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Divide and conquer: intermediate levels of population fragmentation maximize cultural accumulation

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Identifying the determinants of cumulative cultural evolution is a key issue in the interdisciplinary field of cultural evolution. A widely held view is that large and well-connected social networks facilitate cumulative cultural evolution because they promote the spread of useful cultural traits and prevent the loss of cultural knowledge through factors such as drift. This view stems from models that focus on the transmission of cultural information, without considering how new cultural traits actually arise. In this paper, we review the literature from various fields that suggest that, under some circumstances, increased connectedness can decrease cultural diversity and reduce innovation rates. Incorporating this idea into an agent-based model, we explore the effect of population fragmentation on cumulative culture and show that, for a given population size, there exists an intermediate level of population fragmentation that maximizes the rate of cumulative cultural evolution. This result is explained by the fact that fully connected, non-fragmented populations are able to maintain complex cultural traits but produce insufficient variation and so lack the cultural diversity required to produce highly complex cultural traits. Conversely, highly fragmented populations produce a variety of cultural traits but cannot maintain complex ones. In populations with intermediate levels of fragmentation, cultural loss and cultural diversity are balanced in a way that maximizes cultural complexity. Our results suggest that population structure needs to be taken into account when investigating the relationship between demography and cumulative culture.

This article is part of the theme issue 'Bridging cultural gaps: interdisciplinary studies in human cultural evolution'.

1. Introduction

From the accumulation of innovations driving the emergence of complex technologies to the accumulation of knowledge paving the way to increasingly accurate scientific theories, cumulative cultural evolution has set the stage for the remarkable ecological success of our species. Thus, identifying the determinants of cumulative cultural evolution is a key issue in the interdisciplinary field of cultural evolution.

Much interest has focused on demography as a determinant of the rate of cumulative evolution [1–15]. In general, larger populations are thought to facilitate cumulative cultural evolution because they host a larger number of innovators and are less likely to suffer from random loss or incomplete transmission of cultural traits.

A number of empirical studies have explored the relationship between population size and cultural complexity. Results have been mixed: some studies reported an effect in line with theoretical expectations [3,4] while others found no effect [16–18]. These inconsistencies have raised concerns among some scholars about the veracity of the link between population size and cultural complexity [19–21]. However, others have stressed that theoretical models specifically predict a positive relationship between cultural complexity and the *effective* population size, i.e. the size of the population that shares information [2,22]. Empirical studies that used *census* population size, i.e. the estimated size of a particular group without taking into account contacts with other groups, should thus be interpreted with caution. When tested under controlled conditions, the positive relationship between population size and cultural complexity is well supported: a growing body of laboratory experiments show that groups composed of a larger number of individuals produce more complex cultural traits than smaller groups [9–12].

A recent experimental study, however, suggests that partially connected groups produce more complex cultural traits than fully connected groups of the same size when innovation depends of the recombination of existing cultural traits [13]. These results seem to be at odds with theoretical models of cultural evolution that predict that increasing the degree of connectedness, whether within or between populations, will positively affect a population's ability to accumulate cultural information. Increasing the degree of connectedness, the argument goes, gives individuals access to a larger number of social models and promotes individuals' opportunity to build upon each other's solutions [1–3,9]. Most models of cultural evolution, however, focus on the transmission of cultural traits, without considering the processes underlying the production of new traits. For instance, many models fail to capture the fact that rates of innovations are determined, in part, by the level of cultural diversity that exists in a population.

In many fields, population structure is considered as a strong driver of the amount of diversity that exists in a population. Population geneticists, most notably Sewall Wright, have emphasized how populations subdivided into small and partially isolated subgroups would explore a more diverse set of solutions than populations with unconstrained gene flow [23]. Similarly, organization scientists have shown that groups that are well connected tend to lose cultural diversity faster than less-connected groups because individuals' propensity to learn from successful cultural models cause the entire population to converge rapidly on the same solution [24–27].

In this paper, we argue that population structure is likely to critically affect cumulative culture through its effects on both production and maintenance of innovations. First, there exists a relationship between population connectedness and the exploration of the design space [13,24,25,27]. This suggests that populations subdivided into partially isolated subgroups will produce more diverse cultural traits than fully connected populations. Second, evidence from various fields suggests that innovation rates are affected by the level of cultural diversity that exists in a population [28]. This suggests that populations divided into partially isolated subgroups will exhibit more innovative abilities than fully connected populations. Third, theoretical and experimental studies of cultural evolution show that there is a relationship between the size of a population and its ability to maintain complex cultural traits [1,2,9]. This suggests that populations divided into partially isolated subgroups will be less likely to maintain complex cultural traits than fully connected populations.

In the following sections, we aim at incorporating these different ideas within a single cultural-evolution framework to investigate the effect of population fragmentation on cumulative culture. We begin by reviewing the literature from various fields to highlight how increasing connectedness can decrease cultural diversity and stifle populations' innovative ability. We then use a simple agent-based model to show that for a given population size, there exists an intermediate level of population fragmentation that maximizes cumulative cultural evolution. Finally, we discuss the relevance of considering population fragmentation to explain patterns of cultural change in a wide range of contexts.

2. The benefits of reduced connectedness on cultural diversity

Agent-based models from organization science show that population structure affects individuals' ability to solve problems associated with rugged fitness landscapes. Rugged fitness landscapes are hard to search because they have multiple peaks and so it is easy to get stuck at a local maximum. In fully connected populations, individuals are more likely to observe, and imitate, the same set of successful models, which can cause the entire population to converge rapidly to a suboptimal peak. In less-connected populations, individuals observe only a subset of cultural models and so do not benefit from the same cultural information. This can lead to more thorough exploration of the design space because it reduces populations' probability of prematurely converging on suboptimal solutions [24,25,27].

Models investigating search in rugged landscapes differ from models of cumulative cultural evolution because they assume landscapes with a limited set of solutions and they focus on identifying the conditions that allow a population to find the most rewarding solution. By contrast, models of cumulative culture aim to capture an open-ended process that generates increasingly complex solutions. The ultimate goal of these models is to identify the conditions that promote the production and maintenance of complex cultural traits. Nevertheless, the literature about search in rugged landscapes can inform cultural evolution theory because the production of complex cultural traits can benefit from thorough exploration of the cultural landscape.

Economists have pointed out that among all the possible directions technological development may take, only a small portion is ever realized [29]. Furthermore, it has been acknowledged that evolutionary change exhibits *path dependence* because early innovations constrain the future direction of change [30–33] (the notion is similar to what evolutionary biologists call *phylogenetic inertia* [34]). The QWERTY keyboard, for example, was invented in order to prevent jamming of the keys in the case of mechanical typewriting. With the invention of computer keyboards, the jamming problem disappeared but the QWERTY layout persists nowadays despite more efficient solutions [35].

In models of search in complex landscapes, some structural isolation is beneficial because it promotes the exploration of several peaks and increases the population's likelihood of finding the highest peak. In an open-ended landscape, it suggests that populations subdivided into partially isolated subgroups should explore a more diverse set of trajectories than fully connected populations do. Moreover, in a cumulative framework, the partial isolation of subgroups might result in a feedback loop between cultural diversity and innovation because occasional contacts between groups will bring a variety of cultural traits together and will promote combinatorial opportunities.

3. The making of new knowledge

Economists studying the evolution of technology have long stressed the importance of the horizontal transfer of knowledge and innovations between different, but complementary, technological trajectories (e.g. [29,36,37]).

Such transfers can take place between related trajectories [38–40]. For instance, phylogenetic analyses show that the evolution of the cornet, a brass wind musical instrument, was propelled by horizontal transfers between different coexisting types of cornets, as were other musical instruments such as the Baltic psaltery, a plucked stringed instrument [38]. Horizontal transfers between related lineages have also been documented among modern technologies such as programming languages [39]. The incorporation of solutions from different lineages is actually so common in the evolution of material culture that it limits the relevance of using biological phylogenetic methodology to infer historical patterns of material culture [41].

Recombination and horizontal transfer can also take place between unrelated branches of knowledge [42]. For instance, in order to invent the electric light, Thomas Edison combined innovations made in electricity generation, the manufacture of conducting filaments and the removing of gas molecules from sealed volumes [36]. Barely modified traits can also serve a new function in a different domain. For example, pintle and gudgeon hinges that were used to mount sternpost rudders on medieval sailing boats during the late thirteenth century were borrowed from newly developed iron hinges from large castle and cathedral doors [43].

But the merging of knowledge extends well beyond the domain of technology. Science, for example, benefits from borrowing ideas, concepts and methods between disciplines [44]. An analysis of 17.9 million academic papers shows that the papers that are built upon unusual combination of prior knowledge (e.g. work from unrelated disciplines) are more likely to have a high impact [45]. Similarly, economics and social psychology studies suggest that exposure to foreign cultures fosters innovation. Skilled migrants have been shown to positively contribute to knowledge creation in host countries (measured either by the number of patents applied for or by the number of citations to published articles) [46]. Consistently, experiments showed that ethnically diverse groups can generate better ideas than homogeneous groups during brainstorming sessions [47] and that studying abroad positively affects creative thinking among Western students [48].

These studies suggest that innovation is fuelled by the combination of unrelated bodies of skills, technology and knowledge. This, in turn, indicates that a population's ability to innovate should depend on how culturally diverse it is.

4. The trade-off between innovation, production and maintenance

Models of cumulative cultural evolution aim at identifying the conditions promoting the evolution of complex cultural traits. So far, we have suggested that low levels of connectedness might increase the production of new cultural traits because structural isolation promotes cultural diversity and combinatorial opportunities. However, theoretical models suggest that populations composed of partially isolated subgroups will be more likely to suffer from random loss of cultural traits than well-connected populations because the probability of inaccurate transmission is negatively related to the number of cultural learners [1,2]. In less-connected networks, information travels slower so that fewer individuals will be exposed to novel adaptive cultural traits. Experimental studies of cultural evolution demonstrated that cultural traits are more likely to become deteriorated, or even lost, when groups of cultural learners are small [9,11].

These facts suggest that population fragmentation is a double-edged sword. On the one hand, it allows the production of more complex cultural traits, and on the other hand, it restrains populations' ability to maintain these traits. This suggests that for any given population size, there should be an intermediate level of fragmentation that maximizes cumulative cultural evolution, by balancing cultural loss and cultural diversity.

5. Aims of the model

We use an agent-based model to explore the effects of population fragmentation on cultural accumulation. To do so, we integrate into a single cultural evolution framework the ideas discussed above and that are scattered across different fields. Studies from the field of organization science have explored the effect of population structure on the diversity of observed solutions. However, these studies are usually based on finite landscapes where cultural diversity only serves the pinpointing of an optimal solution [24,25,27]. The effects of connectedness on cultural diversity are also well known in the field of cultural diffusion but these models usually condition the act of copying on cultural similarity, or rates of adoption, rather than on the success of cultural models (e.g. [49]). Moreover, both these fields do not deal with cultural traits of varying complexity. Cultural-evolution models have extensively investigated the relationship between traits' complexity and their probability of being lost [1,2,50]. However, these models often neglect the processes that underlie the production of these traits. In particular, most of the existing models of cumulative cultural evolution do not account for how cultural diversity affects the production of new knowledge (e.g. [2,3,14]).

6. Model

We model cumulative cultural evolution as a walk on a tree in order to capture the idea that past innovations shape future evolution (figure 1). Each branch on the tree denotes a different trajectory and the nodes represent different cultural items. The hierarchical level at which an item lies specifies its complexity. From the base of the tree two alternative items of a complexity level of 1 can be produced, *A* and *B*. Each of these items can then be improved in two different ways. Item *A*, for example, can give rise to *AA* or *AB*, which are items with a complexity level of 2. Alternatively, item *B* can give rise to *BA* or *BB*. The number of cultural items that can be produced at any given level of complexity C equals 2^C as each new item opens two alternative pathways.

Highly complex items are composed of simpler items along the same trajectory. An increase in cultural complexity is represented as a climb up the tree, and cultural loss as a walk down it. This captures the fact that the accumulation of cultural traits leads to new branching possibilities, that is new opportunities for cultural diversity.

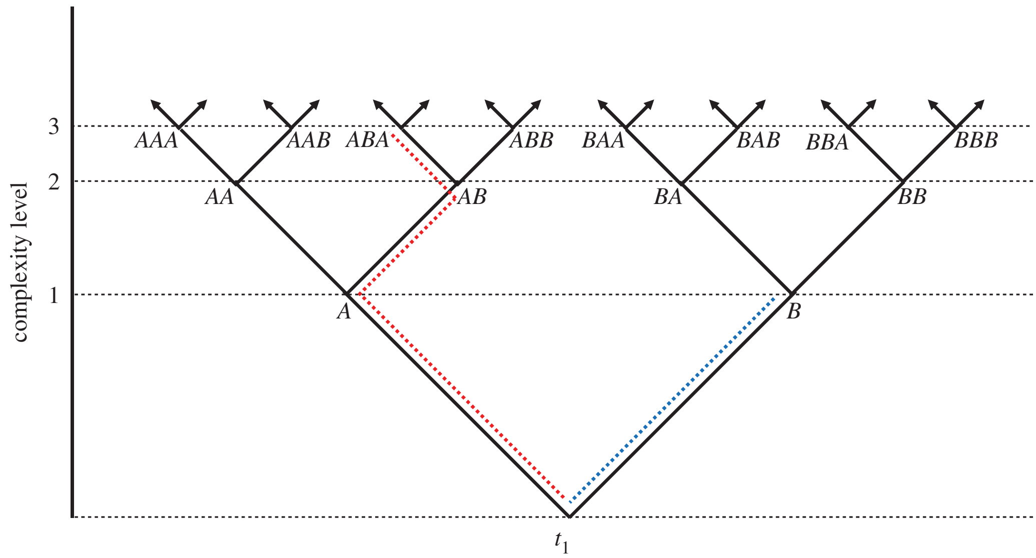

Figure 1. The cultural landscape is modelled as a branching tree. Each node represents a cultural item that can give rise to two new cultural items. More complex items are composed of an increasing number of sub-items. Progress along different trajectories leads to cultural divergence. The number of alternative items increases with cultural complexity according to 2^C. The coloured lines are examples of progression within the landscape. The individual in red produced *A* then *AB* then *ABA*. The diversity level of her cultural repertoire is 3 (she knows *A*, *AB* and *ABA*) and its complexity level is 3 (that is the complexity level of *ABA*, the most complex item in the repertoire). The individual in blue produced *B*. The diversity level of her cultural repertoire is 1 and its complexity level is 1. If these two individuals could learn from each other, they could end up with four items in their cultural repertoire (*A*, *AB*, *ABA* and *B*). The diversity level of their cultural repertoire would be 4 with a complexity level of 3 (as ABA is the most complex item of this repertoire). The number of cultural items that can be produced is theoretically unlimited.

In the model, cultural complexity refers to the level at which innovations lie in the tree-shaped landscape—climbing the tree means higher complexity. Cultural diversity refers to the number of nodes that are explored by a population and captures populations' ability to produce a variety of cultural items. Because groups can diverge, this model differs from cultural dissemination models where cultural diversity can only go down across time (e.g. [49]).

(a) Population structure

We simulated technological evolution in a population of size n and fragmented equally into f subpopulations. For instance, when $n = 600$ and $f = 1$, the population is composed of one single group of 600 individuals. Similarly, when $n = 600$ and $f = 5$, the population is composed of five subpopulations of 120 individuals each.

(b) Mechanics of the model

(i) Innovation

At the start of a simulation, individuals do not possess any cultural items. At the beginning of each time step, they innovate with probability p. Individuals innovate from their most complex item. If an individual possesses more than one item with the same level of complexity, she picks one randomly. When an innovation occurs, individuals acquire one of the two alternative solutions with the same probability. An individual having discovered item *B*, for example, can only produce *BA* or *BB* and not *AA* or *AB*. This simulates the effect of early innovation events on future direction of change and individuals' tendency for local search (empirical evidence from many fields suggests that individuals, and firms, tend to search locally for new solutions by building upon their established technology and expertise [36,51,52]). Thus, isolated individuals progress along a single trajectory and will not explore a diverse set of branches. Individuals, however, can acquire items from various branches through social learning although they always innovate from the most complex item in their toolkit. This captures the effect of specialized knowledge on innovation.

(ii) Social learning

After individuals have had a chance to innovate, they learn socially by copying the items of the members of their subpopulation. When individuals observe more than one technology belonging to the same technological trajectory, they adopt the most complex one. For instance, if individuals observe items *BBA* and *B*, they learn *BBA* (which includes *B*). Errors may occur during the social learning phase: individuals can fail to properly acquire an item and sometimes end up with a less complex form of that item. For example, an individual may observe item *AAA*, but end up with *AA* or even *A*. The extent of the error, i.e. the number of hierarchical levels that separates the item observed from the one learnt, is binomially distributed with parameter ϵ, a constant probability of error and a sample size equal to the complexity of the trait being innovated. Thus, the more complex an item is, the harder it is to learn accurately.

(iii) Connectedness

After the social learning phase, individuals visit other subgroups with probability m. When individuals visit a subpopulation, they choose one population randomly and spend the next time step in that subpopulation. After the next time step is over, visiting individuals return to their primary subgroup. For simplicity, individuals carry all their items when they visit.

(iv) Implementation of the dependence of innovation on cultural diversity

Our model aims to capture the idea that cultural diversity promotes opportunities to innovate. Cultural diversity can

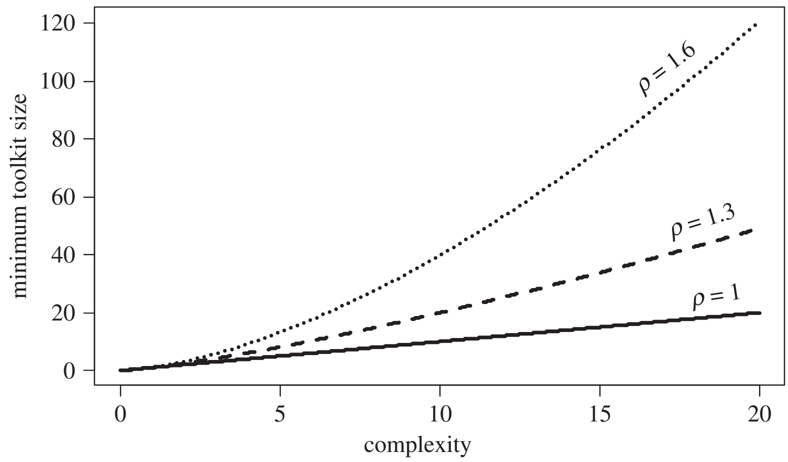

Figure 2. Minimum number of unique cultural items required to innovate, as a function of the level of complexity of the trait being innovated, for $\rho = 1$, 1.3 and 1.6. When $\rho = 1.3$, an individual needs at least eight different items in order to innovate on an item with a level of complexity of 5. When $\rho = 1.6$, an individual needs at least 13 different items.

promote innovation in many ways; however, for simplicity, we suppose that there is a positive relationship between cultural diversity and the opportunity to create complex traits. This assumption is based on the fact that higher amounts of cultural diversity create new combinatorial opportunities and more complex traits are as usually composed of an increasing number of sub-components.

The parameter ρ determines the minimum number of items that an individual has to possess in order to innovate, C^{ρ}, where C is the complexity of the item picked by the individual for innovation (figure 2).

When $\rho = 1$, cultural diversity does not affect innovation. Individuals can innovate without having any knowledge about other trajectories because any item is composed from a sufficient number of sub-items to match C^{ρ}. For instance, an individual who picked an item with a complexity level of 3 to innovate necessarily possesses a cultural repertoire of size 3 which is the number of items required to innovate when $\rho = 1$ (figure 1).

When $\rho > 1$, individuals must possess items from more than one branch in order to innovate. For example, if $\rho = 1.3$, an individual needs at least four different items in order to innovate on an item with a level of complexity of 3 (because $3^{1.3} \approx 4$). This condition cannot be met when individuals progress along a single trajectory (figure 1). When ρ increases, still more diversity has to be produced in order to innovate. For example, if $\rho = 1.6$, individuals need at least six different items in order to innovate on an item with a level of complexity of 3 (because $3^{1.6} \approx 6$). Thus, when ρ increases, generating innovations demands increasingly high levels of cultural diversity, and a population that specializes in one or just a small set of trajectories will soon be unable to produce innovations. Figure 2 shows how the minimum number of items required to innovate varies as a function of ρ and the complexity of the trait being innovated.

The diversity of individuals' cultural repertoires also affects social learning. Individuals can acquire new items through social learning only when they possess in their cultural repertoire the minimum number of items required to innovate, C_i^{ρ}, as described above. If they do not meet this requirement, individuals acquire the most complex item on the trajectory that their cultural repertoire can support. For example, if an individual observes *ABAA* (complexity level of 4) but has a cultural repertoire that is not diverse enough to produce traits of complexity level of 4, he will acquire a simpler version of that trait (such as *ABA*).

7. Results

(a) Fragmentation reduces cultural complexity when innovation does not depend on cultural diversity

When innovation does not depend on cultural diversity ($\rho = 1$), fragmentation results in lower levels of cultural complexity (figure 3). Fragmentation affects cumulative cultural evolution in two related ways. First, it slows down the spread of innovation between individuals, affecting individual's capacity to build upon each other's innovation and decreasing the pace of cumulative cultural evolution. Second, it affects populations' capacity to maintain complex items. When cultural items get more complex, they also get harder to learn. Because each individual has some probability of making learning errors, the probability of inaccurate transmission is negatively related to the number of cultural learners. Complex cultural traits can arise in fragmented populations but they are likely to quickly disappear because few individuals will be exposed to them, increasing the likelihood of failed transmission. More fragmented populations thus exhibit less complex cultural items when they reach their cultural complexity steady state.

Increasing the error rate ε does not qualitatively change these results. Higher rates of error lead to lower levels of cultural complexity in all populations because accurate learning events become uncommon at lower levels of cultural complexity (electronic supplementary material, figure S1). Changing the innovation probability, p, mainly affects the time it takes populations to reach their cultural steady state without affecting the level of cultural complexity (electronic supplementary material, figure S1).

These results are in line with most theoretical models and experimental studies that investigated the relationship between effective population size and cumulative culture [1–5,7–15]. For simplicity, we assume a constant error rate of 0.2 and a constant probability of innovation of 0.005 in the simulations below.

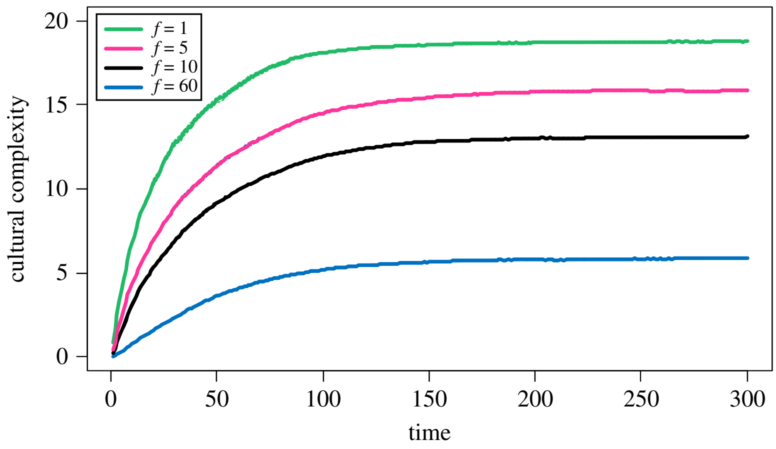

Figure 3. Effect of fragmentation (f) when innovation does not depend on cultural diversity ($\rho = 1$). When $\rho = 1$, cultural complexity, defined as the most complex cultural items possessed by individuals, is negatively affected by population fragmentation. Lines show the value ($\pm$s.e.m.) found after 300 time steps averaged over 30 simulations. Other parameters: $n = 600$, $p = 0.005$, $m = 0.01$, $\varepsilon = 0.2$.

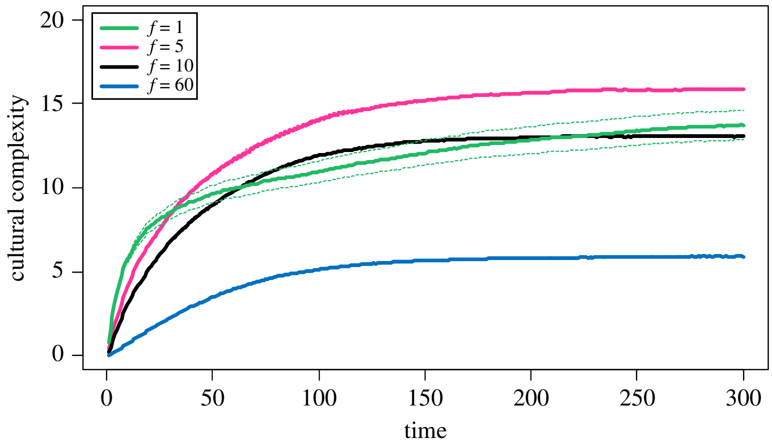

Figure 4. Effect of fragmentation (f) when innovation weakly depends on cultural diversity ($\rho = 1.3$). Weakly fragmented populations produce the most complex cultural items when innovation weakly depends on cultural diversity. This is because weakly fragmented populations ($f = 5$) are able to both stabilize complex cultural items and produce enough cultural diversity to generate them. In comparison, well-connected populations ($f = 1$) suffer from a lack of cultural diversity to innovate, while cultural accumulation in moderately ($f = 10$) and highly ($f = 60$) fragmented populations is limited by populations' ability at maintaining complex cultural items. Lines show the value ($\pm$s.e.m.) found after 300 time steps averaged over 30 simulations. Other parameters: $n = 600$, $p = 0.005$, $m = 0.01$, $\varepsilon = 0.2$.

(b) Intermediate levels of fragmentation maximize cultural complexity when innovation depends on cultural diversity

When innovation depends on cultural diversity (i.e. $\rho > 1$), cultural accumulation in non-fragmented populations is reduced because non-fragmented populations suffer from cultural homogenization, and this prevents them from generating the diversity of traits required to produce highly complex cultural traits. This means that cultural complexity in non-fragmented populations is not limited by what these populations are able to maintain but by what they are able to produce.

Highly fragmented populations suffer from the opposite effect. They produce a variety of cultural traits but cannot stabilize them above a certain level of complexity. Thus, cultural complexity in highly fragmented populations is mainly limited by what these populations are able to maintain.

In populations with intermediate levels of fragmentation, cultural loss and cultural diversity are balanced in a way that maximizes cultural complexity (figures 4 and 5). Weakly fragmented populations exhibit higher levels of cultural diversity than non-fragmented populations, which fuels the innovation process and promotes the emergence of highly complex cultural items. At the same time, low levels of fragmentation do not drastically reduce populations' ability to maintain complex cultural items because many learners will be exposed to innovations.

The optimal level of population fragmentation depends on the extent to which innovation relies on cultural diversity. The more the innovation process depends on cultural diversity, the more fragmented populations must be in order to produce the level of cultural diversity required for further innovation (figures 4 and 5). However, highly fragmented populations become unable to maintain complex cultural traits because few individuals will be exposed to innovations when they appear. The highest level of cultural complexity is thus reached at the minimal level of fragmentation that provides populations with enough cultural diversity to keep innovating.

(c) High rates of migration can reduce the benefits of fragmentation

Fragmentation can increase cultural accumulation because it positively affects cultural diversity. However, when migration

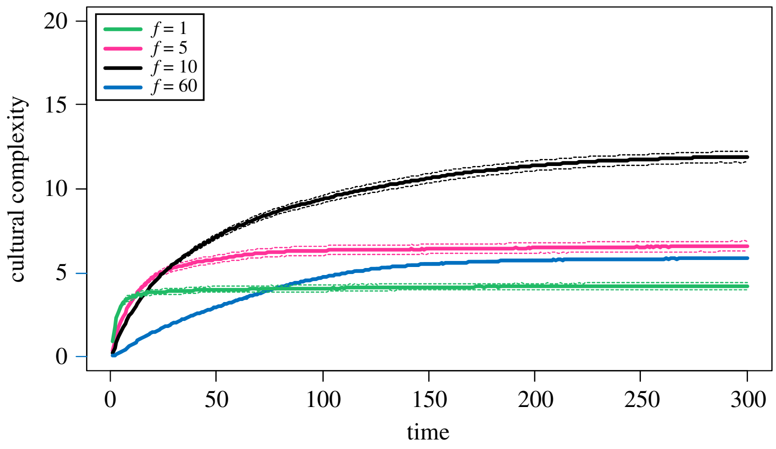

Figure 5. Effect of fragmentation (f) when innovation strongly depends on cultural diversity ($\rho = 1.6$). When innovation requires large amounts of cultural diversity, moderately fragmented populations ($f = 10$) produce the most complex cultural items. Well-connected ($f = 1$) and weakly fragmented populations ($f = 5$) do not generate enough cultural diversity to produce complex items, while highly fragmented populations ($f = 60$) remain limited by their ability at stabilizing complex cultural traits. Lines show the value ($\pm$ s.e.m.) found after 300 time steps averaged over 30 simulations. Other parameters: $n = 600$, $p = 0.005$, $m = 0.01$, $\varepsilon = 0.2$.

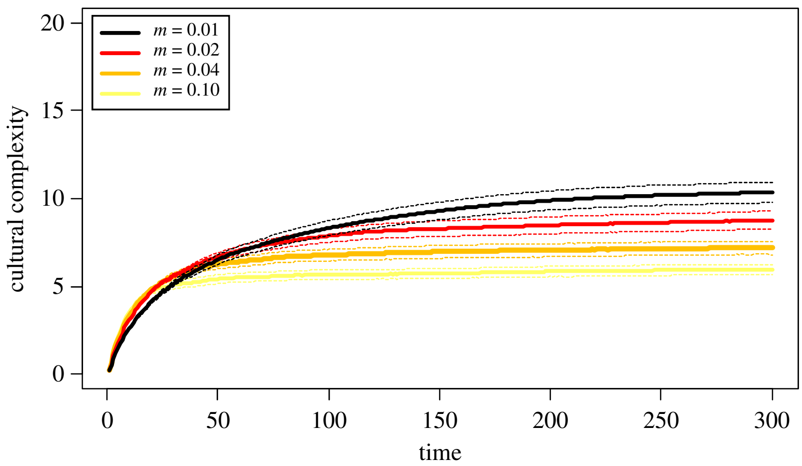

Figure 6. Effect of migration (m) on the performance of moderately fragmented populations ($f = 10$) when innovation strongly depends on cultural diversity ($\rho = 1.6$). As migration rate increases, subpopulations' cultural repertoires become homogenized despite of fragmentation. As a result, populations produce less-complex cultural traits. Other parameters: $n = 600$, $p = 0.005$, $\varepsilon = 0.2$.

rates are high, subpopulations do not diverge because they share cultural information before alternative solutions are produced. Thus, as migration rate increases, the benefit of fragmentation decreases (figure 6).

8. Discussion

Our model shows that populations that are partially fragmented can reach higher levels of cultural complexity than populations that are fully connected when generating complex cultural traits depending on cultural diversity.

Well-connected populations do better than fragmented ones when the production of complex traits is independent of the level of cultural diversity because the steady-state level of cultural complexity is determined only by populations' ability to maintain innovations. In fragmented populations, a smaller number of individuals observes novel cultural traits, which makes innovation more likely to be lost. The effect of fragmentation becomes more acute as cultural traits increase in complexity because more complex traits are more difficult to learn without error. Thus, when the process of innovation does not depend on cultural diversity, less-fragmented populations exhibit more complex cultural traits. This result is consistent with most theoretical models and experimental studies that investigated the relationship between effective population size and cumulative culture [1–5,7–15].

However, evidence suggests that innovation rates are affected by cultural diversity [28,46]. The studies reviewed above suggest that innovation often takes the form of recombination of unrelated technologies, skills and knowledge, and higher levels of cultural diversity makes recombination more fruitful.

When innovation depends on cultural diversity, cultural accumulation is driven by both populations' ability to produce new traits and to maintain them. Fragmented populations are more likely to explore different technological trajectories, and individuals migrating between subpopulations allows diverse cultural traits to be brought together (electronic supplementary material, figure S2). This increase in cultural diversity fuels innovation and allows fragmented populations to produce more complex cultural traits than non-fragmented populations.

The optimal level of fragmentation depends on how strongly the production of complex cultural traits is dependent on cultural diversity. In theory, the populations that produce the most diverse cultural repertoires should be the most innovative. However, highly diverse cultural repertoires cannot be produced without increasing the level of fragmentation, which reduces populations' ability to maintain complex traits. When populations are too fragmented they cannot maintain complex cultural traits and cannot accumulate innovations, even if they have very diverse cultural repertoires. Thus, the most complex cultural traits are produced when populations are fragmented in a way that minimizes cultural loss but generates enough cultural diversity to keep innovating. When innovation is increasingly dependent on cultural diversity, more-fragmented populations tend to perform better while less-fragmented populations tend to perform worse (figures 3–5).

Interestingly, we found that small rates of learning error can promote cumulative culture in non-fragmented populations when innovation weakly depends on cultural diversity. This is because errors allow individuals to shift to a new trajectory after having failed to properly acquire a cultural trait. This leads to a more thorough exploration of the space of possibilities and increases cultural diversity in the overall population. This result is consistent with previous work suggesting that learning errors can benefit cultural diversity [53]. Non-fragmented populations become limited in their ability to innovate due to low levels of cultural diversity but benefit from the diversity arising from learning errors to slowly reach higher levels of cultural complexity (figure 2). This effect is, however, limited as in many cases it does not provide non-fragmented populations with enough cultural diversity to keep innovating (figure 5; electronic supplementary material, figure S3).

In our simulations, the most fragmented populations did not attain the highest levels of cultural diversity because they could not stabilize complex cultural traits (electronic supplementary material, figure S2). As a consequence, highly fragmented populations, despite being composed of many semi-isolated groups, exhibit relatively low levels of cultural diversity because only a few different solutions can be produced at low levels of complexity (figure 1). It could be argued that this result is an artefact of modelling technological evolution as a branching tree. Yet it is worth noting that in real life the space of possible solutions does tend to increase with cultural complexity because more-complex innovations are made of an increasing number of sub-components. Thus, in many situations, the number of directions that innovation can take increases with the number of sub-components because sub-components can be refined in many different ways. Moreover, the addition of sub-components creates new combinatorial opportunities, which further widen the range of possible innovations [54]. Note, however, that highly fragmented populations might produce more cultural diversity in landscapes with more branching possibilities [55].

These simulations predict that the amount of cultural diversity produced by fragmented populations depends on the number of subpopulations and the level of migration between these subpopulations. When migration rate increases, cultural traits spread faster and cultural repertoires are homogenized despite population fragmentation (electronic supplementary material, figure S4). This is in line with a recent agent-based model that showed that higher migration rate can negatively affect cultural accumulation by preventing a culturally distinct toolkit to evolve [15]. As a result, higher migration rates reduce the populations' cultural complexity steady state when innovation depends on cultural diversity (figure 6). The migration rate that maximizes cultural complexity ultimately depends on innovation rate. Lower innovation rates reduce cultural diversity unless migration rates are also lower. In our model, migration events did not affect average population size, as individuals returned to their primary subgroup after social learning. As a consequence, the threshold of cultural complexity that can be maintained by fragmented populations remains determined by the size of their subpopulations. This means that in our simulations lower levels of migration will always lead to higher cultural–complexity steady states, although at lower rates of accumulation. Note that a recent model that considered the joint effect of cultural contact, innovation, and modifiers of biological carrying capacity showed that intermediate rates of migration are better for cultural accumulation [15]. This suggests that low rates of migration could be detrimental to cumulative culture when feedback effects between population size and cultural complexity are more realistically considered.

9. Implications

Our results are consistent with recent experimental and theoretical studies showing that population interaction can be a strong driver of cultural accumulation [13,15]. However, our model also indicates that population interaction does not necessarily increase cultural complexity. When semi-isolated populations are small, cultural complexity is primarily determined by populations' ability to maintain cultural traits. Contact between populations has little effect on cultural accumulation because populations cannot benefit from cultural exchange. When contacts occur between sizeable groups, intergroup contacts promote cumulative culture because contacts increase cultural diversity and foster the emergence of more-complex traits. This suggests that population structure can have important effects on cultural accumulation and should be taken into account when it comes to investigate the relationship between demography and cumulative culture.

Taking into account the role of population structure on cumulative culture may help explain ancestral and historical patterns of cultural change [13]. For example, the Middle Palaeolithic (MP) in Eurasia is characterized by little evidence of change in stone tool technology as compared with later periods such as the Upper Palaeolithic (UP) in Europe or the Late Stone Age (LSA) in Africa [3,56]. The increase in cultural complexity that characterized the UP and LSA has been interpreted as resulting from an increase in effective population size because of the positive effect of demography on cultural transmission [1,3,57,58]. The present results suggest an alternative mechanism, namely that the rise of intergroup interaction that took place during the Palaeolithic could have driven up cultural complexity by bringing diverse cultural traits together, thereby promoting populations' opportunities to innovate (see also [13,15]).

In more recent times, the effect of population structure might also have played a role during the Industrial Revolution in Western Europe in the eighteenth century. Explaining why Europe has been the scene of remarkable technological development over the last centuries has been the focus of much attention in various fields [59–61]. Among economists, one of the most common explanations is that the long political fragmentation of Europe encouraged scientific and technological innovation through competition. According to this view, unified civilizations, such a China, did not experience comparable rates of technological advancement because they had no adversaries to compete with. Emulation, as well as many other factors, certainly contributed in the Industrial Revolution. Yet it is worth noting that Europe's political and cultural fragmentation might have promoted the pursuit of different technological trajectories. In his book *Guns, Germs and Steel*, Jared Diamond notes that 'Europe's geographic balkanization resulted in dozens or hundreds of independent, competing statelets and centers of innovation. If one state did not pursue some particular innovation, another did' [60]. Diamond also stresses that although Europe's barriers were sufficient to prevent political unification, they did not halt the spread of technology and ideas between countries. According to our results, this population structure might have benefited technological progress because it promotes cultural diversity and spurs innovation (although many other factors probably contributed to that phenomenon).

It should be noted that the exploration of alternative portions of the space of possibilities does not require subpopulations to be spatially isolated. Modern communication technologies such as the Internet guarantee access to knowledge accumulated in any disciplines in any part of the world. Thus, the academic world could be considered to be a fully connected population. Nonetheless, it has been shown that the geographical and cultural fragmentation of the research community serves an adaptive role in facilitating the resistance of more diverse ideas and preventing global homogenization even within a single discipline [62]. More generally, because of division of labour and specialization, individuals carry different subsets of information and explore different trajectories within the space of possibilities [63]. Physics scholars, for example, are more likely to make discoveries about elementary particles than biologists. Yet breakthroughs in one branch of science can have a large impact on seemingly unrelated fields. Discoveries about nuclear spin in physics in the 1940s, for example, led to the development of magnetic resonance imaging techniques that led, in turn, to new discoveries in fields of medicine and biology [44]. Thus, the role of population structure on cultural accumulation is not limited to cases where populations are geographically fragmented. Division of labour and other mechanisms that prevent cultural homogenization at the population level are likely to have comparable effects to those observed in our model [55,64]. For example, an empirical study that investigated the relationship between groups' connectivity and their ability to produce innovative ideas in a firm's research and development department found that intermediate levels of connectivity were of most benefit to the production of high-quality ideas [65].

The present paper suggests that it is important to take into account the processes that underlie the emergence of new cultural traits, i.e. the innovation process [13,15,63,66]. Much of the work in the field of cultural evolution has focused on transmission fidelity, as it is considered as one of the main drivers of cumulative cultural evolution [50]. The present model indicates that when the processes that underlie the emergence of new traits are taken into account, cumulative cultural evolution is driven by both transmission fidelity and innovation production. Population structure through its effect on cultural diversity can be a strong driver of cultural accumulation and may help better explain ancestral and historical patterns of cultural change.

Data accessibility. The simulation code is available as the electronic supplementary material.

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