# Cumulative cultural evolution within evolving population structures

**Authors:** Maxime Derex[1]* & Alex Mesoudi[2]

[1] Institute for Advanced Study in Toulouse, UMR 5314, Centre National de la Recherche Scientifique, Toulouse 31015, France.

[2] Human Behaviour and Cultural Evolution Group, Department of Biosciences, University of Exeter, Penryn TR10 9FE, United Kingdom.

Correspondence to: maxime.derex@iast.fr (M. Derex)

**Keywords:** cultural evolution; cumulative culture; demography; group problem-solving; population size; population structure; social learning

## Abstract

Our species possesses 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 synthesise empirical and theoretical studies from multiple fields to highlight how both population size and structure 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. This form of problem solving, however, 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) - 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 ideas from 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.

## Strength in numbers

Demography has long been considered a potential explanation for cultural changes documented in the archaeological 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 main idea behind 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 (see Box 1). In Henrich's seminal model [11], for instance, individuals belong to a population of constant size and possess 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 (Figure 1). These results suggest that decreases in effective population size (due to phenomena such as plagues, war or volcanic eruptions) might result in losses in individuals' level of skills (often proxied in the archaeological literature as the number of tools, or toolkit complexity) by constraining CCE. Several regional losses of cultural traits documented in the archaeological record, such as prehistoric Tasmania, have consequently been attributed to decreases in population size and connectedness [11, 19]. Conversely, the emergence of more complex cultural traits have 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 lab experiments. Typically, participants who are part of groups of different sizes are tasked to improve a piece of technology. To date, 5 experiments from 4 different research groups provide support for a positive effect of group size on cultural complexity [27-31] (but see [32, 33]). One study, for instance, exposed naïve participants in groups of 2, 4, 8 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 were 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 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). Most, for instance, 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. Some experiments that have relied on the former design, however, 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]. Yet mechanisms that are not part of Henrich's model, such as combining information from multiple demonstrators to generate new solutions, certainly 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, nor 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 archaeological data. Results with this approach have been mixed. Some studies support the hypothesis [13, 14, 34, 35], but others do not [36-39] (although [40] point out that some of these studies rely on the same datasets, and should not count as independent tests).

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 archaeologists 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 inter-connected populations, which is typically challenging (but see [34]). Proponents of demographic hypotheses have therefore argued that studies which 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. One study, for instance, found no evidence that larger populations support more complex folk tales, with complexity operationalised as number of tale types, number of narrative motifs within tales, and 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. The function of folktales, for instance, 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 produce more new words nor 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 might 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].

It is also worth stressing that, 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. The risk hypothesis, for instance, holds that populations living in harsh environments create more numerous and specialised 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 (see 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 can be mediated by numerous factors ([58, 62-66]), and that there are numerous challenges in detecting demographic effects on CCE in real-world data (see 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 more broadly how 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 consist of 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 on CCE was already acknowledged in early theoretical models [11, 13]. A simulation model that explicitly implemented migratory activity among subdivided populations, for instance, 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.

More recent work, however, 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 modelling the pathways that give rise to innovation [62, 67-69]. Recent models, for instance, 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 homogenising cultural behaviours. This effect is illustrated by a recent lab experiment in which individuals could innovate by producing incremental changes within path-dependent technological trajectories (**refinement**) and by combining traits that have evolved along different trajectories (recombination) [67]. Results show 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 homogenising cultural behaviours. 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 macroscale and the microscale. At the macroscale, human population have been historically fragmented due to geographic barriers, conflicts and other factors, resulting in long-standing culturally differentiated sub-populations. In this context, increased levels of between-group connectedness are unlikely to homogenise cultural behaviours. Nevertheless, recent models suggest that, because of new opportunities for recombination, contacts between culturally differentiated groups should result in rapid cultural changes whose magnitude far exceed 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 might 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. Network and organization scientists, for instance, have jointly shown that behaviours 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 groups 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 that individuals are exposed to and can draw on to make inferences, which in turn can impact populations' abilities to develop and maintain cultural traits. The benefits of sparsely interconnected networks on CCE in natural populations, however, 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/groups might 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. In noisy environments, however, interactions with multiple carriers 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. Dense networks, for instance, 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 whose efficiency 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 might be better understood by paying greater attention to the structure and evolution of human social networks. Mapping past, or even recent, social networks, however, is challenging. Archaeologists 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 among archaeologists, but many challenges have still to be solved before being able to distinguish spatio-temporal patterns in social interactions from noise in archaeological data [82-84].

Comparative and ethnographic studies, however, are already providing valuable information about human population structure. Comparisons between human hunter-gatherer societies and non-human primate societies, for instance, have shed light on what has been called the deep social structure of human societies [85]. Contrary to most non-human primate societies, which are composed of 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]. Data on interactions between same-sex adults from two hunter-gatherer populations, for instance, reveal that individuals typically interact with more than 300 same-sex adults in a lifetime (although including opposite-sex adults and children results in estimates as high as 1000). In comparison, male chimpanzees are estimated to interact with only about 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 more finely characterize hunter-gatherer networks. One study, for instance, 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 (Figure 2). 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 are made of multiple levels of clustering, and simulations suggest that this sparsely interconnected hierarchical network structure might accelerate CCE by allowing the coexistence of multiple cultural lineages and promoting the emergence of innovations (but see Box 4).

The few studies that have investigated networks in hunter-gatherers, however, 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. Investigation of the co-occurrence of plant uses in dyads in one hunter-gatherer population, for instance, showed that not all knowledge is equally shared [91]. More specifically, results show that medicinal plants were mostly shared between spouses and kin, while plants that serve other functions were shared much more widely. This suggests that knowledge-sharing networks are content-specific and supports the idea that hunter-gatherer multi-level 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. Contact between different ethnolinguistic groups, for instance, can potentially bring different cultural traits together due to significant between-group cultural distance. However, language barriers, endogamy, rivalry and other behavioural 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 ties (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. Anthropological studies, for instance, 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 individuals form ties ultimately feeds back into the evolution of social networks (homophily, for instance, 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 seems 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 has been 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 behavioural choices (e.g. adjustments to out-group contacts due to perceived immediate benefits) and/or unconscious influence on behaviour (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 behavioural barriers that tend to reduce opportunities for cultural transmission between unrelated individuals. Moreover, increasing contacts is only one part of the problem, as 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]. Among the Ache and Hadza, for instance, ritual relationships, mediated by activities such as club fight rituals, have been shown to promote inter-band interaction. Quantitative analyses have revealed that ritual relationship is a more important predictor than kinship for different types of interactions, 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 to other groups [101]. This suggests that groups that possess cultural institutions that promote information sharing and/or mobility might have attained higher cultural complexity and outcompeted groups with cultures less conducive to CCE [17, 101]. It is also worth noting that 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]. Kin naming systems, for instance, 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 nor physical cohabitation [104].

The question of whether humans' social structure might in part result 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. Archeologists, for instance, 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. The hypothesis that CCE directly shapes network structure by acting on conscious behavioural choices, for instance, 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 (Box 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 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 might 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 the 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.

## 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 possesses 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, warm clothing) around 10-12kya 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 possesses 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 processes. Learning error, determined by $\alpha$, 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 naive individual is drawn from a Gumbel distribution (Figure 1). 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 sub-populations show that increasing the migration rate has a similar effect to increasing the size of an isolated population on CCE, because both increase variation within sub-populations and so reduce the risk of losing cultural information [13]. Recent studies have more explicitly modelled the pathways that give rise to innovation and revealed that the effect of migration can even be 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].

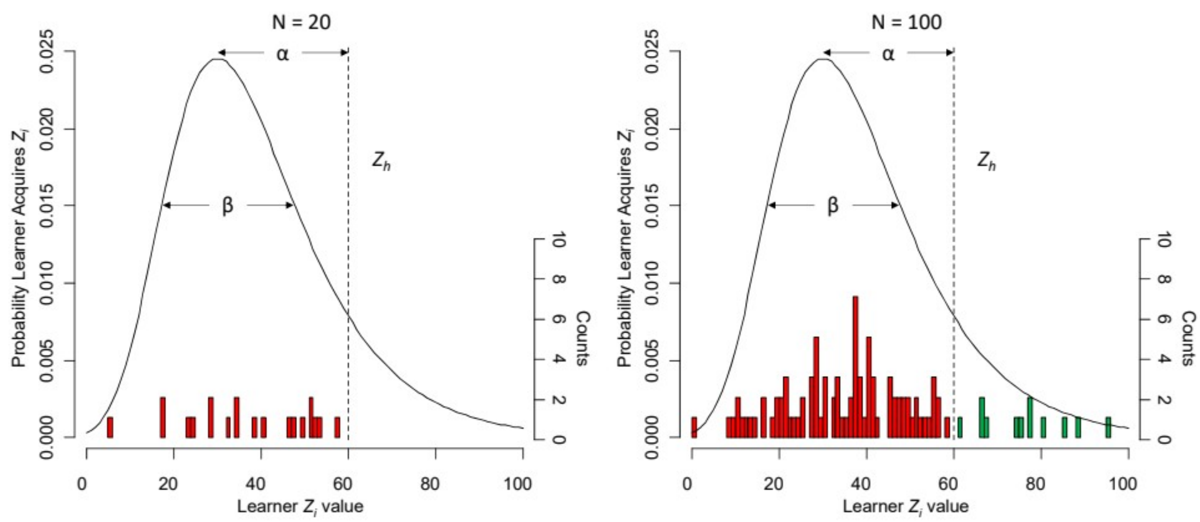


**Figure 1**: **Gumbel distribution from Henrich’s Tasmanian model**

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 $\alpha$, 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 each 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 $z_h$. On the left, a small population (N=20) results in a population-level decline in skill, as no learner matches or exceeds $z_h$. On the right, a large population (N=100) features some learners who exceed $z_h$, resulting in an improvement in the next generation.

## Box 2: Linking models and data in the lab

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 behaviour (rather than modellers' assumptions about human behaviour) [111, 112].

As noted in the main text, the majority of 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 remarkably diverse in experimental tasks, group sizes and inter-individual interactions. Yet, it is worth highlighting that most experimental designs significantly deviate from the models they claim to test. In the main text we discuss 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 (see Box 1). 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). 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 which they cite.

Maybe 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. A recent experiment, for instance, had chains of participants make and throw paper airplanes, with each participant able to learn from 1, 2 or 4 previous participants [33]. Apparently contrary to the demographic hypothesis, flight distance only increased in the 1-demonstrator condition, not the 2- and 4-demonstrator conditions. Yet 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 minutes each. Yet, Henrich's model 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. Fay et al.'s results are consistent with the former in showing that larger groups produce greater variation in distance flight and give participants access to more efficient planes. But the constraints imposed on social learning strategies inhibited 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.

## Box 3: Linking models and data in the wild

Several studies have investigated whether there exists 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 in real world data.

One difficulty concerns limitations in what can be measured [58]. Henrich's model (see Box 1) describes the level of skill of an individual within a population, a variable that in an archaeological context can be interpreted as the number of tools or tool components attributable to an individual. Yet, archaeological 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 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 archaeological studies. In the main text we discuss 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]. Some models, for instance, 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 archaeologists 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 archaeologists 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].

## 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 2A-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. Previous work has shown, for instance, 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.

Maybe 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 2C).

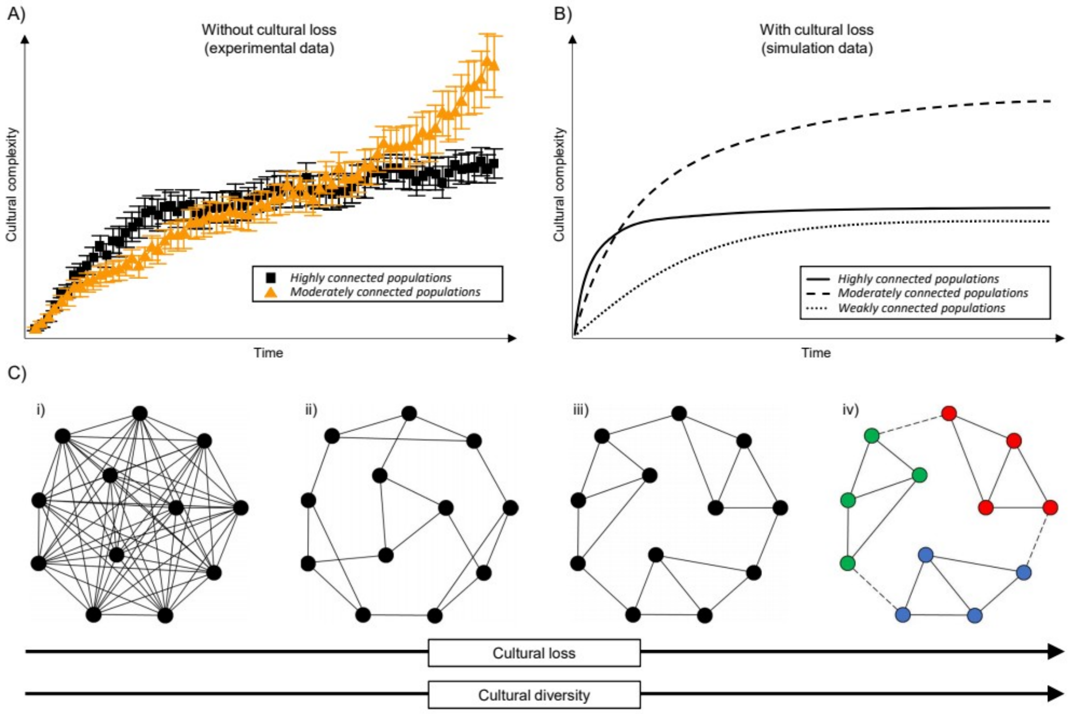


**Figure 2: Trading cultural loss and diversity in structured populations.** (A) Experimental results show that moderately connected populations are slower at accumulating innovations but eventually reach higher levels of cultural complexity than highly connected populations when innovation depends on cultural diversity. Adapted from [67]. (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). Adapted from [69]. (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 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 composed of 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) but also more likely to suffer from cultural loss.

## Glossary

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

**Cumulative cultural evolution (CCE):** the repeated modification and social learning of behavioural 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)

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

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

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

**Tasmanian model:** an influential early model of how population size constrains CCE (see Box 1)

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

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

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

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

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

**Acknowledgments**

We thank four reviewers and Rob Boyd for valuable comments on the manuscript. MD thanks Alex Alvergne, Slimane Dridi and Vivek Venkataraman for helpful discussions. This work was supported by the French Agence Nationale de la Recherche (under the Investissement d'Avenir programme ANR 17-EURE-0010) and the European Union's Horizon 2020 research and innovation programme (under Marie Sklodowska-Curie grant agreement number 748310).

## References


1. Richerson, P.J. and Boyd, R. (2005) Not by genes alone, University of Chicago Press.

2. Henrich, J. (2015) The secret of our success: how culture is driving human evolution, domesticating our species, and making us smarter, Princeton University Press.

3. Boyd, R. et al. (2011) The cultural niche: Why social learning is essential for human adaptation. Proceedings of the National Academy of Sciences of the United States of America 108, 10918-10925.

4. Boyd, R. et al. (2013) The cultural evolution of technology: facts and theories. Cultural evolution: society, technology, language, and religion, 119-142.

5. Mesoudi, A. and Thornton, A. (2018) What is cumulative cultural evolution? Proceedings of the Royal Society B: Biological Sciences 285 (1880), 20180712.

6. Derex, M. et al. (2019) Causal understanding is not necessary for the improvement of culturally evolving technology. Nature Human Behaviour 3 (5), 446-452.

7. Muthukrishna, M. and Henrich, J. (2016) Innovation in the collective brain. Philosophical Transactions of the Royal Society of London B: Biological Sciences 371 (1690).

8. Cavalli-Sforza, L.L. and Feldman, M.W. (1981) Cultural transmission and evolution: A quantitative approach, Princeton University Press.

9. Boyd, R. and Richerson, P.J. (1985) Culture and the evolutionary process, University of Chicago Press.

10. Mesoudi, A. (2011) Cultural Evolution: How Darwinian Theory Can Explain

Human Culture and Synthesize the Social Sciences, University of Chicago Press.

11. Henrich, J. (2004) Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses - The Tasmanian case. American Antiquity 69 (2), 197-214.

12. Eerkens, J.W. and Lipo, C.P. (2007) Cultural Transmission Theory and the Archaeological Record: Providing Context to Understanding Variation and Temporal Changes in Material Culture. Journal of Archaeological Research 15 (3), 239-274.

13. Powell, A. et al. (2009) Late Pleistocene Demography and the Appearance of Modern Human Behavior. Science 324 (5932), 1298-1301.

14. Marquet, P.A. et al. (2012) Emergence of social complexity among coastal hunter-gatherers in the Atacama Desert of northern Chile. Proceedings of the National Academy of Sciences 109 (37), 14754-14760.

15. French, J.C. (2016) Demography and the Palaeolithic Archaeological Record. Journal of Archaeological Method and Theory 23 (1), 150-199.

16. Mackay, A. et al. (2014) Coalescence and fragmentation in the late Pleistocene archaeology of southernmost Africa. Journal of Human Evolution 72, 26-51.

17. Greenbaum, G. et al. (2019) Was inter-population connectivity of Neanderthals and modern humans the driver of the Upper Paleolithic transition rather than its product? Quaternary Science Reviews 217, 316-329.

18. Kuhn, S.L. (2012) Emergent Patterns of Creativity and Innovation in Early Technologies. In Developments in Quaternary Sciences (Elias, S. ed), pp. 69-87, Elsevier.

19. Riede, F. (2009) The loss and re-introduction of bow-and-arrow technology: a

case study from the Northern European Late Paleolithic. Lithic Technology 34 (1), 27-45.

20. Jones, R. (1973) Emerging Picture of Pleistocene Australians. Nature 246 (5431), 278-281.

21. Cavalli-Sforza, L. and Feldman, M.W. (1973) Models for cultural inheritance I. Group mean and within group variation. Theoretical Population Biology 4 (1), 42-55.

22. Neiman, F.D. (1995) Stylistic Variation in Evolutionary Perspective: Inferences from Decorative Diversity and Interassemblage Distance in Illinois Woodland Ceramic Assemblages. American Antiquity 60 (1), 7-36.

23. Shennan, S. (2001) Demography and Cultural Innovation: a Model and its Implications for the Emergence of Modern Human Culture. Cambridge Archaeological Journal 11 (01), 5-16.

24. Tomasello, M. et al. (1993) Cultural Learning. Behavioral and Brain Sciences 16 (3), 495-511.

25. Tennie, C. et al. (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. Philosophical Transactions of the Royal Society B-Biological Sciences 364 (1528), 2405-2415.

26. Lewis, H.M. and Laland, K.N. (2012) Transmission fidelity is the key to the build-up of cumulative culture. Philosophical Transactions of the Royal Society B-Biological Sciences 367 (1599), 2171-2180.

27. Derex, M. et al. (2013) Experimental evidence for the influence of group size on cultural complexity. Nature 503, 389-391.

28. Wisdom, T.N. et al. (2013) Social Learning Strategies in Networked Groups.

Cognitive Science 37 (8), 1383-1425.
29. Muthukrishna, M. et al. (2014) Sociality influences cultural complexity. Proceedings of the Royal Society B: Biological Sciences 281 (1774), 20132511.
30. Kempe, M. and Mesoudi, A. (2014) An experimental demonstration of the effect of group size on cultural accumulation. Evolution and Human Behavior 35 (4), 285-290.
31. Derex, M. and Boyd, R. (2015) The foundations of the human cultural niche. Nat Commun 6, 8398.
32. Caldwell, C.A. and Millen, A.E. (2010) Human cumulative culture in the laboratory: Effects of (micro) population size. Learning & Behavior 38 (3), 310-318.
33. Fay, N. et al. (2019) Increasing population size can inhibit cumulative cultural evolution. Proceedings of the National Academy of Sciences, 201811413.
34. Kline, M.A. and Boyd, R. (2010) Population size predicts technological complexity in Oceania. Proceedings of the Royal Society B-Biological Sciences 277 (1693), 2559-2564.
35. Collard, M. et al. (2013) Population Size and Cultural Evolution in Nonindustrial Food-Producing Societies. PLOS ONE 8 (9), e72628.
36. Collard, M. et al. (2005) Causes of Toolkit Variation Among Hunter-Gatherers: A Test of Four Competing Hypotheses. Canadian Journal of Archaeology / Journal Canadien d'Archéologie 29 (1), 1-19.
37. Collard, M. et al. (2013) Risk, mobility or population size? Drivers of technological richness among contact-period western North American hunterâ€“gatherers. Philosophical Transactions of the Royal Society B: Biological

Sciences 368 (1630).

38. Collard, M. et al. (2013) Population Size as an Explanation for Patterns in the Paleolithic Archaeological Record: More Caution Is Needed. Current Anthropology 54 (S8), S388-S396.

39. Buchanan, B. et al. (2015) Drivers of technological richness in prehistoric Texas: an archaeological test of the population size and environmental risk hypotheses. Archaeological and Anthropological Sciences, 1-10.

40. Henrich, J. et al. (2016) Understanding cumulative cultural evolution. Proceedings of the National Academy of Sciences 113 (44), E6724-E6725.

41. Acerbi, A. et al. (2017) Cultural complexity and demography: The case of folktales. Evolution and Human Behavior 38 (4), 474-480.

42. Arthur, W.B. (2009) The nature of technology: What it is and how it evolves, Simon and Schuster.

43. Nettle, D. (1995) Segmental inventory size, word length, and communicative efficiency. Linguistics 33 (2), 359-367.

44. Hay, J. and Bauer, L. (2007) Phoneme Inventory Size and Population Size. Language 83 (2), 388-400.

45. Moran, S. et al. (2012) Revisiting population size vs. phoneme inventory size. Language, 877-893.

46. Wichmann, S. et al. (2011) Phonological diversity, word length, and population sizes across languages: The ASJP evidence. 15 (2), 177.

47. Wichmann, S. and Holman, E.W. (2009) Population Size and Rates of Language Change. Human Biology 81 (3), 259-274, 16.

48. Bromham, L. et al. (2015) Rate of language evolution is affected by population size. Proceedings of the National Academy of Sciences.

49. Greenhill, S.J. et al. (2018) Population Size and the Rate of Language Evolution: A Test Across Indo-European, Austronesian, and Bantu Languages. Frontiers in Psychology 9 (576).

50. Kirby, S. et al. (2008) Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. Proceedings of the National Academy of Sciences of the United States of America 105 (31), 10681-10686.

51. McElreath, R. et al. (2003) Shared norms and the evolution of ethnic markers. Current Anthropology 44 (1), 122-129.

52. Rogers, D.S. and Ehrlich, P.R. (2008) Natural selection and cultural rates of change. Proceedings of the National Academy of Sciences of the United States of America 105 (9), 3416-3420.

53. Vaesen, K. et al. (2016) Population size does not explain past changes in cultural complexity. Proceedings of the National Academy of Sciences 113 (16), E2241-E2247.

54. Torrence, R. (1989) Re-tooling: towards a behavioral theory of stone tools. Time, energy and stone tools, 57-66.

55. Collard, M. et al. (2011) What drives the evolution of hunter-gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. Philosophical Transactions of the Royal Society B: Biological Sciences 366 (1567), 1129-1138.

56. Grove, M. (2018) Hunter-gatherers adjust mobility to maintain contact under climatic variation. Journal of Archaeological Science: Reports 19, 588-595.

57. Kobayashi, Y. and Aoki, K. (2012) Innovativeness, population size and cumulative cultural evolution. Theoretical Population Biology 82 (1), 38-47.

58. Aoki, K. (2018) On the absence of a correlation between population size and 'toolkit size' in ethnographic hunter-gatherers. Philosophical Transactions of the Royal Society B: Biological Sciences 373 (1743), 20170061.

59. Lehmann, L. et al. (2011) On the number of independent cultural traits carried by individuals and populations. Philosophical Transactions of the Royal Society B: Biological Sciences 366 (1563), 424-435.

60. Vaesen, K. (2012) Cumulative Cultural Evolution and Demography. Plos One 7 (7).

61. Mesoudi, A. (2011) Variable Cultural Acquisition Costs Constrain Cumulative Cultural Evolution. Plos One 6 (3), e18239.

62. Kolodny, O. et al. (2015) Evolution in leaps: The punctuated accumulation and loss of cultural innovations. Proceedings of the National Academy of Sciences 112 (49), E6762-E6769.

63. Fogarty, L. and Creanza, N. (2017) The niche construction of cultural complexity: interactions between innovations, population size and the environment. Philosophical Transactions of the Royal Society B: Biological Sciences 372 (1735), 20160428.

64. Fogarty, L. et al. (2017) The Driving Forces of Cultural Complexity. Human Nature 28 (1), 39-52.

65. Aoki, K. (2019) Cultural bistability and connectedness in a subdivided population. Theoretical Population Biology.

66. Bentley, R.A. and O'brien, M.J. (2011) The selectivity of social learning and the tempo of cultural evolution. Journal of Evolutionary Psychology 9 (2), 125-141.

67. Derex, M. and Boyd, R. (2016) Partial connectivity increases cultural accumulation within groups. Proceedings of the National Academy of Sciences 113 (11), 2982-2987.

68. Creanza, N. et al. (2017) Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. Journal of The Royal Society Interface 14 (130).

69. Derex, M. et al. (2018) Divide and conquer: intermediate levels of population fragmentation maximize cultural accumulation. Philosophical Transactions of the Royal Society B: Biological Sciences 373 (1743), 20170062.

70. Lazer, D. and Friedman, A. (2007) The Network Structure of Exploration and Exploitation. Administrative Science Quarterly 52 (4), 667-694.

71. Fang, C. et al. (2009) Balancing Exploration and Exploitation Through Structural Design: The Isolation of Subgroups and Organizational Learning. Organization Science 21 (3), 625-642.

72. Mason, W.A. et al. (2008) Propagation of innovations in networked groups. Journal of Experimental Psychology: General 137 (3), 422-433.

73. Mason, W. and Watts, D.J. (2012) Collaborative learning in networks. Proceedings of the National Academy of Sciences 109 (3), 764-769.

74. Barkoczi, D. and Galesic, M. (2016) Social learning strategies modify the effect

of network structure on group performance. Nature Communications 7 (1), 13109.

75. Burt, R.S. (2004) Structural Holes and Good Ideas. American Journal of Sociology 110 (2), 349-399.

76. Flynn, E. and Whiten, A. (2010) Studying children's social learning experimentally "in the wild". Learning & Behavior 38 (3), 284-296.

77. Centola, D. and Macy, M. (2007) Complex Contagions and the Weakness of Long Ties. American Journal of Sociology 113 (3), 702-734.

78. Carja, O. and Creanza, N. (2019) The evolutionary advantage of cultural memory on heterogeneous contact networks. Theoretical Population Biology 129, 118-125.

79. Malinsky-Buller, A. and Hovers, E. (2019) One size does not fit all: Group size and the late middle Pleistocene prehistoric archive. Journal of Human Evolution 127, 118-132.

80. Mazet, O. et al. (2016) On the importance of being structured: instantaneous coalescence rates and human evolution—lessons for ancestral population size inference? Heredity 116 (4), 362-371.

81. Kovacevic, M. et al. (2015) Simulating Geographical Variation in Material Culture: Were Early Modern Humans in Europe Ethnically Structured? In Learning Strategies and Cultural Evolution during the Palaeolithic (Mesoudi, A. and Aoki, K. eds), pp. 103-120, Springer Japan.

82. Mills, B.J. (2017) Social Network Analysis in Archaeology. Annual Review of Anthropology 46 (1), 379-397.

83. Peeples, M.A. (2019) Finding a Place for Networks in Archaeology. Journal of Archaeological Research 27 (4), 451-499.

84. Romano, V. et al. (2020) A multilevel analytical framework for studying cultural evolution in prehistoric hunter–gatherer societies. Biological Reviews n/a (n/a).

85. Chapais, B. (2013) Monogamy, strongly bonded groups, and the evolution of human social structure. Evolutionary Anthropology: Issues, News, and Reviews 22 (2), 52-65.

86. Hill, K.R. et al. (2011) Co-Residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure. Science 331 (6022), 1286-1289.

87. Hill, K.R. et al. (2014) Hunter-Gatherer Inter-Band Interaction Rates: Implications for Cumulative Culture. PLoS ONE 9 (7), e102806.

88. Bird, D.W. et al. (2019) Variability in the organization and size of hunter-gatherer groups: Foragers do not live in small-scale societies. Journal of Human Evolution 131, 96-108.

89. Migliano, A.B. et al. (2017) Characterization of hunter-gatherer networks and implications for cumulative culture. Nature Human Behaviour 1 (2), 0043.

90. Migliano, A.B. et al. (2020) Hunter-gatherer multilevel sociality accelerates cumulative cultural evolution. Science Advances 6 (9), eaax5913.

91. Salali, Gul D. et al. (2016) Knowledge-Sharing Networks in Hunter-Gatherers and the Evolution of Cumulative Culture. Current Biology 26 (18), 2516-2521.

92. Durham, W.H. (1992) Applications of Evolutionary Culture Theory. Annual Review of Anthropology 21, 331-355.

93. Tehrani, J.J. and Collard, M. (2013) Do Transmission Isolating Mechanisms (TRIMS) Influence Cultural Evolution?, Berghahn.

94. Apicella, C.L. et al. (2012) Social networks and cooperation in hunter-gatherers.

Nature 481 (7382), 497-U109.
95. Centola, D. et al. (2007) Homophily, cultural drift, and the co-evolution of cultural groups. Journal of Conflict Resolution 51 (6), 905-929.
96. Kandler, A. and Caccioli, F. (2016) Networks, homophily, and the spread of innovations. In The connected past: Challenges to network studies in archaeology and history, pp. 175-198, Oxford Univ. Press.
97. Smolla, M. and Akçay, E. (2019) Cultural selection shapes network structure. Science Advances 5 (8), eaaw0609.
98. Henrich, J. and Gil-White, F.J. (2001) The evolution of prestige - Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. Evolution and Human Behavior 22 (3), 165-196.
99. Mesoudi, A. (2008) An experimental simulation of the "copy-successful-individuals" cultural learning strategy: adaptive landscapes, producer-scrounger dynamics, and informational access costs. Evolution and Human Behavior 29 (5), 350-363.
100. Derex, M. et al. (2014) How does competition affect the transmission of information? Evolution and Human Behavior 35 (2), 89-95.
101. Henrich, J. (2009) The Evolution of Innovation-Enhancing Institutions. In Innovation in Cultural Systems: Contributions in Evolution Anthropology (Shennan, S.J. and O'Brien, M.J. eds), MIT.
102. Wiessner, P. (1981) Hxaro: A Regional System of Reciprocity for Reducing Risk Among the !Kung San, University of Michigan.
103. Wiessner, P. (1997) Seeking guidelines through an evolutionary approach: style

revisited among the! Kung San (Ju/'hoansi) of the 1990s. Archeological Papers of the American Anthropological Association 7 (1), 157-176.

104. Machin, A. and Dunbar, R. (2016) Is Kinship a Schema? Moral Decisions and the Function of the Human Kin Naming System. Adaptive Human Behavior and Physiology 2 (3), 195-219.

105. Langergraber, K.E. et al. (2007) The limited impact of kinship on cooperation in wild chimpanzees. Proceedings of the National Academy of Sciences 104 (19), 7786-7790.

106. Lewis, H.M. et al. (2014) High mobility explains demand sharing and enforced cooperation in egalitarian hunter-gatherers. Nature Communications 5 (1), 5789.

107. Macfarlan, S.J. et al. (2014) Lethal coalitionary aggression and long-term alliance formation among Yanomamö men. Proceedings of the National Academy of Sciences 111 (47), 16662-16669.

108. Bentley, R.A. et al. (2004) Random drift and culture change. Proceedings of the Royal Society of London. Series B: Biological Sciences 271 (1547), 1443-1450.

109. Bell, A.V. (2015) Linking Observed Learning Patterns to the Evolution of Cultural Complexity. Current Anthropology 56 (2), 277-281.

110. Andersson, C. and Read, D. (2016) The Evolution of Cultural Complexity: Not by the Treadmill Alone. Current Anthropology 57 (3), 261-286.

111. Mesoudi, A. (2007) Using the methods of experimental social psychology to study cultural evolution. Journal of Social, Evolutionary, and Cultural Psychology 1 (2), 35-58.

112. Mesoudi, A. and Whiten, A. (2008) The multiple roles of cultural transmission

experiments in understanding human cultural evolution. Philosophical Transactions of the Royal Society B-Biological Sciences 363 (1509), 3489-3501.

113. Enquist, M. et al. (2011) Modelling the evolution and diversity of cumulative culture. Philosophical Transactions of the Royal Society B-Biological Sciences 366 (1563), 412-423.

114. Basalla, G. (1988) The evolution of technology, UK: Cambridge University Press.

115. Fleming, L. (2001) Recombinant Uncertainty in Technological Search. Management Science 47 (1), 117-132.

116. Fogarty, L. (2018) Cultural complexity and evolution in fluctuating environments. Philosophical Transactions of the Royal Society B: Biological Sciences 373 (1743), 20170063.

117. Enquist, M. et al. (2008) Why does human culture increase exponentially? Theoretical Population Biology 74 (1), 46-55.

118. Kolodny, O. et al. (2016) Game-Changing Innovations: How Culture Can Change the Parameters of Its Own Evolution and Induce Abrupt Cultural Shifts. PLOS Computational Biology 12 (12), e1005302.

119. Premo, L.S. (2012) Local extinctions, connectedness, and cultural evolution in structured populations. Advances in Complex Systems 15 (01n02), 1150002.

120. Watts, D.J. and Strogatz, S.H. (1998) Collective dynamics of ‘small-world’ networks. Nature 393 (6684), 440-442.