Hunter-gatherers adjust mobility to maintain contact under climatic variation

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Abstract

Population density and mobility are fundamental population parameters for hunter-gatherer groups, and their reconstruction for prehistoric populations has long been an aim of archaeological research. This endeavour has become more important than ever in recent years, with the recognition that these parameters play a key role in determining rates of cultural transmission. Potential archaeological proxies for population density and mobility are often hard to interpret, creating a need for more generic, reliable, and easily calculated indicators. Climatic variables provide considerable promise in this area, and the analyses reported here test the efficacy of six climatic variables as potential predictors. Significant predictors are then incorporated in path analyses that assess the causal relationships between climatic variables, population density, and mobility. Results suggest that the previously established strong reciprocal relationship between population density and mobility is not due purely to common determination by climatic variables. Instead, the best supported model is consistent with the hypothesis that hunter-gatherers adjust levels of mobility so as to maintain contact with neighbouring groups at varying population densities. This ensures that opportunities for cultural transmission are maintained at similar levels regardless of climatic variation. The results lead to a number of archaeologically testable predictions concerning the relationships between climatic variables, population density, mobility, and assemblage complexity.

Keywords: hunter-gatherer; climatic variability; mobility; population density; cultural transmission.

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1. Introduction

As well as being fundamental population parameters themselves, population density and mobility are heavily implicated in patterns of cultural transmission (e.g. Powell et al. 2009; Grove 2016). For a given level of mobility, individuals or groups experiencing higher population density will encounter one another more frequently per unit time. Similarly, at a given population density, more mobile individuals or groups will encounter one another more frequently per unit time. Thus increases in the number of individuals per unit area or the area covered per unit time will increase the encounter rate, with each encounter providing an opportunity for the transmission of information. The estimation of population densities and levels of mobility associated with archaeological sites is therefore of considerable importance to both studies of palaeoecology and research into rates of cultural transmission.

Variation in population density and mobility is generally considered to reflect underlying differences in climatic variables that account for the density of subsistence resources, and most studies of hunter-gatherers support such conclusions (e.g. Kelly 1995; Binford 2001; Grove 2009). High resource densities should sustain high population densities and require minimal mobility, whilst low resource densities should sustain only low population densities, requiring greater mobility. In addition to these basic expectations, mobility is viewed as a means of maintaining equitable relations with distant groups to ensure that they can be called upon to share resources in times of local hardship. The existence of such 'safety nets' is a common theme in considerations of hunter-gatherer mobility strategies (e.g. Wiessner 1982; Whallon 2006), and reinforces the link between demographic variables and underlying resource structure.

A growing number of archaeologists are making use of demographic variables in explaining changes in assemblage diversity, complexity, or sophistication through time or across space (e.g. Brumm and Moore 2005; James and Petraglia 2005; Zilhao 2007; Langley et al. 2011). Much of this work is influenced by the theoretical models of Shennan (2001) and Henrich (2004), which relate population size to the 'cultural fitness' or 'skill level' attainable within that population. Henrich's (2004) analysis features a particularly effective model of the cultural transmission process, and has had considerable impact within archaeology. The model introduces a basic sampling problem in which all members of a population copy a target individual with a degree of error. Most copying errors are detrimental, but a small number will be beneficial; a larger population size therefore increases the probability that at least one member of the population will produce a copy that is better than the original, thus ensuring cumulative improvement in technology.

Powell and colleagues (2009) embedded the Henrich (2004) model within a broader simulation framework, demonstrating that population density and mobility are more realistic correlates of cultural sophistication than is population size. Grove (2016) confirmed the lack of a population size effect, and noted that both population density and mobility are proxies for the rate of encounters between individuals. The encounter rate model both unifies previous models and explains why empirical studies that focus on population density alone are unlikely to find significant effects. In parallel, theoretical modelling by Premo (2012) has emphasized the 'connectedness' of populations as playing a key role in the resilience of their material culture traditions. An intriguing archaeological case study in this vein is provided by Riede (2008, 2016), who argues that the eruption of the Laacher See volcano in western Germany around 12,920 BP had considerable implications for Late Glacial human demography in northern Europe. In particular, Riede (2008:596) postulates that a “significant and sudden” reduction in the connectedness of populations led to the loss of bow-and-arrow technology and regional technological simplification. An important strand linking both theoretical and empirical work is that decreases in population density, mobility, or ‘connectedness’ can lead to decreases in the pool of cultural interactants, thus limiting the potential for cumulative cultural evolution.

Despite the growing use of demographic arguments, few studies link demographic variables to climatic variables, despite the relatively well established patterns emerging from the hunter-gatherer literature. This omission is part of a wider problem in that few studies examine proxies for demographic variables in parallel with evidence for variation in assemblage sophistication. Hypotheses linking demography with cultural transmission are therefore frequently employed as explanations, but rarely tested with archaeological data (see Collard et al. 2016). One possible reason for this trend is that, whilst there are numerous aspects of archaeological assemblages that might act as proxies for demographic variables, they are often subject to confounds that are difficult to eliminate. Raw material or artefact transfer distances might act as proxies for mobility (e.g. Taborin 1993; Féblot-Augustins 1997; Pearce and Moutsiou 2014), but in many cases it is impossible to distinguish between the signatures of mobility and trade. Artefact or faunal densities, particularly in landscape-level studies, may correlate with population densities, but will also correlate with localised group sizes and site occupation durations (e.g. Grove 2009; Tryon and Faith 2016). The frequent occurrence of palimpsest data and the difficulties of establishing true contemporaneity between sites serve to further cloud this picture (Schacht 1984; Stern 1993; Grove 2011).

The study of relationships between basic climatic and demographic variables in hunter-gatherer groups has the potential to considerably improve our understanding of prehistoric demography. Not only can such relationships provide baseline information about likely demographic parameters, but they can also be used to verify inferences drawn directly from archaeological assemblages, providing independent and complimentary lines of evidence (*sensu* Wylie 1989). Given the ever wider availability of high resolution palaeoclimatic data, it is becoming increasingly important to fully explore the structure of relationships between climatic variables, population density and mobility in recent hunter-gatherer groups. This will not only facilitate inferences about prehistoric demographics, but will also enable archaeologists to make more informed, robust conclusions about the potential for cultural transmission in prehistoric societies.

Given the theoretical relationships between resource density, population density, and mobility highlighted above in relation to the potential for cultural transmission, it is important to distinguish between three viable hypotheses concerning the interaction of these variables. Grove (2016) empirically demonstrated a strong negative correlation between population density and mobility in hunter-gatherer populations. This result was interpreted in a social context as suggesting that mobility is increased as population density decreases, to ensure maintenance of a sufficient number of encounters between neighbouring groups. However, the causal links between resource density, population density and mobility were not directly tested in Grove (2016). There remain two further hypotheses that could feasibly account for the observed patterning. Firstly, the relationship between population density and mobility could result purely from their common determination by resource density. When resources are at low density, foragers dependent on those resources will have their population densities constrained; similarly, they will be required to cover a greater area in order to fulfil energetic requirements. Secondly, if groups are required to cover greater areas to obtain resources, they may increase distances between groups to avoid depleting the same areas as their neighbours, thus decreasing population density.

The analyses detailed below therefore test three alternative hypotheses:

H1. The relationship between population density and mobility is due purely to their common determination by resource density.

The two other hypotheses can be most succinctly framed as different responses to decreasing resource density:

H2. Groups increase mobility to maintain contact with neighbouring groups who are forced by low resource densities to live further apart (i.e. at lower population densities);

H3. Groups decrease population density (i.e. move further apart) to avoid depleting the same areas as neighbouring groups who are forced by low resource densities to increase mobility.

These hypotheses differ only with respect to the *direct* effects of resource density. H1 suggests that resource density directly affects both population density and mobility; H2 suggests that resource density affects population density directly but mobility only indirectly; H3 suggests that resource density affects mobility directly but population density only indirectly. A schematic of these direct and indirect causal paths is provided in Figure 1.

It is important to distinguish between these three hypotheses as they have a direct bearing on how climatic variables are likely to affect rates of cultural transmission in prehistory. Specifically, the structure of dependence between these variables affects the extent to which opportunities for cultural transmission are seen as imposed directly by climatic variables as opposed to arising from social responses to those variables. Whilst feedback mechanisms between climatic and social systems are inevitable, and the former can be seen as ultimately constraining the possibilities of habitation, it is often argued that the latter specify the ways in which climatic constraints are addressed by a particular society (e.g. Ingold 1981; Gamble 1986; Kelly 1995). In these terms, support for H1 would suggest that social systems – in as far as they are defined by basic variables such as population density and mobility – are heavily constrained by climatic variables. Support for H2 or H3, by contrast, would suggest a greater measure of flexibility in how human societies meet climatic challenges.

H1 can be assessed purely via partial correlation analyses; if the strong relationship between population density and mobility remains when the effects of resource density on both are controlled for, H1 is not supported. The causal structures of H2 and H3, however, immediately suggest path analysis as the appropriate statistical technique. Path analysis is rarely used in archaeology and anthropology, but is ideal when evaluating hypotheses that involve multiple causal steps (see Wright 1921, 1934; Li 1975). It is a relatively simple extension of regression analysis, and can be paired with model selection statistics to allow powerful discrimination between competing hypotheses.

2. Data

There exists no direct measure of global variation in resource density, but a number of climatic variables can be calculated that act as useful indices. In particular, a long history of research into biome classification has established that the productivity of different biomes is determined primarily by levels of temperature and precipitation (e.g. Holdridge 1947; Whittaker 1975; Olson et al. 2001; Walter and Breckle 2002; Cox et al. 2016). In order to adequately represent resource density, data on four primary climatic variables (mean annual temperature, standard deviation of annual temperature, mean annual precipitation and standard deviation of annual precipitation) were collected. Two composite variables were also calculated. Net above-ground productivity (NAGP) provides an estimate of net primary productivity (the mass of new plant growth per year) from a combination of temperature and precipitation measures (Rosenzweig 1968). Effective temperature (ET) employs a global model to simultaneously represent both the length and the warmth of the growing season (Bailey 1960). These six climatic variables were combined with data on hunter-gatherer population density and mobility.

Data on population density, mobility, and net above-ground productivity (NAGP) for the hunter-gatherer sample were gathered from Binford (2001). Binford’s (2001) full sample was reduced to only those groups that are fully mobile (i.e. those for which his GRPPAT variable is equal to 1), yielding a sample of 175 groups. Mobility (distance moved per annum) was converted from miles to kilometres prior to analysis, and the population density variable was converted from individuals per 100km^2 to individuals per km^2.

Climatic variables, with the exception of NAGP, were calculated from the global high-resolution databases archived at NOAA/OAR/ESRL PSD (Boulder, Colorado, USA, see http://www.esrl.noaa.gov/psd/ and Willmott and Matsuura 2001). These databases provide monthly mean measurements of air temperature (interpolated from 12,587 stations) and precipitation (interpolated from 12,857 stations) on a .5 × .5 degree global grid. Mean annual temperature (MAT), mean annual precipitation (MAP), standard deviation in annual temperature (SDT) and standard deviation in annual precipitation (SDP) were calculated via linear interpolation of the 12 monthly mean temperatures in the global grid using the longitude and latitude data given in Binford (2001). Finally, effective temperature (ET) was calculated following Bailey (1960:4) as $ET = (18\bar{w} - 10\bar{c})/(8 + \bar{w} - \bar{c})$, where $\bar{w}$ denotes the mean temperature of the warmest and $\bar{c}$ the mean temperature of the coldest month of the year.

To satisfy the requirement of the statistical techniques employed below for normally distributed data, variables with substantial positive skew (population density, MAP, SDP, ET, and NAGP) were natural log transformed, and variables with moderate positive skew (mobility and SDT) were square root transformed. MAT showed moderate negative skew and was transformed using the equation $t_i = -\sqrt{u_{\max} - u_i}$, where t is the transformed variable and u the raw variable (Tabachnick and Fidell 2007). All variables were then standardized (i.e. converted to z-scores) prior to analysis, as this prevents the need to calculate intercepts, increasing the accuracy of the path analyses (Li 1975) and the reliability of model comparisons. It further entails that the standardized and unstandardized regression coefficients are identical (i.e. B = β).

3. Methods

The first stage of the analysis involved performing two separate multiple regressions of (1) population density and (2) mobility on the six climatic variables. Multiple regressions were run using the 'enter' routine in IBM SPSS Statistics 24; this routine produces partial regression coefficients for each independent variable, making the results identical to those achieved via simple path analysis. Confidence intervals for all regression (β) and correlation (r) coefficients were produced using SPSS. Due to the functionality of the software confidence intervals for regression coefficients were produced analytically, whereas for bivariate and partial correlation coefficients they were produced via bootstrap sampling. All bootstrap confidence intervals were produced from 10,000 samples.

To assess H1, climatic variables found to be significant predictors of either mobility or population density were included as control factors in partial correlations. A result demonstrating that the correlation between population density and mobility becomes non-significant when the relevant climatic variables are controlled for is consistent with H1. Conversely, if the partial correlation remains significant, H1 is rejected. Comparing the simple bivariate correlation between the two variables with the partial correlation gives an impression of the proportion of the correlation accounted for by the climatic variables.

To assess H2 and H3, variables found to be significant predictors of either mobility or population density were included in path analyses that were set up as two sets of causal models. The models in Set 1 represent H2, that climatic variables affect mobility primarily indirectly, via their effects on population density. The models in Set 2 represent H3, that climatic variables affect population density primarily indirectly, via their effects on mobility. Differences between models in a given set are due to different configurations of paths from the exogenous (climatic) to the endogenous (population density and mobility) variables. Regardless of the configuration of the climatic variables, models comprising Set 1 include a directed path from population density to mobility, whereas models comprising set 2 include a directed path from mobility to population density. It is expected that increases MAP, MAT, NAGP and ET will lead to increases in resource density, and therefore to increases in population density and reductions in mobility. The variables that index variation in temperature and precipitation – SDT and SDP respectively – are more complex, but in line with previous research (Dyson-Hudson and Smith 1978; Winterhalder 1986; Kelly 1995; Johnson and Earle 2000) greater climatic variation is expected to reduce population density and increase mobility.

For each model a log-likelihood, a sample size corrected AICc value, and a delta value were calculated; these in turn enabled the calculation of relative model likelihoods and probabilities given the data and the set of models considered (see Burnham & Anderson 2002; Burnham et al. 2011). This method allows not only for the identification of the most supported model, but also for assessment of the relative merits of all the models comprising Set 1 as opposed to all the models comprising Set 2. Path analyses were conducted in IBM SPSS Amos 24, with additional calculations based on the raw AIC values and parameter numbers output by the program, following Burnham and Anderson (2002).

4. Results

A multiple regression of population density on the six climatic variables found that only SDT (β = -.734 [95% CI: -1.013, -.454], p < .001) and SDP (β = .433 [.190, .675], p < .001) were significant predictors. Isolating these two variables demonstrated that together they explain 49.4% of the variance in population density (R^2 = .494, F(2,173) = 84.379, p < .001). The multiple regression of mobility on these six variables found that, again, only SDT (β = .885 [.582, 1.188], p < .001) and SDP (β = -.435 [-.698, -.173], p = .001) were significant predictors. Isolating these two variables demonstrated that together they explain 38.0% of the variance in mobility (R^2 = .380, F(2,173) = 53.059, p < .001).

The assessment of **H1** involved first calculating the simple bivariate correlation between population density and mobility, yielding r = -.830 [-.913, -.747], n = 175, p < 0.001. As only SDT and SDP were found to be significant predictors of population density and mobility, partial correlations were run controlling for SDT, controlling for SDP, and controlling for both. As a final verification, a partial correlation was run controlling for all six climatic variables. Bootstrap confidence intervals for r (10,000 samples) were produced for each partial correlation. The results, presented in Table 1, demonstrate that the correlation between population density and mobility remains strong and significant in all cases, rejecting the hypothesis that this correlation is due purely to common determination by the climatic variables.

The finding that SDT and SDP were the only significant predictors of both PD and DISMOV made it possible to run an exhaustive series of exploratory path analyses on the two exogenous variables (SDT and SDP) and two endogenous variables (population density and mobility). The twelve possible models are shown in Figure 2; Models 1-6 comprise Set 1 and represent variations on H2, whereas Models 7-12 comprise Set 2 and represent variations on H3. Model 2 represents the strongest embodiment of the hypothesis that the climatic variables affect mobility only indirectly (H2); similarly, model 8 represents the strongest embodiment of the hypothesis that climatic variables affect population density only indirectly (H3).

Results of the path analyses on the 12 models are shown in Table 2, with full path diagrams for the four best models presented in Figure 3. The first result to note is that models 1 and 7 are saturated (i.e. the maximum possible number of paths are present), and thus are not amenable to reliable statistical analysis. For the remaining models, it is important to note that better models have low AICc and delta values and high relative likelihoods (L_i) and probabilities (w_i). Thus model 2 is the best model, and model 8 is the worst model. The evidence ratio, calculated by dividing the probability of model 2 by that of model 8 (see Burnham et al. 2011), demonstrates that the empirical support for model 2 is over 44 million times that for model 8.

Assessing the two sets of models provides more conservative results. Summing the probabilities of the five valid Set 1 models (2-6) and the five valid Set 2 models (8-12) and dividing the former by the latter demonstrates that the empirical support for Set 1 is ≈5.86 times that for Set 2. This relatively moderate evidence ratio is due to the performance of model 11, which is the only reasonably supported model from Set 2. However, comparing model 11 to its topological equivalent from Set 1 (model 3) demonstrates that the latter receives ≈2.68 times more support. In summary, the results support Set 1 over Set 2, and therefore support the hypothesis that climatic variables affect mobility primarily indirectly, via their effects on population density (H2). Support is strongest for model 2, which is the simplest and strongest embodiment of this hypothesis.

5. Discussion

The results presented above provide the most support for the hypothesis that climatic variables determine population density, which in turn determines mobility (H2). However, they also suggest that it is primarily changes in the standard deviations of temperature and precipitation rather than changes in their means that affect these demographic variables. That variables indexing climatic variability provide the key to demographic patterns is an important conclusion, suggesting not only that such variability has a powerful effect on sustainable population densities, but also that contact between neighbouring groups is crucial in mitigating the challenges it creates. Surprisingly, ET and NAGP, which are often considered to be good indicators of resource density (e.g. Kelly 1995; Binford 2001; Grove 2009), play no part in the final models. Whilst the relationship between SDT and population density is as predicted, the relationship between SDP and population density runs counter to the prediction, with increasing variability in precipitation found to *increase* population density. This result is surprising, and merits further scrutiny.

One possible explanation arises from the fact that the relationship between SDT and SDP is itself significant and negative ($r = -.734$ [$-.787$, $-.675$], $df = 173$, $p < .001$). At the locations represented by the hunter-gatherer groups within the sample, higher variability in temperature tends to be associated with lower variability in precipitation. It could be argued, therefore, that higher SDP leads to higher PD simply because both show significant positive relationships with SDT. Note, however, that this goes against the structure of the models presented above; if all the explained variability in PD were due purely to variation in SDT, then SDP would not achieve significance as a predictor. To reinforce this point, a partial correlation of SDP and PD was performed whilst controlling for SDT. The resultant correlation remains significant and positive ($r = .236$ [$.086$, $.379$], $df = 172$, $p = .002$), suggesting that this explanation is not sufficient.

A second possible explanation arises from the positive correlation between SDP and MAP ($r = .859$ [$.783$, $.936$], $df = 173$, $p < .001$), suggesting that perhaps high SDP leads to high population densities simply because it correlates with MAP, higher values of which were expected to lead to higher population densities. To test this possibility, a partial correlation of SDP and PD was performed whilst controlling for the effects of MAP on both variables. The resultant correlation remains significant and positive ($r = .321$ [$.199$, $.429$], $df = 172$, $p < .001$), suggesting that the positive relationship between MAP and SDP alone is not sufficient to explain the finding of higher variability in SDP leading to higher population densities.

Finally, it may be that the widely assumed link between lower SDP and higher resource density is itself inaccurate or mistaken. Some authors have argued that resource *diversity* might be more important to hunter-gatherer groups than resource density (e.g. Yesner 1977; Erlandson 1994), and it is not unreasonable to suspect that greater variability in precipitation might lead to a greater diversity of floral resources, and hence a wider range of secondary consumers. Further to this, SDP is a valuable index of, but does not fully reflect, differences in seasonality between regions at the macro-scale. The four seasons of the temperate zones, for example, create different rainfall regimes than those experienced in the tropics, which experience only two seasons, often with two distinct periods of increased precipitation. Locations at widely divergent latitudes, therefore, could demonstrate equivalent SDP but experience different annual patterns of rainfall, leading to different relationships between SDP and population density.

To test this latter possibility, the data were divided into three subsets by latitude: the Tropical subset includes those groups between the tropics of Cancer and Capricorn; the Temperate subset includes those between the Arctic Circle and the Tropic of Cancer, and between the Tropic of Capricorn and the Antarctic Circle; finally, the Polar subset includes those north of the Arctic Circle or south of the Antarctic Circle. Population density was then regressed on SDP separately for each of these three subsets. The results, shown in Table 3, demonstrate that SDP has less of an effect on population density among Tropical hunter-gatherers than it does within the other two subsets. The standardized coefficients, however, remain positive and significant in all cases, suggesting that greater variability in precipitation does indeed lead to greater population densities at all latitudes. In future studies, however, it may prove useful to further quantify the profiles of seasonal variability that exist at different latitudes, as these may reveal finer-grained patterning.

The results shown in Table 2 demonstrate that model 2 is the best model, and together with the path diagrams of Figure 3 allow some useful comparisons to be made with the second, third, and fourth best models. Firstly, note that models 3 and 4 are each equivalent to model 2 with an extra path added (SDT -> M in model 3, SDP -> M in model 4). The path coefficients show that the added path in model 3 explains only 0.0064% of the variance in mobility (i.e. 0.08^2), whilst the added path in model 4 contributes essentially nothing to the explanation of this variance. This pattern is reinforced by the results in Table 2. Since the AIC is calculated as $\mathrm{AIC} = -2\ln(L) + 2k$, where $\ln(L)$ is the log-likelihood and k is the number of parameters, adding an extra parameter to a model must increase the log-likelihood by >1 to produce a better model (an equivalent but more complex logic applies to the sample-size corrected AICc). Model 3 increases the log-likelihood by <1, whilst model 4 does not increase it at all. Model 11 is identical to model 3 but for the inversion of the path between population density and mobility; this inversion decreases the log-likelihood by 0.985 (thus increasing the AIC by 1.97), demonstrating the greater explanatory power of models in which the causal path leads from population density to mobility.

The principal finding of these analyses, that climatic variables exert direct effects on population density but only indirect effects on mobility, is consistent with the hypothesis that hunter-gatherers adjust mobility so as to maintain contact with neighbouring groups. This suggests that continued social contact between groups over often considerable distances is a fundamental aspect of hunter-gatherer adaptation; networks of contact between groups are imposed upon, not by, the environmental substrate. Flexibility in mobility ensures that encounter rates between groups are maintained at similar levels *regardless of climatic variation*, a fact that has important implications for patterns of cultural transmission both within extant hunting and gathering groups and in archaeologically documented populations.

A number of recent studies have focused on the elements of hunter-gatherer sociality that might facilitate the spread of cultural variants (e.g. Apicella et al. 2012; Hill et al. 2014; Derex and Boyd 2016; Salali et al. 2016; Migliano et al. 2017). The conclusions of many of these studies mirror aspects of research by Granovetter (1973; see also Watts and Strogatz 1998) that stressed the importance of occasional far-reaching links to other individuals or groups. The idea of an optimal balance of within-group to between-group transmission is therefore once again coming to the fore. For example, Migliano and colleagues (2017) suggest that the efficiency of cultural transmission depends on the structure of links between families. If each member of Family 1 establishes a link to a member of Family 2, there will be considerable redundancy in information flow along those links, and Family 1 will remain isolated from all families other than Family 2. By contrast, if each member of Family 1 establishes a link to a *different* family (i.e. Member 1 links to Family 2, Member 2 to Family 3, etc.), then Family 1 will be thoroughly enmeshed in the wider network, ensuring a comprehensive flow of information from all quarters. In such cases, any innovations that occur in the wider population should be rapidly transmitted to Family 1, who can proceed to adopt them if they choose. In terms of cultural transmission, establishing individual links to multiple families is a better strategy than establishing multiple links to a single family.

The above scenario is intuitively appealing, but an intriguing counterpoint is provided by the study of Derex and Boyd (2016). Performances on the experimental computer task employed by these authors suggest that partially connected groups will produce solutions that are both more complex and more diverse than those of fully connected groups. These findings are best explained by noting that greater diversity is inevitable when groups are not connected – alternate solutions should be expected when groups cannot communicate their ideas – but that the few connections that *do* exist allow the foremost achievements of each group to be periodically combined into more complex and superior solutions. Derex and Boyd (2016) argue that in fully connected groups variation in solutions is swamped by high levels of copying, such that only a small number of possible solutions are actually explored. By contrast, partial connectivity results in a fuller exploration of the full space of possible solutions. Thus there may be an optimal degree of connectivity that balances the need to generate and maintain variation with the need to fully exploit the beneficial innovations that the exploration of different solutions creates.

The degree of social contact between groups may therefore play a key part in the production and transmission of innovations, ensuring that variation is maintained whilst simultaneously spreading useful information between groups. In many ways, this concern directly mirrors the need to maintain genetic diversity by ensuring that inbreeding is avoided, a problem that is particularly acute in small populations. Large-scale mobility, and the links that it provides between distant groups, is an important means of alleviating this problem. In a broad sample of Amazonian societies, Walker (2014) demonstrated that rates of exogamy are in fact considerably higher in hunter-gatherer groups than among horticulturalists, suggesting that the mechanisms of inbreeding avoidance in hunter-gatherer society are highly developed. Incest taboos and exogamy rules are common features of hunter-gatherer culture (e.g. Wobst 1975; Turner and Maryanski 2005), and a particularly clear example is given in Headland's (1987) study of the Casiguran Agta of the Philippines. The exogamy rule among the Agta states that "one may not marry any person whom he already calls by any kinship term" (Headland 1987:267); it thus prevents marriages between existing affines, and ensures that any two family groups of Agta are linked by only a single matrimonial tie. More importantly, it ensures that each family is linked to a number of others through matrimony; a rule that is enforced in order to avoid incest thus has the additional benefit of creating a network topology that displays the 'partial connectivity' quality identified by Derex and Boyd (2016).

Two recent studies have provided evidence that expanded social networks of the kind found in contemporary hunter-gatherers may have considerable antiquity within human lineages. Sikora and colleagues (2017) analysed the genomes of four individuals considered to be members of a single human group from the Upper Palaeolithic site of Sunghir, Russia. None of the four were closely related, leading the authors to conclude that they belonged to a society whose cultural rules prevented significant endogamy. Levels of inbreeding were similar to those found among modern hunter-gatherers, prompting Sikora and colleagues (2017:662) to propose that, by around 34 ka, "complex family residence patterns, relatively high individual mobility, and multilevel social networks were already in place". Brooks and colleagues (2018) suggest that the formation of networks of exchange and procurement over extended areas may date back even further in time, to the roots of the Middle Stone Age. By around 300 ka at Olorgesailie, Kenya, hominin foragers were transporting obsidian from seven separate sources at between 25 km and 50 km from the site. Raw materials from these seven sources together constitute 78% of the obsidian sample, suggesting an established, extensive network rather than occasional forays. Brooks and colleagues (2018) stress the potential for such networks to provide responses to increasing climatic variation of the kind shown above to directly influence population densities.

From an archaeological perspective, the finding that just two climatic variables explain approximately 50% of the variance in hunter-gatherer population densities suggests that the reconstruction of demographic variables via climatic correlates is likely to be a beneficial enterprise. More importantly, the finding that mobility is adjusted so as to maintain contact between groups under varying population density implies a number of archaeologically testable corollaries. Regions in which palaeoclimatic data are of sufficient resolution to show high variability in precipitation and low variability in temperature should support dense human populations, particularly at temperate latitudes. Archaeological sites within these regions should demonstrate archaeological evidence of both high population densities *and* low levels of mobility. To give one example, site densities should be high, whilst lithic transfer distances should be low. Conversely, regions for which palaeoclimatic data demonstrate low variability in precipitation and high variability in temperature should manifest low archaeological site densities, with sites linked by high lithic transfer distances. Despite these differences in population density and mobility, encounter rates should be similar, implying that levels of potential assemblage sophistication or complexity should be essentially invariant to differences in climatic regimes.

This final point could be interpreted as contradicting the prediction made by Torrence (1983, 1989), that groups living at higher latitudes should develop more complex toolkits. Torrence's (1983, 1989) logic is that prey animals will be encountered less often at high latitudes due to their lower density, and therefore that greater investment in technology is merited to minimize the risk of failing to successfully harvest any animals that *are* encountered. This 'risk hypothesis', as it is often described, is a hypothesis about a *cause* of toolkit complexity. The 'encounter rate hypothesis', as outlined here and elsewhere (e.g. Henrich 2004; Powell et al. 2009; Grove 2016), is a hypothesis about a *constraint* on toolkit complexity. Complex toolkits should appear in ethnological or archaeological contexts only when both the constraint is obviated (through a sufficiently high number of encounters with other groups) and the cause is present (due to a demonstrable need for more complex technology). Though they are frequently treated as such, there is no clear rationale for regarding these two hypotheses as mutually exclusive; indeed, future studies would benefit from reconciling them by differentiating between the potential for producing complex artefacts and the actual requirement to do so.

6. Conclusions

The results presented above suggest that basic climatic variables account for a considerable amount of variation in hunter-gatherer population densities, and that the standard deviations of climatic variables are of greater consequence than their means. Path analyses show the greatest support for a model in which climatic variables influence mobility only indirectly, via their effects on population density. This finding is consistent with the hypothesis that hunter-gatherers adjust levels of mobility so as to maintain contact with neighbouring groups at varying population densities, a mechanism that ensures encounter rates remain at similar levels regardless of climatic variation. In line with previous research, this suggests that hunter-gatherers maintain an optimised level of connectivity between groups to facilitate the transmission of both genetic and cultural information. The results further entail a number of testable predictions concerning the relationships between climatic variables, population density, mobility, and the complexity of archaeological assemblages.

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Table 1. Partial Pearson product-moment correlations between population density (individuals per km^2) and distance moved per annum (km), controlling for climatic variables. 'Lower' and 'Upper' columns give the 95% confidence intervals of each correlation, based on 10,000 bootstrap samples. 'All' indicates that MAP, MAT, SDP, SDT, ET & NAGP are all controlled for.

	Correlation (r)				
Control	**Mean**	**Lower**	**Upper**	**df**	**p**
None	-0.830	-0.913	-0.747	173	<0.001
SDT	-0.715	-0.787	-0.632	172	<0.001
SDP	-0.760	-0.818	-0.692	172	<0.001
SDT & SDP	-0.711	-0.783	-0.626	171	<0.001
All	-0.709	-0.783	-0.620	167	<0.001

Table 2. Performance of the 12 models shown graphically in Figure 2. Delta values (or 'AICc change'), relative likelihoods (L_i) and relative probabilities (w_i) are calculated as per Burnham et al. (2011). K is the number of parameters calculated in fitting a model, and $LN(L)$ is the model's log-likelihood.

Set	Model	K	LN(L)	AIC	AICc	Δ_i	L_i	w_i
1	1	10	0.000	-	-	-	-	-
1	2	8	-1.359	18.718	19.585	0.000	1.000	0.385
1	3	9	-0.374	18.749	19.840	0.254	0.881	0.339
1	4	9	-1.359	20.717	21.808	2.222	0.329	0.127
1	5	9	-5.000	28.000	29.091	9.505	0.009	0.003
1	6	9	-17.431	52.861	53.952	34.366	3.447E-08	1.327E-08
2	7	10	0.000	-	-	-	-	-
2	8	8	-18.974	53.948	54.815	35.230	2.238E-08	8.619E-09
2	9	9	-4.015	26.030	27.121	7.535	0.023	0.009
2	10	9	-3.872	25.744	26.835	7.249	0.027	0.010
2	11	9	-1.360	20.719	21.810	2.224	0.329	0.127
2	12	9	-14.917	47.834	48.925	29.339	4.256E-07	1.639E-07

Table 3. Regression analyses of latitudinal subsets of the population density data on the standard deviation in annual precipitation (SDP). 'Lower' and 'Upper' columns give the 95% confidence intervals of the beta coefficient. Degrees of freedom are $n-2$ in all cases.

	Beta				
Subset	**Mean**	**Lower**	**Upper**	**n**	**p**
Tropical	0.290	0.027	0.526	61	0.023
Temperate	0.625	0.485	0.745	99	<.001
Polar	0.625	0.334	0.849	15	0.013
All	0.618	0.517	0.701	175	<.001

Figures

Figure 1. The three hypotheses shown as simple path diagrams. Arrows indicate hypothesized causation.

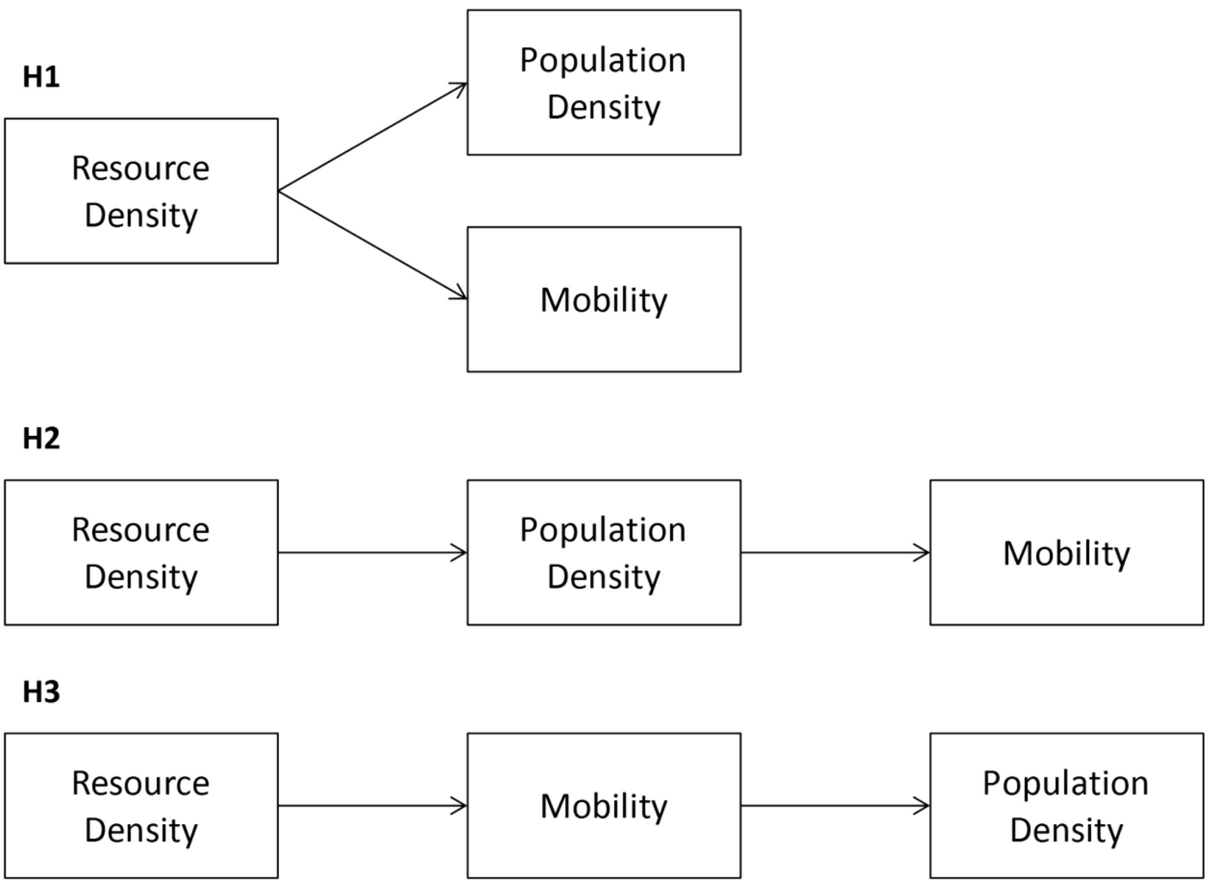

Figure 2. The 12 possible causal models relating the two exogenous variables (SDT and SDP) to the two endogenous variables (PD and M). Models 1-6 represent variations of Hypothesis 2, whereas models 7-12 represent variations of Hypothesis 3. Model 2, the strongest embodiment of Hypothesis 2, and Model 8, the strongest embodiment of Hypothesis 3, are highlighted with grey boxes. Arrows indicate causal paths for which path coefficients are calculated; curved double-headed arrows indicate correlations. SDT = standard deviation of temperature, SDP = standard deviation of precipitation, PD = population density, and M = mobility.

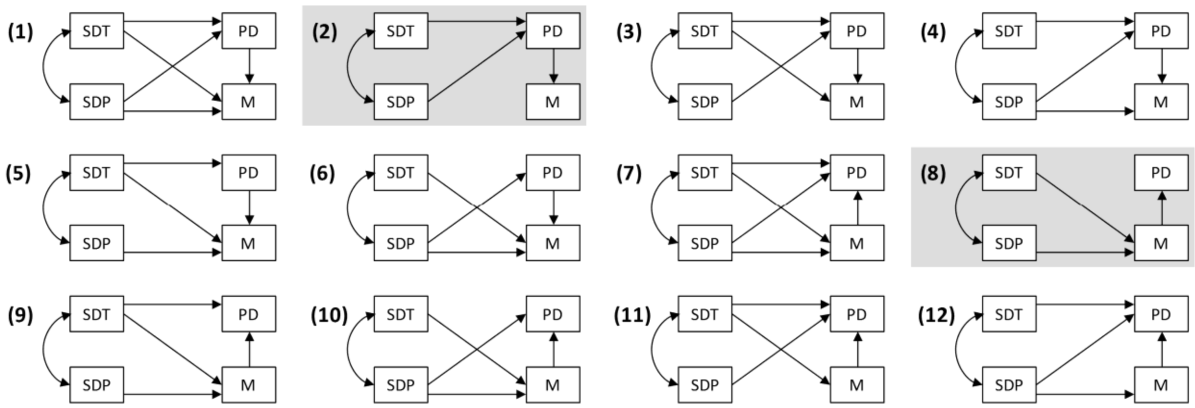

Figure 3. The four best performing models from Figure 2 (see also the statistical output in Table 2). Calculated correlations and path coefficients are included. Labels in boxes are coefficients of determination (R^2) for the endogenous variables. For consistency, the models are numbered as they are in Figure 2 and Table 2.