Trends in Cognitive Sciences

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Review

Cumulative Cultural Evolution within Evolving Population Structures

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Our species has the peculiar ability to accumulate cultural innovations over multiple generations, a phenomenon termed 'cumulative cultural evolution' (CCE). Recent years have seen a proliferation of empirical and theoretical work exploring the interplay between demography and CCE. This has generated intense discussion about whether demographic models can help explain historical patterns of cultural changes. Here, we synthesize empirical and theoretical studies from multiple fields to highlight how both population size and structure can shape the pool of cultural information that individuals can build upon to innovate, present the potential pathways through which humans' unique social structure might promote CCE, and discuss whether humans' social networks might partly result from selection pressures linked to our extensive reliance on culturally accumulated knowledge.

Problem-Solving in Populations over Multiple Generations

A central feature of our species is our unprecedented capacity to develop sophisticated cultural practices that have allowed us to colonize and permanently occupy environments for which we are poorly suited genetically [1,2]. This capacity can be viewed as a form of problem-solving by which humans have successfully solved complex ecological challenges. However, this form of problem solving is peculiar in that it operates at the population level, rather than solely within individuals, and over multiple generations [2,3]. Both traditional and more modern technologies have not been produced by a single individual, but have emerged over centuries through incremental improvements resulting from the efforts of multiple generations of individuals. This process, known as **cumulative cultural evolution** (**CCE**; see Glossary), is powered by our ability to selectively learn adaptive social information, which results in the gradual accumulation of **innovations**, and can give rise to cultural traits (such as technologies) that are beyond individuals' inventive capacities [2–7].

Drawing predominantly on evolutionary theory, anthropologists, biologists, and psychologists have developed a rigorous theoretical framework that applies the notion of descent with modification to material culture, and have investigated the role of population dynamics in the production, transmission, and maintenance of cultural traits [8–10]. An influential finding of early theoretical models is that our social learning abilities interact with **demography** to affect CCE and, more specifically, that the size of the population within which cultural information is shared strongly constrains CCE [11].

Recent years have seen a proliferation of empirical and theoretical work exploring the interplay of demography and CCE, and demographic factors are increasingly invoked to explain historical patterns of cultural changes [11–19]. While this research has advanced our understanding of the link between demography and CCE and opened up promising new avenues, it has also revealed a need to better articulate empirical research and theoretical models. Here, we present the theory, discuss misconceptions, outline future challenges, and highlight new directions in research on demography and CCE.

Highlights

Our species' ecological success is supported by our ability to selectively learn beneficial social information, resulting in the accumulation of innovations over time. Population size affects the social information available to subsequent generations of learners and constrains cumulative culture.

Population structure constrains the flow of social information and can promote the accumulation of innovations by bringing culturally distinct groups into contact. Effective population structure results from a combination of structural barriers (e.g., lack of contact between individuals) and behavioral barriers (e.g., unwillingness to share social information).

Compared with non-human primates, humans live in large networks of unrelated individuals that might be conducive to the accumulation of cultural innovations. This social structure might partly result from selection pressures linked to our extensive reliance on culturally accumulated knowledge.

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Strength in Numbers

Demography has long been considered a potential explanation for cultural changes documented in the archeological record [20–22], but it is with the theoretical work of Shennan [23] and Henrich [11] that the idea gained prominence among evolutionary human scientists. The key underlying demographic models of cultural evolution is that, given that CCE only operates when at least some information is transmitted socially between generations [24–26], the **effective population size** (which depends on both population size and interconnectedness) can buffer the risk of losing cultural information (Box 1). In Henrich's seminal model [11], for instance, individuals belong to a population of constant size and have a psychological propensity to learn from successful individuals. This propensity creates a selective force that promotes the transmission of beneficial cultural traits and outweighs the degrading effects of learning errors when populations are large enough (see Figure I in Box 1). These results suggest that decreases in effective population size, due to phenomena such as plagues, war, or volcanic eruptions, result in losses in individuals' level of skills (often proxied in the archeological literature as the number of tools, or toolkit complexity) by constraining CCE. Several regional losses of cultural traits documented in the archeological record, such as prehistoric Tasmania, have consequently been attributed to decreases in population size and connectedness [11,19]. Conversely, the emergence of more

Box 1. Demographic Models of Cultural Change

Cultural Drift

Some of the earliest cultural evolution models adapted early 20th-century models of genetic drift to the cultural case [8,22,23,108]. Drift, whether genetic or cultural, is essentially sampling error. Drift models typically assume 'unbiased transmission' or 'random copying': each of N individuals within a finite and fixed-sized population has one of a set of discrete cultural traits. Each generation or timestep, individuals select another individual at random and acquire their cultural trait. This process results in the inevitable loss of trait variation. The speed with which traits are lost is dependent on N: smaller populations lose variation quicker. This is a highly simplistic model, but provides a useful base for exploring the effects of processes, such as innovation, and complex population structures, such as island chains or bottlenecks, on CCE, and has been used to explain archaeological assemblage diversity [22,108].

The 'Tasmanian' Model

Perhaps the most influential demographic model of cultural evolution was formulated by Henrich [11]. This model was inspired by the empirical case of prehistoric Tasmania, which apparently lost complex technological traits (e.g., bone tools and warm clothing) around 10 000–12 000 years ago when Tasmania was cut off from the Australian mainland, thus decreasing the effective population size [20]. The model incorporates more psychologically plausible processes than simple drift models. Each of N individuals has a value of culturally transmitted 'skill' (e.g., basket making), represented by a continuous variable z. Each timestep, each individual attempts to learn the skill value z_h of the highest-skilled member of the previous timestep, h (i.e., success biased transmission). Learning is imperfect, and affected by two kinds of process. Learning error, determined by α, always results in worse skill than z_h. Another parameter, β, determines the extent of inferences, experiments, luck, and other factors that ,on average, make skill levels worse, but sometimes better, than z_h. Combining these, Henrich assumed that the skill of a naïve individual is drawn from a Gumbel distribution (Figure I). N interacts with the latter β term: the more individuals there are, the more likely one of those individuals is to exceed z_h, representing an increase in cumulative cultural knowledge/skill. If N is too small, then all learners will acquire values around the mode of the distribution, which is less than z_h, resulting in a decrease in cultural complexity. Subsequent empirical work has shown that this Gumbel distribution is a reasonable approximation of social learning dynamics [109] (but see [110] for a critique of this model).

Population Structure and Trait Recombination

Subsequent models have extended the **Tasmanian model** to investigate in greater detail how the structure of the population impacts both the maintenance and the production of cultural traits. Stochastic simulations of the Tasmanian model with multiple subpopulations showed that increasing the migration rate has a similar effect to increasing the size of an isolated population on CCE, because both increase variation within subpopulations and so reduce the risk of losing cultural information [13]. Recent studies have more explicitly modeled the pathways that give rise to innovation and revealed that the effect of migration can be even more pronounced when cultural traits can combine to form innovations that are 'greater than the sum of their parts' [68]. However, too frequent contact might not be beneficial to CCE because it prevents populations from remaining culturally distinct, and reduces opportunities to innovate [68,69].

Glossary

Behavioral barriers: blocks on information flow due to behavioral tendencies, such as an unwillingness to teach hard-to-learn skills, despite contact,

Cultural drift: cultural change due to random sampling error, which is heavily dependent on population size and structure (see Box 1 in the main text).

Cumulative cultural evolution (CCE): the repeated modification and social learning of behavioral traits from individual to individual and over successive generations, such that the cultural traits improve in some desired measure of efficiency (typically a proxy for fitness).

Demography: the size and structure of a population of individuals within which CCE occurs.

Demonstrator: an individual who serves as a source of social information.

Effective population structure: the structure, resulting from the combined effects of structural and behavioral barriers, that constraints the flow of cultural information.

Innovation: the generation of novel cultural variation, either via refinement or recombination.

Recombination: the bringing together of existing cultural traits to form a new functional trait.

Refinement: improving an existing cultural trait, typically through a small, gradual change.

Structural barriers: blocks on information flow due to the structure of the population (e.g., individuals simply not coming into contact with one another).

Tasmanian model: an influential early model of how population size constrains CCE (see Box 1 in the main text).

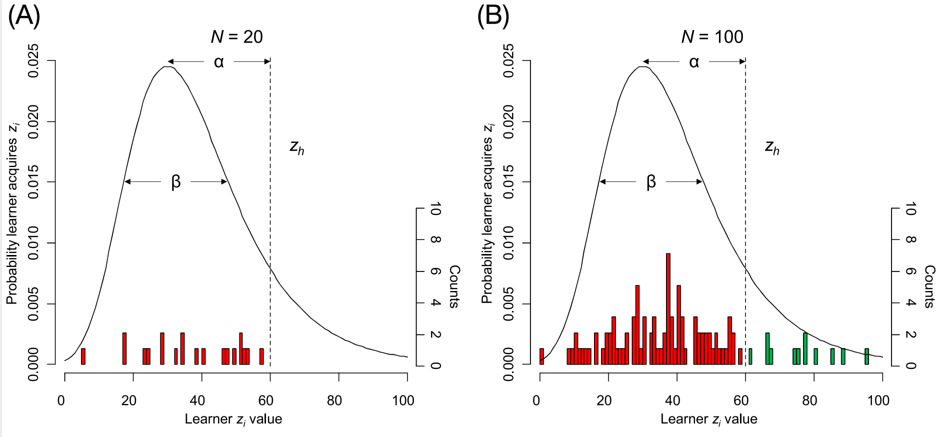

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Figure I. Gumbel Distribution from Henrich's Tasmanian Model. The distributions depict the probability of a learner i acquiring different values of skill, z (z_i), for two different population sizes N. The vertical dotted line shows the z value of the highest-skilled demonstrator being copied (z_h). Learning error, determined by α, reduces the likelihood of z_h being reached. Inferences, experiments, and luck, determined by β, increase the chances of the learner improving on z_h (the area under the curve to the right of the dotted line). Vertical bars show N random draws from the Gumbel distribution, representing N learners' z_i values. Red bars represent inferior z_i relative to z_h, green bars represent superior z_i relative to z_h. (A) A small population (N = 20) results in a population-level decline in skill, because no learner matches or exceeds z_h. (B) A large population (N = 100) features some learners who exceed z_h, resulting in an improvement in the next generation.

complex cultural traits has been hypothesized to result from increases in population sizes and/or densities [13,14].

Experimental Tests of the Relationship between Population Size and CCE

One approach that has been used to evaluate the plausibility of demographic models of CCE involves laboratory experiments. Typically, participants put in groups of different sizes are tasked to improve a piece of technology. To date, five experiments from four different research groups provide support for a positive effect of group size on cultural complexity [27–31] (but see [32,33]). For instance, one study exposed naïve participants in groups of two, four, eight, and 16 to demonstrations showing how to produce virtual arrowheads and fishing nets, and tracked the efficiency of those tools across time [27]. The larger the group, the less likely tools were to deteriorate, the more likely they were to improve, and the more likely a diversity of tool types was to be maintained. Using chains of participants and alternative tasks involving image-editing and knot-tying techniques, another study similarly showed that the deterioration of a technique is less likely (and its improvement more likely) in larger groups [29]. Additionally, these experiments show that individuals use cues, such as success, to choose from whom they learn, lending plausibility to the assumption of Henrich's model [11] that individuals selectively learn from successful **demonstrators**.

Importantly, some of these experiments relied on designs that only loosely reflect Henrich's initial assumptions (Box 2). For instance, most provide individuals with the opportunity to simultaneously learn and combine information from multiple demonstrators (a several-among-many design) [28–31], while Henrich's model assumes that individuals always select a *single* source of information from a larger pool of demonstrators. However, some experiments that have relied on the former design allowed participants to allocate their learning time strategically, which means that individuals' learning strategies might still, in practice, be consistent with Henrich's assumptions [29]. Nevertheless, mechanisms that are not part of Henrich's model, such as combining

Box 2. Linking Models and Data in the Laboratory

Experimental approaches are useful for investigating the relationship between demography and CCE because essential elements of theoretical models can be implemented under tightly controlled conditions, and tested against actual human behavior (rather than modelers' assumptions about human behavior) [111,112].

As noted in the main text, most experimental studies have found support for the general predictions of demographic models [27–31]. This is all the more surprising given that these studies are quite diverse in experimental tasks, group sizes, and interindividual interactions. Yet, most experimental designs significantly deviate from the models they claim to test. In the main text, we discussed one example, where experiments offer social learners the opportunity to combine information from multiple cultural demonstrators [29–31], rather than learn from a single successful demonstrator as in the most-cited demographic models. The role of recombination across existing cultural traits has been stressed by scholars from multiple fields [113–115], and increased opportunities for recombination certainly is one pathway by which effective population size might affect CCE [101]. Yet, most experiments are presented as tests of models that do not feature recombination between existing traits and in which effective population size mostly affects CCE by buffering the risk of losing cultural information (see Box 1 in the main text). Still other experiments have relied on tasks in which cultural loss is unlikely to occur [31]. Thus, even though these experiments support the population size hypothesis, it is not always clear whether they provide appropriate tests of the theoretical models that they cite.

Perhaps more problematic are experiments where results showing no relationship between demography and CCE are used to question the validity of theoretical models despite featuring different assumptions to those models. For instance, a recent experiment had chains of participants make and throw paper airplanes, with each participant able to learn from one, two, or four previous participants [33]. Apparently contrary to the demographic hypothesis, flight distance only increased in the one-demonstrator condition, not the two- and four-demonstrator conditions. However, this experimental design prevented participants from learning from the demonstrator of their choice. Instead participants were forced to attend to multiple, randomly ordered demonstrators for 1.5 min each. This differs from Henrich's model which explicitly holds that it is the combination of the amount of beneficial cultural information (which increases in larger groups) and the selective choices of cultural learners that promotes CCE. The results of this experiment are consistent with the former in showing that larger groups produce greater variation in flight distance and give participants access to more efficient planes [33]. However, the constraints imposed on social learning strategies inhibit CCE in large groups by making learning more difficult in those groups.

Discrepancies between experiments and models are not inherently a problem: the assumptions of models can always be challenged and mechanisms other than those considered in theoretical models are worth investigating. Yet, the experimental literature would benefit from being more explicit about the theoretical basis underpinning the specifics of experimental designs and how they relate to theoretical models.

information from multiple demonstrators to generate new solutions, did play a role in these experiments [29–31]. Due to this disconnect between experimental tests and theoretical models, it is not always clear whether experimental studies showing positive effects of demography offer genuine support for specific theoretical claims, or whether purported failures to detect any effect of demography are valid challenges to theoretical models (see Box 2 for further discussion).

Real-World Tests of the Relationship between Population Size and CCE

A complementary and more direct approach to test the relationship between population size and CCE is to look for a correlation between toolkit size and population size using real-world ethnographic and archeological data. Results with this approach have been mixed. Some studies support the hypothesis [13,14,34,35], but others do not [36–39] (although others point out that some of these studies rely on the same data sets, and should not count as independent tests [40]).

The difficulty with testing demographic models using real-world data is that human populations are typically embedded within extended networks of cultural exchange, making it difficult to gather meaningful estimates of population size. This constitutes a major obstacle for anthropologists and archeologists because theoretical models explicitly link cultural complexity to the size of the population that shares information (i.e., the effective cultural population size) [11]. This implies that tests of demographic hypotheses should control for contact rates between interconnected populations, which is typically challenging (but see [34]). Therefore, proponents of demographic hypotheses have argued that studies that reported null results are invalid because they do not take contact rates into account and typically treat culturally connected groups as independent, culturally isolated populations [40] (see Box 3 for other mismatches between models and empirical tests).

Other studies have tested demographic effects where they may not be predicted to occur. For instance, one study found no evidence that larger populations support more complex folk tales, with complexity operationalized as the number of tale types, the number of narrative motifs within tales, and the number of component details within tales [41]. Yet, folk tales are very different to the technology that is the focus of most demographic models. Tools that are more efficient and have higher payoffs are typically associated with an increasing number of component elements [42], which means that they tend to be more complex. However, if complexity is not associated with higher payoffs, then theoretical models do not predict that population size should necessarily affect it. For example, the function of folktales is to convey meaning. If similar meaning can be conveyed by simpler folktales, we should not necessarily expect to observe the most complex folktales in larger populations. The same line of reasoning applies to the evolution of language, which functionally adapts to the needs of efficient communication [43]. Studies that have investigated the relationship between speaker population sizes and phoneme inventory sizes [44–46] or rates of language change [47–49] have yielded mixed results. However, because language also evolves to become more learnable [50], we should not necessarily expect larger populations to

Box 3. Linking Models and Data in the Wild

Several studies have investigated whether there is a correlation between toolkit size or composition and population size in natural populations [13,14,34–39], but there remain serious challenges in testing demographic effects on CCE using real-world data.

One difficulty concerns limitations in what can be measured [58]. Henrich's model (see Box 1 in the main text) describes the level of skill of an individual within a population, a variable that, in an archeological context, can be interpreted as the number of tools or tool components attributable to an individual. Yet, archeological studies typically only have access to population-level rather than individual-level data. This makes purported tests that use population-level assemblage measures largely irrelevant to Henrich's predictions [58]. Even though a recent model incorporating the appropriate population-level variable does predict a positive relationship between population size and toolkit size [58], these discrepancies illustrate the need to use appropriate measures when attempting to test a model and/or to adapt models so that they can properly be tested using empirical data.

A second difficulty is that demography has multiple aspects that can be difficult to fully take into account in ethnographic and archeological studies. In the main text, we discussed one example of this, where empirical data regarding census population sizes are used to test (and purportedly fail to support) the Tasmanian model without taking contact rates into account. Furthermore, recent models suggest that historical variations in population size and connectedness are as important as immediate demographic contexts in determining cultural complexity in a population [58,64,68]. For instance, some models show that the number of traits in a population should depend not only on the current population size, but also on the history of population growth and decline [58,64]. This can blur the relationship between population size and CCE because growing populations can have fewer cultural traits than smaller, declining populations. Similarly, two populations of the same size might be associated with toolkits of different sizes due to different demographic trajectories. Models also suggest that changes in interconnectedness can result in different outcomes, including transient increases in cultural complexity [68]. The effects of population histories represent a challenge for archeologists whose data represent a record of aggregated events spanning long periods of time during which both population size and interconnectedness might have varied. Further models are needed to determine what testable signatures these dynamics might have left in the past for archeologists and historians to detect.

Finally, demographic factors determine an upper boundary to the level of cultural complexity that can be reached by a population, but do not entirely determine the actual level reached by a population. Assuming that increased cultural complexity is beneficial, increases in population size should result in increases in cultural complexity, but only because this relaxes constraints on CCE. A full understanding of CCE in natural populations requires both drivers of CCE and constraints to be taken into account. To that end, more research is needed to identify the factors that combine with demography to determine CCE in natural populations, such as environmental harshness [54] and instability [116] or accumulated cultural traits themselves [61,117,118].

produce more new words or have larger phoneme inventory size. Furthermore, folk tales and other forms of expressive culture may serve as markers of group membership and some models have suggested that smaller groups will have more exaggerated markers [51]. This suggests that a clearer picture about the relationship between demography and the evolution of expressive cultural traits will emerge by moving away from arbitrarily chosen measures of complexity and by taking into account that functional and symbolic cultural traits exhibit different evolutionary dynamics [52].

Contrary to recent claims [53], no theoretical work ever predicted that population size should solely determine the number of tools (or any other measure of cultural complexity) found in human populations. Many factors are expected to affect toolkit complexity in natural populations, including mobility, subsistence practices, and ecological factors. For instance, the risk hypothesis holds that populations living in harsh environments create more numerous and specialized tools to mitigate the risk of resource failure due to stochastic variation [36–39,54,55]. Importantly, the risk hypothesis and the population size hypothesis differ in what they aim to explain [56]. The risk hypothesis explains what determines the size and complexity of toolkits (i.e., what creates the need for cultural complexity). The population size hypothesis is about the constraints imposed on CCE. Claims that the absence of correlation between population size and toolkit complexity disprove demographic models are based on misconceptions about those models (Box 3).

Inconclusive studies about the relationship between population size and CCE have had the merit of stimulating new work and led to important refinements to early theoretical work. Models with different assumptions have shown that the effects of effective population size hold when more conservative or alternative assumptions are considered (e.g., restricting potential demonstrators to a limited number of acquaintances [57]; conformist transmission [58,59] but see [60]; adding costs to acquiring knowledge [61]; and alternative pathways to innovation [62]). However, recent studies also suggest that the relationship between effective population size and CCE is mediated by numerous factors ([58,62–66]), and that there are numerous challenges in detecting demographic effects on CCE in real-world data (Box 3).

Despite these challenges, there is little doubt that changing the effective size of a population will alter the cultural information available to subsequent generations of learners, which will most likely constrain what can be achieved by individuals. In this context, promising new work has started to investigate how broader constraints on information flow within populations can further promote or hinder the gradual accumulation of cultural innovations.

Beyond Numbers: CCE in Social Networks

Human populations do not comprise a collection of isolated groups of varying sizes. Multiple groups are typically connected by migratory and trade activities, which results in wide, heterogenous social networks. The role of connectedness in CCE was acknowledged in early theoretical models [11,13]. For instance, a simulation model that explicitly implemented migratory activity among subdivided populations showed that increasing the migration rate has a similar effect to increasing the size of an isolated population [13]. This is because increases in both population size and migratory activity increase the effective number of individuals available as demonstrators, and so reduce the risk of losing cultural information.

However, more recent work has started to investigate in greater detail how the structure of the population impacts the accumulation of cultural information. Unlike early models, recent studies decouple the maintenance of existing traits and the production of new traits, more explicitly modeling the pathways that give rise to innovation [62,67–69]. For instance, recent models assume that existing traits can not only be refined, but also combined with other existing cultural traits. When **recombination** between existing traits is incorporated as a pathway towards innovation, increases in population size and connectedness can have different effects on CCE [68,69]. This is because, while increases in population size systematically benefit CCE by reducing the risk of cultural loss, increases in connectedness can reduce opportunities for innovation by homogenizing cultural behaviors. This effect is illustrated by a recent laboratory experiment in which individuals could innovate by producing incremental changes within path-dependent technological trajectories (**refinement**) and by combining traits that had evolved along different trajectories (recombination) [67]. Results showed that high levels of connectedness make individuals more likely to converge on similar solutions, which results in lower levels of cultural diversity and slower rates of innovation compared with less connected groups.

These results suggest that understanding the effect of demography on CCE requires us to consider not only how changes in connectedness affect the number of individuals available as demonstrators, but also how it shapes the cultural diversity to which individuals are exposed. When these two effects are considered simultaneously, models show that optimal rates of accumulation are reached for intermediate levels of connectedness [68,69]. This is because low levels of connectedness increase the risk of cultural loss by decreasing access to demonstrators, while high levels of connectedness reduce opportunities to innovate by homogenizing cultural behaviors. At intermediate levels of connectedness, groups can accumulate cultural information while remaining culturally distinct, which keeps fueling innovation.

These results have implications for CCE both at the macro- and the microscale. At the macroscale, human populations have been historically fragmented due to geographic barriers, conflicts, and other factors, resulting in longstanding culturally differentiated subpopulations. In this context, increased levels of between-group connectedness are unlikely to homogenize cultural behaviors. Nevertheless, recent models suggest that, because of new opportunities for recombination, contacts between culturally differentiated groups should result in rapid cultural changes, the magnitude of which far exceeds what is predicted by models that incorporate cultural loss alone [68]. This also suggests that population structures that allow for contacts between culturally differentiated groups act as endogenous drivers of cultural change [67,68], even though it should not be assumed that populations will develop and maintain more complex cultural repertoires without appropriate incentives to do so (Box 3).

Patterns of connectedness might also affect CCE at the microscale by influencing individuals' exploration of the design space. For instance, network and organization scientists have shown that behaviors are more likely to become homogeneous in well-connected than in partially connected groups when learners preferentially acquire information from the same demonstrator [70–72] (but see [73,74]). Sociologists have similarly argued that behaviors tend to be more homogeneous within than between groups and that individuals with ties to otherwise unconnected groups have greater opportunities to develop new ideas because they are exposed to a broader diversity of information [75].

These studies illustrate how patterns of connectedness impact the quantity and diversity of information to which individuals are exposed and that they can draw on to make inferences, which in turn can impact the abilities of populations to develop and maintain cultural traits. However, the benefits of sparsely interconnected networks on CCE in natural populations remain to be properly evaluated. Complex cultural traits are typically hard to learn, and several experiments have stressed the importance of multiple demonstrations and multiple learning attempts in the acquisition of complex skills [27,76]. This suggests that occasional contacts between different individuals and/or groups do not allow complex skills to spread properly. Additionally, network scientists have stressed the importance of the number of sources of exposures for the adoption of unproven new solutions [77]. Experiments typically provide participants with accurate information about alternative solutions, which allows them to confidently adopt the most rewarding ones. However, in noisy environments, interactions with multiple sources might be critical for individuals to adopt alternative solutions [77] (see also [78] for an example of how the mean number of connections within a network affects the spread of cultural traits). Future research should test whether the optimal level of connectedness differs depending upon the characteristics of the cultural traits one is looking at. For instance, dense networks might be critical for the cultural evolution of hard-to-learn traits (for which transmission is the key bottleneck), while the cultural evolution of easy-to-learn traits, the efficiency of which can be readily assessed, might be faster in sparsely connected networks.

Characterizing Human Social Networks in the Wild

The effects of population interconnectedness on CCE suggests that cultural changes would be better understood by paying greater attention to the structure and evolution of human social networks. However, mapping past, or even recent, social networks is challenging. Archeologists and geneticists are still struggling to infer past population sizes [15,79,80], let alone population structures [81]. In recent years, approaches relying on social network analyses have seen a rise in use among archeologists, but many challenges have still to be solved before being able to distinguish spatiotemporal patterns in social interactions from noise in archeological data [82–84].

However, comparative and ethnographic studies are already providing valuable information about human population structure. For instance, comparisons between human hunter-gatherer societies and non-human primate societies have shed light on what has been called the ‘deep social structure of human societies’ [85]. Contrary to most non-human primate societies, which comprise independent, single-group structures, human societies are federations of multifamily groups [85,86]. This unique multigroup structure results in extensive networks of unrelated individuals that might be conducive to CCE [87]. For example, data on interactions between same-sex adults from two hunter-gatherer populations reveal that individuals typically interact with >300 same-sex adults in a lifetime (although including opposite-sex adults and children results in estimates as high as 1000). By comparison, male chimpanzees are estimated to interact with only ~20 other males in a lifetime [87] (see also [88] for a discussion on the large-scale social networks of hunter-gatherer groups).

Other studies among hunter-gatherer populations have started to characterize hunter-gatherer networks more finely. For instance, one study used trackers to map in-camp networks in two hunter-gatherer populations and showed that individuals invest early in their childhood in a few close friends who bridge densely connected families [89]. These strong friendships increase the global efficiency of hunter-gatherer in-camp networks, which might facilitate the flow of social information (see Figure I in Box 4). More recently, characterization of hunter-gatherer networks has been extended to between-camp interactions and has been used to simulate the accumulation of cultural innovations over real networks [90]. Results confirm that hunter-gatherers’ social structures comprise multiple levels of clustering, and simulations suggest that this sparsely interconnected hierarchical network structure accelerates CCE by allowing the coexistence of multiple cultural lineages and promoting the emergence of innovations (but see Box 4).

However, the few studies that have investigated networks in hunter-gatherers have been limited to interview data and proximity measures [87,89,90]. Actual measurements of cultural transmission remain scarce, and the extent to which proximity networks accurately reflect transmission networks is currently unknown. For example, investigation of the co-occurrence of plant uses in dyads in one hunter-gatherer population showed that not all knowledge is equally shared [91]. More specifically, results showed that medicinal plants were mostly shared between spouses and kin, while plants that serve other functions were shared more widely. This suggests that knowledge-sharing networks are content specific and supports the idea that hunter-gatherer multilevel social structure enables culturally differentiated units to remain stable despite occasional co-residence [90]. This work also suggests that both **structural barriers** (i.e., lack of contact between individuals) and **behavioral barriers** (i.e., unwillingness to share cultural knowledge) have to be taken into account to properly evaluate the effects of population structure on CCE. Indeed, structural and behavioral barriers combine to result in an effective population structure that ultimately determines opportunities for cultural transmission. For instance, contact between different ethnolinguistic groups can bring different cultural traits together due to significant between-group cultural distance. However, language barriers, endogamy, rivalry, and other behavioral barriers, such as in-group conformity, might limit opportunities for cultural exchange between those groups [92,93].

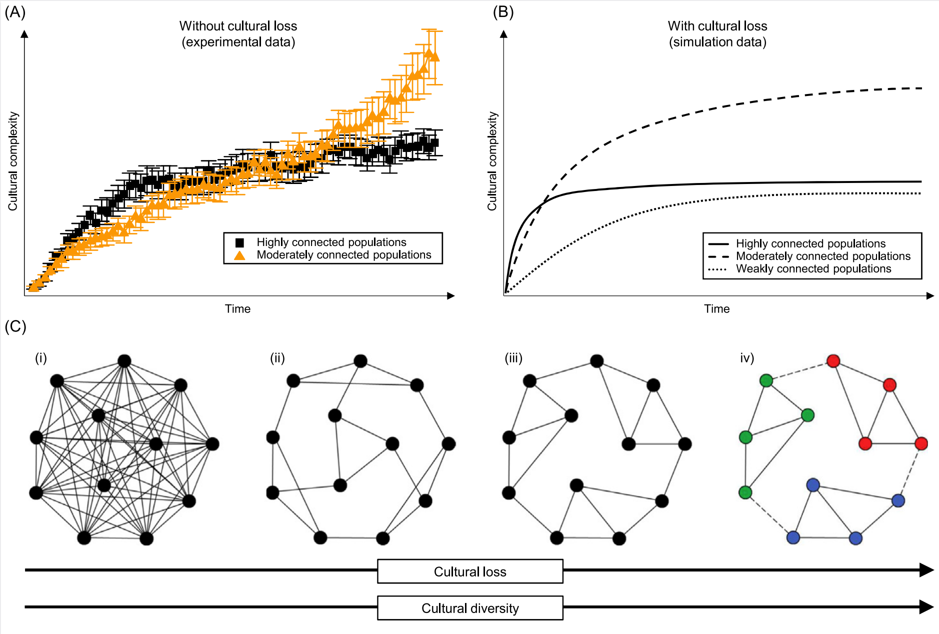
These results suggest that our understanding of the relationship between demography and CCE would benefit from a better understanding of how and why individuals form social ties both within- and between-groups and the extent to which different types of tie (such as kin based, affine based, and friendship based) are conducive to cultural transmission. This will permit more realistic implementation of cultural transmission into theoretical models. Indeed, while the combination of vertical cultural transmission (i.e., learning from parents) and success-biased learning is empirically supported and provides a useful first approximation of the dynamics of social learning in groups [40], multiple factors are likely to affect opportunities for social learning. For instance, anthropological studies have shown that social ties are more likely to form between people who share similar traits (i.e., homophily [94,95]). Furthermore, understanding how individuals form social ties is an important avenue for future research because the way in which individuals

Box 4. Is Human Multilevel Social Structure Beneficial to CCE?

Recent theoretical and experimental studies have challenged the assumption that anything that maximizes the flow of cultural information should positively impact innovation rates (Figure IA,B). These results have led scholars to wonder whether CCE in human populations has benefited from our unique multilevel social structure via the partial constraints it imposes on information flow [67]. A recent simulation study provided support for this by showing that real hunter-gatherers' social networks allow the coexistence of multiple cultural lineages, thus promoting the emergence of innovations [90].

However, while characterizing actual networks is useful for understanding how cultural information is expected to spread, many (still largely unknown) parameters need to be taken into account before establishing whether, and if so why, human multilevel social structure promotes CCE. For instance, previous work showed that the effect of network structure on CCE is mediated by factors such as individuals' probabilities of innovating (because even strong constraints on information flow prevent cultural diversification if innovation rates are low [69]) and the extent to which innovation depends on cultural diversity (because constraints on information flow both slow down and limit CCE when innovation does not depend on recombination [69]). In the aforementioned simulation study [90], both individuals' opportunity to innovate, and possibilities for recombination, were determined by the properties of an artificial cultural fitness that was designed to permit innovation through incremental improvement and recombination [67], but whose relevance to rates of CCE in natural populations is uncertain.

Perhaps more importantly, the effect of network structure on cultural loss was not considered in those simulations [90]. When cultural loss is not taken into account, constraints on information flow necessarily benefit CCE by promoting cultural diversification. In more realistic situations, constraints on information flow expose populations to higher rates of cultural loss, which can prevent cultural diversification [119]. Moreover, even if they have diverse cultural repertoires, sparsely connected populations can be unlikely to reach high levels of cultural complexity because of their inability to maintain complex cultural traits [69]. Thus, given our current limited knowledge about rates of loss and innovation, and opportunities for recombination, in real-world populations, it is not clear whether the network structure documented in [90] positively affects CCE or whether cultural complexity in hunter-gatherer populations would benefit from more connectedness by being less susceptible to cultural loss. Answering this question will require an evaluation of how sparse networks made of strong ties (e.g., kin and friendship ties) balance cultural loss and cultural diversity (Figure IC).



Trends in Cognitive Sciences

Figure I. Trading Cultural Loss and Diversity in Structured Populations. (A) Experimental results show that moderately connected populations are slower at accumulating innovations but eventually reach higher levels of cultural complexity compared with highly connected populations when innovation depends on cultural diversity. (B) Simulation models show that optimal rates of accumulation are reached for intermediate levels of connectedness when populations are exposed to cultural loss. Relative rates of accumulation between variously connected populations depend on parameters such as rates of innovation and cultural loss, and the extent to which innovation depends on cultural diversity (not shown). (C) Patterns of connectedness affect both cultural loss and diversity. (i) In fully connected networks made of permanent links (solid lines), the average number of steps required to connect any two individuals (i.e., path length) is minimal and the efficiency with which information spreads is maximal. This reduces the risks of cultural loss but decreases cultural diversity. (ii) Removing ties increases the average path length between individuals and results in less efficient networks (e.g., from i to ii). (iii) Networks comprising individuals tied to the same number of neighbors can also vary in efficiency due to differences in average clustering coefficients (a measure that reflects the 'cliquishness' of a network [120]). Increasing the average clustering coefficient results in less efficient networks (e.g., from ii to iii). (iv) Intermittent links between different parts of a network (dotted lines) further constrain information flow and result in substructures that are more likely to culturally diverge by isolation (illustrated by different colors), and also more likely to suffer from cultural loss. Adapted from [67] (A) and [69] (B).

form ties ultimately feeds back into the evolution of social networks (e.g., homophily is known to introduce local structure into networks [95,96]).

How Did Human Social Networks Get Their Shape?

Even if questions remain regarding the effects of specific network properties on CCE, it appears clear that humans live within unusually large and uniquely structured social networks. This raises questions about how and why humans have come to form large networks of unrelated or weakly related individuals.

Recently, it was argued that, because individuals from culturally differentiated groups might have greatly benefited from increased between-group interactions, selection might have acted at the individual level to affect individuals' propensity to interact with out-group members [17]. This might have involved changes in conscious behavioral choices (e.g., adjustments to out-group contacts due to perceived immediate benefits) and/or unconscious influence on behavior (e.g., decreased fear of foreigners or tendency to disperse) [17]. Congruently, a recent simulation model that investigated whether network structure itself can evolve as a result of ecological pressures related to skill acquisition confirmed that selection can impact individuals' propensity to form random ties (such as non-kin ties) [97]. Yet, it is not clear whether the acquisition of social information creates sufficiently strong incentives for individuals to overcome rivalry and other behavioral barriers that tend to reduce opportunities for cultural transmission between unrelated individuals. Moreover, increasing contacts is only one part of the problem, because many cultural traits are unlikely to be properly acquired without a demonstrator's willingness to share information [98–100].

Another possible way by which selection might have promoted the emergence of networks that are conducive to CCE is by acting on variation that exists at the group level [17,101]. Indeed, anthropologists have long stressed the role of cultural institutions in promoting both information sharing and interactions between non-kin [87,101–103]. For example, among the Ache and Hadza, ritual relationships, mediated by activities such as club fight rituals, have been shown to promote interband interactions. Quantitative analyses revealed that ritual relationship is a more important predictor than kinship for different types of interaction, including opportunities for cultural transmission (such as observing tool-making skills) [87]. Furthermore, anthropologists have stressed that certain groups have cultural beliefs that connect envy and harm, which make successful individuals more likely to hide information from other group members, thus inhibiting CCE compared with other groups [101]. This suggests that groups that have cultural institutions that promote information sharing and/or mobility attain higher cultural complexity and outcompete groups with cultures less conducive to CCE [17,101]. The maintenance of large networks of unrelated or weakly related individuals might have been further supported by the emergence of cultural innovations, such as kin naming systems and stylistic markers of group identity, that typically promote cooperative interactions between unrelated individuals [103]. For example, kin naming systems allow familial relationships to extend to affine, distant kin, and even non-kin [103] and might permit individuals to maintain privileged relationships with large numbers of individuals without requiring much cognitive effort or physical cohabitation [104].

The question of whether humans' social structure might result in part from selection pressures linked to our extensive reliance on culturally accumulated knowledge will have to be carefully evaluated. Indeed, chimpanzees also live among nonrelatives [105] and humans' propensity to form ties with non-kin might be due to reasons unrelated to CCE and that just happened to be conducive to the accumulation of cultural innovations. For instance, archeologists noted that an incest avoidance rule would give rise to the same kind of sparsely connected networks that might benefit CCE [56]. Alternative determinants of outgroup contacts include resource distribution [56], reciprocal cooperative exchange [106], and coalition formation [107], among others. Specific predictions should be formulated and properly tested to disentangle the respective effects of these various mechanisms on network structure. For instance, the hypothesis that CCE directly shapes network structure by acting on conscious behavioral choices would predict that individuals should flexibly reinforce or weaken their investment in non-kin ties depending on the usefulness of the information they provide.

Concluding Remarks and Future Directions

The proliferation of work exploring the interplay of demography and CCE has recently led to many misconceptions due to loose interpretations of early theoretical models (Boxes 2 and 3). Empirical tests that operationalize models in ways that are consistent with theoretical assumptions provide support for the hypothesis that effective population size constrains CCE. However, testing these models using real-world data remains difficult because multiple factors combine with demography

Outstanding Questions

Are human population structures especially conducive to CCE? If so, did they emerge because they promote CCE or for reasons unrelated to CCE, such as inbreeding avoidance?

What are the respective roles of structural and behavioral barriers in shaping effective population structures?

What type of population structures permit populations to exchange cultural information while remaining culturally distinct? Are those structures best for CCE?

Do hard-to-learn cultural traits require different network structures than easy-to-learn cultural traits to spread effectively?

What determines the emergence of non-kin ties in human societies? How flexible are these non-kin ties? Do individuals adjust their investment in ties depending on the information those ties provide?

What is the role of friendship ties in the spread of hard-to-learn cultural practices?

To what extent are knowledge sharing networks content specific or domain general? For example, do medicinal practice networks resemble tool-making networks, or are they distinct?

Are some cultural domains (e.g., technology) more likely to be influenced by population size and structure than others (e.g., art, literature, or language)?

What are the cognitive and cultural underpinnings of the large numbers of social ties that humans maintain?

What was/is the role of multilevel selection in the emergence of large and structured social networks?

What are the implications of the relationship between demography and CCE for cultural evolution in non-human species, which may exhibit some but not all features of human CCE?

to determine CCE and human populations are typically embedded within extended networks of cultural exchange. While these extended networks of contacts make it difficult to gather meaningful estimates of population size, recent research suggests that they also affect CCE in ways that are not yet fully appreciated. Understanding how population structure affects CCE will require us to understand precisely how structural and behavioral barriers constrain information flow in natural populations (Box 4).

The effects of connectedness on the accumulation of cultural information raise many questions about the relationship between humans' unique social structure and CCE (see Outstanding Questions). Through the study of the nature and emergence of non-kin ties, both within groups and between groups, as well as knowledge-sharing networks in natural populations, it will be possible to illuminate how humans have managed to accumulate cultural information in such an unprecedented way and determine whether our unique social structure results in part from selection pressures linked to our extensive reliance on culturally accumulated knowledge.

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