

Population size does not explain past changes in cultural complexity

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Demography is increasingly being invoked to account for features of the archaeological record, such as the technological conservatism of the Lower and Middle Pleistocene, the Middle to Upper Paleolithic transition, and cultural loss in Holocene Tasmania. Such explanations are commonly justified in relation to population dynamic models developed by Henrich [Henrich J (2004) *Am Antiq* 69: 197–214] and Powell et al. [Powell A, et al. (2009) *Science* 324(5932): 1298–1301], which appear to demonstrate that population size is the crucial determinant of cultural complexity. Here, we show that these models fail in two important respects. First, they only support a relationship between demography and culture in implausible conditions. Second, their predictions conflict with the available archaeological and ethnographic evidence. We conclude that new theoretical and empirical research is required to identify the factors that drove the changes in cultural complexity that are documented by the archaeological record.

cultural evolution | demography | Upper Paleolithic transition | Tasmania | cultural complexity

The idea that demography affects cultural evolution has a long history in archaeology. The relationship has been characterized in two main ways. The older of the two, which is rooted in the work of Malthus and Boserup, focuses on the interaction between demography and the environment, especially the effects of population pressure (1–9). Recently, this Malthusian–Boserupian approach has been eclipsed by what may be called the “population size approach” (10–13). This approach contends that population size alone affects cultural evolution. Its key claim is that increases in population size lead to increases in cultural complexity, whereas decreases in population size result in decreases in cultural complexity.

The population size approach has had a major impact on archaeology in the past few years. For example, several authors have suggested that the appearance of indicators of behavioral modernity results from an increase in population size rather than from a change in cognitive abilities (10, 14–16). Others have used population size decrease to explain the loss of certain technologies, such as the abandonment of the bow and arrow in Northern Europe during the Late Glacial period (17, 18). Still others have invoked population size to explain apparent instances of cultural stability. Hopkinson et al. (19), for example, suggest that small population size explains the conservatism of the Acheulean. Such has been the growth of interest in the population size approach that the author of a recent review describes it as having “changed how archaeologists think about socio-cultural change” (ref. 20, p. 11).

The putative link between population size and cultural complexity that is at the core of the population size approach was identified with formal models. This paper offers a combined theoretical and empirical assessment of the most influential of these models (11, 12). For a model to provide a credible explanation for a pattern in the archaeological record, it must meet two conditions: Its components (i.e., its assumptions, simplifications, definitions) must be defensible, and it must be consistent with empirical data from relevant cases. Accordingly, we begin by describing the models of Henrich (11) and Powell et al. (12). We then investigate whether their assumptions and definitions can be

justified. Subsequently, we evaluate the fit of the models to ethnographic and archaeological data. The results of our evaluation cast doubt not only on the use of the models of Henrich (11) and Powell et al. (12) to explain patterns in the archaeological record but also on the population size approach in general.

Models of Henrich and Powell et al.

In this section, we briefly outline the main elements of the models of Henrich (11) and Powell et al. (12). More technical descriptions of the models are provided in *Supporting Information* and *Figs. S1–S4*.

Henrich (11) developed his model to explain a key part of Jones' (21) interpretation of the archaeological record of Tasmania. Jones (21) argued that Tasmania experienced a slow cultural decline from the beginning of the Holocene until contact with Europeans. Henrich (11) avers that the decrease in the complexity of the Tasmanians' technology has to do with their isolation from mainland Australia following the rise of sea levels 12–10 kya. Henrich (11) contends that the latter event would have reduced the pool of interacting social learners, and that this reduction would have led to reduced cultural complexity.

At the heart of Henrich's model (11) is a process of cultural transmission we will call “Best.” In Best, each individual in the older generation has a skill level that expresses how proficient he or she is at performing a given skill. Individuals in the younger generation learn the skill from the most skilled member of the older generation, but this copying process is inaccurate. Consequently, members of the younger generation will, on average, be worse at the skill than members of the older generation. It is at this point that strength in numbers becomes important: Larger populations have a higher probability of giving rise to learners who achieve a level of skill as high as or even higher than the level of skill of the most skilled member of the older generation. Conversely,

Significance

Archaeologists have long tried to understand why cultural complexity often changed in prehistory. Recently, a series of highly influential formal models have suggested that demography is the key factor. According to these models, the size of a population determines its ability to invent and maintain cultural traits. In this paper, we demonstrate that the models in question are flawed in two important respects: They use questionable assumptions, and their predictions are not supported by the available archaeological and ethnographic evidence. As a consequence, little confidence can be invested in the idea that demography explains the changes in cultural complexity that have been identified by archaeologists. An alternative explanation is required.

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preferring Henrich's definition (11) over those definitions put forward by other researchers. Therefore, the results of Henrich's model (11) are dependent on an unjustified definition of cultural complexity, as well as on an unjustified assumption about the nature of cultural transmission.

One major problem with Complexity Regression is that it treats an individual's skill level as fixed, which is inconsistent with the large body of literature on skill acquisition that has been published over the past 30 y. The literature in question indicates that skill level is heavily influenced by practice time (40). Learners can thus improve their ability to perform a given skill by practicing it, which in turn implies that a population can counter the effects of the loss of gifted learners on skillfulness by investing more time in learning skills.

Complexity Regression is problematic in yet another respect. Consider a population that uses fishing nets and is able to catch 100 fish per day. The population is struck by an infectious disease and loses some members. As a consequence of this loss, their skill level decreases and they are now worse at catching fish (e.g., they can only catch 90 fish per day). How might they respond? One option is to switch to a simpler skill like hand-line fishing, which is what Henrich (11) assumes will happen. However, there are several other possibilities. One is that the population might do nothing because population pressure has relaxed to such an extent that its members can survive on the lower returns from net fishing, because the decreasing benefits of net fishing are offset by decreasing costs (e.g., catching fewer fish per day requiring a smaller fishing team), because switching costs do not outweigh the lower returns from net fishing, and/or because tradition demands it. Alternatively, the population might compensate for the lower returns by relying more on other resources, by storing more food, or by engaging in more trade with other populations (5, 41–43). In these cases, if the strategy prevents a further decline in population size, the population can continue fishing with nets rather than switching to a simpler skill. Generally, whereas the outcome of an analysis of costs and benefits can be expected to vary greatly from case to case, Complexity Regression assumes only one possible outcome.

In sum, then, Henrich's model (11) does not withstand theoretical scrutiny. There are problems with both of its key assumptions and with the definition of cultural complexity it relies on.

Powell et al.'s Model. Given that Powell et al. (12) use the same definition of cultural complexity as Henrich (11), and that we have already explained why that definition is problematic, we will focus on the two assumptions made by Powell et al. (12) when constructing their model: Payoff and Complexity Maximization. To reiterate, Payoff is the assumption that cultural transmission is a two-stage process in which learners first undergo vertical transmission and then have the opportunity to improve their skill level by selecting another cultural parent proportional to the parent's skill level, whereas Complexity Maximization is the assumption that when a population increases in size, its members will always opt to adopt more complex cultural traits.

Payoff suffers from the same problems as Best. The fact that Vaesen (23) has shown that a number of copying processes do not yield an association between population size and skillfulness means that the results of Powell et al.'s model (12) also are not independent of the transmission process they assume. Equally problematically, there is no empirical support for Payoff. The first part of Payoff is in line with the available ethnographic evidence, which, as we explained earlier, suggests that vertical transmission is important early on (24–28). However, Payoff's second part cannot be justified on empirical grounds. One study has reported evidence for payoff biases in the transmission of skills related to fishing, growing yams, and using medical plants among indigenous Fijians (44), but the aforementioned studies by MacDonald (34) and Jordan (35) indicate that other societies use other forms of oblique transmission. Consequently, Payoff cannot be assumed to be universal.

Complexity Maximization has shortcomings too. One of these shortcomings is the fact that a number of the items that appear

during the Upper Paleolithic are tools or tool parts. The issue here is that increasing the complexity of a tool can, beyond a certain level, negatively affect its performance. This phenomenon is well known in industry (45), but it also applies to the tools produced by small-scale societies. Consider the type of harpoon used by contact-era Inuit to hunt seals in open water. Such harpoons typically had floats attached to them to make it more difficult for the seal to dive. It is obvious that there is a point at which adding more floats would make such a harpoon more difficult to use. The harpoon would be more complex but less effective. Given that complexity can negatively affect the performance of tools, it is unlikely that a population will always opt to adopt more complex tools.

It is difficult to justify Complexity Maximization in relation to the other elements of the Upper Paleolithic as well. There is no evidence that contemporary people maximize the complexity of their symbolic behavior, ritual artifacts, musical instruments, etc. Recent history certainly offers examples of change leading to increased complexity, but it also provides plenty of instances of change that reduced complexity. Given this fact, there is no reason to assume that ancient populations were "cultural complexity maximizers" in relation to their symbolic behavior, ritual artifacts, musical instruments, etc.

Complexity Maximization might be thought to fit with Boserup's suggestion that increased population density may induce subsistence stress and that such stress prompts innovation. However, both theoretical and empirical work has shown that increased population density cannot be assumed to lead to innovation (5, 46–48), let alone innovation of a complexity-increasing kind. We have already outlined one reason for the failure to establish a robust link between increased population density and innovation: Innovation is only one of several options available to people to relieve subsistence stress. The alternatives to innovation include migration, exchange, and higher reliance on resources already in the subsistence base (5, 41–43). A further problem with justifying Complexity Maximization by means of Boserup's hypothesis is that it is not clear what Powell et al.'s model (12) adds. If population growth forces populations to innovate, there is no need to invoke cultural transmission processes to explain increases in cultural complexity.

So, Powell et al.'s model (12) does not withstand theoretical scrutiny either. Its key assumptions are problematic, and so is the definition of cultural complexity it relies on.

Empirical Assessment of the Predictions of the Models of Henrich and Powell et al.

In the previous section, we showed that there are theoretical reasons to be skeptical about the use of the models of Henrich (11) and Powell et al. (12) to interpret the archaeological record. In this section, we demonstrate that the predictions of the models are inconsistent with the available empirical evidence. We begin by showing that the models do not do a good job of explaining the archaeological patterns they were developed to explain. Subsequently, we review studies in which ethnographic and archaeological data have been used to test one of the key predictions of the models of Henrich (11) and Powell et al. (11) and the other models that underpin the population size approach, namely, that there should be a positive correlation between population size and cultural complexity. We show that the majority of these studies do not support this prediction.

Henrich's Model and the Cultural History of Tasmania. As noted earlier, Henrich (11) developed his model to explain a key part of Jones' (21) interpretation of the archaeological record of Tasmania, which is that the Tasmanians experienced a loss of cultural complexity during the Holocene. Drawing on the results of his model, Henrich (11) argued that Tasmania's isolation from the mainland led to a reduction of the pool of social learners, and that this reduction, in turn, resulted in the Tasmanians being unable to sustain the skills necessary to produce a complex toolkit. This hypothesis has been widely accepted as accurate, so much so that the idea that decreases in population size have a negative impact on cultural complexity is now often referred to as

“the Tasmanian effect” (e.g., ref. 49, p. 272). However, it is not, in fact, supported by the available ethnographic and archaeological data.

For Henrich’s hypothesis (11) to be correct, the skills abandoned by the Tasmanians must have been more complex than those skills they practiced afterward. Bone points are the only type of artifact that the Tasmanians are known to have stopped producing (22). Bone points have been recovered at several sites that date to the Late Pleistocene or Early Holocene (50), but bone points were not among the tools used by Tasmanians at the time of contact with Europeans. Hence, there is no doubt that sometime in the past few thousand years, probably *ca.* 4 kya, the Tasmanians stopped making bone points. Consequently, the key question is “Were any of the skills that the Tasmanians practiced after they stopped producing bone points more complex than bone point manufacture?”

The bone points produced by Late Pleistocene/Early Holocene Tasmanians would not have been difficult to make. Their production involved a few simple actions, including fracturing long bones and rubbing the broken ends on an abrasive surface (50). As such, they would have been easier to produce than some of the artifacts that the Tasmanians made after 4 kya. Among these more-difficult-to-manufacture items are woven baskets, seaworthy bark canoes, waterproof shelters, and certain stone tools (51). The skills involved in the production of bone points would also have been less complex than the skills involved in a number of the economic and ritual activities that Tasmanians engaged in after 4 kya. These activities include the mining, alteration, and distribution of ochre (52); the creation of necklaces from human bones and pierced shell beads (53); body scarification (54); and funerary rituals (53). Thus, a number of the skills that the Tasmanians practiced after they stopped producing bone points were more complex than bone point manufacture.

It is also worth noting that much knowledge transfer in Tasmanian Aboriginal society took place through song, dance, and stories. Robinson’s (55) diaries make numerous references to the Tasmanians’ cosmology and creation myths. Similarly, Clark (56) describes a rich repertoire of song and dance that persisted into the 1830s. There can be no doubt that many of these songs, dances, and stories would have been more difficult to learn, and therefore more complex according to Henrich’s definition of cultural complexity (11), than bone point production. Thus, Henrich’s hypothesis (11) fails on this count too.

Given that many of the activities that the Tasmanians were recorded doing at the time of contact with Europeans were more complex than manufacturing bone points, there is no reason to believe that the Tasmanians experienced a loss of cultural complexity as a result of the negative impact on skillfulness of their isolation from groups on the Australian mainland. (For a more detailed treatment of the Tasmanian case, we refer the reader to [Supporting Information](#).)

Powell et al.’s Model and the Upper Paleolithic Transition. To reiterate, Powell et al.’s goal (12) was to explain the interregional variation in the timing of the Upper Paleolithic transition. Having developed their model, they carried out a two-step empirical analysis. First, they used molecular data to estimate when different regions of the world would have reached the same population density as Europe at the start of the Upper Paleolithic. They then compared the population estimates with the timing of the Upper Paleolithic transition in the other regions of the world. Their rationale was that if the start of the Upper Paleolithic in Europe represents a substantial increase in cultural complexity as most archaeologists believe, and if cultural complexity is dependent on population size, then the Upper Paleolithic transition should occur in other regions when they have reached the same population density as Europe at the start of the Upper Paleolithic.

However, Powell et al.’s analysis (12) is inadequate as a test of their model. According to the model, populations should accumulate complexity whenever their size increases and not just when they reach a critical size, let alone a critical density. A better procedure is to examine whether the Upper Paleolithic transition

in various regions of the world took place around the time population size started to increase. Such a reanalysis, in which one assumes that Powell et al.’s (12) population estimates are reliable, that their dates for the Upper Paleolithic transition in various parts of the world are accurate, and that it is unproblematic to use a package of traits to characterize modernity [but see the severe criticism by other researchers (57–62)], yields nontrivial violations of the predicted association in Sub-Saharan Africa, Northern and Central Asia, Southern Asia, and Australia (a more detailed treatment is provided in [Fig. S5](#)).

Some of these incongruities also appear in Powell et al.’s two-step analysis (12). The authors suggest these incongruities are due to the low resolution of their single-locus population estimates, which were taken from Atkinson et al. (63). However, a recent multilocus study (64) does not settle the issue in favor of Powell et al.’s analysis (12). These new estimates give rise to a different set of mismatches. Most notably, they suggest that the Upper Paleolithic transition took place in Africa at a time when populations were shrinking (90–75 kya) and that the Upper Paleolithic appeared in Europe at a historic population low ([Fig. S6](#)). The fact that this new set of population size estimates challenges the lynchpin of Powell et al.’s analysis (12), the coincidence between the Upper Paleolithic transition and a relatively high population density in Europe, clearly calls into question the reliability of Powell et al.’s results (12).

Significantly, it is not just a question of which set of genetic data-derived population size estimates to believe. Recent studies by Klein and colleagues (e.g., 65) address whether larger human population sizes might explain the sporadic occurrence of more complex behavior in the South African Middle Stone Age and whether long-term population increase over the course of the Middle Stone Age could explain the emergence of the Later Stone Age at roughly 50 kya. For both cases, they failed to find any association.

Thus, Powell et al.’s model (12) also fails to explain convincingly the archaeological pattern it was developed to explain. There is no clear link between the Upper Paleolithic transition and demography.

Tests of the Predicted Correlation Between Population Size and Cultural Complexity. Population size is not the only factor that has been argued to affect cultural complexity. Environmental risk (66, 67) and mobility (68, 69) have also been suggested to influence it. Therefore, an adequate test of the prediction that there should be a positive correlation between population size and cultural complexity is one in which population size is evaluated alongside at least one other putative driver. So far, eight studies meet this criterion (67, 69–75).

The results of two of the studies are consistent with the prediction. Kline and Boyd (71) found an association between toolkit complexity and population size in a sample of 10 fisher-farmer groups from Oceania, whereas Collard et al. (72) found the same thing in a sample of 45 small-scale food-producing groups from several continents. In contrast, the results of the other six studies are not consistent with the prediction (67, 69–75). None of them identified a relationship between population size and cultural complexity when other potential driver variables were taken into account. Four of them found that cultural complexity was only correlated with proxies for environmental risk (67, 70, 73, 75). Another found that cultural complexity was correlated with both environmental risk and mobility. The remaining study concluded that a change in ecological and demographic conditions is more likely to have caused the relevant change in cultural complexity than is population size (74). Thus, the prediction has not fared well in the studies in which it has been adequately tested. The most that can be said about the relationship between population size and cultural complexity is that it is an inconsistent one.

In fact, even this conclusion may overstate the support for the population size approach. Larger societies tend to have a more complex social organization (76, 77), which often includes specialization of tasks (67, 73, 78). Task specialization has the potential to affect the complexity of a society’s cultural repertoire because individuals need not master all skills and can focus on learning a small number of more complex tasks (e.g., blacksmithing, carpentry). Task specialization and the mechanism of

the formal models of Henrich (11) and Powell et al. (12) work differently. In the former case, complexity is regulated by increased practice time and by the number of types of specialists; in the latter, complexity is regulated by a population's size-dependent ability to bring forth gifted individuals. Critically, for present purposes, the introduction of task specialization into a population is likely to increase complexity even though it implies a reduction of the effective population size for certain skills (i.e., a reduction from the entire pool of possible cultural parents to a pool merely consisting of specialist parents). Consequently, unless task specialization is controlled for, finding a correlation between population size and cultural complexity does not support the hypothesis that population size drives cultural complexity via the former's impact on transmission accuracy. Neither Kline and Boyd (71) nor Collard et al. (72) included task specialization as a control variable. Thus, their results do not necessarily support the population size approach.

Concluding Remarks

The recent rise in popularity of the population size approach within archaeology has, to a large extent, been based on the formal models presented by Henrich (11) and Powell et al. (12) and their apparent ability to explain the decline in cultural complexity in Tasmania in the Early Holocene and the regional variation in the timing of the Upper Paleolithic transition, respectively. In this paper, we have shown that these models have serious shortcomings from a theoretical perspective. Their results are dependent on their assumptions, and their assumptions cannot be justified empirically. In addition, there is no reason to prefer the definition of cultural complexity they use over any of the other definitions that have been put forward. We have also shown that the models fit the available empirical data poorly. The ethnographic and archaeological data from Tasmania are not consistent with Henrich's model (11), and the available evidence pertaining to the Upper Paleolithic transition is not in line with Powell et al.'s model (12). Thus, the models do not fit the archaeological patterns they were developed to explain. Furthermore, most adequate tests of the most basic prediction of the models—that there should be a positive correlation between population size and cultural complexity—have returned results that are inconsistent with the prediction.

We contend that these findings cast serious doubt on the population size approach within archaeology. The fact that the two most influential models have serious shortcomings is clearly

a cause for concern. However, the problem is wider than that. The prediction that there should be a positive correlation between population size and cultural complexity is not specific to the models of Henrich (11) and Powell et al. (12). It is a prediction of all of the models that have been developed by proponents of the population size approach (10, 13). Thus, the failure of the majority of tests of the prediction to support it casts doubt not just on the models of Henrich (11) and Powell et al. (12), but on the population size approach in general.

What then, if not population size, drives the increases and decreases in cultural complexity that are documented by the archaeological record? We have already briefly mentioned the three most obvious possibilities. One is changes in population pressure as per the Malthusian–Boserupian approach. Another is changes in the degree of task specialization in the context of changes in the degree of social complexity. The third possibility is changes in environmental risk. None of these potential explanatory factors is free of problems. That population size does not correlate with cultural complexity in the majority of studies discussed in the previous section is difficult to square with the Malthusian–Boserupian idea that population pressure spurs innovation, or at least it is to the extent that population size is a good proxy for population pressure, and that innovation involves increases in complexity. It is also difficult to square with the notion that changes in task specialization drive changes in cultural complexity, because the latter predicts a correlation between population size and cultural complexity. One problem with the hypothesis that changes in cultural complexity are driven by changes in the level of environmental risk is that although a number of studies have supported its predictions (67, 70, 73, 75), some have failed to do so (72, 79). The implication of this is that environmental risk is probably not a universal driver of changes in cultural complexity. Further theoretical and empirical research is required to identify the factor or, as we think more likely, the set of factors that drove the changes in cultural complexity that are documented by the archaeological record.

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Supporting Information

Vaesen et al. 10.1073/pnas.1520288113

1. Technical Explanation of the Models of Henrich and Powell et al.

Henrich (11) invites us to imagine a process of cultural transmission, in which parent generations pass on their skills to generations of cultural offspring (a graphical representation is provided in Fig. S1). We start with a parent population of N individuals, where each individual has a skill level, z , concerning a skill involving at least some transmittable component (e.g., producing a bone point). The offspring generation, also consisting of N individuals, tries to imitate the most skilled parent of the first generation (i.e., the parent with the highest z -value). However, for complex skills in particular, this process is inaccurate. As a result, after learning, the offspring will usually end up with a lower skill level (z -value) than the parent.

Assume, for instance, that, on average, this copying error amounts to \bar{c} . Crucially, not all cultural learners will exhibit the same error (i.e., some learners are better at imitation than others). To determine the error, c , of a particular learner, one draws a random number from a continuous probability distribution (e.g., Gumbel distribution, logistic distribution, normal distribution) centered around \bar{c} . It is at this point that population size becomes an issue: Larger populations are more likely to contain a cultural learner whose error is drawn at the extreme right of the distribution, so that this individual's skill level (z -value) will be at least as high as (or even higher than) the skill level of the parent she is trying to imitate. Conversely, smaller populations are at risk for lacking such gifted learners. Even their best individual would perform worse than the parent she learns from; over the generations, the average skill level should be expected to decrease (Fig. S1).

Importantly, when talking about cultural complexity (or changes therein), we refer to \bar{c} (or changes therein), not to \bar{z} (or changes therein; more on this below). The intuition behind this idea is as follows: A complex skill is a skill that is difficult to learn, and hence, one that should be expected to be associated with high transmission inaccuracy.

Assuming this kind of transmission process, Henrich (11) was able to derive a set of equations that relate changes in average population skillfulness (not complexity), $\Delta\bar{z}$, to both population size N and cultural complexity (expressed as \bar{c}). So, Henrich's equations (11) tell us how much, for a given population size and a given level of cultural complexity, the population's average skill level can be expected to change per time step. Positive values for $\Delta\bar{z}$, for example, would simply mean that the N -sized population will, per time step, become better at, say, producing a bone point, a skill that is complex to the extent \bar{c} .

Now, by setting $\Delta\bar{z}=0$ in these equations, one can derive, for a given level of cultural complexity, what Henrich (11) calls the critical population size, N^* . Assuming copying error to follow a Gumbel distribution, N^* is given by

$$N^* = e^{(\bar{c}-\varepsilon)}, \quad [\text{S1}]$$

where e is Euler's number and ε is the Euler–Gamma constant ≈ 0.577 . [Henrich (11) gives a similar derivation for logistic distributions; Vaesen (23) does so for normal distributions. For these two derivations, \bar{c} corresponds to transmission inaccuracy *simpliciter*; for Gumbel distributions, as in the equation in the main text, \bar{c} , in fact, refers to transmission inaccuracy divided by the spread of the Gumbel. However, nothing in what we say depends on this ambiguity.] N^* is the minimum

population size needed to sustain a skill of complexity \bar{c} (i.e., to pass the skill on without loss of skill).

Figs. S2–S4 plot Eq. S1. The curve gives combinations of N and \bar{c} for which $\Delta\bar{z}=0$. As such, it demarcates two regimes: a regime of increasing ($\Delta\bar{z}>0$; the region below the curve) and a regime of decreasing ($\Delta\bar{z}<0$; the region above the curve) skill levels.

In and of itself, Eq. S1 does not provide us with a dependence of complexity (\bar{c}) on population size (N). What we can, at most, infer from Eq. S1 and Figs. S2–S4 is that larger populations are more likely to experience increases in skill levels (not in complexity); conversely, smaller populations are at a higher risk of having to face reductions in skillfulness. So, intrinsically, there is nothing inconsistent in accepting Eq. S1, while, at the same time, believing that \bar{c} and N (not N^*) are uncorrelated.

To account for a reduction in complexity, one needs to make an additional assumption (22), which we will call “Complexity Regression.” Complexity Regression posits that populations of cultural learners experiencing loss of skill will return to or cross the equilibrium state (i.e., $\Delta\bar{z}\geq 0$) by (re)adopting simpler technologies (downward arrow in Fig. S2). Henrich (11) invokes this assumption to account for the Tasmania case: A drop in the Tasmanian population (leftward arrow in Fig. S2) would have been followed by a movement along the vertical “regressive” arrow in Fig. S2.

Henrich's model (11) was later adapted by Powell et al. (12) to account for the substantial increase in technological and cultural complexity during the Upper Paleolithic transition. The core of their model is identical to Henrich's model (11). It assumes a process in which cultural parents transmit their skills to subsequent generations of cultural offspring; parents have a skill level z , which offspring typically are unable to replicate; on average, offspring individuals end up with a skill level z that is lower, to an extent \bar{c} , than the skill level of their parents; and \bar{c} is taken to be a measure of skill complexity. In line with the above, positive increases in \bar{c} are thus what demography is supposed to explain.

To tailor the model to the Late Pleistocene, Powell et al. (12) implement three modifications. First, rather than assuming one large population, Powell et al. (12) assume a metapopulation consisting of various subpopulations, which are connected by migratory activity and which might pass on skills to one another. Second, naive individuals do not just learn from selected cultural parents (oblique transmission) but also from their biological parents (VERTICAL-biased transmission). More specifically, all individuals undergo, consecutively, vertical and oblique transmission. Third, as regards oblique transmission, offspring select parents proportional to their skill level (Payoff-biased transmission), rather than learning from the single best individual in the parent generation.

Powell et al. (12) find that migratory activity has the same effect on skill accumulation as increasing the size of a single isolated population and, moreover, that the results for their extended transmission process (including VERTICAL and Payoff) are equivalent to Henrich's analytical result (11). Hence, for the sake of clarity, we shall simply use Fig. S3 to illustrate Powell et al.'s explanation (12). Referring to mtDNA analyses performed by Atkinson et al. (63), Powell et al. (12) argue that during the Late Pleistocene, human populations increased in all parts of the world, geographic variation in the precise timing notwithstanding. These events correspond to the arrow labeled “demographic change” in Fig. S3. For these populations to reach a state of increased cultural complexity, they must still undergo a movement upward. So, by a process other than the transmission process assumed in the formal model, populations should achieve more complex culture

(i.e., invent and settle on skills more intricate than previous ones). This process is what is called Complexity Maximization in the main text.

Complexity Maximization can be construed in two ways. On a first, weakly demographic reading, the assumption may stipulate that after demographic change, population size will no longer act as a constraint. Innovation itself, however, would be dependent on factors other than population size; that is, innovation would be prompted by any of the other drivers of complexity advanced in the literature, both on theoretical and empirical grounds, such as population pressure, risk of resource failure, mobility, or migration to new habitats (main text), or by more endogenous factors, such as cognitive innovations or social (re)organization (6, 80–82). Because these more traditional forces would do much (if not most) of the explanatory work, any explanation along these lines will qualify as demographic only to a minimal extent.

Powell et al. (12) do not refer to any of these nondemographic factors, either in the presentation of their model or in the interpretation of their results. Cognitive change is even explicitly put aside, because they write “demographic factors can thus explain [...] the first appearance of modern behavior” (ref. 12, p. 1298). Such a full-fledged demographic explanation would need to rely on a demographic reading of Complexity Maximization. Moreover, in particular, the assumption must now be that populations, in virtue of their increased size, are conducive to the invention of more complex skills, as well as generally attracted to the adoption of these more complex skills.

Importantly, the shift to higher levels of complexity can be considered a general pattern of populations in a regime of skillfulness gain ($\Delta\bar{z} \geq 0$), only if one accepts that, generally, these populations are complexity maximizers, in either of the two senses just defined. It implies, on the first reading, that they are generally subject to said nondemographic forces, and generally produce more complex culture in response, and, on the second reading, that increased size generally increases complexity.

Powell et al. (12) might avoid reliance on Complexity Maximization altogether if they were to treat \bar{z} (or changes therein), rather than \bar{c} , as the dependent variable, and thus as a measure of complexity. However, such a reading would sit uncomfortably with the way in which they consistently refer to transmission inaccuracy (here denoted by \bar{c}) as an expression of skill complexity, as well as with Henrich’s original formulation that complex skills are related to “tools that are hard to learn to make, and easy to screw up” (ref. 83, p. 776). Further, Powell et al.’s model (12) would become counterintuitive. On this construal, demographic change would have allowed human populations to move along the horizontal line in Fig. S3, from an equilibrium state to a regime of skill accumulation ($\Delta\bar{z} \geq 0$). However, the only two certain conditions under which populations will indeed become more skillful ($\Delta\bar{z} \geq 0$) is when \bar{c} decreases or is kept fixed. If both N and \bar{c} increase, populations may just remain in equilibrium ($\bar{z} = 0$) and, because z is now being assumed to indicate complexity, not reach a higher level of complexity. Consider now an example that Powell et al. (12) give, namely, the advent of functional and ritual bone, antler, and ivory artifacts. For these artifacts to be explained in terms of demography, we need to suppose several things, namely, that the processing and transformation of bone, antler, and ivory into functional and ritual artifacts is the very same skill as the processing and transformation of materials default in earlier periods (e.g., stone, wood); that the production of functional and ritual bone, antler, and ivory artifacts arose as a result of errors made during imitation of stone/wooden tool-making skills; and that, completely opposite to the idea that increases in N “will out-weigh the degrading effect of low-fidelity transmission” (ref. 12, p. 1300), the two modes of production are either equally hard to master or the newer is easier to learn than the older (i.e., $\bar{c}_{\text{stone/wooden tools}} \geq \bar{c}_{\text{bone/antler/ivory artifacts}}$). Significantly, even if one is prepared to accept these puzzling premises, support

for the demography hypothesis is weak in light of the fact that it fails to hold under conditions more conservative and plausible than Payoff (main text).

Another assumption, which we will call “Complexity Optimization,” is required if one wishes to infer from the formal models that, irrespective of demographic change, population size directly determines the level of cultural complexity achieved. For there to be a positive relationship between population size and cultural complexity, a given population level of complexity should be higher than the level of complexity of a population of smaller size but lower than the level of complexity of a larger population. So, if the relationship in question is not to collapse, a population in a regime of skill accumulation must increase its level of cultural complexity relative to the level of cultural complexity of a smaller population, but not so much that it exceeds the level of cultural complexity of a bigger one. Put differently, the population must engage in Complexity Maximization until it starts experiencing decreasing skill levels. Conversely, a population in a regime of skill loss must engage in Complexity Regression, but only to the point where skill levels stop going down. Social learners thus must be assumed to optimize complexity, achieving a level of complexity that is neither too high nor too low (Fig. S4).

2. More on the Tasmanian Archaeological Record

Henrich (11) focuses on the isolation of Tasmania from the Australian mainland following the postglacial rise in sea levels (between 12 and 10 kya). He argues that this event would have reduced the effective population size (i.e., the pool of interacting social learners) considerably, and that this reduction would have caused the cultural decline that Jones (21) argued was observable in the archaeological record of Tasmania. Here, we show that the empirical evidence does not support the claim that there was a loss of cultural complexity in Tasmania after 12–10 kya. We then highlight uncertainties concerning the reduction of the size of the pool of interacting social learners. In short, we demonstrate that neither part of the story that Henrich (11) developed his hypothesis to explain withstands scrutiny.

2.1. Technological Decline. Jones (21) first developed the idea that the Tasmanian Aborigines experienced a slow cultural decline during the Holocene. Excavating shell middens in the northwest islands in the 1960s, he noticed an absence of fish bones after about 3.5 kya, as well as a disappearance of bone points about the same time, an observation that was subsequently repeated at other sites in Tasmania. Jones (21) argued that after millennia of isolation, the Tasmanians had forgotten how to catch fish and lost the use of many of their tools and even the ability to make fire. Henrich (11) simply built on Jones’ “maladaptive” reading of the Tasmanian record (21), framing it as a “pattern of change from a more complex tool kit to a less complex one” [although Henrich (11) was more willing to ascribe to the Tasmanians the ability to produce fire]. Aspects of Henrich’s argument (11) have been criticized before (22, 50). Based on the work of Hiscock (50), Andersson and Read (22) have recently pointed out that the only documented loss of a tool is the loss of bone points. These tools, these researchers explain, are simpler than some of the stone tools that Tasmanians continued to make after 4 kya, which means that they (the bone points) do not support Henrich’s claim that the Tasmanians experienced a loss of cultural complexity due to a reduction in the pool of cultural learners. Andersson and Read (22) argue that it is more likely that environmental factors explain why Tasmanians stopped making bone points:

With but one exception, where the points may have been used for making nets, bone points only occur during extremely cold periods [...] when “simple clothing” (84) was made in response to environmental conditions. After the climate substantially ameliorated at the end of the last Ice Age, the need for clothing diminished (85). They

continued, moreover, to make and wear simple skin cloaks during the colder parts of the year (84).

With regard to fish consumption, some workers (86) have pointed to historical records suggesting that some Tasmanian groups continued to eat fish after 3 kya, whereas others have explained the nonconsumption of fish (as opposed to the massive collection of shellfish) as due to the fact that fish were needed for neither protein nor as a source of carbohydrates. Under such conditions, these researchers contend, the investment required to obtain fish may have been maladaptive (22). Thus, even if it were the case that the Tasmanians abandoned fishing, there is an alternative explanation for them doing so.

The problems with Henrich's argument (11) do not stop there. A review of the Tasmanian ethnographic and archaeological records reveals several other activities that the Tasmanians engaged in after 4 kya that are more complex than the production of bone points. For example, the archaeological record and reports by early European observers indicate that the Tasmanians practiced complex funerary rituals, created necklaces from modified human skeletal remains (mandibles and femur), and manufactured beads by piercing shells (ref. 53, p. 364). There is also good evidence for the mining, gender-specific preparation, and distribution of ochre (51, 52). In addition, Plomley (54) has studied the prevalence and geographic distribution of body scarification (cicatrices) and has shown not only that the designs were complex but also that they varied by region. Most of these activities involved behaviors that are more difficult to learn than those activities involved in the production of bone points. By implication, it is problematic to argue that bone points were lost because the population was too small to retain the skills necessary to produce them. Obviously, if the population was big enough to sustain skills that are more complex than those skills involved in the production of bone points, it must have been big enough to sustain the skills involved in the production of bone points.

It is also worth noting that Henrich (11) focuses on material culture, whereas the complexity of cultures is often reflected in the existence of abstract thought and ideas (e.g., related to resource information). Ethnographically, we know that much knowledge transfer in Tasmanian Aboriginal society took place in the realms of song, dance, and mythology. There are numerous references to cosmology and creation myths in Robinson's diaries (55), whereas Clark (56) describes the rich fabric of song and dance that pervaded their society well into the 1830s, even after the catastrophic impact of European invasion 25 y earlier. Again, it is clear that many of the songs, dances, and myths in question were more difficult to learn than the activities involved in the production of bone tools. So, the Tasmanians' intangible culture also undermines Henrich's hypothesis (11).

Lastly, Henrich's argument (11) is difficult to square with the longer term history of Australia. Australia was colonized by small groups who crossed the open sea between Sunda and Sahul by boat, and population size did not increase appreciably until the Holocene (14, 87). As Cosgrove et al. (88) have pointed out, this low level of population did not restrict the development of seafaring by 50 kya (89), the development of deliberate burial (90), raw material movement over 300 km (91), montane plant exploration by 45 kya (92), or development of hafted axes by 44 kya (93, 94). It also did not prevent the development of grinding technology and symbolic expression by 35 kya (95–98), early deep sea fishing (94) and animal translocation by 20 kya (99–101), or the development of backed artifacts by 15 kya (102) (table 14.1 of ref. 89).

Summarizing, the available archaeological and ethnographic data do not, contrary to what Henrich suggests (11), document a pattern of change from a more complex tool kit to a less complex one.

2.2. Population Size Reduction. Much of the population part of Henrich's argument (11) consists of assumptions based on Jones' initial calculations (21), using the numbers of tribes and bands as observed by G. A. Robinson. Robinson was the Conciliator of the Aborigines, and he made several journeys across Tasmania in the 1830s with Aboriginal people, a few decades after Europeans arrived (55). However, Robinson's numbers say nothing about pre-European demography, and we have, as yet, no robust way of calculating population size from the archaeological record. The most we can do is estimate relative changes in population size, and even that process is controversial, as is well illustrated by the recent debate between Mellars and French (103) and Dogandžić and McPherron (104).

Population sizes are judged by what they are compared with. The Tasmanian Late Pleistocene archaeological record does not show a clear plummeting line, but fluctuating numbers of sites, artifact/faunal densities, discard rates (105, 106), and pulses of radiocarbon dates (107). There are peaks and troughs, at regional levels, that possibly indicate more intensive occupation followed by a decrease or disappearance of populations, respectively. The regional pulse for southwest Tasmania is clear, but it is impossible to make statements about population size estimates for the whole of Tasmania at this time.

Archaeological evidence from sites with occupations <3.5 kya, such as Warragarra Shelter, Parmerpar Meethaner, Billop Rockshelter, Kangaroo Apple Shelter, and Ouse River Site number 7, all show an increase in occupation intensity, tied to greater economic opportunity and increasing use of landscapes and seascapes (105–109). Deepwater marine shells and freshwater mussels have been found in archaeological sites in the central Tasmanian uplands dated to 1.38 ± 0.06 kya. The transport of *Neotrigonia margaritacea* (brooch shell) up to 80 km from the coast and its use are not mentioned in the ethnographic records (ref. 105, pp. 82–84) and underline the incompleteness of early European observations about Tasmanian Aboriginal culture. Vanderwal (110) suggested that the increasing use of Maatsuyker Island in southern Tasmania and the development of watercraft were Late Holocene initiatives. Williams et al. (111) used a comprehensive dataset of continental-wide archaeological radiocarbon data and applied geospatial techniques and optimal foraging theory to explore mobility patterns of human movement and settlement across Australia throughout the Holocene. Their Australia-wide modeling suggests an increase in populations during the onset of the Holocene climatic optimum (9–6 kya), also for Tasmania, in contrast to the decrease after the Early to Mid-Holocene inferred by Henrich (11).

Furthermore, Henrich (11) implicitly assumes that before the sea level rise of the Holocene, the foragers inhabiting what is now Tasmania formed a pool of interacting social learners with groups from what is now Bass Strait and mainland Australia. However, there is nothing, archaeologically, to suggest any social connections between the mainland and Tasmania. No exotic Tasmanian artifact raw materials, such as Darwin glass, brecciated chert, or blue chert of Late Pleistocene age, have ever been found in Victorian mainland sites dated to the same period (51; ref. 88, p.182; 112).

The same applies to the few sites on islands in what is now Bass Strait. Cave Bay cave on Hunter Island was first occupied circa 23 kya, circa 35 km from the nearest coast, whereas Mannalargenna Cave on Prime Seal Island was about 70 km from the nearest coast when first occupied circa 23 kya and Beeton Rockshelter on Badger Island in Bass Strait was also initially occupied circa 23 kya (113). These sites would have been part of the Bass Plain during the Last Glacial maximum. They have small amounts of material compared with southwest Tasmania and contain no indications, such as exotic raw materials, to suggest movement of populations. In fact, at Mannalargenna Cave, 98% of the tools are made out of local quartz with a couple of shell tools, whereas at Beeton Rockshelter, 96% of the artifacts are quartz. In southwest Tasmania, there is archaeological

— Upper Paleolithic transition (estimated by Powell et al)

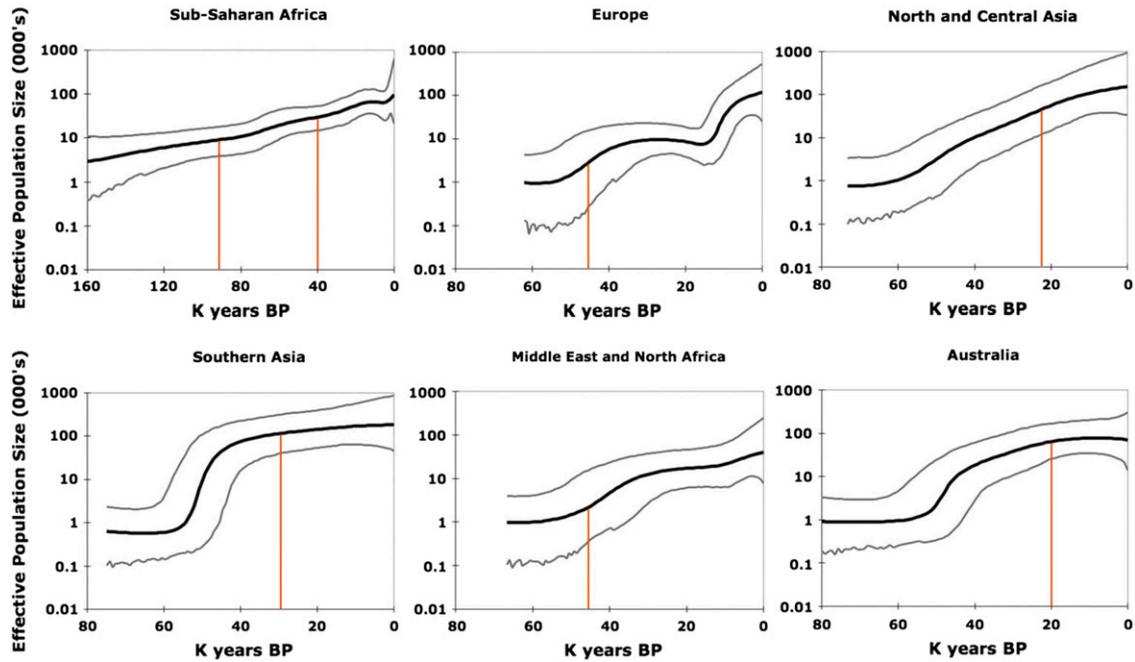


Fig. S5. Estimated effective population sizes for *Homo sapiens* [borrowed by Powell et al. (12) from Atkinson et al. (63)]. The orange lines indicate estimated dates for the Upper Paleolithic transition [estimates were taken from Powell et al. (12)]. According to the model of Powell et al. (12), populations should accumulate complexity whenever their size increases. This prediction is violated in the following ways. Concerning Sub-Saharan Africa, populations grow steadily from 160 kya onward, yet the transition to full modern human behavior appears only around 90–75 kya, and the package of modern human behavior disappears, despite population growth, between 75 and 40 kya. Population growth in Northern and Central Asia starts ~55 kya, whereas the onset of the Upper Paleolithic transition is around ~43 kya; the full package of modern human behavior evolves only 22 kya. Southern Asian populations increase very markedly from 55–45 kya, after which they stabilize; it is in the latter period, not during expansion, that the Upper Paleolithic transition takes place. In Australia, the transition starts fairly suddenly ~20 kya, much after the pronounced population increase 50–45 kya. Adapted from ref. 63 (Atkinson et al.) (Copyright 2008, Oxford University Press).

