Demography and Cultural Evolution

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Abstract

Trying to explain the increase in cultural complexity over the long term of human history has long been an interest of anthropology and of historical social sciences more generally. In recent years, interest has grown rapidly in the idea that a key factor in accounting for it might be the size of the human population itself and the extent of interaction between people, because of the effect these have on the innovation rates in populations and on the success with which innovations are transmitted. An important driver of this growth of interest has been the emergence of the new interdisciplinary field of cultural evolution, which makes extensive use of mathematical techniques, especially methods derived from population genetics. The result has been the development of a range of analytical and computer simulation models that make various predictions about the way in which population size influences cultural change, and in particular the growth of cumulative culture, including the processes that have led from the very simple forms of culture possessed by other great apes to those characteristic of *Homo sapiens*. The aim of this review is to distinguish them, so that future work can focus on evaluating their strengths and weaknesses and the circumstances in which they are useful.

INTRODUCTION

The past decade or so has seen an enormous increase in interest in the relationship between population patterns and processes on the one hand and patterns of cultural change and adaptation, on the other; in particular, the extent to which population size and interaction rates have an effect on innovation rates and on the growth of cultural complexity or cumulative culture. *Cumulative culture* refers to the idea that over time the number of cultural elements present in human societies tends to increase, and that the presence of complex cultural or technological innovations, for example, the internal combustion engine, requires the prior existence of a number of other traits. A major driver of this new interest has been the development of the interdisciplinary field of cultural evolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981), which takes a Darwinian theoretical perspective on cultural variation and change, seeing it in terms of innovation, transmission, and

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selection processes. Associated with this perspective has been the application to studies of cultural data of methods derived from evolutionary biology, especially population genetics. More specifically, the development of this new field has led to the growth of interest in exploring the existence or otherwise of cultural traditions in animals, not least our closest living relatives, the great apes (e.g., Whiten *et al.*, 1999). Much if not most of the work on the relationship between population and cultural complexity has been of a generalizing nature, based on the construction of relatively abstract models, though there has been a particular interest in the long-term evolutionary question of how the cultural complexity of present-day human societies could have emerged from the much simpler culture of other nonhuman species.

There is now a range of different models and suggestions in the literature relating to the role of population processes in cultural accumulation and change, and the aim of this review is to distinguish them, so that future work can focus on evaluating their strengths and weaknesses and the circumstances in which they are useful. An initial distinction can be made between studies that have placed particular emphasis on the detailed processes of cultural transmission and innovation and those that pay less attention to mechanisms and look more at general trends. I will begin with the latter, which have a longer history, but the vast majority of research on this topic has only been published in the twenty-first century and is still the subject of intense debate, hence the distinction between foundational and cutting-edge research is a difficult one to make.

FOUNDATIONAL RESEARCH

MACROSCALE ECONOMIC MODELS

At the end of the eighteenth century, Thomas Malthus proposed that the growth of human populations rapidly outstrips available resources and that they are held in check by disease, famine, and warfare. As many have pointed out since, while this was true in the past, Malthus was writing at a time when the situation was changing. The Industrial Revolution and subsequent technological developments have meant that resources have been able to keep up with population, which has risen to unprecedented levels. Marx criticized Malthus on these grounds, and much more recently, Boserup (1965) proposed that the deterioration in living conditions produced by "population pressure" created incentives in human societies to innovate to overcome existing limits. Kremer's (1993) model of long-term technological evolution and its relation to population size is in the spirit of Malthus and Boserup. Population is limited by the carrying capacity of the environment given the availability of a specific technology. Technological innovation can increase the carrying capacity, and population will then rise to a new limit. However, the rate of innovation is not independent of population size. Other things being equal, a larger population will contain more innovators, so there will be a feedback relationship between technology and population size, with one dependent on the other. This further implies that the rate of growth of a population at a given time is proportional to its size at that time, in contrast to models where technological improvement is independent of population size, determined by other factors. Kremer shows that, at least until recently, the predictions of this model are consistent with long-term human population history, and that it can be extended to a more general version that factors in variations in research productivity, which can additionally account for the recent decline in population growth rates with increased incomes. He also considers the geographical implications of his model, pointing out that for the same level of technology and population density, regions with larger areas and therefore larger starting population sizes will have faster rates of technological change and over a given period will reach higher levels of population and technology. Again, he shows that this prediction is met by data on estimated population sizes of different regions of the world at 1500 AD just before European expansion into the New World. Finally, he notes that his model does not include the possibility of technological loss, as appears to have occurred in prehistoric Tasmania after it was cut off from the Australian mainland, potentially leading to a negative spiral in technology and population. Kremer ascribes the relationship between technological complexity and population size to the “nonrivalry” of technology, the fact that one person’s use of it does not preclude the use by others.

Richerson, Boyd, and Bettinger (2009) also develop an economic model within the Malthus–Boserup framework, proposing, like Boserup, that as population approaches a given carrying capacity and individual income goes down, people will innovate and intensify, but also suggesting, in line with the diet-breadth model in behavioral ecology (e.g., Kaplan & Hill, 1992), that if incomes increase, for example, as a result of the appearance of new resources, perhaps as a result of climate change, people can also “deinnovate” or deintensify, at least for short periods until population catches up. Apart from such short periods, “population pressure” is always present; so long-term population trends depend on the rate of innovation that increases the environmental carrying capacity. Interestingly, the earliest evidence we have for pressure on resources is only 50,000 years ago, with indications of the overexploitation of tortoises in the Middle East (Stiner, Munro, & Surovell, 2000), and Richerson *et al.* (2009, pp. 223–224) suggest that before this, the limits to human population size might have come from competition with other carnivores, postulating social and technical innovations that could have made modern humans more successful competitors. They go on to suggest, following Marx, that, at least in the Holocene, the limiting factor on cultural evolution may have been the rate of social rather than technical innovation, and conjecture that at the broadest social and temporal scale, a model in which the innovation rate is dependent on the population size will lead to exponential growth in technological sophistication (2009, p. 228).

CUTTING-EDGE RESEARCH

Macroscale Innovation-Transmission Models

Ghirlanda, Enquist, and Perc (2010) take a rather different approach to the relation between population and culture by focusing more closely on the processes involved. To understand the relationship between population and culture, we need to consider the balance between individual creativity and the effect of cultural innovations on environmental carrying capacity, on the one hand, and the rate of cultural loss, on the other. If the former outstrips the latter, then cultural accumulation or complexity, together with the population size, can increase. This can arise as a result of an increased effect of culture on carrying capacity, increased innovation or increased transmission fidelity. Ghirlanda *et al*. also introduce the possibility that an innovation that initially increases carrying capacity may not continue to do so, for example, the use of firearms for hunting may initially increase returns but then lead to a decrease as resources are overexploited. They show that varying the effect of culture on carrying capacity and the impact of what they call the corruption rate, the rate at which adaptive features become nonadaptive, can result in very different dynamics, ranging from stability to unlimited growth to population extinction. Unsurprisingly, the introduction of a parameter that allows for “adaptive filtering,” the ability to detect and discard features that have become maladaptive, increases the space in which unlimited growth occurs.

Finally, they return to the question of the hyperbolic rate of human population increase over the long term, generally assumed, as in Kremer’s model, to arise from the fact that innovations increase both the environmental carrying capacity and the rate of population increase, because larger populations have more innovations, and suggest a possible alternative explanation that the rate of increase in innovations with population size may be faster than linear. The relevance of this suggestion is borne out by the study of Bettencourt, Lobo, Helbing, Künhert, and West (2007) showing that the rate of increase in innovations in cities is not a linear function of the population size but of population size to the power 1.2, which leads to growth that is faster than exponential. On the other hand, it is clear that until very recent times, cities were population sinks, with low birth rates and high death rates, maintained only by large-scale immigration from the countryside [Knauft, 1986, cited by

Richerson *et al*. (2009), cf. Barnes, Duda, Pybus, & Thomas, 2001]. How the accumulation of innovations and increased population would have emerged from these different forces remains to be explored.

The long-term mutual dependency of technology and population size is clear from all the studies outlined so far; however, the view of technology, or adaptive culture, represented, important though it is, is a one-dimensional one and does not consider what we might call the internal dynamics of cumulative culture itself. As pointed out earlier, *cumulative culture* refers to the idea that, beyond the very simplest level, cultural attributes generally depend on one another, in the sense that the presence of one cultural attribute affects the likelihood that another will be present; the strongest cases being those where one is a prerequisite for the other, and, at the other extreme, where one precludes the other. Enquist, Ghirlanda, and Kimmo Eriksson (2011, pp. 415–418 and Figure 1) show that there is variety of ways that such dependencies can arise: directional change in a single dimension, where to get from state (a) to state (c) you have to go through state (b); branching differentiation, where a given state can give rise to two or more states, which then change independently of one another; pairwise combinations, where the state of one attribute is affected by the state of two others; and finally, "systems of cultural elements" in which there may be multiple influences, positive and negative, between attribute states, including reciprocal ones. Unsurprisingly, simulation studies show that "systems of cultural elements" result in cultures whose number of elements increases at a far faster rate than any of the others and also produce corresponding increases in the histories of individual elements, that is to say, "the number of evolutionary events that created the element, starting from a cultural seed" (Enquist *et al*., 2011, p. 418, Figure 5). Systems characterized by these complex interdependencies are strongly path-dependent, both because of the very large number of possible links and because there is a strong stochastic element as the links are not deterministic ones. The authors argue that there is strong evidence in many domains for the predicted exponential increase in the diversity and complexity of culture (Enquist, Ghirlanda, Jarrick, & Wachtmeister, 2008, Figure 1). In summary, the rate of accumulation of culture at a given point depends on its rate at the previous point purely as a result of the increase in cultural interdependencies. However, as Enquist *et al*. emphasize, this is a very abstract model and it does not address transmission processes at the individual level, nor does it consider the demographic aspects that they and others have shown elsewhere to be important, as we have seen earlier. The role of selection in winnowing out ineffective combinations of traits is also not considered.

MODELS OF SPECIFIC INNOVATION-TRANSMISSION PROCESSES

The best-known model that looks at the implications of specific innovation and transmission processes and their link to demography is that of Henrich (2004). This is based on a model of learning in which individuals attempt to imitate the most skilled individual available to them. Most individuals will fail to reach that level, so there will be a distance between the modal skill level in the population and the best. However, there will be a certain probability that an individual will exceed the current best and a new, higher, most skilled level will result. In these circumstances, given a constant gap between the best level and the modal level, the result will be an improvement in the modal level. The probability of improvement or decline in the population modal level depends on the ratio of the gap between the mode and the best, on the one hand, and the dispersion of the distribution of skill levels on the other. If the gap is small and the dispersion is large, then improvement will be far more probable than in the opposite case. For a given ratio, though, Henrich demonstrates that what happens will depend on population size, as improbable events will occur more often in larger populations. For very complex technologies where the gap between the modal level and the best is large and the variation between individuals is small, then a large population will be required to maintain or improve the technology. Thus, if external forces cause a decline in the population size, the most complex technologies are likely to be lost. Simpler ones, even if they are lost, have a much higher probability of being reinvented. Henrich showed that this process could account for the well-known and apparently deeply puzzling cultural impoverishment of the aboriginal Tasmanians after Tasmania was cut off from the Australian mainland at the end of the past Ice Age. More generally, “It is the selective transmission of lucky errors and occasional experiments that drives much of the evolution of adaptive technology, skills, beliefs, and practices” (Henrich, 2004, p. 202), and makes it strongly dependent on population size. Henrich’s result has subsequently been confirmed by Kobayashi and Aoki (2012), who showed that a version of the model with the more satisfactory assumption of overlapping rather than discrete generations produced an even stronger population effect.

The substantive assumption in Henrich’s argument that real improvements are difficult to make because of the sheer amount of cultural knowledge embedded and embodied in human artifacts and cultural practices is supported by the ethnoarchaeological work of Roux (2010), who makes the point that training in any production process that involves the acquisition of high levels of expertise that take a long time to acquire is likely to restrict innovation, because the whole process of learning is designed to fix particular sets of skills and knowledge; this may be particularly the case with physical expertise and motor skills. Only the most expert, those who have complete control of all aspects of a process and its associated knowledge, are likely to transcend the limits of what they have learned and invent something new. Roux cites (2010, p. 224) the example of inventions in the field of pyrotechnology by traditional craftsmen in India, which were only made by those who were most skillful, individuals "exceptional as much for their skills as for their rarity."

It is important to note that the *population size* in such cases refers to the "effective population size," not the total local population but the relevant interacting population of learners and teachers. Thus, in the case of Henrich's proposal for Tasmania, the interacting population size decreases because of the loss of contact with the mainland, not because of local population decline, though this probably occurred. Where there is craft specialization, the effective population size may be tiny and the skills are correspondingly vulnerable to loss. Thus, Roux (2010) shows that despite the productivity of the technique, the wheel-coiling of pottery was lost on two occasions in the societies of the ancient Levant because it was a highly specialized activity with only a small number of practitioners. When the socioeconomic conditions that sustained it collapsed, a small number of transmission links were broken. It was only later, as the number and spatial extent of transmission links increased, that this technical system became less vulnerable to the effects of external historical events.

Powell, Shennan, and Thomas (2009) simulated a version of Henrich's model and effectively ran it in reverse, to explore the effects of increased population density and increased migration between groups in a meta-population on increases in cultural complexity. They showed that differentials between regions in terms of population density or migration rate could sustain very substantial differences in the skill level as measured in terms of Henrich's model, and proposed that these factors could account for the puzzling appearance and disappearance of features of the so-called behavioral modernity in the African Middle Stone Age, features that had previously been accounted for in terms of biological cognitive evolution, if human populations fluctuated in size or contact rates as a result of changing climate patterns. However, others have emphasized the importance of evaluating the costs and benefits of more and less complex technologies in different environments (Mackay & Marwick, 2011). In any case, it is worth emphasizing that neither Henrich's original model and, Powell *et al.*'s version, nor Kobayashi and Aoki's modification includes any feedback from the improving or devolving technology itself to the population size. Population size is simply an independent variable affecting the innovation and transmission of novel improved ways of doing things.

A different model of the relationship between cultural complexity and population size was explored by Shennan (2001). He modified a genetic model developed by Peck, Barreau, and Heath (1997) on the basis of the ideas of Fisher (1930). Individuals have a number of different attributes or traits that are subject to selection depending on the values of their attribute states. The model starts with a perfectly fit population. Cultural transmission occurs, with the parental value of a cultural trait having a certain probability of not being passed on to its offspring; when this occurs, the individual chosen to be the cultural model is the one with the highest adaptive value chosen from a random selection of individuals in the parental generation; otherwise, the offspring takes the parent's value. In the course of transmission innovations can occur, which can be either beneficial or deleterious. The probability that any given attribute state adopted by an offspring will have just undergone an innovation is represented by the attribute innovation rate. An innovation is assumed to change the adaptive value associated with an attribute by some amount, drawn from a distribution such that the majority of innovations have very little effect but some have a more significant one. The results of the simulations carried out using this model showed that larger populations can evolve to a higher average fitness than smaller ones, because they carry a smaller drift load of deleterious cultural traits, though again there was no feedback to population size.

A similar model has recently been used by Lehmann and Wakano (2013) to look at the effect of the multidimensionality of cultural traits; in other words, where the best payoff depends on getting the right combination of a number of different features, for example, different aspects of size and shape of an artifact. In Henrich's model, everything is collapsed down to a single dimension. With increasing numbers of dimensions, there are far more ways of making things worse than making them better. Where the number of dimensions is very high, then even a learner with very high computational ability going through different combinations and their effects in their imagination will not find the optimum, but a population of payoff-biased learners making uncorrelated errors will be able to reach it if it is sufficiently large. An excellent example of the kinds of complexity and multidimensionality involved is provided by Lombard and Haidle's (2012) construction of what they call the "effective chain" of activities for the production of bows and arrows, based on evidence from Middle Stone Age Africa.

If we think about the different kinds of dependencies between cultural elements described by Enquist *et al*. (2011) and discussed earlier, then clearly the case where there are "systems of elements" in which there may be multiple influences, positive and negative, between attribute states, and whose numbers of elements increase very rapidly as a result, will also be the case where finding an optimum is the most difficult. Once again then, from a different set of premises, successful innovation, and therefore adaptive cumulative culture, depends on population size. The more complex the system of elements becomes, the steeper is the rate of increase in cultural complexity, as Enquist *et al*. (2011) show; correspondingly, the larger the population size needs to be in order to have a high probability of arriving at the optimum combination of trait values.

The general argument about the importance of population size for cultural complexity is supported by Kline and Boyd's (2010) study of marine fishing technology in Oceania. This showed a correlation between the number and complexity of marine fishing tools and the size and connectedness of island populations, with smaller and more isolated islands having fewer and less complex tools than larger and less isolated ones. Importantly, they point out that the pattern is not entirely consistent with the type of Malthus–Boserup model proposed by Kremer in which improved technology produces increased carrying capacity and therefore increased population because this model does not explain why the connectedness of the islands, not just their local population size, also has an effect. They proposed that the pattern could be accounted for by either a drift model of the kind proposed by Shennan or Henrich's process (which they call the *treadmill* model); however, in any case, a model in which the transmission process has a significant role.

Alternative Models of Links between Cultural Complexity and Population

Of course, the models described earlier that show the importance of the effective population size in the process of cumulative cultural evolution are based on the assumption of differential payoffs in influencing outcomes, even if, as we have seen there is no feedback to population size. This seems appropriate when the aim is to understand the adaptive role of culture in human evolution. However, it will not necessarily apply to all or even most cultural traits, many of which will be under very weak selection or indeed completely neutral, that is to say having no fitness or performance differentials. In the latter case, there may still be cumulative evolution in the sense that, for example, a particular decoration pattern on a ceramic vessel may have been arrived at via a series of prior steps, perhaps combining a number of existing variants, but it will not be governed by the same rules. In such cases, we cannot make any predictions about the history of particular variants but the turnover of neutral variants will be determined by a combination of the innovation rate and the population size (e.g., Bentley, Hahn, & Shennan, 2004), so the latter remains important.

The models outlined earlier, although among the best known, are by no means the only ones that have postulated a role for demographic factors in the evolution of more complex human culture in prehistory. Still within the same family as the innovation-transmission models described earlier, Premo and Kuhn (2010) developed a spatially explicit agent-based model that explored the extent to which frequent local extinctions of subpopulations in a meta-population could produce an appearance of stability in the archaeological record. Their model showed that such an extinction process would indeed affect a range of patterns potentially visible in the archaeological record, including the rate of cumulative change and the degree of differentiation between different local groups, because when there are frequent local extinctions, more cumulative change is lost from the meta-population. Importantly, this process affects neutral traits as well as adaptive ones.

However, Moore (2013) has offered a completely different role for demography in the case of increased cultural complexity in prehistoric Australia. He examined the change from simple stone flaking to more complex sequences there and suggested that there was no evidence that they were more efficient or led to the production of more efficient toolkits. By correlating their appearance with other developments, he postulated that their adoption was a consequence of population increase that led to restrictions on group mobility and the growth of closed territories. The increasing role of material-based symbolic communication was part of the development of relations between groups based on ceremony and exchange and involving complex signaling, of which elaborate symbolically loaded stone tools formed a part. As such, the processes generating cultural elaboration here are completely different from those in the models described earlier as they are not based on the relationship between demography and transmission processes but on selection for investment in more complex signaling arising from the consequences of increased population density. In this sense, the model fits into the Malthus–Boserup framework discussed earlier because the socio-technical innovations result in increased carrying capacity.

TRANSMISSION FIDELITY AND THE CONTRAST BETWEEN HUMAN AND NONHUMAN CULTURES

The previous discussion has explored a range of factors affecting cumulative culture and its relationship to demographic processes but it has effectively assumed that the detailed mechanisms affecting the fidelity of transmission are a constant. Of course, this cannot be assumed when we are trying to understand the transition from great ape culture to human culture and there has been much discussion of the relative importance of creativity and transmission fidelity in accounting for the difference. A simulation of a simple cultural transmission model by Lewis and Laland (2012) showed that the most significant factor affecting the buildup of cumulative culture was cultural loss and that a major difference was made by minor improvements in the fidelity of transmission, which led to increased longevity of cultural traits, while forms of innovation involving the combination of existing traits also played a role. In keeping with the central importance of transmission fidelity, they cited a study showing that superior achievement in a sequential problem-solving task was linked to verbal instruction and imitation in children though not in chimpanzees.

Pradhan, Tennie, and van Schaik (2012), on the other hand, reject the idea that the differences between great ape and human culture are explicable by the fact that the former cannot imitate, because in their view, there is evidence that they can transmit complex techniques. On the basis of their knowledge of the social behavior of great ape groups, the authors propose that the key dimension affecting the growth of complexity is differences between the species in terms of sociability and they show by modeling that greater sociability leads to increased technical accumulation. They conclude that "[cultural accumulation] in hominins was induced by changes in social organization that led to higher sociability, brought about by cooperative hunting or scavenging, followed by the adoption of full terrestriality and teaching elicited by systematic food sharing and provisioning, which further improved social transmission of skills" (Pradhan *et al*. 2012, p. 186).

Although the authors do not appear to see it in this way, their model is another version of the demographic arguments outlined earlier, in this case, the trend to increased sociability is a trend toward increased effective population size as far as the acquisition and accumulation of skills is concerned; the total connected population size in their model has no effect on cultural accumulation but there is no reason why we should expect it to. In any event, their proposal makes the important point that structures of social interaction play an important role in affecting the fidelity of transmission. The same is true of the nature of social practices, as Barth (1990) and Whitehouse (1992) have shown in the case of the transmission of ritual in New Guinea societies.

KEY ISSUES FOR FUTURE RESEARCH

Cultural propensities are species-wide but cultures and cultural complexity are not—they are specific to particular populations. Recent work has shown that effective population size—the number of people interacting with respect to a particular learned and transmitted activity—has a major impact on a wide range of cultural evolutionary processes and their outcomes, including cultural accumulation. Different models postulate different mechanisms as responsible for this and an important task for the future must be to create formal models including demography of processes for which they do not yet exist and to compare the predictions of the various models. Introducing feedback from cultural states to population size via considerations of fitness is also important, as is an investigation of the role of population size in relation to attributes where selection is weak to nonexistent.

The emphasis in this review does not mean to imply that effective population size is the only relevant factor affecting cultural evolution, especially the persistence of cultural traits. Costs and benefits, that is to say, selective forces, are relevant and are likely to change through time with respect to any given cultural feature. Transmission forces are also relevant, for example, the importance of conformist transmission bias in affecting the fidelity of transmission. Further psychological experiments and anthropological field studies that address the role of different factors will also be required, so that the models are based on growing knowledge of the psychology of innovation and transmission processes on the one hand and their operation in real social contexts on the other.

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Stephen Shennan studied Archaeology and Anthropology at the University of Cambridge, UK, where he also completed his PhD. He spent the earlier part of his professional academic career at the University of Southampton, UK, before moving to the Institute of Archaeology, University College London (UCL). He is currently Professor of Theoretical Archaeology and Director of the Institute of Archaeology, UCL. His main research interest is the study of cultural evolution on the basis of archaeological evidence, using cultural evolutionary theory to develop and test hypotheses about cultural change in prehistory, and using archaeology to throw light on postulated cultural evolutionary processes. From 2001 to 2005, he was the Director of the Centre for the Evolutionary Analysis of Cultural Behaviour at UCL and he currently holds an Advanced Grant from the European Research Council for the project "Cultural Evolution of Neolithic Europe."

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