origins* included climatic terms in Betti et al. (2009).

Current study

Building on previous research (Balloux et al., 2009; Betti et al., 2009), the present study examined whether diversities appear to contain a climatic signal when the signal of expansion is controlled for.[3] Prior research has used minimum temperature as a climatic variable (Balloux et al., 2009; Betti et al., 2009, 2012; Manica et al., 2007),[4] and minimum temperature was used as such in the present study. Using populations from across the world, earlier research has adjusted genetic diversities for distance from Africa (distance from the same location in Africa for each diversity), and seen if these adjusted diversities are related to minimum temperature (Balloux et al., 2009); this approach was broadly taken in the present study, but with some differences. To counter a potential influence of location in Africa on whether relationships with climate are apparent (Figure 2), several analyses solely featured populations outside of Africa. Those analyses concerned autosomal microsatellite heterozygosity, autosomal SNP haplotype heterozygosity, X-chromosomal microsatellite heterozygosity, and cranial form diversity. Having said that, certain analyses (global/worldwide analyses) did feature African populations. The distance from peak points specific to the relevant diversity (Cenac, 2022, 2023a) were used in the global analyses. These analyses featured the aforementioned autosomal and X-chromosomal diversities, as well as Y-chromosomal microsatellite heterozygosity.

Method

Data

The present study used genetic diversities in Balloux et al. (2009). These diversities were mitochondrial (51 populations, from the Human Mitochondrial Genome Database and GenBank), and heterozygosities (51 populations from the HGDP-CEPH) regarding autosomal microsatellites, autosomal SNP haplotypes, X-chromosomal microsatellites, and Y-chromosomal microsatellites (Balloux et al., 2009). Balloux et al. acquired the haplotype diversities from Li et al. (2008). Additionally, the form diversity of male crania (90 populations) and female crania (34 populations) outside of Africa (Betti et al., 2009) was used (regarding cranial data, Betti et al., 2009, cite Manica et al., 2007).

Geographical distances were from prior research (Betti et al., 2009; Cenac, 2022), some of which (in Cenac, 2022) included distances from i) 99 locations in Africa from Betti et al. (2013), and ii) 32 global locations found in von Cramon-Taubadel and Lycett (2008). Geographical distances (Betti et al., 2009; Cenac, 2022) from peak points (Betti et al., 2009; Cenac, 2022, 2023a) were used to adjust diversities. These distances (Betti et al., 2009; Cenac, 2022) were from peak points i) in Africa for cranial form diversity (Betti et al., 2009), X-chromosomal microsatellite heterozygosity, autosomal SNP haplotype heterozygosity (Cenac, 2022), and autosomal microsatellite heterozygosity (Cenac, 2023a), and ii) in Asia for Y-chromosomal microsatellite heterozygosity (Cenac, 2022). That is to say, peak points are in Africa for each of these diversities (Betti et al., 2009; Cenac, 2022, 2023a) except for the Y-chromosomal diversity, where the peak point is in Asia (Cenac, 2022). Because peak points can vary between diversities (Cenac, 2022), the distances (from peak points) used for adjusting diversities were the ones relevant/specific to the type of diversity. Distances from peak points were utilised even when analyses only consisted of populations outside Africa (despite reasoning in the *Introduction*).

The continents which populations are in concerning the genetic data were known from beforehand (Cenac, 2022); it was clear which populations are inside Africa, and which are not. Labelling employed in Betti et al. (2009) was used to identify which populations featured in their study are outside of Africa.

Minimum temperatures shown in previous research (Balloux et al., 2009; Betti et al., 2009) were used (both Balloux et al., 2009, and Betti et al., 2009, sourced minimum temperatures from WORLDCLIM, and they cited Hijmans et al., 2005, with respect to WORLDCLIM).

Analysis

Analysis took place in R Version 4.0.5 (R Core Team, 2021) and Microsoft Excel. ppcor (Kim, 2015) was used for running semi-partial correlation tests, except for the semi-partial Pearson correlation tests used regarding autosomal microsatellite heterozygosity, and the semi-partial Spearman correlation test employed regarding the diversity of male crania.

Autosomal microsatellite heterozygosity may *appear* to fall linearly when distance from Africa increases (Prugnolle et al., 2005), but this type of diversity stands more strongly with a non-linear trend (quadratic) than a linear decline (Cenac, 2023a). Therefore, autosomal microsatellite heterozygosity was adjusted for a quadratic (rather than a linear) relationship with distance from Africa. It was then seen if the adjusted autosomal diversity is related to minimum temperature. Semi-partial Pearson correlation coefficients concerning adjusted autosomal diversity and minimum temperature were calculated (for populations globally, and only outside Africa). The correlation coefficients were converted to *t*-statistic values using a formula in Kim (2015). A *p*-value can be found for a *t*-statistic value (e.g., Kim, 2015), and *p*-values were indeed calculated for the converted *t*-values.

In Betti et al. (2009), there was a non-linear association between distance from Africa and cranial form diversity for male crania (105 populations across the globe). The model used in Betti et al. (2009) for predicting diversity from distance from the peak point had an intercept, a linear term, and a cubic term; [5] a variant of their model was used to calculate residuals in the present study (the residuals being diversity adjusted for distance from Africa) – the same distances were used as in Betti et al., an intercept was also utilised, as was a linear term, and also a cubic term when trying to predict diversity from distance, but populations were solely outside of Africa. The semi-partial Spearman correlation coefficient for adjusted cranial diversity and minimum temperature was determined. The formula in Kim (2015) was used for converting the correlation coefficient to a *t*-value, for which (like with autosomal diversity) a *p*-value was calculated.

Linear declines (with extending distance from Africa) are shown in autosomal SNP haplotype heterozygosity and X-chromosomal diversity (Balloux et al., 2009), with a quadratic relationship attaining no support (over a linear relationship) (Cenac, 2023a). And so, adjusting those diversities for linear distance from Africa (e.g., Balloux et al., 2009) would seem to be acceptable, and therefore analysis in the present study set out to adjust those diversities for linear distances.

Y-chromosomal microsatellite heterozygosity has a peak point in Asia it seems (and indicates an origin of expansion which possibly is exclusive to Asia), with a linear decline from there (Cenac, 2022), and an absence of support for a non-linear relationship (Cenac, 2023a). Therefore, it was planned for the present study to adjust Y-chromosomal diversity for linear distance from Asia (Balloux et al., 2009, adjusted for linear distance from Africa).

When data were analysed parametrically, datapoints which have *z*-scores of residuals over |3.29| were noted as being atypical (e.g., Field, 2013). The Surui population (Balloux et al., 2009) had an atypical standardised residual in some analyses (see *Results and discussion*). In the absence of atypical datapoints, it was seen whether heteroscedasticity was indicated. It was also seen if the presence of heteroscedasticity was resolved in the absence of any one population. To visually assess whether heteroscedasticity was present (in parametric analysis), adjusted diversity (*y*-axis) was placed

against minimum temperature (*x*-axis) in graphs. Several graphs of this sort are presented in Balloux et al. (2009).

To see whether positive spatial autocorrelation was present amongst residuals, the three-step method of Chen (2016) was employed. This was done utilising a spreadsheet available in Chen (2016). Spatial Durbin-Watson values (spatial *DW*s) are produced in the three-step method, and Durbin-Watson bounds are applicable to the spatial *DW* (Chen, 2016). Consequently, (5%) Durbin-Watson bounds (Savin & White, 1977) were referred to in order to assess if positive spatial autocorrelation was at hand. Regarding the cranial data, population longitudes and latitudes were not stated in Betti et al. (2009); the present study used semi-partial Spearman correlation tests when it came to cranial diversity in the event that there was positive spatial autocorrelation in parametric analyses concerning cranial diversity.

The Bonferroni correction (reviewed in Abdi, 2010, alongside other methods of adjusting *p*-values) was used on *p*-values in the current study; *p*-values were multiplied by five (as there were five types of diversity of interest in this study) regarding the genetic diversities, but multiplied by 10 concerning cranial diversity (multiplied by five given the five types of diversity, and multiplied by two because there were separate analyses of males and females).

Results and discussion

Outside of Africa

As described above, when only populations outside of Africa were featured in an analysis, diversities were adjusted for distance from Africa. For populations outside of Africa, diversity (adjusted for distance from Africa) correlated positively with minimum temperature when the diversity was X-chromosomal microsatellite heterozygosity, $sr(40) = .40$, $p = .040$, spatial $DW = 1.91$. This was following Surui not being included due to an atypical standardised residual ($z = -3.70$) (as in part of Figure 2A). Adjusted autosomal SNP haplotype heterozygosity had no correlation with minimum temperature, $sr(41) = .10$, $p = 1.00$, spatial $DW = 1.71$. The same can be said for adjusted autosomal microsatellite heterozygosity, $sr(39) = .25$, $p = .57$, spatial $DW = 1.92$ (in the absence of Surui due to their standardised residual, $z = -3.41$). As for adjusted cranial form diversity, it was not found to have a correlation with minimum temperature for females, $sr_s(31) = -.13$, $p = 1.00$, or for males, $sr_s(86) = -.02$, $p = 1.00$.

Worldwide

When analyses were not limited to only populations outside of Africa, diversities were adjusted for distance, but not necessarily distance from Africa (as covered in the *Method*). X-chromosomal microsatellite heterozygosity (adjusted for distance from Africa) was found to have a positive association with minimum temperature, $sr(46) = .39$, $p = .031$, spatial $DW = 1.92$, but there were caveats, with this correlation not featuring two of the populations. When using 51 populations, Surui had an atypically low standardised residual ($z = -3.52$). Whether with or without Surui,

heteroscedasticity was indicated. In the absence of Surui, out of the 50 remaining populations, any one of the populations was removed to see if any particular population may be driving the heteroscedasticity amongst the 50 populations. The absence of the Mbuti Pygmy population (Balloux et al., 2009) seemed to (visually) have the most impact. Indeed, without Mbuti Pygmy, heteroscedasticity appeared to be absent; amongst the 50 populations, it seemed like Mbuti Pygmy may have resulted in the heteroscedasticity. And so, without Surui and Mbuti Pygmy, there was a correlation between adjusted X-chromosomal diversity and minimum temperature.

X-chromosomal peak point

Autosomal SNP haplotype heterozygosity (adjusted for distance from Africa) was not observed to be associated with minimum temperature, $sr(48) = .16$, $p = 1.00$, spatial $DW = 1.81$. Additionally, autosomal microsatellite heterozygosity (controlling for distance from Africa) did not yield a correlation with minimum temperature, $sr(46) =.28$, $p =.28$, spatial $DW = 1.92$ (without Surui because of their standardised residual, $z = -3.69$). For Y-chromosomal microsatellite heterozygosity (adjusted for distance from Asia), a correlation was not found with minimum temperature, $sr_s(48) = -.11$, $p = 1.00$. A semi-partial Spearman test was used regarding Y-chromosomal diversity because heteroscedasticity seemed apparent in parametric analysis, and it persisted when any one population was absent.[6]

The intention was to adjust diversity for distance from the peak point. The peak point used with respect to X-chromosomal diversity was found by using 51 populations (Cenac, 2022). Peak points may be substantially influenced by African populations (Cenac, 2022). So, without Mbuti Pygmy (and Surui, i.e., using 49 populations), X-chromosomal diversity may generate a markedly different peak point than when 51 populations are used. The location of the peak point does likely affect the correlation between diversity (adjusted for distance) and minimum temperature (Figure 2). When using 49 populations, the peak point was more southern, with its location being (30°S, 20°E).[7] When X-chromosomal diversity is adjusted for distance from (30°S, 20°E) and 51 populations are used, Surui still had a very low standardised residual ($z = -3.56$), and, in the absence of Surui, Mbuti Pygmy seemed to still be driving heteroscedasticity. Using 49 populations (no Surui or Mbuti Pygmy), the correlation coefficient for the relationship between X-chromosomal diversity [adjusted for distance from (30°S, 20°E)] and minimum temperature was, $r = .39$, i.e., the same (to two decimal places) as was found when using the peak point calculated from the 51 populations. And so, no matter whether the peak point for 51 or 49 populations was used, the correlation coefficient did not seem to be notably affected.

Context

Previous research had not found support for a climatic signal in autosomal diversity, Y-chromosomal diversity (Balloux et al., 2009), or cranial form diversity (Betti et al., 2009). This lack of support was matched in the present study. On the other hand, this study departed from previous research (i.e., Balloux et al., 2009) when it came to X-chromosomal diversity. In Balloux et al.

(2009), a climatic signal was not indicated in X-chromosomal diversity for populations worldwide, unlike in the current study, where a signal was indicated.

This disagreement between studies is unlikely to be because distances were from different African locations; distances in Balloux et al. (2009) and the ones used in the present study regarding X-chromosomal diversity (from Cenac, 2022) were actually from a similar location (see *Introduction*). Rather, the disagreement possible arose due to correlation tests in the present study having omitted populations due to an atypical standardised residual (Surui) and then heteroscedasticity (Mbuti Pygmy). Balloux et al. (2009) included those populations in their analysis; what are correlation coefficients like in the present study with the inclusion of Surui and Mbuti Pygmy? In the present study, if the correlation coefficient (for adjusted diversity and minimum temperature) is calculated when including the two populations, the correlation coefficient is numerically smaller in magnitude, $r = .18$, than when the populations are absent. Without Surui, the correlation coefficient is also numerically smaller, $r = .28$. It is also worth stating that when using populations outside of Africa, the inclusion of Surui (who had an atypical standardised residual) leads to a numerically weaker correlation coefficient ($r = .31$) than when Surui were absent (see above).

Would Balloux et al. (2009) have likely observed a climatic signal in X-chromosomal diversity if the two populations were not featured in their analysis? In Figure 3D of Balloux et al. (2009), adjusted X-chromosomal diversity is graphed against minimum temperature. When comparing Figure 3D of Balloux et al. (2009) to a graph made in the present study,[8] it could very well be that Surui would have been an atypical datapoint in Balloux et al. and perhaps Mbuti Pygmy as well, and it does seem like heteroscedasticity is indeed indicated in Balloux et al. Looking at Balloux et al. Figure 3D, and given results in the current study, heteroscedasticity would likely have been absent in Balloux et al. without the two populations. Without them, Figure 3D of Balloux et al. could actually hint at a positive trend between adjusted X-chromosomal diversity and climate.

An association between adjusted X-chromosomal diversity and minimum temperature could suggest that climate is related to i) a male:female ratio in migration, or ii) reproduction (Balloux et al., 2009 – see Balloux et al. for more information). Therefore, it could very well seem like relationships between climate and either of those two possible *factors* might underlie the correlation between adjusted X-chromosomal diversity and climate. However, the diversity ratio with respect to the sex chromosomes has no relationship with minimum temperature, which suggests that the relationship between mitochondrial diversity and climate is not explainable by minimum temperature being linked to either of the possible factors (Balloux et al., 2009), and this lack of explanation could therefore apply to the relationship between adjusted X-chromosomal diversity and minimum temperature.

Conclusion

In agreement with previous research (Balloux et al., 2009; Betti et al., 2009), a climatic signal does not seem to be evident in autosomal, Y-chromosomal, or cranial form diversities. Mitochondrial diversity appears to have a climatic signal, and, in contrast to previous research (Balloux et al., 2009),

X-chromosomal diversity now seems to as well. The reason for why a climatic signal seems to be present in X-chromosomal diversity is not clear.

Footnotes

[1] Diversity was adjusted for distance by fitting a linear trend for the relationship between diversity and distance, and calculating residuals – the residuals were diversity adjusted for (linear) distance (Balloux et al., 2009).

[2] Nonetheless, for a number of cranial dimensions, their diversity and the climate are related (Manica et al., 2007).

[3] Several diversities were of interest in the present study. These were: autosomal heterozygosity (microsatellite, and SNP haplotype separately), X-chromosomal microsatellite heterozygosity, Y-chromosomal microsatellite heterozygosity, and cranial form diversity. Each does undergo a decline with more distance from Africa (Balloux et al., 2009; Betti et al., 2009; Cenac, 2022; Prugnolle et al., 2005). Of the genetic diversities, consistent with global expansion originating from Africa alone are autosomal microsatellite heterozygosity (Manica et al., 2007), autosomal SNP haplotype heterozygosity, and X-chromosomal microsatellite heterozygosity, whereas, Y-chromosomal microsatellite heterozygosity actually corresponds to expansion from elsewhere than Africa (Cenac, 2022). As for cranial form diversity, when the diversity is of male crania, it does indicate an expansion beginning only in Africa (Betti et al., 2009; Cenac, 2022). With respect to the cranial form diversity of females, Betti et al. (2009) found the area from which the expansion likely originated was an area that was not utterly in Africa. In research elsewhere, however, the area was in Africa in its entirety (Cenac, 2022). Moreover, cranial form diversity appears to lead to a larger area of origin than cranial shape diversity does (Cenac, 2022). Therefore, the area in Betti et al. (2009) likely would have been in Africa alone had they used cranial shape diversity (given that the peak point was in sub-Saharan Africa in their study). Hence, whilst the area of origin was not exclusive to Africa in Betti et al. for the form diversity of female crania, it still makes sense to adjust the cranial form diversity of females for distance from Africa in order to account for the signal of expansion from Africa.

[4] In addition to minimum temperature, Betti et al. (2009, 2012) and Manica et al. (2007) also included other climatic variables in their analyses.

[5] However, without two populations (both Patagonian), there was a linear relationship (Betti et al., 2009 – see Betti et al., 2009, for discussion about this).

[6] Figure 3 in Balloux et al. (2009) may indicate heteroscedasticity with respect to parametrically testing for relationships between heterozygosity (adjusted for distance from Africa) and minimum temperature when the heterozygosity used was of X-chromosomal microsatellites, autosomal microsatellites, autosomal SNP haplotypes, and Y-chromosomal microsatellites (Balloux et al. did also employ partial Mantel tests).

[7] Distances calculated in other research (Cenac, 2022) were used. These were distances between coordinates in the continent of Africa from Betti et al. (2013) and HGDP-CEPH populations (Cenac, 2022). Previous research has used those distances to calculate peak points (Cenac, 2022), and they were used for that reason in the current study.

[8] A graph was produced (like in Balloux et al., 2009) when using the 51 populations with minimum temperature on the *x*-axis and adjusted X-chromosomal diversity on the *y*-axis.

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