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Ingroup-Biased Copying Promotes Cultural Diversity and Complexity

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Abstract

Studies have found that when innovation involves recombining cultural traits, partially-connected populations produce higher levels of cultural complexity than fully-connected populations by avoiding cultural homogenization. However, population connectedness is only one of many factors that could promote cultural diversity and thus cultural complexity. Here, we examine whether people's preference for copying members of their own social group could also fill this role. Our simulations reveal that even in fully-connected populations, ingroup-biased transmission results in greater cultural complexity than unbiased transmission. Moreover, in partially-connected populations, this bias interacts with population structure to produce even higher levels of cultural complexity than population structure alone. Finally, by incorporating population turnover into our model, we shed light on the trade-off between promoting cultural diversity versus limiting cultural loss.

Keywords: cultural diversity; innovation; cumulative cultural evolution; ingroup copying bias; connectedness

Introduction

Humanity's unprecedented technological and cultural sophistication has been widely attributed to our capacity for cumulative cultural evolution (Boyd & Richerson, 1985). Over time, we have accumulated an increasingly diverse and complex set of cultural products and practices, including technologies, scientific theories, and forms of social organization that far exceed what any single generation could devise on its own (Tomasello, 1999). This accumulation can be observed across a variety of interrelated measures (Enquist, Ghirlanda, Jarrick, & Wachtmeister, 2008), such as in the efficiency, amount, and complexity of our cultural traits (behaviors, concepts, material products, etc.). Various factors are thought to affect this cultural accumulation, including transmission fidelity (Lewis & Laland, 2012; Montrey & Shultz, 2020), intelligence (Stout & Hecht, 2017), behavioral conservatism (Marshall-Pescini & Whiten, 2008), life history (Wakano & Miura, 2014), and prosociality (Tomasello, 1999).

However, one of the most influential lines of inquiry has been into the role of demography. Theoretical models predict that larger populations should support more complex culture because frequent opportunities for social learning stem the rate of cultural loss (Henrich, 2004; Powell, Shennan, & Thomas, 2009). Otherwise, complex cultural traits are lost with the death of their creators, forcing future generations to rediscover or reinvent rather than build upon existing

knowledge. While this idea has drawn criticism (Andersson & Read, 2016) and empirical evidence is mixed (Buchanan, O'Brien, & Collard, 2015; Collard, Buchanan, O'Brien, & Scholnick, 2013), proponents have argued that cultural complexity is not expected to covary with population size per se. Rather, it is expected to covary with effective population size, defined as the number of individuals actively engaged in social learning (Derex & Mesoudi, 2020). At minimum, this means that the frequency of intergroup contact (i.e., population connectedness) needs to be considered, which varies considerably according to ethnographic studies (Kline & Boyd, 2010; Migliano et al., 2020).

Population structure may affect cultural complexity in other ways as well. Historical analysis (Basalla, 1988) and theoretical models alike (Lewis & Laland, 2012) suggest that innovation (the production of new or better cultural traits) frequently involves recombining existing traits (Enquist et al., 2008). For example, examination of U.S. patent records from 1790 to 2010 reveals that the majority of inventions patented during this period combined at least two earlier technologies (Youn, Strumsky, Bettencourt, & Lobo, 2015). Cumulative cultural evolution can thus be characterized as an autocatalytic process (Gabora & Steel, 2020), where each additional trait presents new opportunities for recombination, eventually sparking a positive feedback loop (Gabora & Steel, 2017). This could help explain why human culture has been observed to grow exponentially (Enquist et al., 2008) in domains ranging from the technological evolution of Paleolithic stone tools (Stout, 2011) to the rate of contributions to chemistry, biology, economics, mathematics, and medicine since the early modern period (Lehman, 1947).

One important consequence of this view is that cultural diversity (possessing a wide range of cultural traits) drives cultural complexity (Enquist, Ghirlanda, & Eriksson, 2011). This is well-illustrated by organizational research, which shows that ethnically diverse groups tend to produce higher quality ideas (McLeod, Lobel, & Cox, 1996). However, this also means that population structure has another avenue for influencing cultural complexity: by either speeding or delaying cultural homogenization (people's tendency to converge on a similar set of cultural traits). Both experimental (Derex & Boyd, 2016; Fay, De Kleine, Walker, & Caldwell, 2019) and theoretical findings (Cantor et al., 2021; Derex, Perreault, & Boyd, 2018; Migliano et al., 2020) corroborate this

idea. These reveal that partially-connected populations produce greater cultural complexity than fully-connected populations by giving diverse cultural traditions the opportunity to flourish.

That being said, population connectedness is only one of many factors that could promote cultural diversity by slowing cultural homogenization. Barriers to the flow of social information are often not just structural, in that individuals lack contact, but also behavioral, in that they are unwilling to share information (Derex & Mesoudi, 2020). For example, ethnographic studies reveal that certain types of knowledge, such as medicinal plant use, are shared more freely between kin than non-kin (Salali et al., 2016), and theoretical models suggest that such kin-biased transmission can promote cultural diversity (Migliano et al., 2020).

In addition to kin-biased transmission, people employ a wide variety of other social learning strategies (Kendal et al., 2018) that could affect cultural diversity. For example, analysis of contemporary hunter-gatherer societies shows that interaction rates tend to be governed more strongly by ritual relationships than kinship (Hill, Wood, Baggio, Hurtado, & Boyd, 2014). The apparent importance of non-kin social relationships, such as who participates in particular rituals together (Hill et al., 2014), aligns with recent psychological findings. These reveal that people use social group membership to determine whom to observe and copy, even when these groups are arbitrary, novel, and devoid of intergroup competition (Montrey & Shultz, 2022). Surprisingly, this bias has also been found to produce intergroup differences in behavior in intermixed groups (Montrey & Shultz, 2022). This raises the possibility that even in a fully-connected population, the mere perception of a group identity could bias copying along group lines and spur the creation of distinct cultural traditions.

Here, we examine whether an ingroup copying bias could slow cultural homogenization enough to promote cultural complexity. Because previous models of population connectedness have typically examined highly isolated subpopulations (Derex et al., 2018), it is not readily apparent whether a probabilistic copying bias could have a similar effect, particularly in intermixed groups. To answer this question, we develop a model where innovation depends on recombination. We then introduce ingroup-biased transmission into fully-connected populations and test how this affects cultural complexity. Next, we examine how this bias interacts with population structure. In the context of cultural complexity, the issue of how population structure and transmission biases interact has only recently begun to be examined (Migliano et al., 2020). It is therefore unclear whether these factors will mitigate or reinforce one another. Finally, by implementing population turnover, we address how cultural complexity varies with the reliability of social learning. Because models of cultural evolution have traditionally focused on either innovation or social learning, they have often ignored the trade-off between cultural diversity, which collapses when copying is

too frequent, and cultural loss, which accelerates when copying is not frequent enough.

Methods

We model a population of n individuals divided into g equally sized groups. Each individual is described by its group membership and cultural repertoire. This repertoire consists of the set of cultural traits the individual possesses (e.g., its toolkit). Each trait is characterized by its type (a unique random string) and level of complexity (C).

Innovation

During the innovation phase, each individual innovates with probability $p_{innovate}$. If the individual's cultural repertoire is empty, it discovers a novel trait of a new type and complexity level $C = 1$. If the individual's repertoire is not empty, it tries to innovate on the trait it is currently exhibiting, which yields a new trait of the same type but with complexity level $C + 1$.

Models of cumulative cultural evolution often capture the relationship between innovation and cultural diversity in one of two ways. The explicit approach involves specifying precise relationships between cultural traits that determine whether they can be recombined into new traits of higher complexity (Enquist et al., 2011; Gabora & Steel, 2020; Migliano et al., 2020). The implicit approach abstracts away from these details and describes the relationship between innovation and cultural diversity as a mathematical function instead (Creanza, Kolodny, & Feldman, 2017; Derex et al., 2018; McElreath, 2010).

Here, we adopt an implicit similar scheme to the one used by Derex et al. (2018). We assume that for an individual to successfully innovate on a trait of complexity C , the size of its cultural repertoire must equal or exceed C^μ (rounded to the nearest whole number). Parameter μ reflects how strongly innovation depends on cultural diversity, and thus describes how often innovation involves recombination rather than refinement (Enquist et al., 2011). If $\mu = 1$, innovation does not depend on cultural diversity at all because any individual trying to innovate on a trait of complexity C already has at least $C^1 = C$ traits in its repertoire. This removes any upper bound on trait complexity and captures scenarios where innovation revolves exclusively around refinement. When $\mu > 1$, innovating on a trait requires a larger repertoire containing multiple types of traits. For example, if $\mu = 1.2$, innovating on a trait of complexity $C = 3$ requires a repertoire of $3^{1.2} \approx 4$ traits. If $\mu = 1.8$, innovating instead requires a repertoire of $3^{1.6} \approx 7$ traits, which reflects a stronger relationship between cultural diversity and innovation. This reflects scenarios where innovation involves recombining existing traits.

Social Learning

During the social learning phase, with probability p_{copy} , each individual learns from a random neighbor by observing the trait it is currently exhibiting. If the trait is of an unfamiliar type, the individual learns a rudimentary version ($C = 1$). If the trait is of a known type, then the individual compares

the trait’s complexity (C') to that of its own similar trait (C). Less complex traits ($C' < C$) are disregarded, whereas more complex traits ($C' > C$) allow the individual to learn an incrementally more complex trait of the same type ($C + 1$).

This captures two important features of human social learning. First, simple traits are learned quickly, whereas complex traits require a greater investment of time (Wakano & Miura, 2014). Second, because copying a complex trait is a multi-step process, individuals can have more than one cultural parent (Enquist, Strimling, Eriksson, Laland, & Sjöstrand, 2010). This aligns with the observation that highly complex traits, such as stone knapping techniques, tend to be learned iteratively through repeated exposure to multiple demonstrators and that relevant aspects of a complex trait are often imperceptible to naïve individuals (Whiten, 2015).

We model ingroup biases in social learning as an increased probability of copying ingroup members. With probability p_{bias} , rather than copying any random neighbor, individuals seek out a neighbor belonging to their own group instead. This reflects the notion that people use social group membership to decide whom to observe and copy (Montrey & Shultz, 2022), a tendency that may even extend to infants (Buttelmann, Zmyj, Daum, & Carpenter, 2013). If $p_{bias} = 0$, individuals ignore group membership and copy entirely at random. To ensure that copying preferences do not alter network topology, we restrict $p_{bias} < 1$.

Behavior

During the behavior phase, each individual exhibits the most complex trait in its cultural repertoire. If multiple traits are equally complex, it selects one at random. We assume that complex traits are favored over simple ones because complexity is often indicative of improvement. For example, the development of increasingly elaborate knapping techniques allowed early hominins to produce ever-more efficient stone tools (Stout, Semaw, Rogers, & Cauche, 2010). This assumption also helps capture the notion of path dependence, where early innovations tend to constrain later ones (David, 2007).

Population Structure

We consider two types of social structure: complete graphs and relaxed caveman graphs. In complete graphs, each individual is fully-connected to all other individuals. Groups are intermixed and there are no structural barriers to the flow of information. In relaxed caveman graphs, intragroup connections are much more common than intergroup connections, which causes groups to form insular cliques. Such graphs are produced by fully connecting group members to one another and then randomly rewiring each connection with probability p_{rewire} . This rewiring results in a limited number of intergroup connections.

Simulation

At the start of the simulation, the population has no cultural knowledge. Each time step begins with the innovation phase,

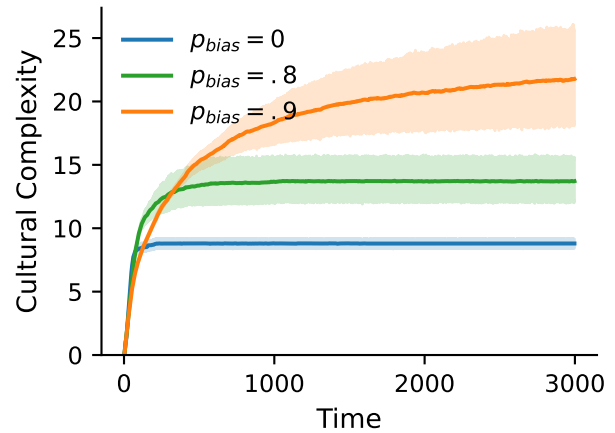


Figure 1: Cultural complexity over time. Ingroup-biased transmission ($p_{bias} > 0$) results in higher levels of cultural diversity and complexity than unbiased transmission ($p_{bias} = 0$). Each population is fully-connected.

in which individuals learn independently, followed by the social learning phase, in which individuals observe one another in random order. This is followed by the behavior phase, in which individuals choose which behavior to exhibit. Finally, individuals are replaced with probability $p_{replace}$ by individuals belonging to the same group but with empty cultural repertoires.

Cultural Complexity

We operationalize cultural complexity as the average complexity level of each individual’s current (i.e., most complex) cultural trait. This reflects a population’s capacity to produce and maintain complex cultural products and practices, a hallmark of cumulative cultural evolution (Tomasello, 1999). It is worth noting, however, that because cultural complexity is contingent on cultural diversity, this measure also reflects the average size of individuals’ cultural repertoires.

Results

By default, we consider a fully-connected population of $n = 400$ individuals divided into $g = 20$ groups, where innovation is rare ($p_{innovate} = .01$), social learning is reliable ($p_{copy} = .8$), population turnover is slow ($p_{replace} = .001$), and innovation depends moderately on cultural diversity ($\mu = 1.5$). We run simulations for 10,000 time steps to allow cultural trends to stabilize. Results are averaged over 20 simulation. Error envelopes represent bootstrapped 95% confidence intervals.

Ingroup Copying Bias

Even in fully-connected populations, a preference for copying ingroup members ($p_{bias} > 0$) yields higher levels of cultural complexity (Figure 1). By slowing the rate of intergroup copying, cultural repertoires homogenize more slowly, giving

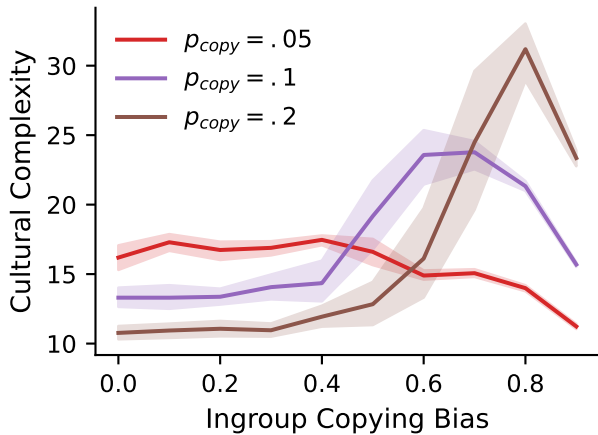


Figure 2: Stabilized cultural complexity as a function of ingroup copying bias strength. If copying is highly unreliable ($p_{copy} = .05$), such biases can result in cultural loss. However, if copying is even slightly more reliable ($p_{copy} = .1$ or $.2$), such biases can slow cultural homogenization without overly restricting the flow of information. Each population is fully-connected.

each group the opportunity to develop a unique set of complex traits before these traits diffuse through the broader population. This increased cultural diversity then spurs further innovation, resulting in even more complex traits.

Cultural Diversity vs. Cultural Loss

When social learning is highly unreliable ($p_{copy} = .05$), ingroup copying biases can have a deleterious effect on cultural complexity (Figure 2). This occurs because the flow of information is too restricted for complex traits to be reliably preserved when individuals are replaced, and strong biases in copying exacerbate this problem. However, as social learning becomes more reliable, the need to stem cultural loss becomes less dire. If social learning is even slightly more reliable ($p_{copy} = .1$ or $.2$), ingroup-biased transmission can slow cultural homogenization without overly restricting the flow of information, resulting in higher levels of cultural complexity.

Connectedness

Having established that social learning strategies, much like population connectedness, can influence cultural complexity, it is worth asking whether these factors interact. For example, in a population structure that promotes cultural complexity, would an ingroup copying bias offer any further advantage? To answer this question, we first place our population on a relaxed caveman graph ($p_{rewire} = .2$). Next, we find the level of population connectedness that maximizes cultural complexity in the absence of an ingroup copying bias. Because groups in this context form insular cliques, with far more intragroup than intergroup connections, we can manipulate connectedness by varying the number of groups (g) in the

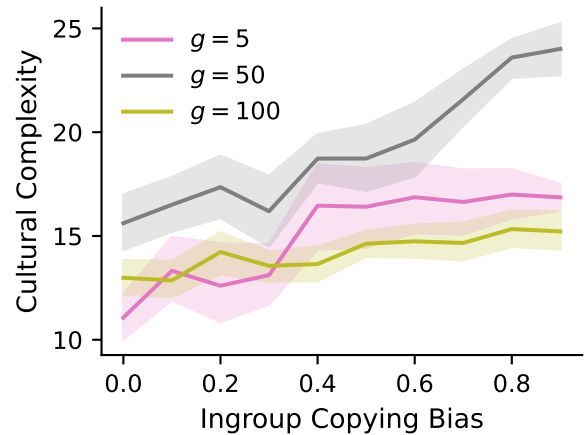


Figure 3: Stabilized cultural complexity as a function of ingroup copying bias strength. Intermediate levels of connectedness ($g = 50$) produce greater cultural complexity than weakly ($g = 100$) or strongly connected ($g = 5$) populations. In all three cases, ingroup-biased transmission promotes cultural complexity. Each population is placed on a relaxed caveman graph.

population (Derex et al., 2018). Intuitively, the more groups there are in the population, the less likely these groups are to be interconnected.

Consistent with previous theoretical (Derex et al., 2018) and empirical (Derex & Boyd, 2016) results, we find that intermediate levels of connectedness ($g = 50$) produce greater cultural complexity than weakly ($g = 100$) or strongly connected populations ($g = 5$). Varying the strength of the ingroup copying bias reveals that ingroup-biased transmission promotes cultural complexity at all three levels of connectedness (Figure 3). Notably, ingroup-biased transmission interacts with intermediate levels of connectedness to produce even higher levels of cultural complexity than population structure alone.

Other Parameters

In the following section, we examine how various parameters affect cultural complexity and, where qualitative differences exist, how they interact with ingroup-biased transmission. In all cases, we consider fully-connected populations.

Population Size Larger populations (n) are conducive to cultural complexity because they create additional opportunities to discover new traits or innovate on existing ones (Figure 4a). This is consistent with classic demographic models of cultural evolution, which predict that larger populations should support more sophisticated cultural traits (Henrich, 2004).

Number of Groups When social learning is unbiased, the number of groups (g) has no effect on cultural complexity because group membership has no behavioral signifi-

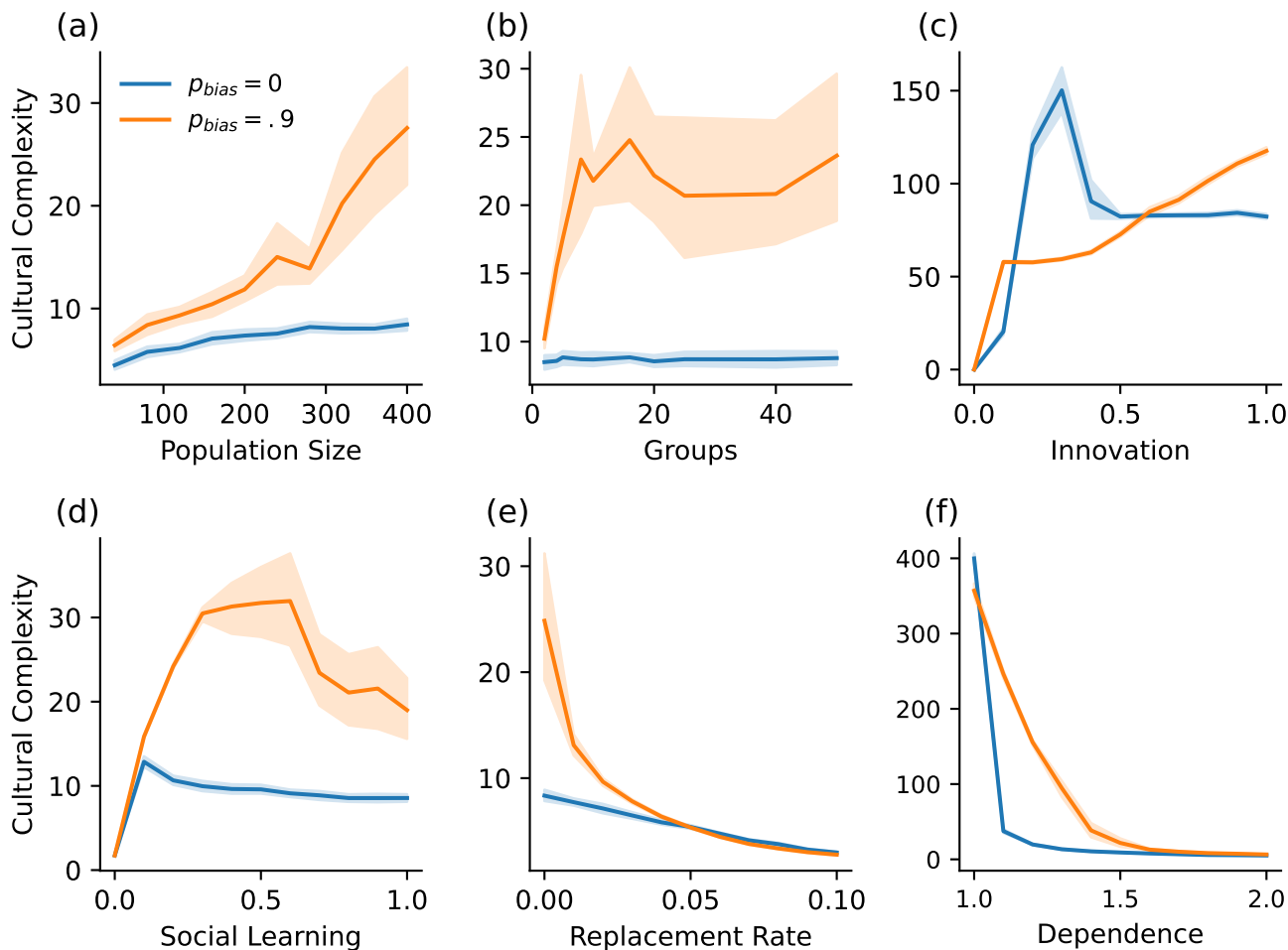


Figure 4: Stabilized cultural complexity as a function of (a) population size, (b) number of groups, (c) innovation rate, (d) social learning reliability, (e) replacement rate, and (f) innovation’s dependence on cultural diversity. Each population is fully-connected.

cance. However, when social learning is biased toward in-group members, dividing the population into smaller groups further restricts the flow of information, which delays cultural homogenization and boosts cultural complexity (Figure 4b).

Innovation As predicted by previous models (Kandler & Laland, 2009), higher rates of innovation ($p_{innovate}$) generally result in greater cultural complexity (Figure 4c). The more innovations occur before cultural traits diffuse and homogenize, the more diverse the population’s cultural repertoire, allowing for more complex innovations. That being said, when social learning is unbiased, extremely high rates of innovation can fail to maximize cultural complexity. This occurs because individuals end up with so many cultural traits that they have difficulty deciding which of these to innovate on.

Social Learning When social learning is unreliable, complex innovations are consistently lost before they can spread through the population. As a result, increasing social learn-

ing reliability (p_{copy}) initially stimulates cultural complexity (Figure 4d). Much of the cumulative cultural evolution literature has focused on this phenomenon and has frequently emphasized the importance of transmission fidelity to the build up of complex cultural traits (Andersson, 2013; Lewis & Laland, 2012; McElreath, 2010; Montrey & Shultz, 2020; Tennie, Call, & Tomasello, 2009). However, when cultural loss has to be balanced against cultural diversity, increasing social learning reliability past a certain threshold hurts innovation more than it prevents cultural loss. As culture rapidly homogenizes, cultural complexity drops.

Replacement Rate The more frequently individuals are replaced ($p_{replace}$), the more often cultural traits are lost before they can spread through social learning. Longer lifespans thus promote cultural complexity by reducing cultural loss (Figure 4e). This aligns with the view that increased longevity played a key role in enhancing human cultural capacities (Kaplan, Hill, Lancaster, & Hurtado, 2000; Montrey

& Shultz, 2020; Stout & Hecht, 2017).

Innovation's Dependence on Cultural Diversity When innovation does not depend on cultural diversity ($\mu = 1$), there is no downside to cultural homogenization. Cultural complexity is limited only by a population's rate of cultural loss. However, as the relationship between innovation and cultural diversity grows stronger, it becomes exponentially more difficult to innovate on existing traits, which sharply curtails cultural complexity (Figure 4f).

Discussion

In recent years, population structure has been increasingly invoked to explain patterns of human cultural evolution (Creanza et al., 2017; Kline & Boyd, 2010; Powell et al., 2009). To date, studies have largely focused on how population structure can impact cultural diversity by constraining the flow of social information (Cantor et al., 2021; Derex et al., 2018; Kobayashi, Ohtsuki, & Wakano, 2016; Migliano et al., 2020). However, the question of whether probabilistic transmission biases can have a similar effect has gone relatively unexplored. We find that a preference for copying ingroup members slows the rate of cultural homogenization and thus promotes cultural complexity. Although this bias interacts with population structure to produce even higher levels of cultural complexity, its effects are observed even in fully-connected populations. Therefore, much like structural barriers, behavioral barriers may play an important role in cultural complexity (Derex & Mesoudi, 2020).

Models of cumulative cultural evolution have traditionally focused on social learning's ability to prevent cultural loss (Andersson, 2011; Enquist et al., 2010; Henrich, 2004; Lewis & Laland, 2012; Montrey & Shultz, 2020). For this reason, frequent and accurate copying has often been viewed as an unalloyed good. While models focusing on how cultural traits are produced have presented an important counterpoint to this perspective by stressing the downsides of excessive social learning (Cantor et al., 2021; Derex & Boyd, 2016; Migliano et al., 2020), these in turn have generally neglected the role of cultural loss (Derex & Mesoudi, 2020). By including population turnover, our model allows us to examine how these competing pressures interact, revealing that ingroup-biased transmission benefits cultural complexity only so long as social learning is reliable. When social learning is unreliable, strong biases do more harm than good because the cultural diversity they produce cannot be preserved.

This could help explain why humans evolved an ingroup copying bias in the first place. As frequent and accurate social learners (Montrey & Shultz, 2020), our species may have been particularly likely to benefit from this bias' tendency to produce cultural diversity. These findings also suggest that transmission biases could have different effects on cultural complexity across various populations. For example, societies with writing (Kempe, Lycett, & Mesoudi, 2014), institutionalized pedagogy (Boyette & Hewlett, 2018), or techniques for accurately transmitting oral traditions (Filliozat,

2004) could benefit more than societies without similar mechanisms for stabilizing cultural transmission.

In our work, we draw a distinction between network topology, which describes the existence of social connections, and the probability that an individual will actually be copied. However, this dichotomy could plausibly be captured using a weighted graph, where some pairs of individuals are more likely to interact than others. In this sense, our results reveal the importance of examining not just the presence or absence of social connections, but the strength between them as well.

Although recent anthropological models have begun to incorporate such connection weight information, for example on the basis of frequency of contact (Migliano et al., 2020), such approaches may nevertheless fail to adequately capture transmission biases for at least two reasons. First, social learning strategies could influence copying probabilities in ways not reflected by frequency of contact alone. For example, the ingroup copying bias has been shown to persist even after controlling for how much more often ingroup members are observed (Montrey & Shultz, 2022). This highlights the benefits of measuring cultural transmission rates through empirical correlations in cultural traits rather than inferring them from social contact (Salali et al., 2016). Second, because some social learning strategies are either context-dependent (e.g., copy if uncertain) or content-dependent (e.g., payoff-biased transmission), it is not apparent how these could be captured through network topology alone.

Finally, our results add to a growing body of research showing that transmission biases are an important factor in cumulative cultural evolution (Kendal et al., 2018). For example, several studies have found that conformity bias can hinder cultural complexity by impeding the spread of novel innovations (Eriksson, Enquist, & Ghirlanda, 2007; Kandler & Laland, 2009). Although the apparent contradiction between conformity bias and cultural complexity has led some researchers to speculate that people may not be as conformist as social psychologists once believed (Kandler & Laland, 2009), our findings highlight another possible explanation: the ingroup copying bias could serve an important anti-majoritarian function in large populations, which invariably comprise diverse social groups. People's tendency to employ multiple social learning strategies in tandem (Kendal et al., 2018) could thus counteract conformity bias' drive toward cultural homogenization, laying a foundation for the cultural diversity and complexity that we widely observe.

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