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Innovation rate and population structure moderate the effect of population size on cumulative technological culture

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Cumulative technological culture is defined as the increase in efficiency and complexity of tools and techniques over generations that allowed humans to conquer the whole Earth. While one part of the puzzling ability of humans to develop such a form of culture lies in their cognitive capacities giving rise to reliable transmission of information, another lies in the impact of demographic factors. Indeed, many studies have examined the impact of population size, innovation rate and population structure on cumulative technological culture. Here, we present a computational model based on a previous model of micro-society that we extended to study the impact of population size and the influence of innovations on cumulative technological culture. Our results showed that population size exhibits an influence on cumulative technological culture, principally in small-scale populations. Additionally, the model suggests that the innovation rate constrains cumulative technological culture and the importance of population size. Indeed, when innovations are frequent, the impact of population size is diminished. Furthermore, our results demonstrate that individuals rely more on themselves than on others to innovate in earlier generations as well as in small populations. However, when populations grow as well as in later stages of evolution, reliance on innovation from others increases. Overall, these results indicate that population size has a limited impact on cumulative technological culture and that other demographic factors such as innovation rate could offer a viable alternative explanation for archeological records.

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Introduction

Our success in expanding and conquering the whole Earth (and even space) has been attributed to our capacity for sharing, maintaining and improving tools and techniques over generations, a phenomenon called cumulative technological culture [hereafter shortened as CTC, see Boyd and Richerson (1988), Derex (2022), and Tomasello et al. (1993). CTC is driven by the transmission of technical knowledge. It is widely accepted that this is supported by social learning, referring to learning about others or the physical world that is influenced by observation of, or interaction with, another individual or its products (Boyd et al. 2011; Derex 2022; Heyes 1994). While CTC has long been linked to humans (Tomasello 1999), contemporary research has uncovered instances of cumulative culture, and even CTC, in non-human animals (Boesch et al. 2020; Jesmer et al. 2018; Mesoudi and Thornton 2018; Sasaki and Biro 2017; Whiten 2021). This challenges the conventional belief that CTC is an exclusively human trait. Nevertheless, the question of the origin of our CTC in our evolutionary history persists.

One part of the puzzle lies in the human cognitive capacities underlying CTC. The main hypothesis in this regard assumes that the emergence of CTC is enabled by a high-fidelity information transmission mechanism. This mechanism allows for the maintenance of CTC, until an innovation occurs and improves it [referred to as the ratchet hypothesis (Tennie et al. 2009; Tomasello 1999; Tomasello et al. 1993)]. This hypothesis focuses on human social cognitive skills that can support high-fidelity transmission [e.g., theory of mind, ToM hereafter, the ability to detect as well as attribute intentions and mental states in others (Piaget 1932; Premack and Woodruff 1978; Whiten 1991)]. While acknowledging the role of social cognitive skills in CTC, recent studies have stressed the importance of understanding the non-social cognitive skills underlying both social and asocial events of transmission (Osiurak et al. 2021; Osiurak et al. 2022; Osiurak and Reynaud 2020; Singh et al. 2021; Vale et al. 2021; Whiten 2022). One such account is the technical-reasoning hypothesis (Osiurak and Reynaud, 2020), stipulating that technical reasoning (shortened as TR hereafter), a specific form of causal reasoning oriented towards the physical world acquired through experience (i.e., both asocial and social learning), allows humans to understand, build and use tools. While claims from both hypotheses allowed for great advancement in the study of the cognitive factors underlying CTC, we are still in the early stage of this investigation and much more needs to be done in this regard (Heyes 2018, 2023).

Another piece of the puzzle lies in demographic factors, which are vital contributors to CTC. Over the past two decades, researchers have concentrated on population size as a key determinant, positing that larger populations foster greater CTC (Shennan 2001). A pivotal study by Henrich (2004) associated population size with cultural complexity. According to this model, larger populations enhance cultural complexity, while smaller populations lead to a decrease in cultural complexity (e.g., fewer tools in a population). These findings have been applied to interpret cultural changes, such as the loss of artefacts in Tasmania post-separation from Australia (Henrich 2004, 2016). Numerous subsequent studies have built on these findings, investigating population structure, toolkit size, learning bias, and validating results through archeological records and laboratory experiments (Andersson and Read 2016; Aoki 2018; Baldini 2015; Derex et al. 2013; Kempe and Mesoudi 2014; Kline and Boyd 2010).

Despite the decade-long prominence of the population-size hypothesis in CTC, recent challenges have surfaced. Archeological studies supporting Henrich's model face limitations, with factors such as abrupt climate change possibly explaining tool loss

in Tasmania (Andersson and Read 2016; Vaesen et al. 2016). Moreover, empirical studies show a limited connection between population size and CTC (Buchanan et al. 2015; Collard et al. 2013; Vaesen 2012). Additionally, several studies using micro-society paradigms [a paradigm where chains of individuals are asked to improve a physical system, for a detailed explanation see Caldwell and Millen (2008)] have shown that increasing the number of demonstrators did not lead to greater CTC (Caldwell and Millen 2010) and could even lead to no CTC at all (Fay et al. 2019). Finally, it is important to note that several studies still showed an effect of population size but it would be significant only in small-scale populations (Andersson and Törnberg 2016; Ben-Oren et al. 2023; Vaesen et al. 2016).

Henceforth, other demographic factors have been put forward to explain how CTC can develop. Indeed, population structure, along with connections between individuals of that population, have been considered important factors (Creanza et al. 2017; Derex and Boyd 2016; Kolodny et al. 2015; Lehmann et al. 2011). More specifically, partially connected populations where subgroups of individuals preferentially interact within their peers than with the rest of the population yield a greater CTC than in fully connected populations in which everyone is interacting with one another (Ben-Oren et al. 2023; Derex et al. 2018). Another factor is the social learning strategies that bias individuals toward copying specific traits or individuals [for a review see Kendal et al. (2018)]. For example, in the model of Henrich (2004) a strong success bias (i.e., copying the most successful individual) is assumed, while others have shown that under unbiased social learning (i.e., copy at random) population size does not correlate with CTC (Andersson and Törnberg 2016; Bentley and O'Brien 2011). It has been shown that the rate at which innovation occurs in a population exhibits great control over the effect of population size, where innovation rate dictates the benefit of increasing the number of individuals in a population (Baldini 2015; Fogarty et al. 2017; Kobayashi and Aoki 2012). Finally, recent studies started using *effective population size*, defined as the relationship between population size and the connectedness of the population (Derex and Mesoudi 2020) rather than simple population size. They have shown that this distinction is critical to understand CTC (Deffner et al. 2022).

Our study aims to integrate both pieces of this puzzle, namely the cognitive and demographic facets of CTC. To do so, we used a computational model (Bluet et al. 2022) based on the micro-society paradigm to explore the influence of various cognitive factors on CTC. Expanding this model, we run multiple transmission chains simultaneously to simulate a population. To demonstrate the significance of this approach, we first replicate known results from the recent literature that the impact of population size on CTC is not linear. Afterwards, we delve into the reasons behind this non-linear relationship, focusing on the dynamics of innovations, their occurrence, and the cognitive factors influencing them. Finally, we investigate the connection between innovation rate and population size. Our results suggest that increasing the population size only impacts CTC in small populations, and that the innovation rate constraints the impact of population size on CTC.

The model

The model we present here is based on a computational model of microsociety (Bluet et al. 2022). This model assumes a transmission chain composed of only one individual per generation (Fig. 1A). In this model, a single technology is passed along individuals, whose goal is to improve said technology. To achieve this goal, individuals learned about the underlying mechanisms of the technology from their predecessors using one of three social
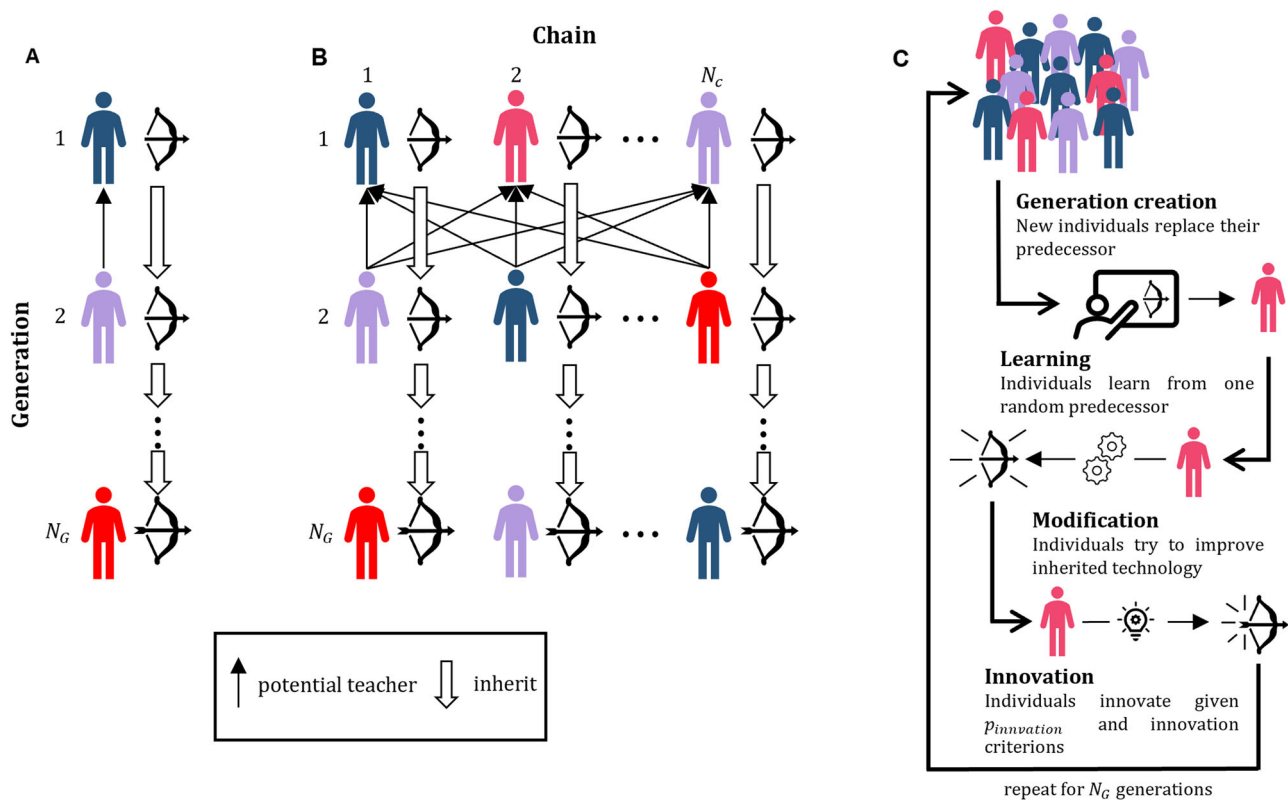
Fig. 1 Overview of the model and its network structure. A Network structure of Bluet et al. (2022) model. In this model, a single transmission chain is run. At each generation, a new individual is introduced in the model. This individual inherits the technology from its predecessor and learn from them. **B** Network structure of the model presented here. The model is composed of N_C chains, akin to population size. At each generation, N_C individual is created and inherits the technology from their direct predecessor. Then, they learn from one of any individuals in the past generation. **C** Model workflow. A population was created, replacing the previous one and inheriting their technology. Each individual from this generation learned from a single individual in the previous generation. Then, individuals modified their inherited technology. Under a certain probability and criteria, individuals innovate, bringing new traits to the technology (in this case, addition of feather to the arrow). This process is then repeated for N_G generation.

learning forms (namely reverse-engineering, observation or teaching). This learning process depends on the two cognitive skills of the individuals: technical reasoning, the ability to reason about the physical properties of objects (Osiurak 2014; Osiurak and Reynaud 2020), and theory of mind, defined as the ability to share attribute mental states to oneself and others (Harris 1991; Mead and Mead 1985; Piaget 1932). From this model, we keep the transmission chain structure, and only teaching[1], the best performing and most reliable social learning forms in Bluet et al. (2022) model.

We extend this model to run multiple transmission chains in parallel, simulating a population (Fig. 1B). A population is composed of N_C chains (akin to the population size) denoted as C, each having its variant T_C of a general technology (for example, each chain has a specific variation of a bow). We assume a cross-learning population, where each individual can socially learn from every other individual in the parent population (Fig. 1C). The general flow of the model is as follows. First, a new generation is introduced in the model. Each individual is allocated to a specific chain C and inherits the technology T_C from their respective chain. The values of their two cognitive skills are then computed. While their theory of mind is drawn from a normal distribution, their technical reasoning is based on the quality of their technological environment, largely derived from the technology T_C they inherited (more on that in section *(b) individuals*). Note that this model does not assume reproduction or genetic inheritance, but only the inheritance of cultural traits. Second, individuals socially learn about the technology, choosing a random single individual from the parent generation (i.e., unbiased

social learning) as their teacher. In the hypothetical case where the teacher has a technology T_c that has undergone innovations that did not happen in the individuals' chain, we assume that they learn these innovations and implement them in their technology. We call this phenomenon *socially acquired innovation*. Third, individuals apply their teaching and modify the technology from their chain (i.e., the one they inherited). Finally, they might have the opportunity to innovate themselves through their own personal experience with the physical environment. We call those innovations *asocial innovations*. Then, the process repeats itself for N_G generations G, as a new generation of individuals is introduced in the model.

To illustrate the model, let us imagine a population of hunter-gatherers using bows where everyone knows each other. Each child inherits the bow of their family when they are born and learn about its underlying mechanisms growing up. When they are at the age of making their own bows, children have the opportunity to learn from anyone in the population by going with them on a hunting episode. After this learning phase, they return home and apply what they have learned to the bow of their family, including modifying existing traits (the modification phase) and implementing the innovations they saw (*socially acquired innovation*) in others. Finally, they may witness a natural event that sprouts new ideas to implement in their bows (*asocial innovation*).

Technology. In the model, a technology T is composed of n distinct independent traits, such that $T = \{trait_1, trait_2, \dots, trait_n\}$, each

trait has a *quality* and a *limit*. The *quality* represents the efficiency of the trait, with an initial value of 1. We assume that the sum of the qualities of each trait gives the quality of the technology T, denoted $quality(T)$ such as:

$$quality(T) = \sum_{i=1}^{n} quality(trait_i).$$

The *limit* represents the maximum potential quality a trait can achieve in its current state, set to an arbitrary natural number ($limit(trait_i) = 2$ if not stated otherwise). Note that limits can move through the generation, as innovations increase the limits of every trait (for more information about innovation, see section *(e) innovation*). As for the quality, the limit of T, denoted $limit(T)$ is computed as:

$$limit(T) = \sum_{i=1}^{n} limit(trait_i).$$

Individuals. In the model, an individual I possess two cognitive skills, namely theory of mind and technical reasoning (hereafter ToM and TR respectively). Their ToM noted ToM_I is drawn from a truncated Gaussian distribution, such that ToM_I belongs to [0, 1] with $\mu = \frac{1}{2}$ and $sd = \frac{1}{6}$. In the model, their TR, noted TR_I, is also drawn from a truncated Gaussian distribution but it belongs to [0, TE] with $\mu = \frac{TE}{2}$ and $sd = \frac{TE}{6}$, where TE is short for technological environment. This value represents the quality of the technological environment where individuals first appear. We assume that the TE of each individual is principally composed of their chain's technology T_C. However, one can imagine that the technology transmitted T_C is not the only technology that composes the TE of the individual. To account for that, we add a noise variable, ε, drawn from a uniform distribution in the range $\left[-\frac{quality(T_C)}{10}, \frac{quality(T_C)}{10}\right]$. ε is based on $quality(T_C)$ because we assume that every technology in the individual TE should be close in terms of quality to the main technology T_C (e.g., every bow owned by the parent should be similar to the one inherited). This gives:

$$TE = quality(T_C) + \varepsilon.$$

The model assumes that the TE of each individual shapes their TR skills because the richer the environment is in technology, the greater the chance an individual has to increase their technical reasoning through either social or asocial learning (Osiurak et al. 2022; Osiurak and Reynaud 2020). Note that the increase in $quality(T_C)$ will lead to an increase in TE, resulting in an increase in the TR skills of individuals. Indeed, we assume that a greater technological environment will lead to greater individuals in terms of technical reasoning skills. To reflect the overall mastery of the technological environment by an individual, we use the ratio between its TR skills and TE, $\frac{TR_I}{TE}$.

Each individual I is also defined according to its understanding about the mechanisms underlying each $trait_{C,i}$ of the technology T_C, such as $I = \{cog_1, cog_2, \ldots, cog_n\}$, with each cog_i corresponding to a specific $trait_{C,i}$. For example, understanding the effect of the length of a bow on the energy stored when stringing it could be stored in cog_1, while the impact of the material used for the string could be cog_2. Each cog_i can take some value between 0 (no knowledge at all) to the *limit* of $trait_{C,i}$ (a total understanding of $trait_{C,i}$). To initialize each cog_i, we first randomly select a random one with replacement and then assign a value drawn in the range $\left[0, limit(trait_{C,i})\right]$. This process is repeated until the pool of knowledge, represented by TR_I, is depleted, such that

$$\sum_{i=1}^{n} cog_i = TR_I.$$

This leads to a heterogeneous distribution of understanding, where some cog_i might centralize a majority of TR_I, while other cog_i are very limited. We argue that this way of allocation cog_i gives a more diverse knowledge landscape in our population, allowing for some individuals to be specialized in a specific $trait_{C,i}$.

Learning. We assume that individuals learn once and choose their teacher at random from their parent generation. This means that while some individuals might learn from their direct parent (i.e., the one from whom they inherited their technology), most individuals learn from someone outside of their chain C, akin to how many people learn from a teacher in school rather than from their parents. In our model, learning is defined using a modified version of the learning equation for teaching from Bluet et al. (2022), for more detail about the modification from the previous model of this equation, please see Supplementary Material S1: *Simplification of* Bluet et al. (2022) *model*]

$$cog'_i = cog_i + \left(\Delta_{RE} * \frac{TR_I}{TE}\right) + \left(\Delta_{OBS} * \frac{TR_I}{TE}\right) + \left(\Delta_{TCH} * \frac{TR_I}{TE} * (ToM_T)\right),$$

(1)

where cog'_i represents the new understanding $trait_{C,i}$ after the learning process, each Δ represents the amount of knowledge that can be learned for each $trait_{C,i}$ compared to what the individual already knows, and ToM_T represents the ToM of the teacher. In this learning equation, three distinct social learning components are at play: reverse engineering (RE), observation (OBS), and teaching (TCH). Let's revisit our example of an individual observing a bow hunting episode. While watching an experienced hunter, the individual can scrutinize the bow, employing reverse engineering to extract vital insights about its construction. Posthunt, the observer may witness the experienced hunter fine-tuning and enhancing the bow based on the hunting results, illustrating observation in line with the transmission chain literature (Caldwell and Millen 2009; De Oliveira et al. 2019; Fay et al. 2019; Osiurak et al. 2016). Throughout the entire hunting episode, the individual also has the opportunity to engage in communication with the experienced hunter, who may provide teachings on how to enhance the bow.

Hence, Δ_{RE} represents the information given by observing the teacher's technology, given by

$$\Delta_{RE} = quality(teacher.trait_{C,i}) - individual.cog_i.$$

This equation reflects to which extent individuals understand a specific $trait_{C,i}$ of their teachers' technology. Δ_{OBS} represents the information gained by observing the teaching improving its own technology, such that

$$\Delta_{OBS} = quality(teacher.T_{C,i}) - quality(teacher.T_{C,i-1}),$$

where $teacher.T_{C,i}$ represents the teacher's technology, and $teacher.T_{C,i-1}$ represents the teacher's technology before modification (i.e., the one it inherited).

Finally, Δ_{TCH} represents the direct comparison between the teacher's and the individual's cog_i, such that

$$\Delta_{TCH} = teacher.cog_i - individual.cog_i.$$

We assume that each Δ are set to 0 if $\Delta<0$. Indeed, in the case where an individual has a better understanding of a trait than their teacher, we assume that they are simply not learning

anything. All three types of learning are influence by the learner TR, represented by the aforementioned $\frac{TR_i}{TE}$. The implication of TR skills in CCE has been suggested by multiple experiments using the transmission chain paradigm [(Osiurak et al. 2016; Osiurak, De Oliveira, et al. 2020; Osiurak et al. 2021), for a review see Osiurak and Reynaud (2020), for an alternative perspective, please see Derex et al. (2019)]. As for the teacher ToM, ToM_T, it can be compared to the teaching ability of an individual in our model, it only impacts the teaching learning form. Indeed, it has been repeatedly suggested that ToM (or more generally mentalizing process) might play an important role in teaching (Herrmann et al. 2007; Tomasello 1999; Tomasello et al. 1993, 2005). In the context of transmission chains, it is particularly the teacher's ToM (Osiurak et al. 2020) that may impact the CCE.

Modification of the technology. After the learning phase is over, individuals modify their technology according to what it has learned. For every $trait_{C,i}$ of a technology T_C, a modification factor β_i is computed such that

$$\beta_i = \beta_{down} + \left(\beta_{up} - \beta_{down}\right) * \frac{cog_i{}'}{trait_{C,i}}, \qquad (2)$$

where $\beta_{up} = 1.2$ and $\beta_{down} = 0.6$ [these values are chosen arbitrarily, but a parameter sweep shows that our results are robust to different values for β_{up} and β_{down}, for more information see Supplementary Material S2: *Parameter sweep*]. Thus, the new quality of T_C after modification is given by

$$quality(T_C) = \sum_{i=1}^{n} qualitiy\left(trait_{C,i}\right) * \beta_i.$$

Innovation. Finally, individuals may have an opportunity to innovate, referred to as *asocial innovation*, with probability $p_{innovation}$. To seize this opportunity, we assume that one of two criteria must be satisfied:

- *TR criterion:* the individual TR skills must be advanced compared to the TE, specifically $\frac{TR_i}{TE} > 0.8$.
- *Optimization criterion:* the technology T needs to be nearly optimized, meaning its quality approaches its limits, specifically $\frac{quality(T)}{limit(T)} > 0.8$.

The reasoning for the first criterion is that individuals with great TR skills will come up with new ways to integrate other traits into their current technology, as their understanding of the mechanisms underlying the technology is outstanding in the population. As for the second criterion, we consider that a near-optimized technology will lead to fewer possible improvements, thus prompting individuals to try new ways to improve the technology, leading to innovations. This is close to the concept of exploitation of Type II CCE and exploitation of natural phenomena proposed by Derex (2022), which proposes that human CTC evolves through a succession of slow improvement periods and brief and rapid boost in efficiency brought by the exploitation of a natural phenomenon [for a similar view in a real-life setting, see Miu et al. (2018)].

If neither of these two criteria are met, no innovation occurs. We called that a *missed opportunity*. Conversely, meeting at least one criterion leads to the individual seizing the innovation opportunity, changing the technology in two ways. First, the technology gains a new trait, which refers to *groundbreaking innovation* (Kolodny et al. 2015). Second, all the traits $trait_{c,i}$ have their limits $limit(trait_{c,i})$ increased by an arbitrary number, representing the *innovative combination* (Kolodny et al. 2015).

As said previously, we assume that innovations are transmitted through social learning, leading to *socially acquired innovations*. Thus, when an individual learns from a teacher with a technology more advanced (i.e., with more traits), the learner first applies the innovation, to its own technology, with similar mechanisms to an *asocial innovation* (i.e., with *groundbreaking innovation* and *innovative combination*). Then, the learner tries to learn from every trait (both old and new) of the teacher's technology. The newly added traits and their related cog_i will start with the lowest quality possible (i.e., 1 and 0 respectively) and the same limit as those of the teacher's technology.

Results

As in the initial version of the model (Bluet et al. 2022), we averaged the quality of the technology over multiple simulation runs as the model incorporates various random elements that may impact a single simulation run. Except when stated otherwise, all the results presented below were obtained using the following set of parameters: $\beta_{up} = 1.2$, $\beta_{down} = 0.6$, and $p_{innovation} = 0.01$, $N_C = 200$. Other parameter values were kept as the based value from the previous model [see Bluet et al. (2022) for more details on the parameters and their impact on the model].

Population size and number of innovations. Our model shows an increase in the quality of the technology as population size grows (Fig. 2A). However, this increase follows a logarithmic-like function. Our results show that an increase in population size has a larger impact on increasing the technology's quality in smaller populations than in larger populations. The model also shows that this limitation is stronger when the population size is at least 100 individuals, i.e., approaching the stage where there is theoretically one *asocial innovation* per generation (with $p_{innovation} = 0.01$).

If a larger population does not always result in greater technology quality, it might be attributed to the fact that larger populations do not necessarily mean more innovations. However, contrary to the technology's quality, the total number of innovations increase in a linear fashion with population size (Fig. 2B). Furthermore, both the total number of opportunities to innovate and the number of missed opportunities increase linearly (Fig. 2C). This means that when the population grows, more opportunities for asocial innovation appear in the population and individuals also convert more of these opportunities. This is consistent with our results, showing that the percentage of missed opportunities reaches an asymptote around a population size of 20 individuals (Fig. 2D).

Overall, these results reveal that the relationship between population size and CTC is not linear. Indeed, the impact of increasing the size of a population on its CTC offers diminishing returns. This result left us with a puzzling question: why does a population that innovate noticeably more not show greater technology's quality? To answer this question, we will first explore the relationship between population size and the type of innovation (*asocial innovation* or *socially acquired innovation*) occurring and take a closer look at which criterion (*TR criterion* and *Optimization criterion*) are met in the case of asocial innovation. We will also investigate the relationship between population size and individual technology knowledge, examine the propagation of innovations within the population, and consider the impact of the *asocial innovation* rate in relation to population size.

Type of innovation. Unsurprisingly, our model shows that there are more *asocial innovations* compared to *socially learned*
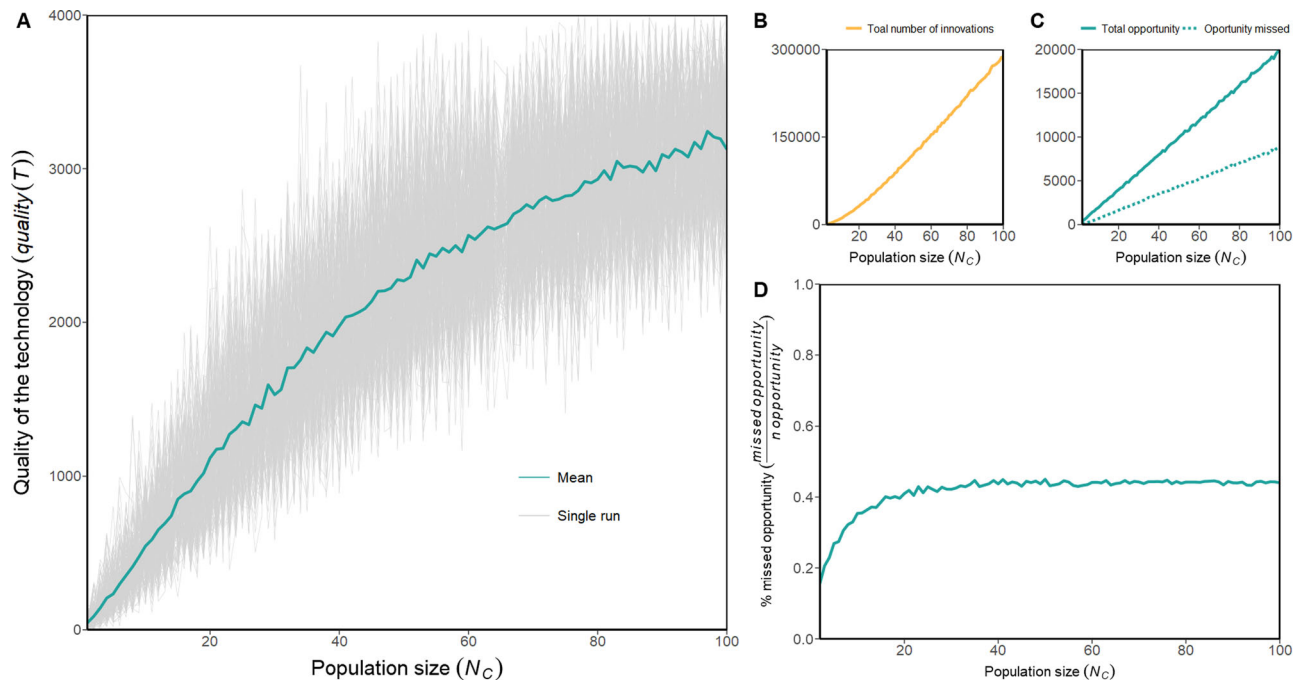
Fig. 2 Population size and number of innovations as a function of population size. A Model results in terms of technology's quality as a function of population size. We run 200 simulations of 200 generations for each population size N_C in the range [0, 100]. Gray lines represent each simulation single simulation run for a specific population size N_C. The blue line represents the averaged technology's quality between simulations. Common parameter values for all models: $n = 2$, $\theta = 5$, $\beta_{UP} = 1.2$, $\beta_{DOWN} = 0.6$, $p_{innovation} = 0.01$. **B** The total number of innovations (both *social* and *asocial*) as a function of population size. **C** The total number of opportunities to innovate (solid line) and missed opportunities (dotted line) as a function of population size. **D** Percentage of missed opportunities compared to the total number of opportunities as a function of population size.
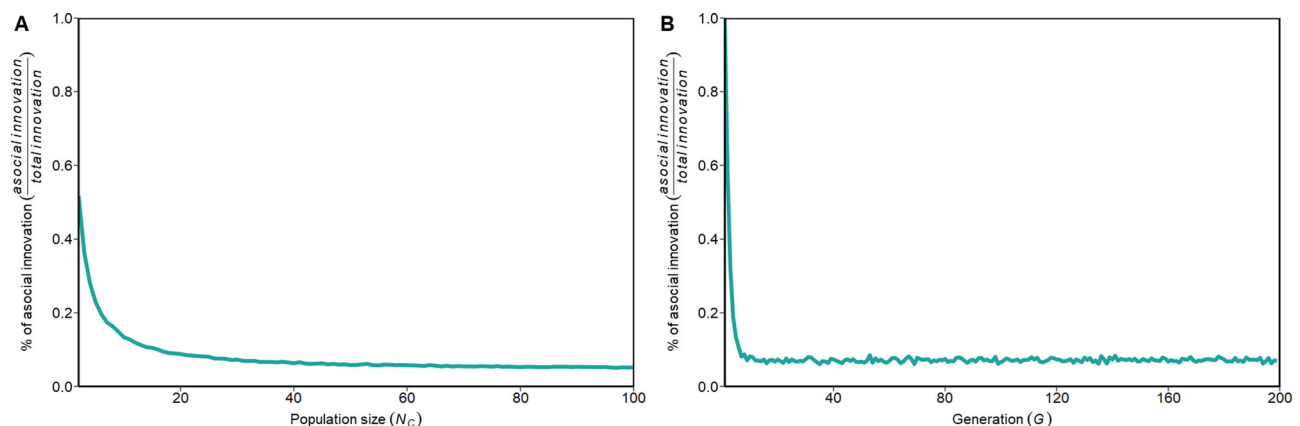
Fig. 3 Proportion of innovation's type as a function of population size and generation. A The proportion of *asocial innovations* compared to total innovations ($\frac{asocial\ innovation}{total\ innovation}$) as a function of population size (N_C). **B** The proportion of *asocial innovations* compared to total innovations ($\frac{asocial\ innovation}{total\ innovation}$) as a function of generations (N_G).

innovations both when the population is small and in the early generations of the population (Fig. 3A, B). In the early generations, this happens because until there is an *asocial innovation*, it cannot be passed on socially. This makes it impossible to see *socially learned innovations*. In smaller populations, fewer individuals lead to less learning interaction, resulting in less *socially learned innovation* overall. We observe that the rate of *asocial innovation* decreases very quickly to about 10% of total innovations. From these results, a question remains: what are the mechanisms leading to *asocial innovation* in different populations size and at different generations? To address this question, we delve into the repartition of the distribution of both the *TR criterion* and the *optimization criterion*.

The repartition of *asocial innovation* based on the *TR criterion* and the *Optimization criterion* suggests that smaller populations tend to rely more on optimized technology for innovation compared to bigger populations that are mainly driven by innovating on the *TR criterion* (Fig. 4, left part). We also observed an equal repartition of the *asocial innovation* type in the early generations (Fig. 4, bottom part). It may be because at the early age of a society, the technology is easy to optimize, and thus the *TE* value is also small, meaning that any individual has access to an optimized technology while also being ahead in terms of TR. Another interesting result is the small resurgence of technology-based innovation in later generations, even for large populations (Fig. 4, top part). An explanation is that in the latter stages of
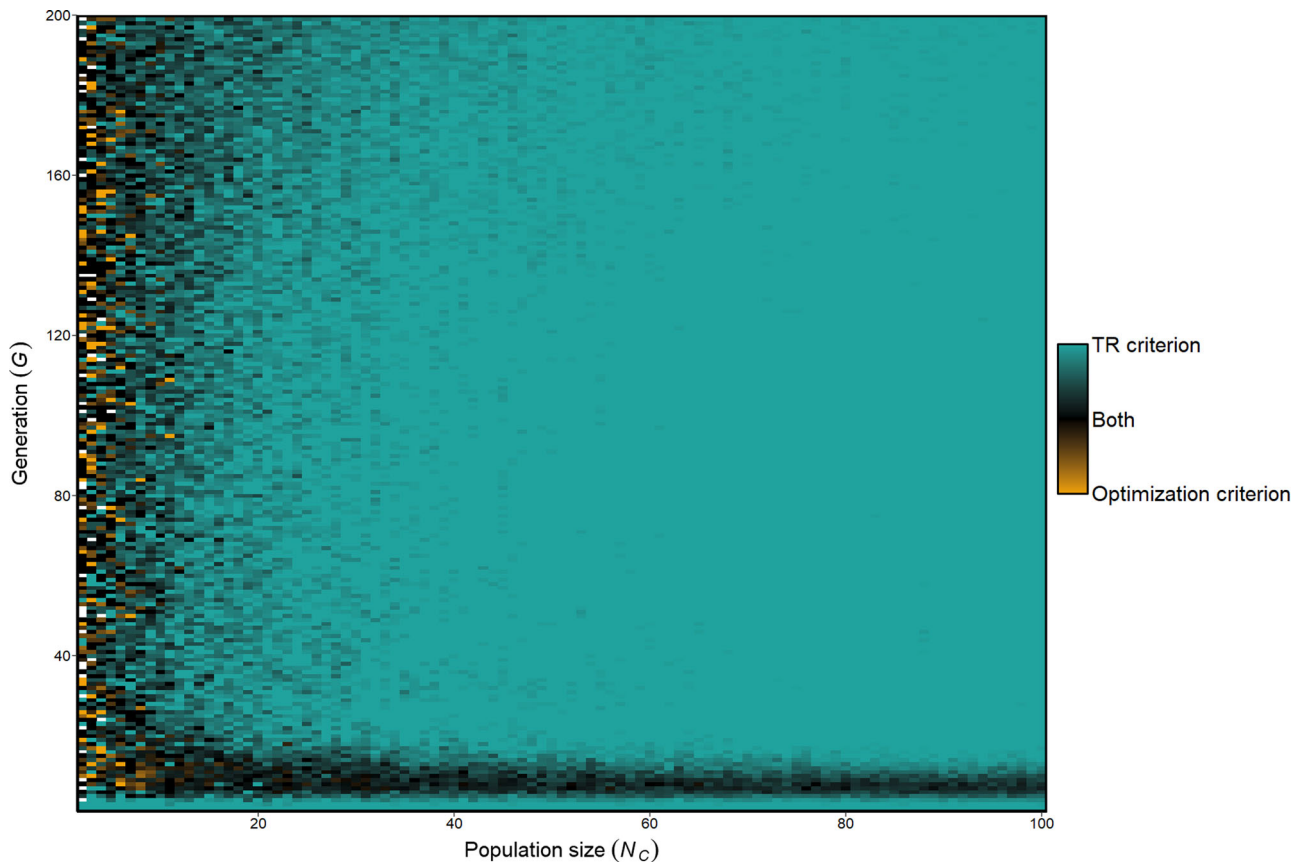
Fig. 4 Repartition of the criteria met for asocial innovations as a function of population size (N_C) and generation (N_G). White areas represent missing values, where no innovation occurred.

populations, technologies are too advanced for individuals to catch up with them in terms of knowledge, meaning that populations need again to rely more on optimized technology than on individuals with great TR.

Relationship between population size and individual knowledge of the technology. We then investigated the relationship between population size and TR skill compared to the *TE* along with the overall optimization status of the technology, defined as the ratio between the technology's quality and its limit, such that $optimization = \frac{quality(T)}{limit(T)}$. The model suggests that individuals exhibit the highest TR skills level in early to middle generations, especially in larger populations (Fig. 5A), while simultaneously, the technology exhibits suboptimal optimization within the same range of generations and population size (Fig. 5B). This indicates that in these early generations, individuals have an overall better understanding of their environment, leading the way to many improvements and *asocial innovations* of the technology, which makes it theoretically excellent [i.e., increases *limit*(T)] but also reduce its *optimization* at the same time [because *limit*(T) will be far greater than quality(T)]. Note that this pattern is absent for very small populations (i.e., less than 5 individuals). This relationship between TR skills and optimization can be explained by the fact that the overall *quality*(T) of the technology dictates the quality of *TE* upon which the TR_I of individuals are drawn. However, our model suggests that even the worst populations in terms of TR are still high ($\frac{TR_I}{TE}$ >0.75) while the technology optimization is very low ($\frac{quality(T)}{limit(T)}$ < 0.85).

This pattern of early bursts of high-skilled individuals followed by a small and steady increase in technology quality is also

present when we investigate the mean number of generations needed to achieve the *asocial innovation* requirements (as a reminder either $\frac{TR_I}{TE} > 0.8$ or $\frac{quality(T)}{limit(T)} > 0.8$, Fig. 6) after an *asocial innovation* occurs. For the TR, our results suggest a slower catchup speed for small populations (Fig. 6A). However, note that the number of generations is very small, as almost every generation in every population size reaches easily the *TR criteria* for *asocial innovation*. This is not true for the mean technology optimization speed, which increases with population size until reaching a plateau value around the 20th generation (Fig. 6B). This value should be taken with caution as there is a lot of fluctuation in our result. Nevertheless, the results show that smaller populations, while having worse technology in terms of quality, optimized their technology faster.

Propagation of the innovation. One might think that greater population size means that it is more difficult for innovation to spread socially. Indeed, it is normal to consider that a larger population goes with a longer transmission of information to all its members. Despite this, our model shows that the speed of innovation propagation (i.e., the number of generations needed for an innovation to spread in all technologies) follows a logarithmic trend as a function of population size (Fig. 7). Thus, the propagation of innovation cannot account for the disparity between the increase in population size and CTC.

This observation, while perhaps not surprising in the context of diffusion mechanisms, is interesting to investigate within our model. This result stems from two conflicting forces: *asocial* and *socially learned innovation*. Indeed, our previous results already illustrated that increasing the population means that more
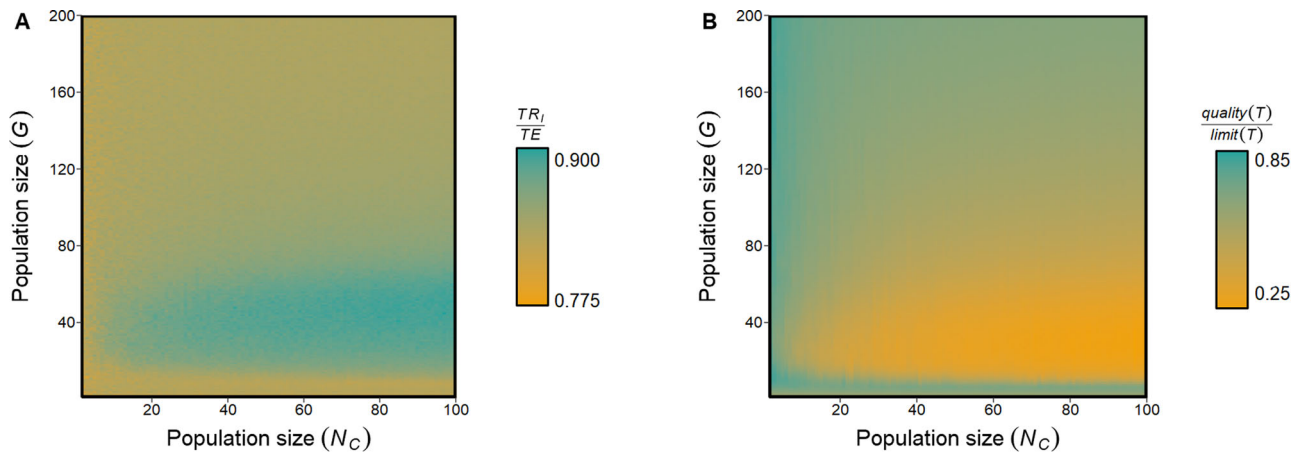
Fig. 5 Relationship between population size, individual knowledge and technology optimization. A The mean overall mastery of the environment in terms of TR, computed with $\frac{l_{TR}}{env}$ as a function of both population size (N_C) and generation (N_G). **B** The mean overall optimization of the technology computed with $\frac{quality(T)}{limit(T)}$ as a function of both population size (N_C) and generation (N_G).
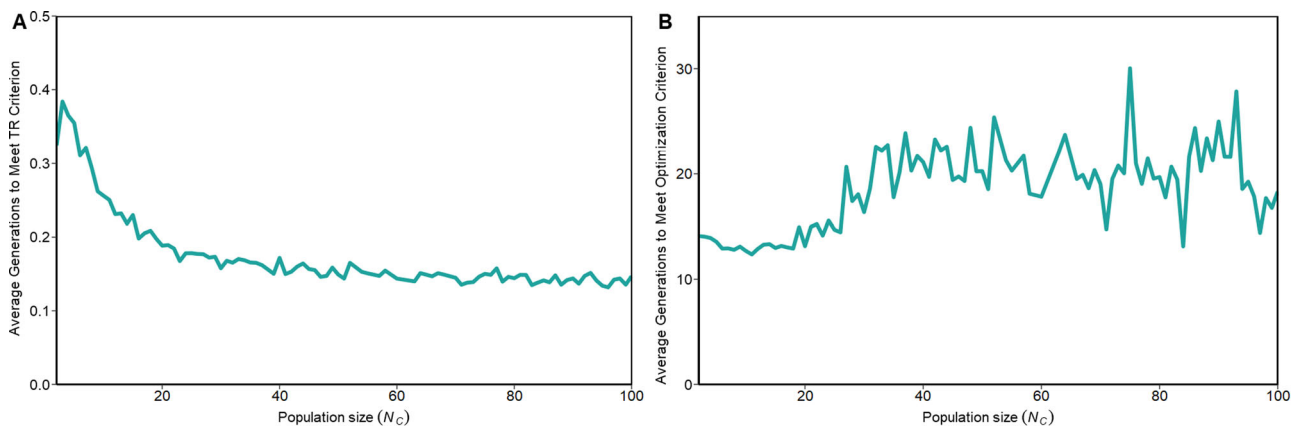

Fig. 6 Relationship between population size and innovation catch-up. A We computed the mean number of generations it takes for individuals to reach the innovation. We computed the mean number of generations it takes for the individual to meet the requirement for *asocial innovation* using TR ($\frac{l_{TR}}{env} > 0.8$) after an innovation occurs as a function of population size. **B** We computed the mean number of generations it takes for the technology to be optimized enough for an *asocial innovation* ($\frac{quality(T)}{limit(T)} > 0.8$) after an innovation occurs as a function of population size.

individuals have the opportunity to innovate, and also that in bigger populations individuals have greater TR skills. On the other side, greater population size means that the chance of learning from an individual that happens to have a technology with innovations when learning is rarer (think of it as a 1% chance to find the chain where an individual just innovates the previous generation for a population of 100 individuals). In summary, increasing population means more *asocial innovation*, but more time to find this innovation in the population for it to be learned socially.

We did a computational model of this trade-off in innovation diffusion mechanisms and the result is qualitatively the same as the one seen in the model (Supplementary Material S3: *Innovation computational model*), suggesting that this result is explained by the innovation dynamics of our model.

Innovation rate. When varying the value of $p_{innovation}$, our model shows that the effect of population size is constrained by the *asocial innovation* rate, as it was previously stated in the literature (Baldini 2015; Fogarty et al. 2017; Kobayashi and Aoki 2012). Indeed, our results show that when the *asocial innovation* rate is low, population size increases the technology quality linearly (Fig. 8A). However, as the value of $p_{innovation}$ increases, the effect of the

population size decreases (Fig. 8B–D). We observe that the quality of this impact decreases rapidly around the value of population size that equals an *asocial innovation* every generation (i.e., around 100 individuals for $p_{innovation} = 0.01$, 20 for $p_{innovation} = 0.05$ and 10 for $p_{innovation} = 0.10$).

Discussion
Here, we propose a model of CTC that simulates the effect of demographic factors from a micro-scale modeling framework of social information transmission. This model is based on a previous model of micro-society (Bluet et al. 2022), a paradigm used to study CTC in the laboratory (Caldwell and Millen 2008; Derex et al. 2019; Osiurak et al. 2022; Osiurak et al. 2020; Osiurak et al. 2020; Osiurak et al. 2016). To create a population using this model, we extend it to run multiple transmission chains in parallel, in which individuals could learn from any other individual. This setup has also been studied in previous laboratory experiments and showed that increasing population size leads to a better CTC (Derex and Boyd 2016; Kempe and Mesoudi 2014). However, contrasting results have been provided by other transmission chain experiments, where bigger group sizes did not lead to a greater CTC (Caldwell and Millen 2010; Fay et al. 2019).
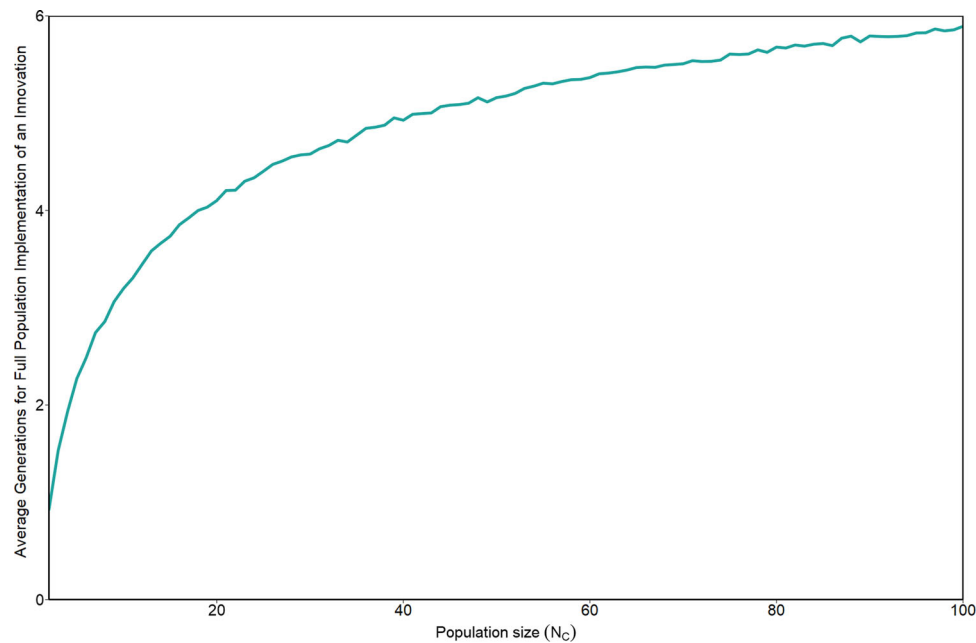
Fig. 7 Average propagation speed of innovation. We computed the average number of generations for the population to all have the last innovation that occurred. We called this the mean propagation speed (MPS) and showed it as a function of population size.
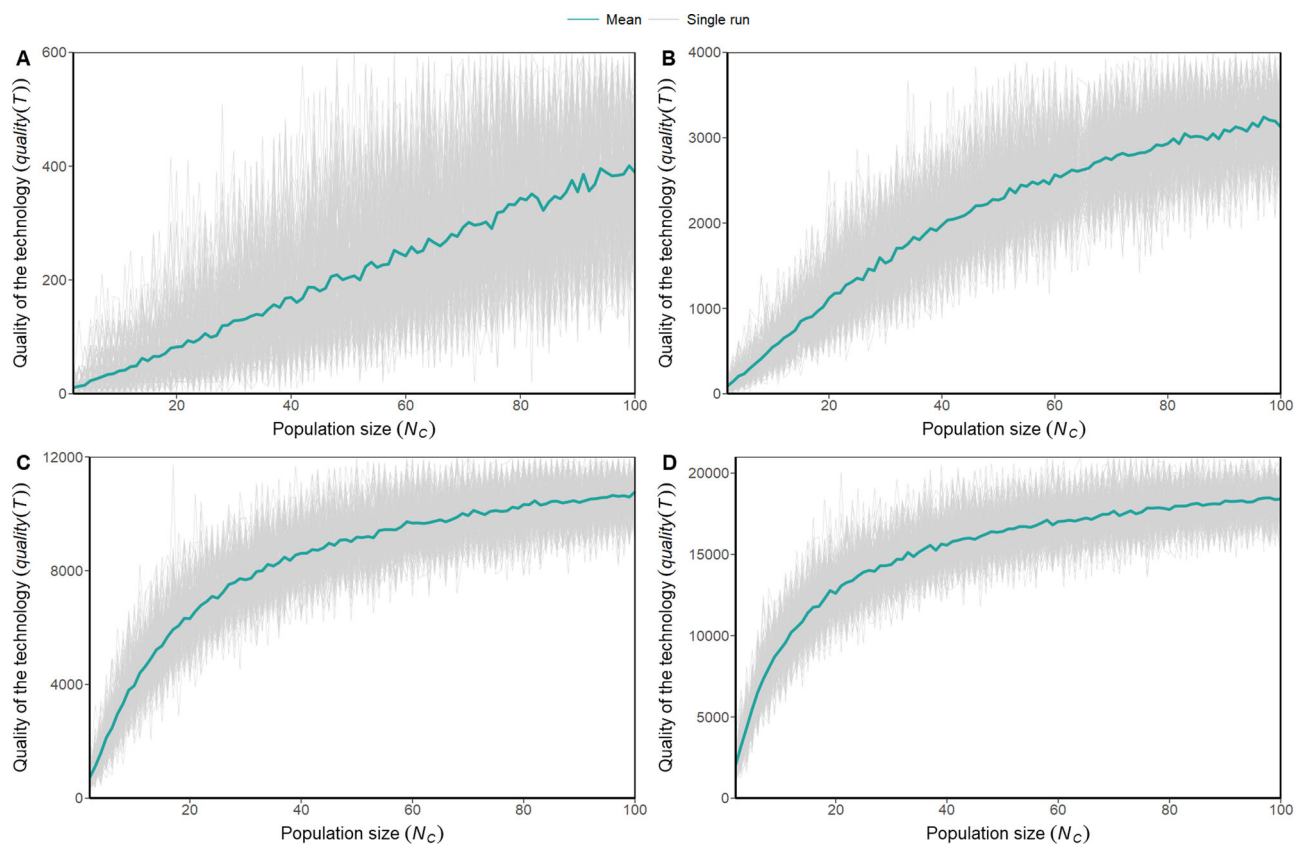

Fig. 8 Model results in terms of technology's quality as a function of population size. We run 200 simulations of 200 generations for each population size in the range [0, 100]. Gray lines represent each simulation single simulation run for a specific population size. The blue line represents the averaged technology's quality between simulations. Common parameter values for all models: $n = 2$, $\theta = 5$, $\beta_{UP} = 1.2$, $\beta_{DOWN} = 0.6$. **A** $p_{innovation} = 0.001$. **B** $p_{innovation} = 0.01$. **C** $p_{innovation} = 0.05$. **D** $p_{innovation} = 0.1$.

Our results are consistent with these last studies, by showing that larger population sizes do not relate to a greater CTC in a linear fashion. More specifically, while the CTC increases with population size, this effect becomes limited as the population grows larger, indicating that the contributions of additional individuals in the population is significant primarily for smaller populations. These results are in line with the literature that shows an effect of population size only when the population is small (Andersson and Törnberg 2016; Ben-Oren et al. 2023; Vaesen et al. 2016). Furthermore, multiple studies show no relationship between population size and the archeological tool record (Andersson and Read 2016; Buchanan et al. 2015; Collard et al. 2013; Schiffels and Durbin 2014; Vaesen 2012). Our model predicts that this is not due to slowing the innovative process in larger populations, as the number of innovations is evolving linearly with population size. It is also not linked to more missed opportunities in big populations, as the model shows that the mean *asocial innovation* loss decreases as the population size increases. Finally, larger populations do not mean a slower spread of innovation. Indeed, our model shows that the innovation spread speed is growing logarithmically. Thus, the question of why larger populations are not linked to greater CTC while they are innovating significantly more than lesser populations remains open. Overall, these results provide insights into the underlying mechanisms of CTC and highlight the effectiveness of our micro-scale modeling framework in exploring demographic factors.

Our model shows that individuals rapidly rely on *socially learned innovations*, meaning that they do not innovate themselves but take the *asocial innovation* of the few individuals who do. This is akin to the free-rider problem expressed by Roger in his 1988 paper (Rogers 1988). In his model, Roger shows that as the frequency of social learning grows, the overall fitness of the population decreases. Indeed, learning socially has less cost than learning asocially, hence an individual should try to learn from others. However, if every individual does so, no one will bring new knowledge to the population, and thus the fitness of the population will decrease. This problem was solved by integrating social-learning bias (Boyd and Richerson 1995; Kameda and Nakanishi 2003). Thus, our results showing the lesser impact of population size in larger populations could be explained because unbiased social learning is assumed in the model. A model integrating social learning bias could lead to a linear increase in CTC as a function of population size. Nevertheless, it is important to note that the implication of social learning biases, particularly the prestige bias [(Henrich and Gil-White 2001) for a review see Kendal et al. (2018)], remains contested in the literature (Chellappoo 2021).

Another result of our model is that in larger populations, individuals rely more on their skills (here, TR) to innovate than on the fact that the technology is already optimized, and thus it can be improved through *asocial innovation* only. This is in contrast to smaller populations, where *asocial innovation* is rooted in both technical reasoning and technological optimization. In later generations, we observe a resurgence of *asocial innovation* relying on technology optimization, even for larger populations. This could be because, in the later stages of a population, the technology is too advanced for individuals to master its underlying mechanism during their lifetime, a known fact in the literature (Mesoudi 2011). In line with this interpretation, our model shows that individuals are at their best in terms of understanding the technology in larger populations and at earlier stages of their development. On the contrary, populations have more optimized technology either when they are small, yielding simpler technology easier to optimize or in the latter generations. This result indicates that while smaller populations may have less diverse or complex technologies, they might have a better understanding of them, while larger, more advanced

populations rely more on others to develop technologies and techniques.

We also tested for the influence of the *asocial innovation* rate on the effect of population size. Our results show that greater *asocial innovation* rates (i.e., more chance to innovate) are linked with a decreased effect of population size on CTC. Indeed, although increasing the rate of *asocial innovation* leads to a better CTC, it also leads more quickly to the asymptote of the population size effect. It has already been suggested that the effect of population size might be limited by the rate of innovation (Baldini 2015; Fogarty et al. 2017; Kobayashi and Aoki 2012). Moreover, this asymptote seems to arrive in our model at the moment when the threshold of one *asocial innovation* per generation is reached (i.e., around 100 individuals for $p_{innovation} = 0.01$, 20 for $p_{innovation} = 0.05$ and 10 for $p_{innovation} = 0.10$), which indicates that once there are enough innovators in the population, it is no longer necessary to increase its size to obtain a better CTC.

While these results contribute to the debate on the involvement of demographic factors in CTC, we would like to point out that our model has its limitations. First, we assume a cross-learning population for simplicity. However, it has been shown many times that population structure has an impact on CTC (Creanza et al. 2017; Derex and Boyd 2016; Kolodny et al. 2015; Lehmann et al. 2011). Furthermore, recent studies have shown the impact of effective population size on CTC (Deffner et al. 2022; Derex and Mesoudi 2020). Because of our assumption of a fully cross-learning population, the effective population size is the same as the population size in our model, thus reinforcing the idea that to study CTC, a non-fully cross-learning population is better suited. It seems important to us that future research on this topic should focus on population structure and connectivity. Second, we assume unbiased social learning, where each individual randomly chooses the predecessor they will learn from. The choice to abstain from social learning biases is a choice that we assume, but integrating these biases into the model could give interesting results, as several studies have already pointed out (Acerbi and Alexander Bentley 2014; Atkisson et al. 2012; Henrich and Gil-White 2001; Jiménez and Mesoudi 2019; Thompson and Griffiths 2021). Finally, as we have shown, our results depend greatly on the way we model innovations and whether they are socially transferable. First, how individuals innovate is derived from the model on which the present work relies (Bluet et al. 2022) which itself bases its innovation process on another model (Creanza et al. 2017; Kolodny et al. 2015) that has been proven successful. Second, the assumption that innovations are socially transmitted is consistent with most models in the literature in which individuals pick up the majority of traits from the person they observe (Andersson and Törnberg 2016; Aoki 2018; Baldini 2015; Ben-Oren et al. 2023; Creanza et al. 2017; Henrich 2004; Kobayashi and Aoki 2012; Miu et al. 2018; Powell et al. 2009). However, the assumption that innovation can be acquired without any cost for the social learner can be questioned. Simple solutions to this problem could either be to add a cost for *socially acquired innovation*, or to implement criterion for this type of innovation, akin to *asocial innovation*. Nevertheless, the potential emergence of a link between innovation and population size could be investigated as a function of the innovative process.

Humanity has relied heavily on technologies to conquer the world, and our success as a species cannot be explained without CTC. Our model suggests that population size is not the sole explanatory reason for our success and that the way innovation arise, are transmitted and their frequencies have a much greater impact on CTC. Thus, future studies should focus more on the process behind innovation and its implication in the demographic factors governing CTC.

Data accessibility

Note

1 Note that in the previous model, the condition was called *communication*. We decided to change it to *teaching* as it led to confusion in the previous paper over the meaning of communication and its implication in CTC [for a more detailed explanation, see Bluet et al. (2022)].

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