# Cumulative Cultural Evolution in Age Structured Populations: a simulation study

A Thesis

Submitted to

Indian Institute of Science Education and Research Pune in partial fulfilment of the requirements for the BS-MS Dual Degree Programme

by

Rishabh Bagawade

20151135

Supervisor: Prof. Sutirth Dey

Indian Institute of Science Education and Research Pune

Dr. Homi Bhabha Road, Pashan, Pune 411008, INDIA.

April, 2020

# Certificate

This is to certify that this dissertation entitled "Cumulative Cultural Evolution in Age Structured Populations: a simulation study" towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study/work carried out by Rishabh Bagawade at Indian Institute of Science Education and Research under the supervision of Prof. Sutirth Dey, Professor, Department of Biology, IISER Pune during the academic year 2019-2020.

Dey

Prof. Sutirth Dey

Date: 6/4/20

Committee:

Supervisor: Prof. Sutirth Dey

TAC member: Dr. Anand Krishnan

# Declaration

I hereby declare that the matter embodied in the report entitled "Cumulative Cultural Evolution in Age Structured Populations: a simulation study" are the results of the work carried out by me at the Department of (Biology), Indian Institute of Science Education and Research, Pune, under the supervision of Prof. Sutirth Dey and the same has not been submitted elsewhere for any other degree.

Rishabh Bagawade

Date: 31/3/2020

6/4/20

# Table of Contents

# List of Figures

# List of Tables

# Abstract:

Cumulative culture, i.e. the knowledge that builds over one another across generations, is considered to be a unique aspect of humans since it provides massive adaptive advantage and allows humans to colonize a wide range of habitats on earth. Culture can be socially transmitted via transmission modes such as vertical (VT), horizontal (HT), and oblique (OT) transmission. These transmission modes have been studied previously in the context of cultural traits which are non-cumulative in nature. We built an age structured individual based model which would capture the effect of pure and mixed transmission modes on cumulative cultural dynamics. Pure transmission modes showed considerable differences in terms of rate of change, complexity reached at equilibrium, as well as the distribution of cultural values at equilibrium. Agreeing with the previous results, the rate of accumulation followed the order HT>OT>VT, however, the complexity of cumulative culture at equilibrium followed the order OT>VT>HT, suggesting the efficiency of transmission modes would depend on the time frame in which one is comparing them. The comparison of mixed transmission modes, in the form of ‘agriculturalist’ and ‘hunter-gatherer’ learning life histories, showed that, keeping all else equal, agriculturalist strategy can sustain more complex cumulative culture than the hunter-gatherers. Further, populations with higher survival showed higher ability to sustain complex cultures. Comparison of learning mechanisms, defined in terms of cost and hierarchy, in tandem with pure transmission modes showed that learning from elders would help reach higher complexity at equilibrium in majority of the cases. Age structure plays a key role in explaining all the results. At the end we suggest several directions in which one can expand this model.

# Acknowledgments:

First and foremost, I would like to express my gratitude to my supervisor, Prof. Sutirth Dey, for providing me immense freedom to choose the direction of the project while providing valuable inputs and directions at the same time. Periodic discussions with him were enlightening and have taught me how to think about an idea in all possible directions. I admire his habit of giving personal attention to the reports and presentations of each student in the lab.

I would also like to thank Abhishek Mishra for mentoring me over the course of two years. He has helped me out in every aspect, from how to write a good report to making sense of some of the results. He has been a part of all the discussions with sir and he could always rephrase some of my half-baked ideas in a coherent manner.

It is really important to have a cheerful and refreshed mind when you get back to work. This wouldn’t have been possible without all the current and previous lab-mates with whom I enjoyed fun-filled activities which refreshed my mind. I am also grateful for their contribution during my presentations in lab, which has given me valuable insights for improving my work.

I would like to use this opportunity to thank IISER Pune, for providing immense flexibility while choosing our courses and giving us an opportunity to work on our thesis projects for a full year. I would also like to express my gratitude to my TAC member, Dr. Anand Krishnan, for his valuable inputs during mid-year evaluation and his support throughout the year.

Finally, I would like to thank my family, and special thanks to Vasanti for being a constant support in every aspect of my life.

## 1. Introduction:

‘Culture’ can be defined as information, including knowledge, beliefs, attitudes, norms, preferences, and skills, which is acquired from other individuals via social transmission (Mesoudi, 2011a). Culture also includes the products of this information embodied in the form of behaviour, and artefacts which can be learned and transmitted to other individuals (Cavalli-Sforza and Feldman, 1981). The words ‘culture’ or ‘cultural traits’ are used to refer to the information which is transmitted socially. Culture can be acquired either from other individuals by ‘social learning’ or can be acquired independent of others by ‘individual learning’ (Ohtsuki et al., 2017). Social learning can occur via processes such as direct instruction (teaching), imitation (copying others), and emulation (reproducing by observing end results of others’ actions) (Boyd and Richerson, 1985; Hewlett et al., 2011); or also from imprinting and conditioning (Cavalli-Sforza and Feldman, 1981). Individual learning can be an outcome of trial-and-error, insight, deduction, or novel combinations of existing cultural traits (Creanza et al., 2017; Enquist et al., 2008; Rendell et al., 2010). For the purpose of this study, we use the words ‘learning’ or ‘transmission’ for social learning and the word ‘innovation’ for individual learning.

It has been argued that culture can evolve similar to biological evolution, and ‘cultural evolution’ is the theory which studies the evolution of cultural traits over time (Mesoudi, 2016). Evolutionary processes such mutation, inheritance, selection, migration, and drift have parallels in cultural evolution in the form of innovation, transmission, cultural selection (learning biases), demic (with physical movement of individuals) and cultural (without physical movement of individuals) diffusion, and cultural drift respectively (Mesoudi, 2017). The similarities and differences between these parallels are extensively discussed in the seminal works done by Boyd and Richerson, (1985); and Cavalli-Sforza and Feldman, (1981). Cultural evolution has been studied extensively since it provides a second inheritance system (apart from genetic inheritance) (Whiten, 2005). It can also provide adaptive advantage to animals in the form of efficient foraging techniques, travel route selection, mate choices, predator avoidance techniques etc.; and to humans in the form of communication (language), tool making, and other scientific and technological advancements (reviewed in Whiten et al., (2017)). Furthermore, culture can modify selection pressure on certain genes, for example, in the case of humans, the emergence of agriculture and cattle farming is considered to be positively selecting the alleles that help us to digest food rich in plant starch and lactose respectively, and this phenomenon is regarded as gene-culture coevolution (Creanza et al., 2017; Richerson et al., 2010).

The ability to accumulate and build upon existing knowledge over several generations is argued to be central in providing distinctive adaptive advantage to humans (Salali et al., 2016; Stout et al., 2019). The accumulated culture can be defined as cumulative culture provided it is built over previous knowledge and is so complex that no single individual can invent it within the individual's lifetime (Dean et al., 2014; Mesoudi and Thornton, 2018). Such accumulation of cultural modification over multiple generations can be called as the 'ratchet effect' (Tennie et al., 2009; Tomasello, 1999), and the process of accumulation itself is regarded as cumulative cultural evolution (CCE) (Mesoudi and Thornton, 2018). CCE is considered a key factor that imparts humans with the ability to generate complex cultural traits that provide adaptive advantage, allowing them to colonize numerous types of environments on earth (Castro and Toro, 2014; Hill et al., 2009; Richerson and Boyd, 2005).

Theoretical studies have compared the importance of individual versus social learning, and the results suggest that individual learning is favoured in fluctuating (both spatial and temporal) environments whereas social learning is favoured in comparatively stable environments (Aoki and Feldman, 2014; Boyd and Richerson, 1988; Feldman et al., 1996). However, both social learning and individual learning (innovation) are considered important to explain cumulative culture (Aoki, 2010; Borenstein et al., 2008; Lehmann et al., 2010); learning spreads the pre-existing knowledge whereas innovation builds upon it, and the innovations are then spread in the population via learning leading to accumulation of culture. There are ample numbers of analytical and/or computational studies in the literature that investigate cumulative cultural dynamics in a variety of contexts. For example, origin and sustenance of cumulative culture (Enquist and Ghirlanda, 2007; Pradhan et al., 2012); evolutionary steady states between learning and innovation (Lehmann et al., 2010); importance of high fidelity transmission to maintain cumulative culture (Castro and Toro, 2014; Lewis and Laland, 2012); effects of innovation rates, population size, population density, network size, network connectivity, etc. on CCE (Baldini, 2015; Derex and Boyd, 2016; Fogarty and Creanza, 2017; Kobayashi and Aoki, 2012; Kobayashi et al., 2016); rarity of cumulative culture in other animals (Kempe et al., 2014); existing cultural elements facilitating or inhibiting accumulation of new cultural elements (Enquist et al., 2011).

As opposed to genetic transmission which is strictly vertical (and rarely horizontal), social transmission can occur via different transmission modes such as vertical transmission (VT), horizontal transmission (HT) and oblique transmission (OT) (Cavalli-Sforza and Feldman, 1981). Individuals learn from their biological parent in VT, learn from their peers in HT, and learn from elder individuals in OT. Analytical and computational models have been used in order to study the differences in spread of cultural traits via different pure transmission modes. For example, Cavalli-Sforza & Feldman (1981) use analytical population genetic models for explaining vertical transmissions, and epidemiological models for explaining horizontal and oblique transmission. They regard vertical transmission to be conservative, i.e. new traits do not spread as rapidly as horizontal or oblique transmission. Other recent studies have used age-structured mathematical and/or simulation models to study the effects of transmission types on culture. For example, Kandler et al., (2017) have investigated the effects of individual level preferences for transmission modes and their effects on population level characteristics such as cultural diversity. They found that vertical transmission shows the slowest rate of change (confirming its conservativeness) whereas oblique transmission leads to lower cultural diversity and slower rates of change as compared to horizontal or age neutral transmission modes. Some studies also look at the effects of fluctuating (in both space and time) environments on the preference towards vertical or oblique transmission (Ram et al., 2018, 2019). While other studies investigate the effects of vertical, horizontal and oblique transmission, on cultural dynamics and demography, where the cultural traits affect survival or fertility of the individuals (Fogarty et al., 2013, 2019).

Apart from pure transmission modes, a few theoretical studies also consider mixture of transmission modes (Fogarty et al., 2019; Kandler et al., 2017). One of the major ways in which mixed modes of learning can be studied is using 'learning life history' which is defined as the dominance of different modes of transmission at different stages of individual's life (Fogarty et al., 2019). There are empirical studies that have investigated learning life histories of different communities and have provided data in the form of age dependent preference to a particular transmission mode. For example, Hewlett et al., (2011) studied *Aka* hunter gatherers and neighbouring *Aka* and *Bofi* agriculturalists in central Africa; Kline et al., (2013) studied life history of learning in Fijian villages; and Aunger, (2000) studied the learning life histories of orally transmitted culture in a society based in Republic of Congo. We have used data from one of these studies (Hewlett et al., 2011), which was also used by Fogarty et al., (2019), in this investigation.

The existing studies (including the ones described above) which incorporate different pure and mixed modes of transmission are in the context of non-cumulative culture i.e. they study the effects on the spread of a single cultural trait or multiple independent cultural traits which do not have the property to accumulate over generations. Therefore, in the first part of this study we aim to investigate the effects of pure transmission modes on the dynamics of cumulative culture. In the second part, we study similar dynamics in the context of 'hunter-gatherer' and 'agriculturalist' learning life histories defined in Fogarty et al., (2019). In order to study transmission modes in the context of cumulative culture we incorporate age structure into our model. Age-structure becomes necessary in order to define the identity of parents, peers, and elders, which in turn define the transmission modes (the pool of individuals from whom a focal individual would learn). It also enables us to define age-dependent learning life histories. In the third part of this study, we explore some other possibilities where there is either some cost associated with learning or there is presence or absence of hierarchy during the process of learning. We define hierarchical transmission as a learning process where learner and demonstrator are pre-defined in a transmission event, and costly transmission where culture can be lost by either of the individuals taking part in a transmission event. We study the cumulative cultural dynamics in terms of the amount of culture accumulated and the rate at which it accumulates. The results show different dynamics for the defined pure and mixed transmission modes. The rate of spread of culture is slower for vertical transmission and oblique transmission than horizontal transmission (agreeing with previous results) but interestingly the amount of culture accumulated in the long run is the highest for the oblique transmission, followed by vertical, and the least for horizontal transmission. Age structure plays a crucial role in explaining the results.

## 2. Methods:

For the purpose of this study, we constructed a uniparental, age-structured, individual-based model with overlapping generations and fixed population size. The model is purely cultural i.e. culture does not affect survival or reproductive ability of the individuals. The cumulative property of the culture is modelled similar to model 2 of a previous study (Kempe et al., 2014). The individuals in this model possess a single cultural trait that has multiple levels/complexity, denoted by whole numbers. We define the maximum level of the culture possessed by an individual as its ‘cultural value’. Cultural value of zero implies the individual does not possess the culture, non-zero value implies the individual possess the culture and higher the value greater is the cultural complexity (for example, possession of a skill, and higher and higher efficiency in performing that skill). There is no predefined upper limit to the number of trait levels. Each individual can innovate and/or learn from others in order to gain new levels. A new level can be learned or innovated only when the individual has all the preceding levels. This signifies the cumulative nature of the cultural trait.

Following existing age-structured models in the cultural evolution literature we built a model discrete in time (discrete age classes) (Baldini, 2014; Fogarty et al., 2013, 2019; Kandler et al., 2017) but with a finer scale i.e. one time step equivalent to one year. This allows us to use age-dependent survival curves, fecundity curves, as well as age dependent preferences to particular transmission modes (learning life histories).

The scope of this study is broadly divided into three parts and each part is studied using slightly different execution of the main simulation model. Model 1 is our main model, which is used to look at the differences in the modes of transmission with respect to the dynamics of the cumulative culture. In Model 2 the transmission is modelled on the basis of life history of learning (i.e. different modes of transmissions being dominant at different stages of life) and in Model 3 we look at cases where cultural transmission is either hierarchical or non-hierarchical and costly or non-costly (2×2, 4 cases). Model 2 and 3 are equivalent to Model 1 except the differences in the cultural transmission (learning) step. Learning step follows the learning life histories in model 2 and the combinations of hierarchical and costly transmission processes in model 3.

The cultural dynamics of the models depend upon several parameters (see table 1). Learning ability ‘a’ is the probability of success per learning attempt and is equivalent to ‘accuracy of social learning’ in Kempe et al, 2014. Every individual gets an opportunity to learn from others at each time step, we call this as a ‘transmission event’. The way learning happens in a transmission event is discussed in section 2.1.3. Every individual gets one innovation attempt per time step, and innovation ability ‘μ’ is the probability of success per innovation attempt. The number of demonstrators from which the focal individual learns will be denoted by ‘k’. Peer Width ‘PW’ is the age range that is considered as the peer group for a particular individual. Apart from these parameters the cultural dynamics may also depend upon other factors such as population size (popsize), survival curve, and fecundity curve. For simplicity, every individual in a given population is considered to have the same parameter values.

*Table 1: Model parameters.*

| **Parameter name** | **Symbol** | **Description** |
|---|---|---|
| Learning ability | a | Probability of successful learning of a cultural level |
| Innovation ability | μ | Probability of successful innovation per attempt |
| Peer Width | PW | Range of age considered as peer group |
| # of demonstrators | k | Number of demonstrators picked for learning |
| Population size | popsize | Number of individuals in the population |

The basic flow for all the models is shown in figure 1. All the steps are discussed in detail in the subsequent sections. Simulations run for 5000 iterations (or more in some cases) and 20 replicates. It is important to note that the model is simplistic and considers cultural transmission similar to that in primitive human societies where the transmission occurs only via social interactions (teaching, imitation, etc.) and the information is not stored in any written or non-perishable form i.e. information will be removed from the population once the individual who possessed it is dead.

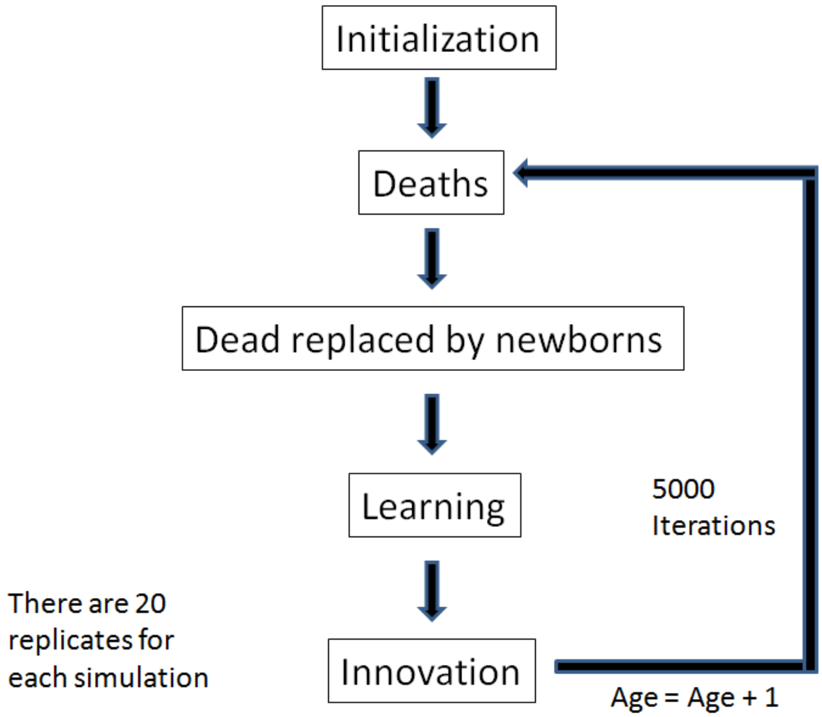



*Figure 1: Basic model flowchart. Each simulation runs for 5000 iterations (more in some cases) and 20 replicates.*

*2.1. Model 1: Comparing cumulative cultural dynamics of pure transmission modes*

This is the central model of our study, where we compare the differences between the dynamics of the cumulative cultural evolution (CCE) when different pure transmission modes are followed, namely, Vertical Transmission (VT), Horizontal Transmission (HT), Oblique Transmission (OT), and Age Independent Transmission (AIT). Model 1 follows the basic steps in figure 1 and is described below in detail.

*2.1.1 Initialization:*

A population of fixed size (popsize) is initialized. Each individual begins with a zero cultural value. Survival curve in figure 2a shows the proportion of individuals in the initial population, y-axis, which would survive till a particular age on the x-axis. This implies the stable age distribution would look similar to the survival curve. Thus, to ensure stable age distribution, age is assigned to each individual in such a way that it mimics the survival curve (figure 2a) i.e. there are higher numbers of younger individuals than the older ones. Stable age distribution makes sure that the age distribution itself is not interfering with the cultural transmission. Parents are assigned randomly in the beginning, one parent per individual. This means that everyone gets a parent assigned and the parent is considered alive if its age is greater than the offspring by at least twelve (i.e. the age where fecundity first becomes non-zero). The birth-death cycle (see section 2.1.2) is iterated 500 times before starting the simulation run (i.e. starting cultural transmission) to make sure that the age structure and parent assignment is stabilized.

<u>*2.1.2. Birth-Death cycle:*</u>

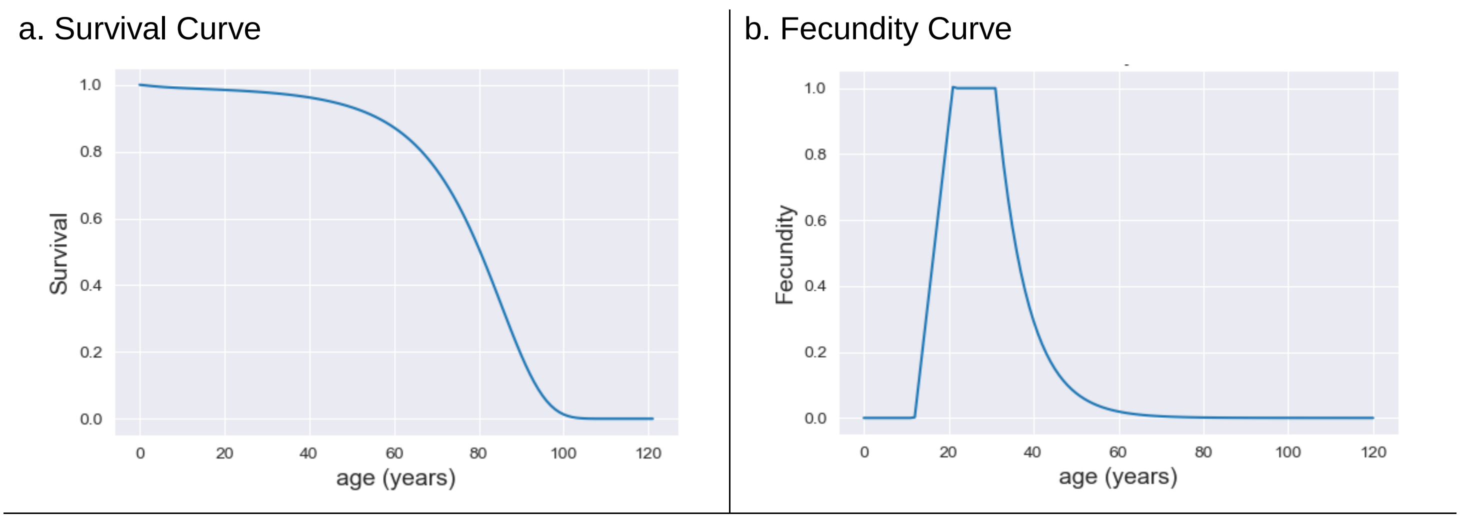



*Figure 2: a) Survival curve. Adopted from Weon, 2003. b) Fecundity curve. Adapted from Noord-Zaadstra et al., 1991.*

The next two steps in figure 1 (deaths and dead replaced by newborns) is elaborated in this section. The survival curve in figure 2a represents the proportion of the initial population, y-axis, which would survive till the particular age on the x-axis. We used a transformed version of this survival data in order to incorporate into our simulations (see appendix 1). The transformed survival curve (see figure A1b in appendix 1) gives us the age dependent probability for an individual surviving from age t to age t+1, and individuals die according to this age dependent probability. Dead individuals in this step are replaced by naïve newborns (culture = 0, age=0) so that the population size remains constant.

The parents of the newborns are decided based on an age-dependent fecundity curve (figure 2b), adapted from Noord-Zaadstra et al., 1991, the values from age 21 onwards are coming from the data from the paper and we have fit a straight line from age 12 till 21 to make up the unavailability of the data before age 21. The curve in figure 2b is relative and shows the age dependent fecundity normalized by the highest value. Parent is assigned in such a way that individuals with higher fecundity have higher chance of getting assigned as a parent of one of the newborns. The model is uniparental i.e. the newborns are assigned to a single parent. Also, in a given time step, an individual is capped to have maximum of one child, this is done keeping in mind that humans, in general (ignoring twins), can have only one child per year (here one time step corresponds to one year). Note that an individual can have multiple offspring but in a single iteration it can have maximum of one offspring. In this study the birth – death cycle does not get affected by culture.

### *2.1.3. Learning:*

Every individual gets a chance to learn at every time step. We call this a 'transmission event'. The cultural values are updated as soon as the transmission event has happened, thus if the same individual takes part in another transmission event then it goes in with the updated value. Individuals learn in randomized order in every time step. The individual from whom the focal individual learns is called a 'demonstrator' and the focal individual itself is called as a 'learner'. At every time step each individual randomly picks k demonstrators from the pool of individuals determined by the transmission mode (see table 2). In VT, learning of the focal individual stops after the parent (demonstrator) dies. If the number of individuals in the pool are less than or equal to k then all of the individuals in the pool are picked. The learner learns from the first demonstrator it picks and then moves on to the next until the learning is attempted from all k demonstrators.

Cultural value of the demonstrator needs to be greater than that of the learner for learning to occur. From each demonstrator, the individual learns the first level that it does not possess with probability ‘a’, if successful it learns the next level with the same probability ‘a’, this goes on until it fails to learn for the first time or reaches the cultural value equal to that of the demonstrator.

*Table 2: Rules to pick demonstrators according to the transmission mode*

| **Transmission Mode** | **Rule to pick the demonstrator** |
|---|---|
| Vertical Transmission (VT) | Pick the parent |
| Horizontal Transmission (HT) | Pick from the peers of age ∈ (own age ± PW) |
| Oblique Transmission (OT) | Pick from the elders of age > (own age + PW) |
| Age Independent Transmission (AIT) | Pick anyone (except parents) |

### *2.1.4. Innovation:*

At every time step, every individual attempts to innovate. Probability of success of an innovation attempt is ‘μ’. If successful, the cultural value of the individual is incremented by one, and if not, the cultural value is not affected.

### *2.2. Model 2: Comparing mixed transmission modes in the form of learning life histories*

While model 1 was employed to study the effects of pure transmission modes, model 2 was used to investigate the effects of mixed (i.e. combinations of) transmission modes through ‘learning life histories’ on the dynamics of cumulative culture. Learning life histories can be defined as the contributions of different modes of learning (vertical and oblique/horizontal) throughout an individual’s life span (Fogarty et al., 2019; Kline et al., 2013). Fogarty et al. (2019) define two such learning life history strategies namely ‘Agriculturalists’ (Agri) and ‘Hunter-gatherers’ (HG). They use empirical data from Hewlett et al. (2011), gathered from *Aka* hunter gatherers and neighbouring *Aka* and *Bofi* agriculturalists in central Africa, to define these two learning life history strategies in terms of relative contribution of vertical and non-vertical (oblique/horizontal) modes of transmission in each age class. The empirical data was in terms of the amount of time spent during the day-time within an arm’s reach of the parent and non-parent individuals and Fogarty et al. (2019) assume that the amount of time spent with the individual is proportional to the amount of culture learnt from that individual. We use the same assumptions in this study. Figure 3 shows the learning life history strategies adapted from Fogarty et al. (2019) and depicts the data in a different format (see appendix 2 for more details).

All other parts of model 2 were similar to model 1 except the learning step (see figure 1). In model 2, every individual has an age dependent probability to learn from vertical and non-vertical (oblique/horizontal) transmission modes (according to figure 3). If the population is following hunter-gatherer learning life history then the probabilities will be according to the red curves and if it is following the agriculturalist learning life history then the probabilities will be according to the blue curves. Learning from vertical or non-vertical mode is decoupled i.e. in every time step the focal individual decides to either learn or not learn from a mode of transmission independent of the other. This is done by feeding probabilities of learning from vertical and non-vertical modes, as the success probabilities, into two different binomial random generators. The outcome of each of these two events can be either success or failure. According to the outcome, the individual has the opportunity to learn via both vertical and non-vertical modes (both success), either of the modes (one success, one failure), or neither of the modes (no success). If the individual is learning via both the modes of transmission then it first learns from that transmission mode for which the individual has higher probability of following the transmission type and then learns from the other transmission mode. Similar to model 1, the model 2 is also run for 5000 iterations and 20 replicates. Age and cultural value of every individual at every time step is recorded.

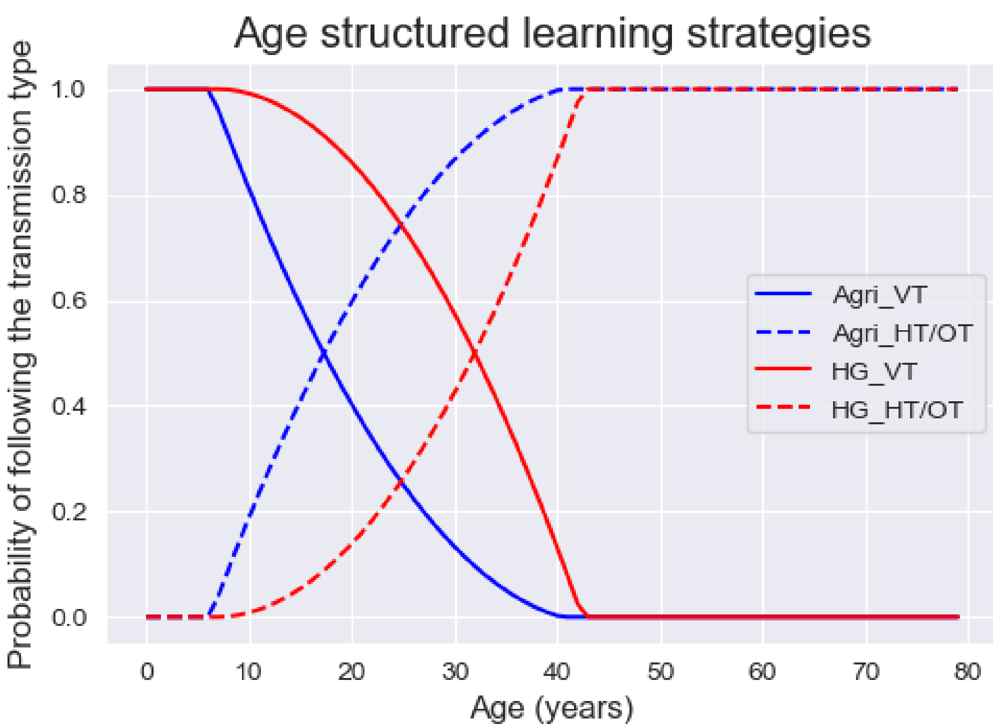



*Figure 3: Age structured learning life history strategies adapted from Fogarty et al. (2019). Blue line denotes agriculturalist and red denotes hunter-gatherer strategy. The solid lines denote the probability of following vertical transmission and the dotted lines denote the probability of following non-vertical transmission.*

## *2.3. Model 3: Comparing different mechanisms of learning defined in terms of hierarchy and cost of learning*

In this part of the study, we consider four different ways (mechanisms) in which learning can occur and compare how they affect the cumulative cultural dynamics. We consider hierarchical and non-hierarchical learning along with costly and non-costly learning. The hierarchical case is where the learner and the demonstrators are predefined whereas the non-hierarchical case is where the learner and demonstrators are not pre-defined before taking part in a transmission event. The costly learning is where the individual loses cultural levels in a transmission event when it interacts with someone who has lower cultural levels. Non-costly learning on the other hand either increases the cultural levels or does not affect it in any way. Taking hierarchy and cost into consideration we have four mechanisms of learning, namely, hierarchical costly (H-C), hierarchical non-costly (H-NC), non-hierarchical costly (NH-C), and non-hierarchical non-costly (NH-NC). Hierarchical non-costly (H-NC) mechanism is the one, which is used in model 1 and 2.

Model 3 runs similar to model 1 except the way an individual learns. Here we compare the four mechanisms of learning defined in the previous paragraph. The schematic in figure 4 demonstrates the way in which we model the mechanisms of learning. The 'H-NC' mechanism is exactly same as model 1, the learner attempts learning when its cultural value is lower than the demonstrator and does not learn anything otherwise (see figure 4a). In the 'H-C' mechanism the learner gains cultural levels when the demonstrator has greater cultural value than learner, loses cultural levels when demonstrator has lower cultural value than the learner, and nothing happens if both have equal cultural levels (see figure 4b). Note that, in hierarchical mechanisms, the demonstrator does not get affected in any way. In 'NH-C' mechanism the learner and the demonstrator are not pre-defined. The individual of lower cultural value gains cultural levels whereas the individual with higher cultural value loses cultural levels and nothing happens when both have equal cultural values (see figure 4c). In this case, loss and gain is decoupled i.e. there is a chance that one individual gains more than the other has lost and vice-versa. In 'NH-NC' mechanism, the learner and the demonstrator are not predefined and, in a transmission event, individual with lower cultural value learns from the one with higher cultural value and there is no loss of culture, nothing happens if the cultural values are equal (see figure 4d).

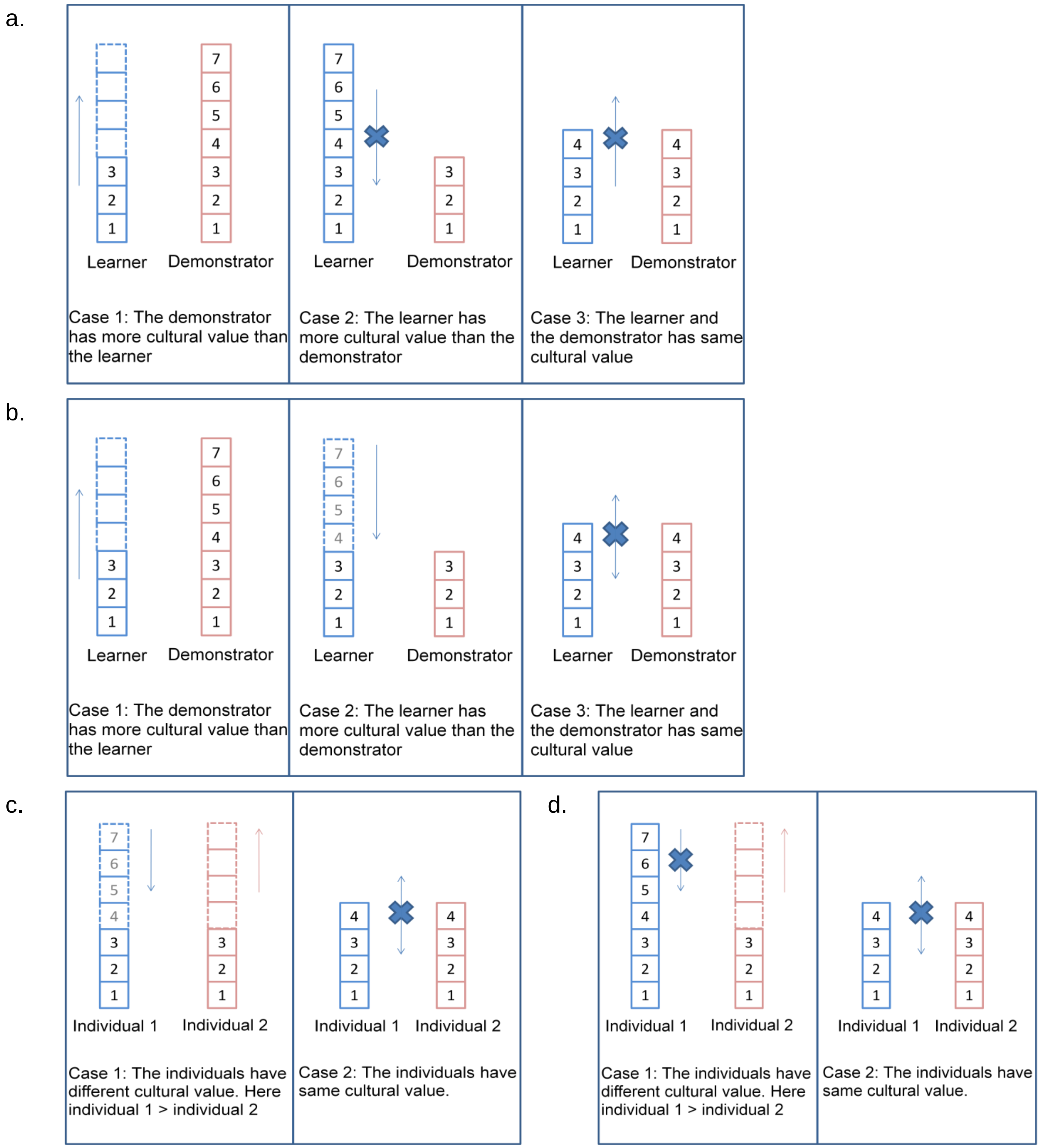



*Figure 4: Schematic for learning mechanisms. a) Hierarchical Non-Costly (H-NC). b) Hierarchical Costly (H-C). c) Non-Hierarchical Costly (NH-C). d) Non-Hierarchical Non-Costly (NH-NC).*

The loss and gain of cultural levels in this model happens the same way as learning happens in model 1 except that the directions are opposite. For simplicity the same value of learning ability ‘a’ is used for both loss and gain of cultural levels.

*2.4. Measures used to quantify the dynamics of cumulative culture*

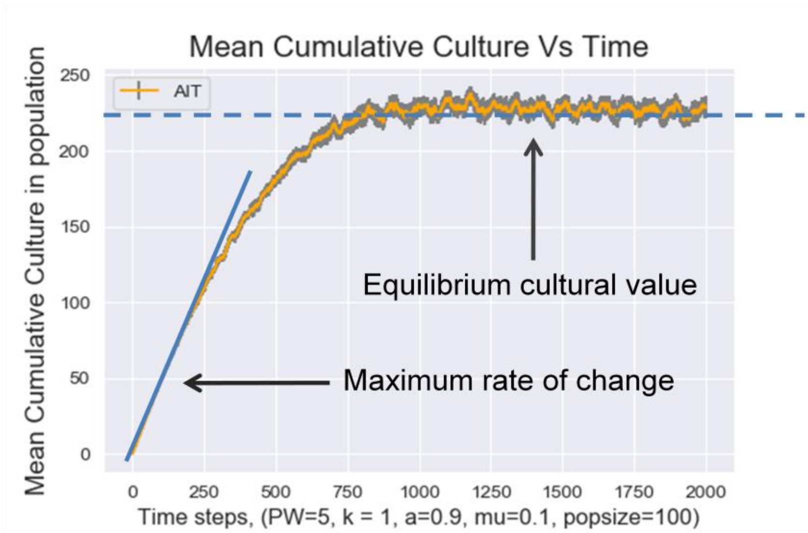



*Figure 5: Time series plot of mean cultural values in the population for Age Independent Transmission (AIT). Error bars are 95% confidence intervals calculated over values form 20 replicates.*

Figure 5 shows that the mean cultural value (mean of cultural values of all the individuals in a population) increases initially and then stabilizes around a value. We call the value where time series stabilizes as the ‘equilibrium cultural value’. We also measure the ‘maximum rate of change’ of cultural value as a proxy for how fast culture can accumulate over time. See appendix 3 for the exact procedure followed to calculate these two quantities.

We first investigated time series of mean cumulative culture in the population for Age Independent Transmission (AIT) (Fig 5) and found that it agrees with qualitative trends (increase and saturation of culture) in previous studies (e.g. (Kempe et al., 2014)). Even though we had not put any upper limit on the cultural levels learnt, the mean cumulative culture reaches an equilibrium value. This is due to the equilibrium reached between learning, innovation and death. Successful learning and innovation is responsible for increase in cumulative culture whereas failed learning attempts and deaths are responsible for removal of culture from the population. These processes balance each other out at the equilibrium. Mesoudi, (2011b) argue that as the complexity of cumulative culture increases, it would be costly for individuals to learn complex cumulative culture and the amount of time required to learn it would be high, resulting in an upper limit of cumulative cultural complexity in a population. Here, without explicitly invoking costs, we get upper limit to the cumulative cultural levels. The time required to learn the higher levels is high, and when this time exceeds the individuals' lifetime then the population reaches an upper limit.

In order to be sure that the above process is actually depicting cumulative culture, we have to show that the culture is accumulating over generations such that no single individual would be able to innovate it in a single lifetime. In order to show this, we plotted the time series with learning ability 'a' to be zero. This implies there is no social learning and the population is accumulating knowledge only through individual innovations. In this scenario, we saw that the equilibrium cultural value reached was only up to 4 (see appendix 4). In figure 5, the mean cultural value becomes greater than 4 pretty quickly, and the equilibrium cultural value is around 225, which implies that the above process is depicting cumulative culture.

## 3. Results and Discussion:

*3.1. Model 1: Comparing the effects of pure transmission modes on the dynamics of cumulative culture*

In this section, the effects of transmission modes on the dynamics of cumulative culture (in terms of equilibrium cultural value and maximum rate of change) are compared.

*3.1.1. Comparison of pure transmission modes*

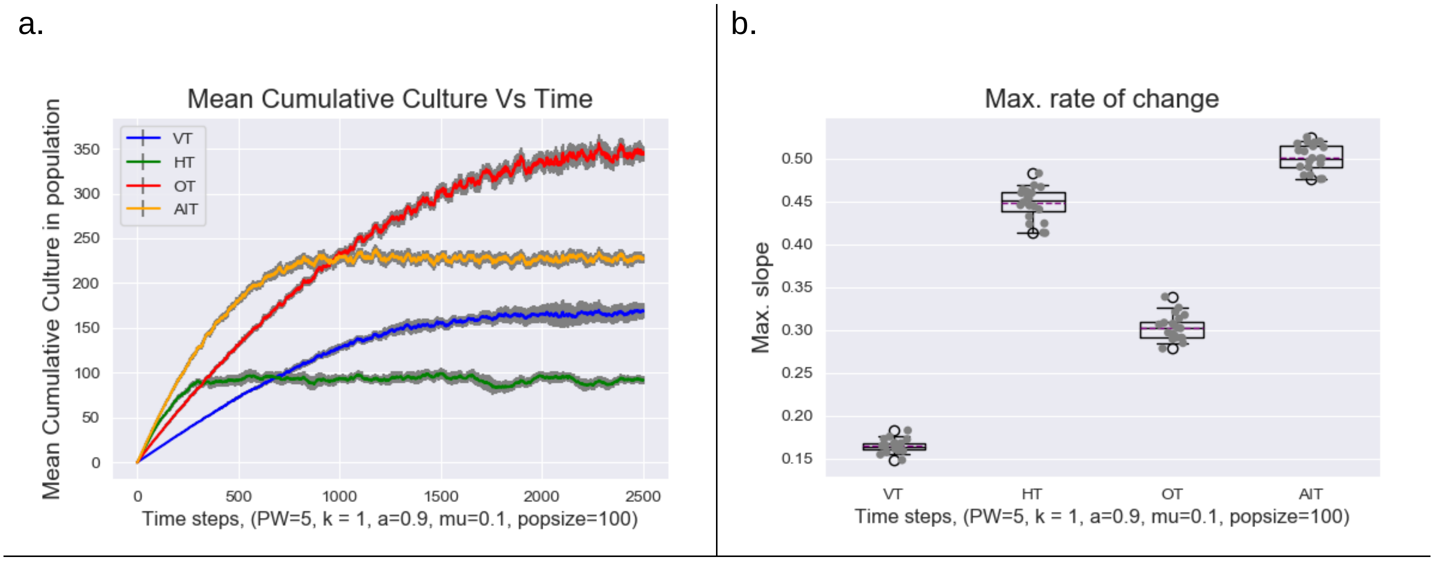



*Figure 6: a) Time series plot for transmission modes. Blue curve corresponds to VT, green corresponds to HT, red corresponds to OT and orange corresponds to AIT. b) Box plot for maximum rate of change for each transmission mode where solid black horizontal line denotes the median and purple dashed line denotes the mean. Parameter values are mentioned on the x-axis label of the plots. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

Figure 6a shows that the time series plots for each transmission mode are different in terms of rate of change as well as equilibrium cultural value. The equilibrium cultural values are in the order OT>AIT>VT>HT. This implies that in the long run; learning from one's elders (OT) appears to be the most beneficial, followed by learning from any random individual (AIT) and learning from your parents (VT), and the least beneficial is learning from one’s peers. Note that these are pure transmission modes, i.e. each population follows only single predefined mode of transmission, and, in many real life situations, this might not be the case. However, studies show that cultural traits can show dominant preference for a particular transmission mode. For example, a study with students from Stanford University showed that traits like political and religious beliefs are predominantly vertically transmitted whereas entertainment preferences are predominantly horizontally transmitted (Cavalli-Sforza et al., 1982). Similarly, sexual health practices are predominantly horizontally transmitted among farmers and foragers of Central Africa (Bailey and Aunger, 1995)).

The maximum rate of change on the other hand follows the order AIT>HT>OT>VT (figure 6b). This implies that culture accumulates the fastest when one learns randomly from anyone (AIT) as well as when one learns from their peers (AIT and HT are pretty close in terms of maximum slope (see figure 6b)). On the other hand, culture accumulates slower in the case of oblique transmission (OT) and it is visibly the slowest in terms of vertical transmission (VT). Similar order for rate of change has been discussed in Kandler et al., 2017, where they compare the dynamics of cultural change (changes in cultural variants) conditioned on vertical, oblique, horizontal, and age-neutral transmission modes. It is important to note that, in our model, higher rate of change does not imply higher equilibrium culture, and hence we can study trends in the two quantities independently.

Another point to observe is that even though HT has very high initial increase in cultural value, it reaches equilibrium quickly and at a much lower value than the others. Similarly, AIT also increases rapidly in the beginning but saturates out well before OT. These dynamics have resulted in the comparison of transmission modes being dependent on the time-frame in which one is trying to compare the mean cumulative culture. For example, before the 300$^{th}$ time step (in figure 6a) HT is higher than both OT and VT but in the next 300 time steps HT becomes the least effective mode of transmission. This implies that the effectiveness of a transmission mode depends on the time-frame in which the transmission modes are being compared. The effectiveness will also depend upon whether a particular cultural traits needs rapid initial accumulation to sustain in the population or it can tolerate slow initial growth but requires higher cultural accumulation in the long-run. HT and AIT will be favourable for the former whereas OT and VT will be favourable for the latter scenario.

Innovations work identically for each transmission type, therefore the differences in the dynamics of each transmission mode must be coming from the learning step. In order to explain the observations so far we would need to consider the characteristics of the pool of individuals from which the learner picks the demonstrators. The characteristics can be the age of the individuals in the pool as well as the size of the pool itself. Another characteristic can be the directionality of the flow of information in the learning process.

In the case of OT and VT, individuals always learn from demonstrators older than them. Since our model is age structured and individuals learn and innovate at every time step, older individuals tend to have high cultural values as compared to the young ones since the older individuals have more chances to learn and innovate (similar arguments are used in (Fogarty et al., 2019)). This gives OT and VT higher chance of getting demonstrators that are more knowledgeable at each learning attempt as opposed to HT, where your peers would have cultural levels similar to you, and AIT, where you would randomly pick anyone from the population as a demonstrator. Therefore, mean cultural value of OT and VT keeps on increasing for a longer time and results in saturation at higher values as opposed to HT. The pool of individuals from which the learner picks the demonstrators is the highest for AIT and in the case of VT, individual can learn only from its parent therefore the pool is the least, resulting in AIT to tap into larger pool of individuals. Hence between AIT and VT, AIT reaches higher equilibrium culture.

The rate of cultural accumulation depends upon the rate of innovations and the rate at which they are spreading. Since the innovation ability 'μ' is the same for all the transmission modes, the rate of occurrence of innovations is the same for all. Hence, the rate of spread of innovations would determine the rate of cultural accumulation. In the case of HT and AIT, the new innovations can spread pretty quickly as the spread is bidirectional i.e. the innovations can spread from older to younger as well as from younger to older individuals. Whereas for OT and VT, the spread is unidirectional i.e.

the innovations can spread only from older to younger individuals. Furthermore, in the case of VT, innovations are transmitted only from the parent to progeny i.e. every family tree needs to innovate and accumulate the culture independently, which drastically slows down the cultural accumulation at the population level. Therefore, AIT and HT have higher maximum rate of change followed by OT and VT. This result agrees with a previous study (Kandler et al., (2017)).

It is important to note that all of the above discussion is valid for the parameters mentioned in the graphs. Whether or not this comparison of transmission modes is conserved across the parameter ranges is discussed in section 3.1.4. Also, in this model, individuals keep on learning and innovating throughout their lifetime. We have also run simulations when learning and innovation stops after certain age and they do not change the qualitative results discussed here (see appendix 5).

### *3.1.2. Different initial cultural values*

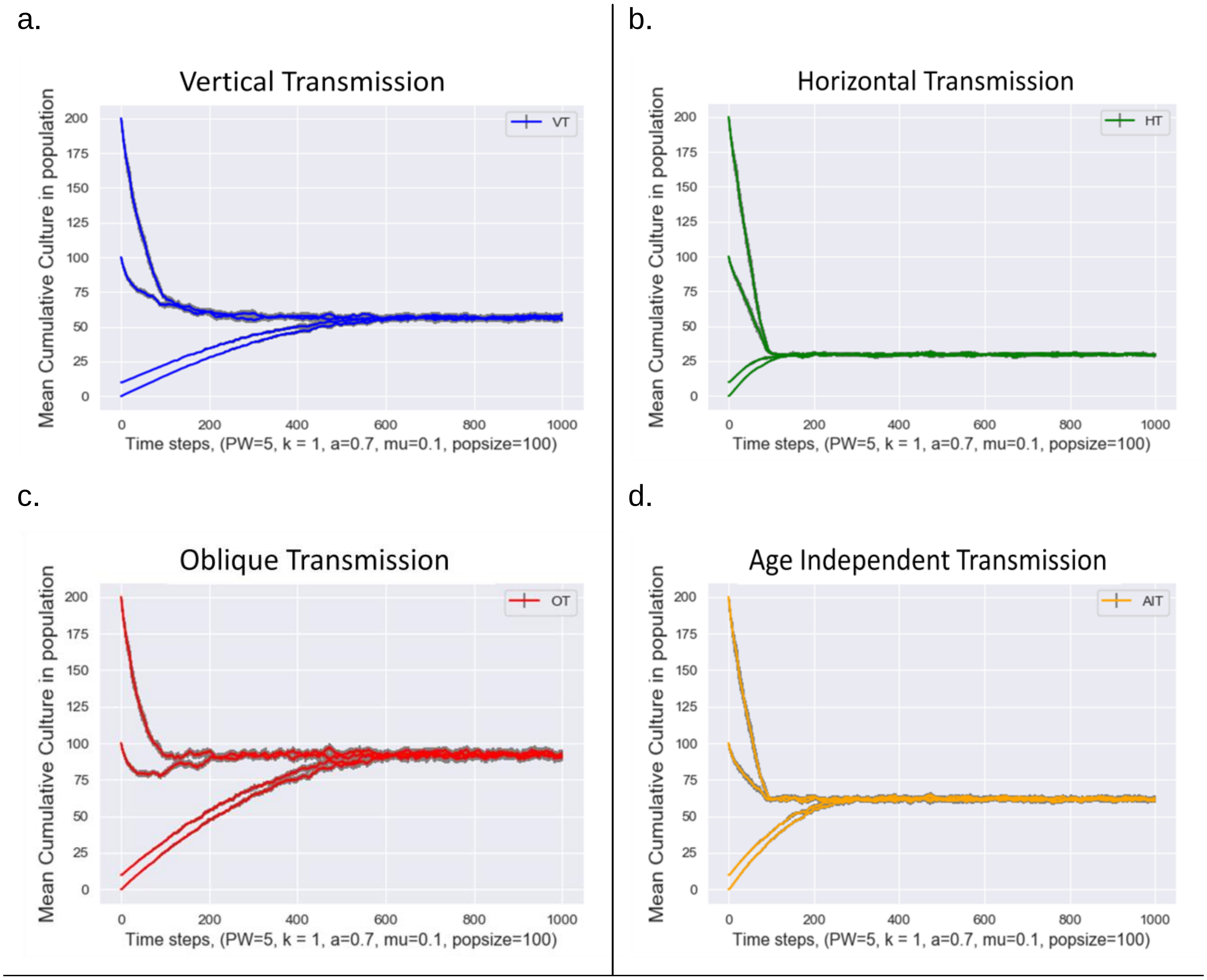



*Figure 7: Time series plots starting with different initial cultural values. The plots a, b, c, and d correspond to VT, HT, OT, and AIT respectively. The starting cultural values chosen are 0, 10, 100, and 200. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

In general, the simulations are started with initial cultural value to be zero i.e. at the beginning every individual has zero cultural value. Figure 7 has the time series plots for the transmission modes when the initial cultural values are not zero. It can be observed that irrespective of the cultural value with which the population starts the cultural transmission process, all the populations reach the same equilibrium cultural value. If the starting cultural value is below the equilibrium then mean culture increases towards equilibrium whereas when the starting cultural value is above equilibrium then the population loses cultural levels to reach towards the equilibrium. These observations are true for all transmission modes.

This implies that only the parameters of the system decide the equilibrium cultural value. In other words, the complexity of the cumulative culture that can be maintained in a given population is determined by the parameters of the population. Even if highly complex (in terms of number of cultural levels) cultural practices (or knowledge) are introduced at some point in the population, the population will lose those practices (or knowledge) until it reaches the complexity which can be maintained in the population. Such, reduction in cultural complexity has been observed empirically. For example, Henrich, (2004) reviewed the case of Tasmania, humans arrived at Tasmania around 34,000 years ago and around 12,000 to 10,000 years ago Tasmania was cut off from mainland Australia due to rising sea levels. In 2000s, contemporary observations and archaeological records showed that the contemporary Tasmanian technologies (e.g. toolkit size and complexities) are much less complex as compared to their own ancestors. This example is to emphasize that the populations can lose cultural complexity. We suggest that the parameters of the population need to be changed (for example, increase a, μ, k, or popsize) in order to maintain higher levels of cultural knowledge. Refer section 3.1.4 to see how cultural dynamics change with the parameters.

### 3.1.3. Distribution of cultural values at equilibrium

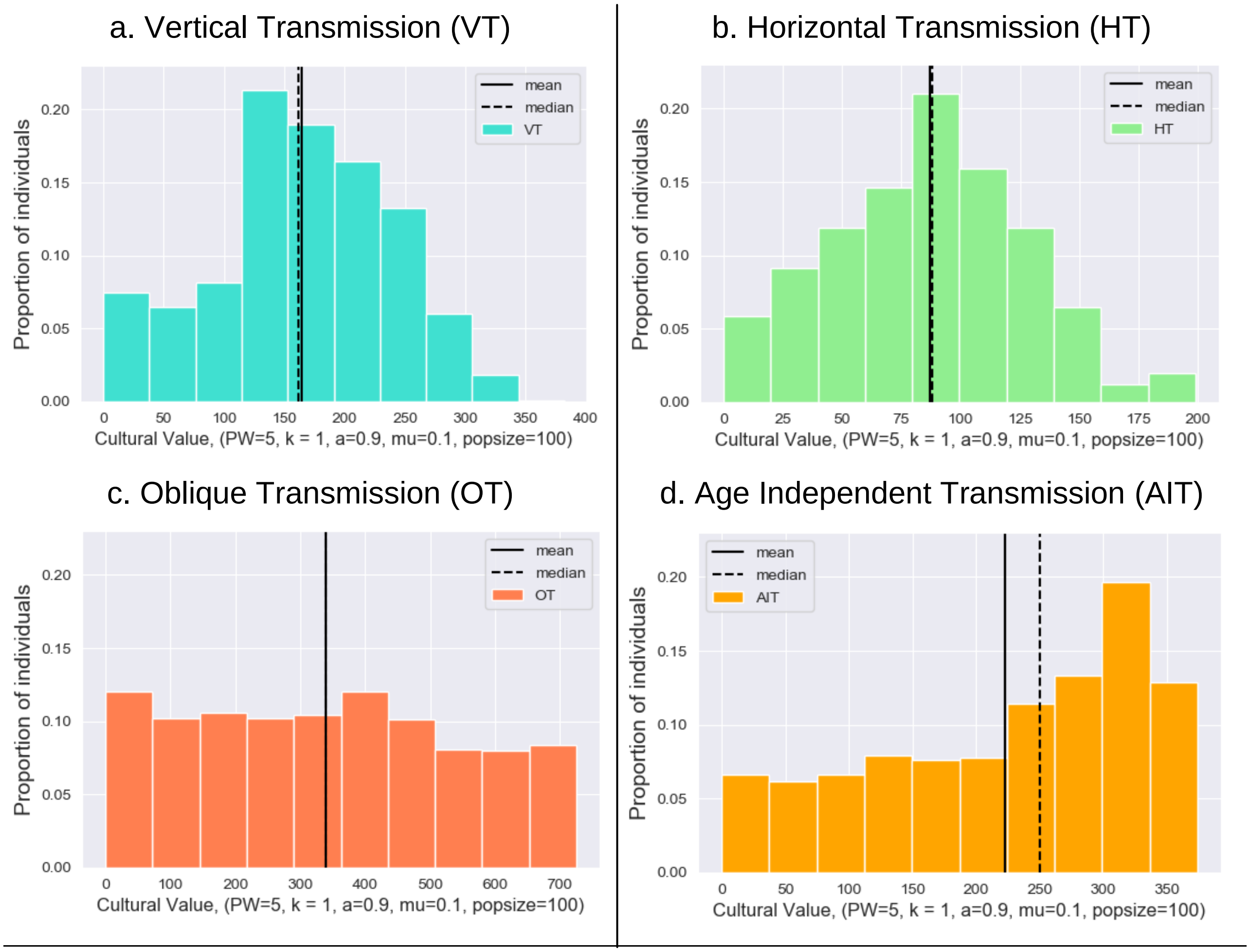



*Figure 8: Distribution of cultural values at equilibrium. The cultural values of all individuals in the last time step (when cultural accumulation has reached equilibrium) along with its 20 replicates are pooled together to plot the distributions. Solid vertical line is mean, and dotted vertical line is the median. Plot a, b, c, and d correspond to VT, HT, OT, and AIT respectively.*

The results till now involved the population level averages of cultural values. Thus, all the information in the population was reduced to a single value. Figure 8 shows the distribution of cultural values once the population has reached equilibrium. We look at the distributions in the form of a histogram where the y-axis shows the proportion of individuals with cultural value lying in the bins on the x-axis. Note that the x-axis scale for the transmission modes is different since each transmission type reaches different equilibrium cultural value. The descriptive statistics of the distributions in figure 8 is plotted in figure 9.

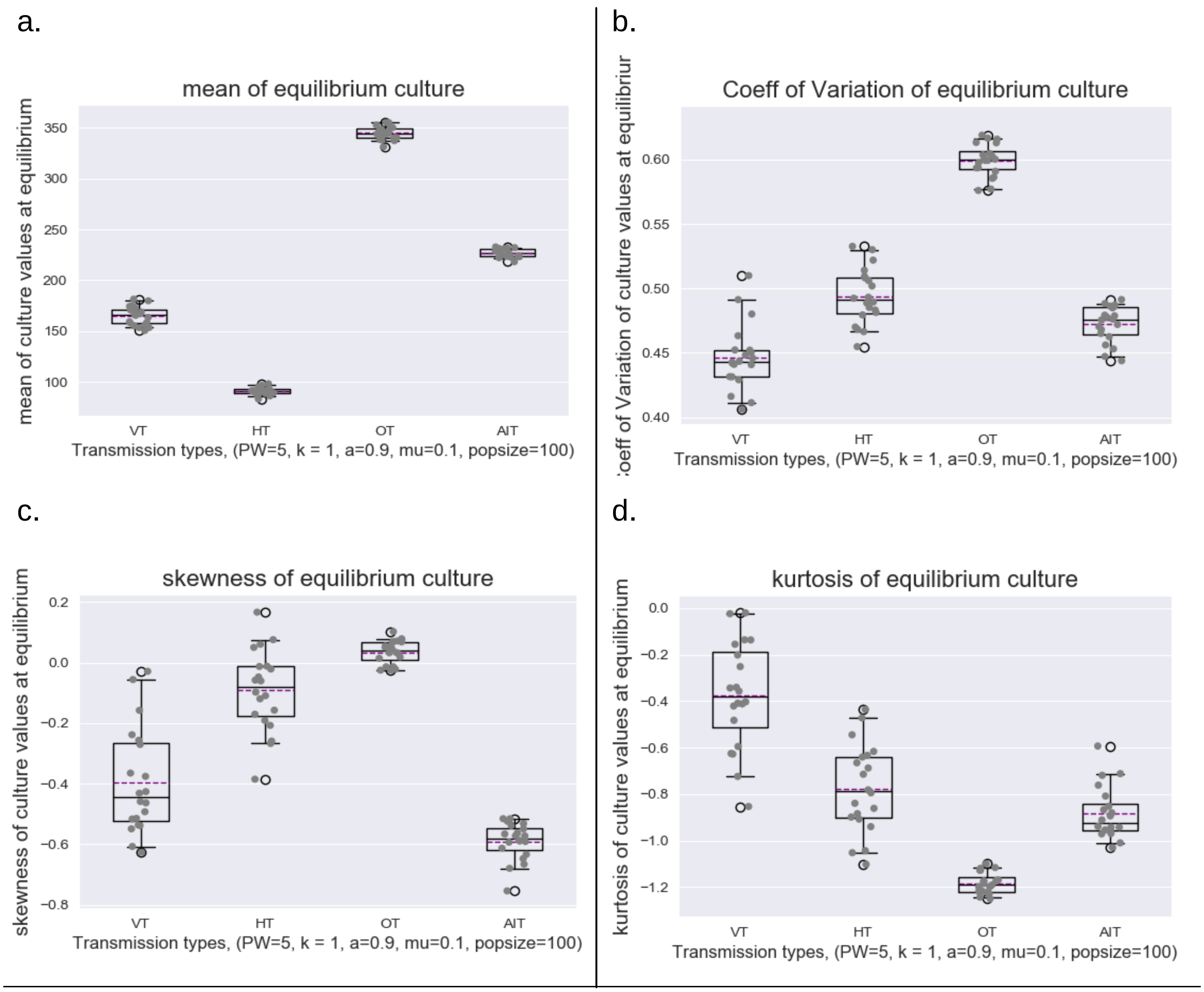



Figure 9: Box plots depicting the descriptive statistics of cultural values at the equilibrium (data same as figure 8). a) Mean, b) coefficient of variation, c) skewness, and d) kurtosis of the cultural values at equilibrium. *Solid black horizontal line denotes the median and purple dashed line denotes the mean.* Whiskers are 95% confidence intervals.

The distribution of cultural values at equilibrium, for the given set of parameters, appears to be distinctive for each transmission mode (figure 8). VT and HT show approximately bell shaped curves which implies maximum proportion of individuals have the intermediate cultural value. OT on the other hand has roughly uniform distribution of cultural values which implies there are equal proportion of individuals having a particular level of cultural complexity. Interestingly, AIT has high negatively skewed distribution which implies most of the individuals in the populaton are at the higher end of the spectrum of cultural complexity (similar distribution is also observed in Kempe et al., (2014)).

In order to understand how these distributions come about, we have plotted the same data but as a scatter plot between cultural value on the x-axis and age of the individual on the y-axis (figure 10). It also shows the projection of the data as a distibution on the x-axis and y-axis. The projection on the x-axis corresponds to the age distribution at equilibrium and it qualitatively agrees with the survival curve in figure 2a. Projection on the y-axis shows the distribution of cultural values at equilibrium and it agrees with distributions in figure 8. Apart from this, the plot also informs us about the way in which cultural values are distributed with respect to age.

VT shows good correlation between age and cultural value for younger individuals (figure 10a). As individuals grow older, the chances of their parents dying increases resulting in stoppage of learning for those whose parent is dead and continuation of learning whose parent is alive. This leads to reduction in correlation between age and cultural value at higher ages. Similar observation can be made of HT (figure 10b). As the individuals grow older there is a chance of most of your peers being dead. Along with this, cultural values within a peer-group would considerably homogenize resulting in less cultural gain per transmission event at later stages of life.

Oblique transmission shows visibly strong correlation between age and cultural value (figure 10c). This is argued to happen due to trickle down of cultural levels from higher aged individuals to lower age individuals (Kandler et al., 2017). In other words, all individuals (except the very old ones) always have someone older (therfore having more cultural value) individuals from which they can keep on learning, leading to higher correlation. In the case of AIT, cultural value is showing saturating relationship with age (figure 10d). This might be because as one grows older and their cultural value increases, the probability of picking a demonstrator more knowledgeable than oneself decreases resulting in the saturating relationship.

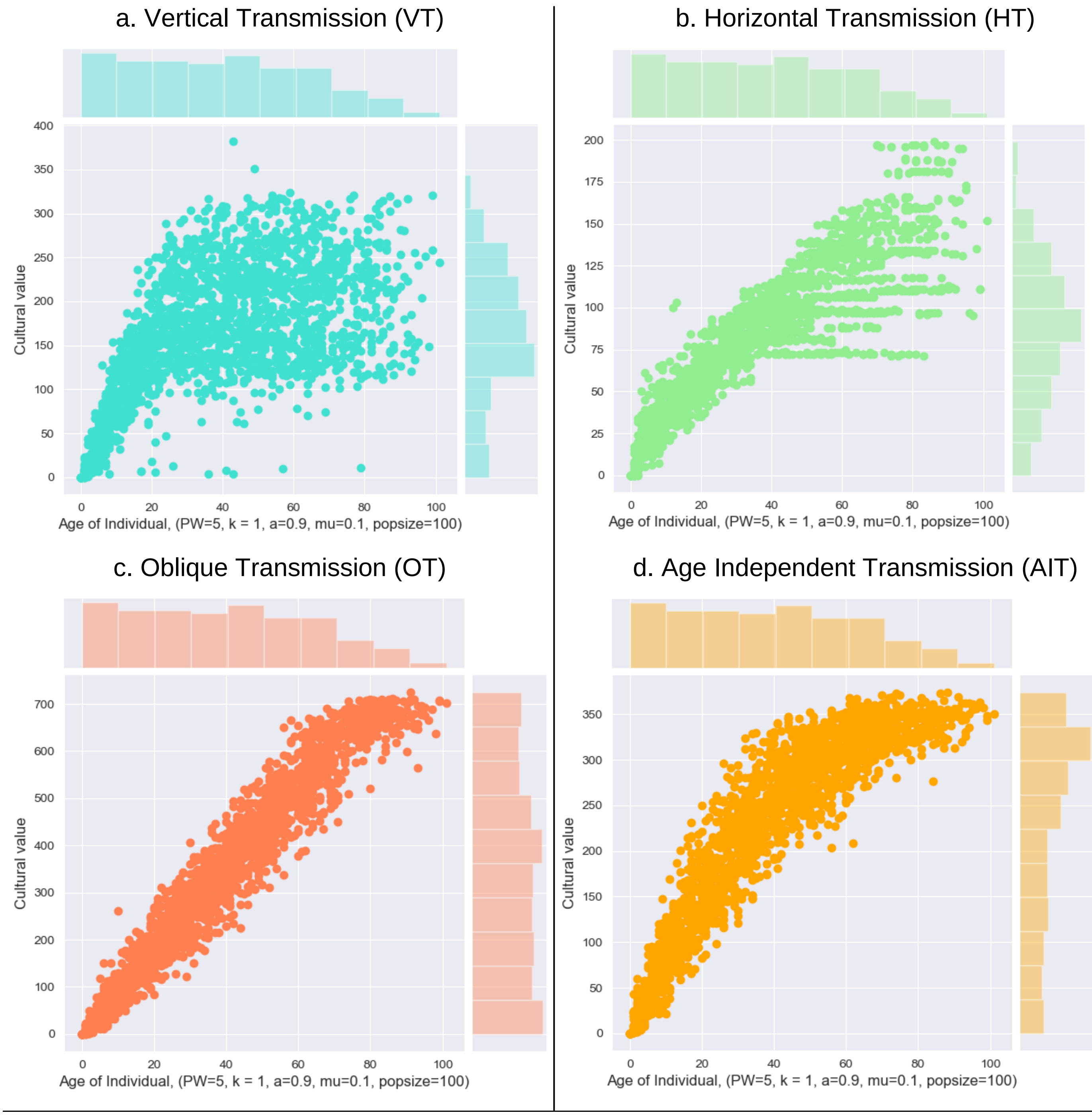



*Figure 10: Scatter plot between cultural values and age of the individuals at equilibrium. Data used is same as in figure 8. Plot a, b, c, and d correspond to VT, HT, OT, and AIT respectively.*

### *3.1.4. Comparison of cumulative cultural dynamics over the parameter sapce*

In this section we look at the equilibrium cultural value and maximum rate of change over the parameter ranges of a, μ, k, PW, and popsize. We also compare the transmission modes over the parameter space and compare the results with section 3.1.1.

#### *3.1.4.1. Equilibrium cultural value and Maximum rate of change with innovation ability 'μ'*

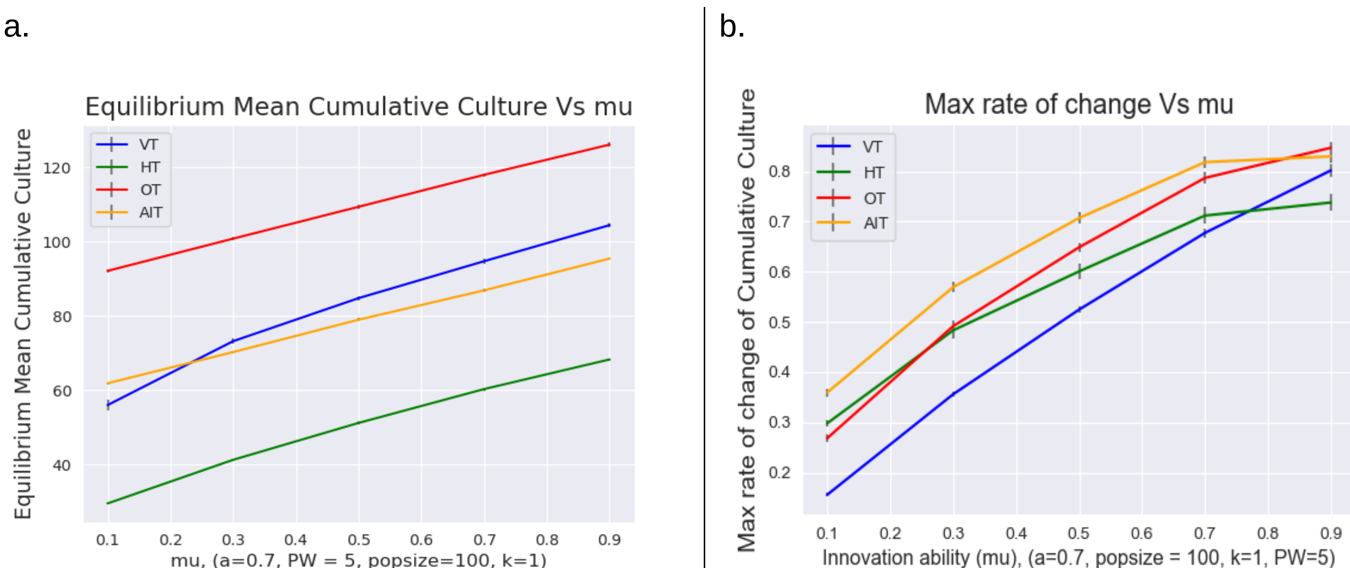



*Figure 11: a. Trend of mean cumulative culture over parameter range of 'μ'. b. Trend of maximum rate of change over parameter range of 'μ'. The colours blue, green, red, and orange correspond to VT, HT, OT, and AIT respectively. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

As observed in figure 11a, the equilibrium cultural value linearly increases with increase in innovation ability 'μ'. This occurs because succesful innovation results in addition of only one cultural level, thus with increase in 'μ' overall successful innovations increase linearly. The difference between the transmission modes also remains constant throughout the parameter range. This is the case because 'μ' affects every transmission mode in the same way. VT is acting a bit differently because it is innovation limited to a large extent. As discussed in section 3.1.1 VT requires every family line to innovate all the cultural levels independently. This might be the reason why the slope with which the trend of VT in figure 11a increases is slightly higher as compared to other transmission modes. As a result after the value of 0.3, VT becomes better than AIT in terms of equilibrium cultural value.

The maximum rate of change is also affected positively by the innovation ability ‘μ’ (figure 11b). This is expected since the accumulation of rate of change would be positively dependent on the rate of emergence of new cultural levels (innovation rate). The order (AIT>HT>OT>VT) discussed in section 3.1.1 is for ‘μ’ value of 0.1. For higher values of ‘μ’ the rate of change of OT and VT are increasing rapidly and they are going close to AIT at the highest ‘μ’.

An important aspect to note here is that the term innovations in this study need not imply the innovated level would be novel to the whole population. We are defining innovation as the cultural levels gained independently of the social interactions (independent learning or non-social learning). This gain in cultural levels can be due to trial and error learning, or novel innovations.

### *3.1.4.1. Equilibrium cultural value and Maximum rate of change with learning ability ‘a’*

a. b.

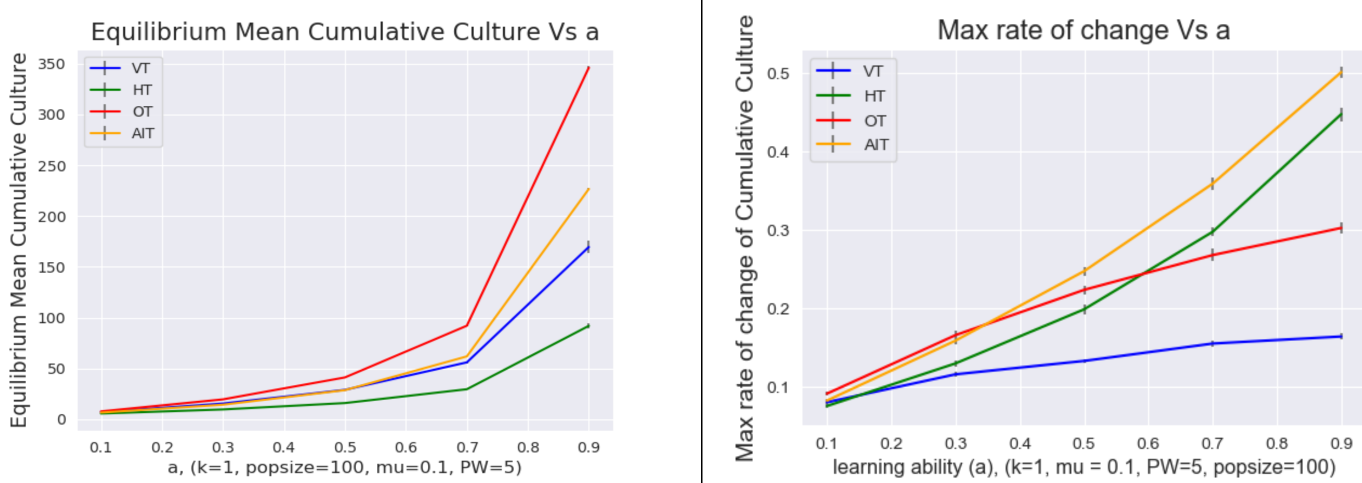



*Figure 12: a. Trend of mean cumulative culture over parameter range of ‘a’. b. Trend of maximum rate of change over parameter range of ‘a’. The colours blue, green, red, and orange correspond to VT, HT, OT, and AIT respectively. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

Figure 12a shows how equilibrium cultural value varies over the parameter range of learning ability ‘a’ for all the transmission modes. We observe that the equilibrium cultural value increases with increase in ‘a’ in exponential fashion. This might be the case because the learning in model 1 is in such a way that, in one transmission event, the learner can keep on learning new levels from the demonstrator until it fails for the first time or equals the cultural value of the demonstrator. Since the success probability of learning every new level is ‘a’ and if the learner successfully learns ‘l’ levels then the overall success probability would be $a^l$. Therefore, increase in ‘a’ increases $a^l$ to a very large extent, resulting in the exponential increase pattern seen in figure 12a.

The order of equilibrium cultural values (OT>AIT>VT>HT) discussed in the section 3.1.1 has value of ‘a’ set at 0.9. We can observe that the order is more or less conserved for all values of ‘a’ (figure 12a). Learning is the only step where the transmission modes differ from each other and learning ability ‘a’ is the major factor that affects learning. Thus the difference between the equilibrium cultural values for each transmission mode is very small for low values of ‘a’ (learning affects the transmission to a lesser extent) and increases with increasing value of ‘a’.

Figure 12b shows the trend of maximum rate of change with learning ability ‘a’. Again we can observe that the differences between the transmission modes is lower for small value of ‘a’ and increases with increase in ‘a’. The order AIT>HT>VT is followed for all of the parameter range. For smaller values of ‘a’ (<0.6) OT behaves somewhere between AIT and HT, the difference between the transmission types is amplified with higher values of ‘a’. Taken together, figure 11a and 11b imply that stark differences between the transmission modes will be seen (as seen in section 3.1.1) for cultural traits which show high values of transmission accuracy ‘a’.

*3.1.4.3. Equilibrium cultural value and Maximum rate of change with number of demonstrators 'k'*

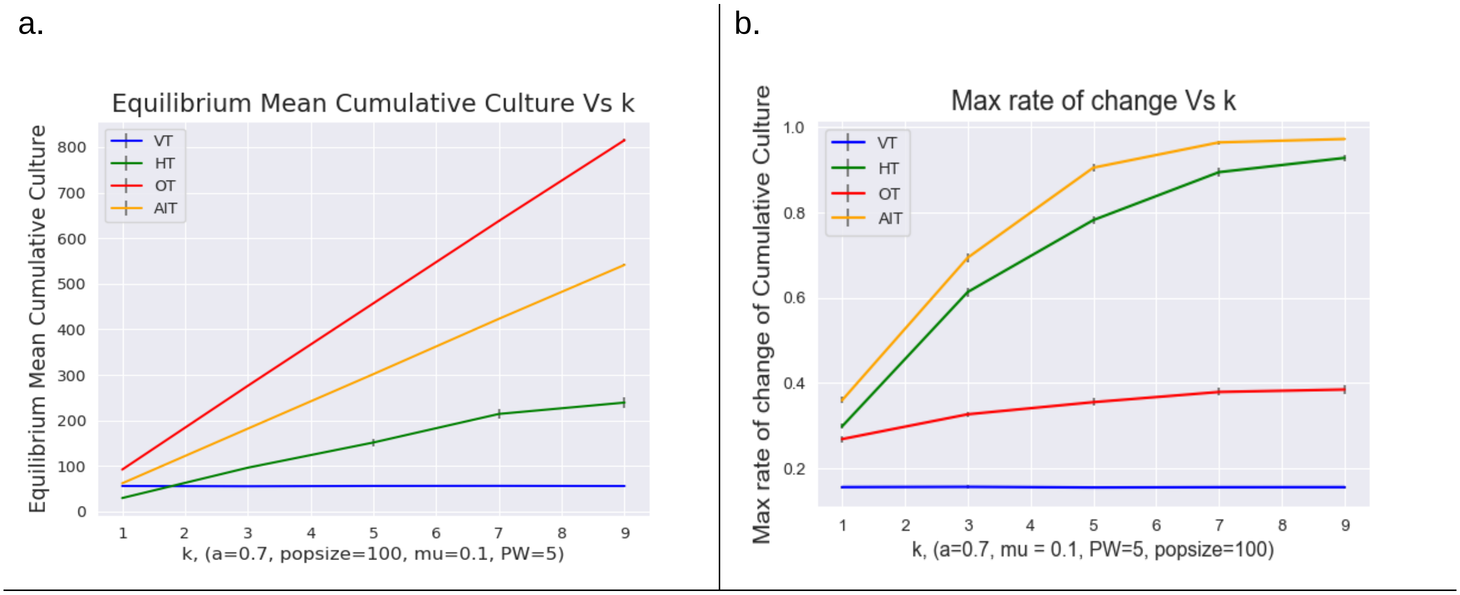



*Figure 13: a. Trend of mean cumulative culture over parameter range of 'k'. b. Trend of maximum rate of change over parameter range of 'k'. The colours blue, green, red, and orange correspond to VT, HT, OT, and AIT respectively. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

In this section, we look at the effect of the number of demonstrators from which the learner learns in a transmission event. Figure 13 shows that the value of 'k' does not affect the dynamics of VT because by definition you have only one parent. For the other transmission types, the equilibrium cultural value increases linearly with 'k' (figure 13a). This trend is in agreement with Kempe et al. (2014). Similar to the effect of learning ability 'a', the difference between the transmission modes are magnified with increase in 'k'. The order of equilibrium cultural value discussed in section 3.1.1 (OT>AIT>VT>HT) is for 'k' equal to one. The order is conserved throughout the tested range of 'k' except that the HT becomes better than VT when focal individual starts learning from multiple peers at every time step.

In the case of maximum rate of change, the transmission modes (except VT) show increasing trend with 'k' (figure 13b). HT and AIT show the most increase because learning from larger number of demonstrators spreads the innovations at a higher rate, which results in faster initial accumulation of culture. On the other hand, in the case of OT, even though an individual is learning from more number of demonstrators, the innovations need to be passed from elder individuals to younger individuals. This is a slower process, resulting in a smaller effect of ‘k’ on maximum rate of change.

### *3.1.4.4. Equilibrium cultural value and Maximum rate of change with population size ‘popsize’*

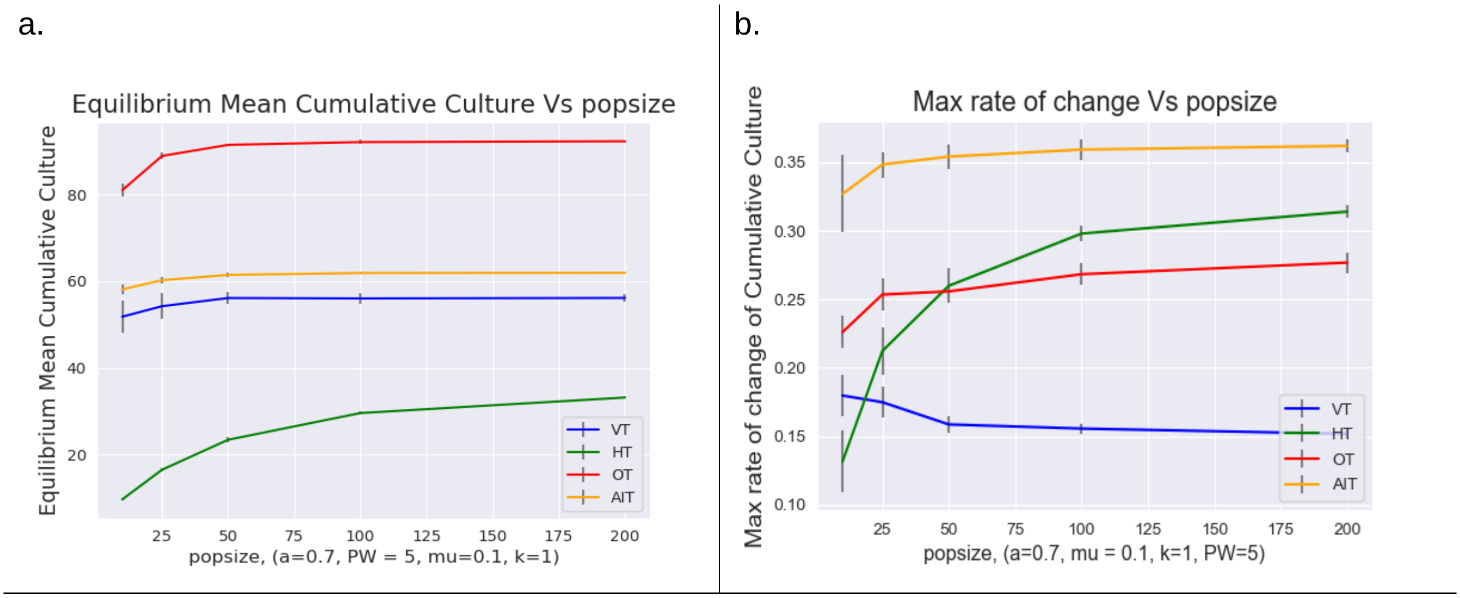



*Figure 14: a. Trend of mean cumulative culture over parameter range of ‘popsize’. b. Trend of maximum rate of change over parameter range of ‘popsize’. The colours blue, green, red, and orange correspond to VT, HT, OT, and AIT respectively. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

Figure 14 shows that the effect of population size on equilibrium cultural value (figure 14a) and maximum rate of change (figure 14b) is weak. The effect is prominent for HT since it has very small pool of individuals who act as a demonstrator and in small population sizes there is higher chance that peer group has no individual. Even if there are individuals in the peer group, they would be very few in number, leading to peers having similar cultural value resulting in less net gain in a transmission event. Thus higher population sizes benefit HT more than the others.

The effect of population size has been discussed previously in the literature. It started from Henrich, (2004) when he claimed population size to be an important parameter responsible in deciding the complexity of culture that can be retained in the population. Later, the effect of population size was disentangled from the number of acquintances from whom you learn and it was observed that population size in itself does not hugely affect the cultural dynamics (Kobayashi and Aoki, 2012). It is also argued that the effect of population is observed only at very low innovation rates and that too only on the rate of change and not on the equilibrium cumulative culture (Baldini, 2015). Our results are in agreement with these studies.

### *3.1.4.5. Equilibrium cultural value and Maximum rate of change with peer width 'PW'*

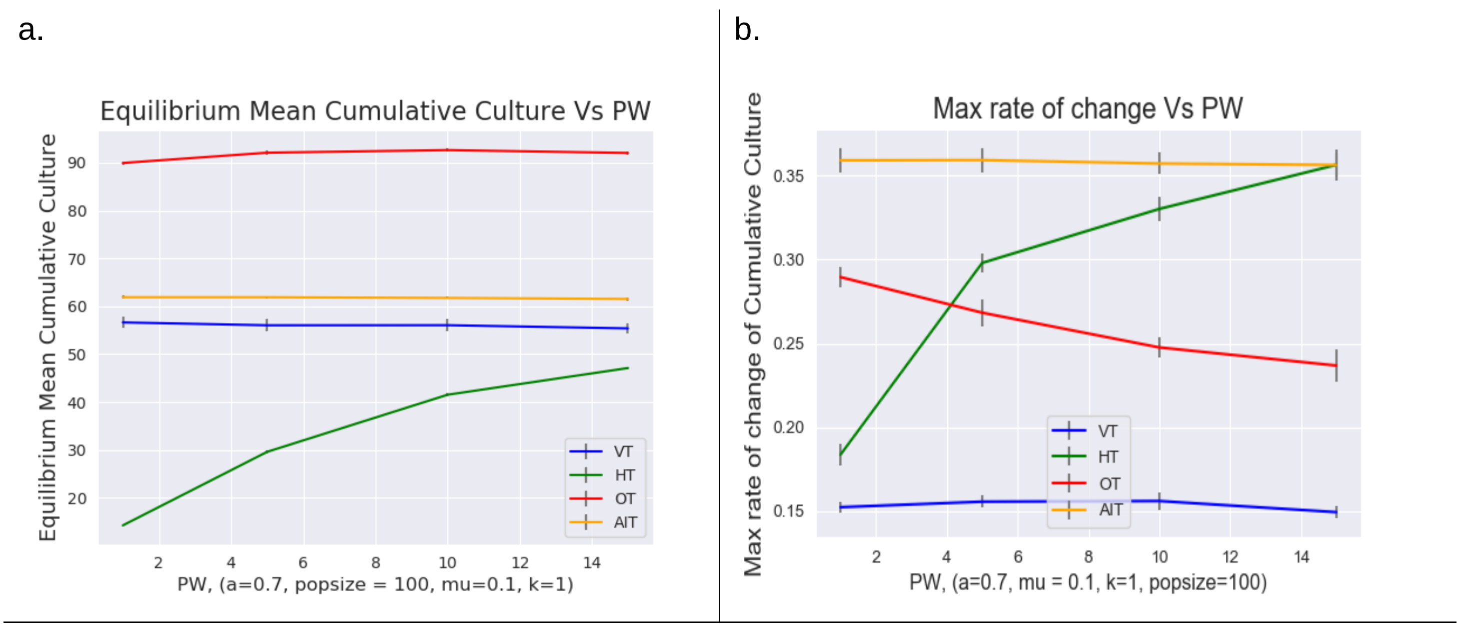



*Figure 15: a. Trend of mean cumulative culture over parameter range of 'PW. b. Trend of maximum rate of change over parameter range of 'PW'. The colours blue, green, red, and orange correspond to VT, HT, OT, and AIT respectively. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

Peer width ‘PW’ decides the age range around the learner’s age from which we pick the demonstrators, hence it affects HT. ‘PW’ also affects OT since we pick the demonstrator from the pool of individuals who have age > learner’s age + PW. Thus increase in ‘PW’ increases the pool of potential demonstrators for HT but reduces the pool for OT. ‘PW’ does not affect VT and AIT. As expected equilibrium cultural value remains same for VT and AIT, it increases positively for HT (figure 15a) since larger pool of individuals lead to larger cultural reservoir from which one can learn. It does not seem to largely affect the equilibrium culture of OT, but the maximum rate of change of OT shows decreasing trend with ‘PW’ since it reduces the pool of potential demonstrators.

Some previous studies in the literature have investigated the effects of the parameters ‘a’, ‘μ’, ‘k’, and ‘popsize’ on equilibrium cumulative culture but not in the context of transmission modes. Hence, we compare trends in previous studies with AIT from our study. Table 3 summarizes this comparison.

*Table 3: Summary of the effect of parameters on the equilibrium cultural value*

| **Parameter** | **Effect on equilibrium cultural value** | **Previous study (Agreeing with AIT)** |
|---|---|---|
| Learning ability ‘a’ | Positive (non-linear, exponential) | (Kempe et al., 2014) |
| Innovation ability ‘μ’ | Positive (linear) | |
| # of demonstrator ‘k’ | Positive (linear) | |
| Population size | Weakly positive (non-linear, saturating) | (Baldini, 2015; Kobayashi and Aoki, 2012) |

### *3.2. Model 2: Comparing the effects of mixed transmission modes on the dynamics of cumulative culture*

In this section, we investigate the effects of mixed modes of transmission on equilibrium cumulative culture and rate of change. Mixed modes are studied in terms of learning life histories (Fogarty et al., 2019), defined in section 2.2.

#### *3.2.1. Effects of learning life histories on the equilibrium cultural value and rate of change*

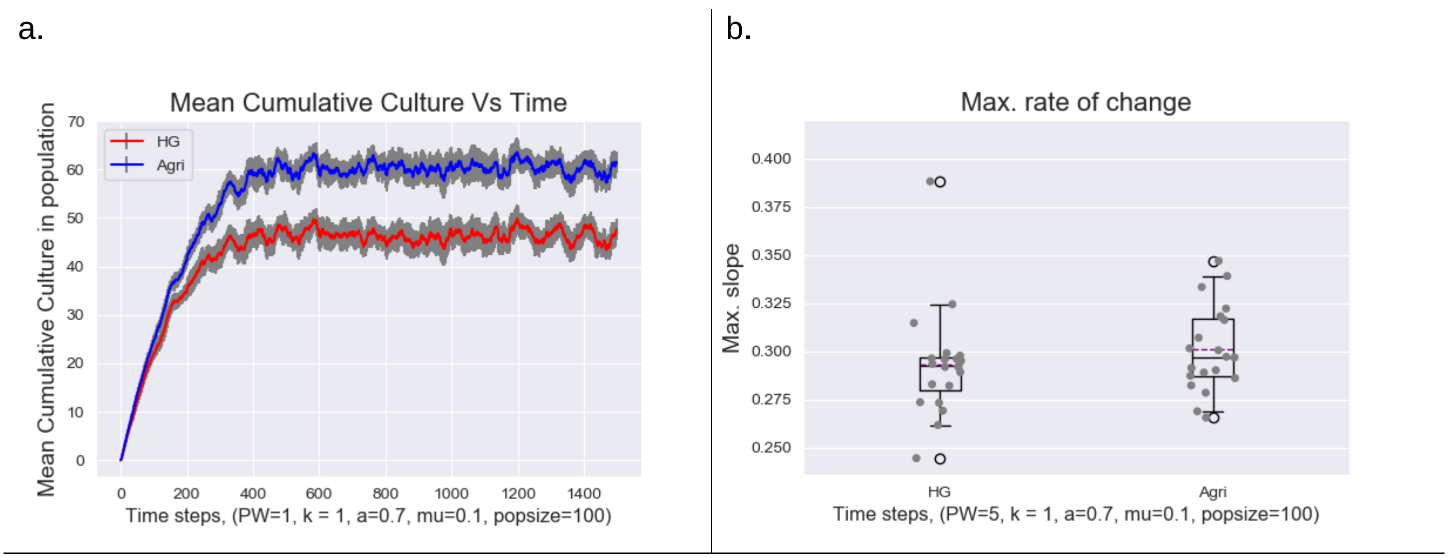



*Figure 16: a) Time series comparing the Hunter-Gatherer (HG) (red) and Agriculturalist (Agri) (blue) learning life histories. b) Box plot for maximum rate of change comparing HG and Agri. Solid black horizontal line in box plot denotes the median and purple dashed line denotes the mean. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

The learning life history strategies considered here are called Hunter-Gatherer 'HG' and Agriculturalist 'Agri' strategies (see figure 3). Figure 16a shows that, all else being equal, 'Agri' learning life history strategy by itself can reach higher equilibrium cultural value than 'HG'. Maximum rate of change, on the other, does not show any stark difference (figure 16b). According to the figure 3, which comes from previous studies (Fogarty et al., 2019; Hewlett et al., 2011), 'HG' have Vertical Transmission (VT) dominant for longer span of their life as compared to their ‘Agri’ counterpart. Conversely, ‘Agri’ start the Non-vertical transmission (NVT), i.e. oblique or horizontal transmission, earlier than their ‘HG’ counterparts. One way to explain this is that, in farming societies, parents spend more time in agricultural activities resulting in the young children relying on oblique or horizontal transmission from a younger age (Fogarty et al., 2019). These differences result in the trend seen in figure 16a. The trend of equilibrium cultural value is conserved throughout the parameter range (see appendix 6).

It is important to note that the data for the learning life history strategies used here comes from a specific group of hunter gatherers and agriculturalists. In reality, different groups might have different learning strategies (for example, see Kline et al., (2013) who study life history of learning in Fijian villages; and Aunger, (2000) who study learning life histories of orally transmitted culture in a society based in Republic of Congo) and these strategies could be easily incorporated in this model.

### *3.2.2. Effects of learning life histories corrected for survival on the equilibrium cultural value and rate of change*

In the previous section (3.2.1), survival curves used for both ‘HG’ and ‘Agri’ were same as the one in figure 2a. We considered another survival curve (also adopted from Weon, (2003)) for ‘HG’ which had a certain level of juvenile mortality associated with it (see appendix 7 for survival curve and the transformed survival curve). Figure 17a shows that when ‘HG’ strategy is combined with hunter-gatherer like survival (green plot) then the resulting difference between ‘HG’ and ‘Agri’ if further enhanced. The maximum rate of change of this case is also lower than the other two (figure 16b).

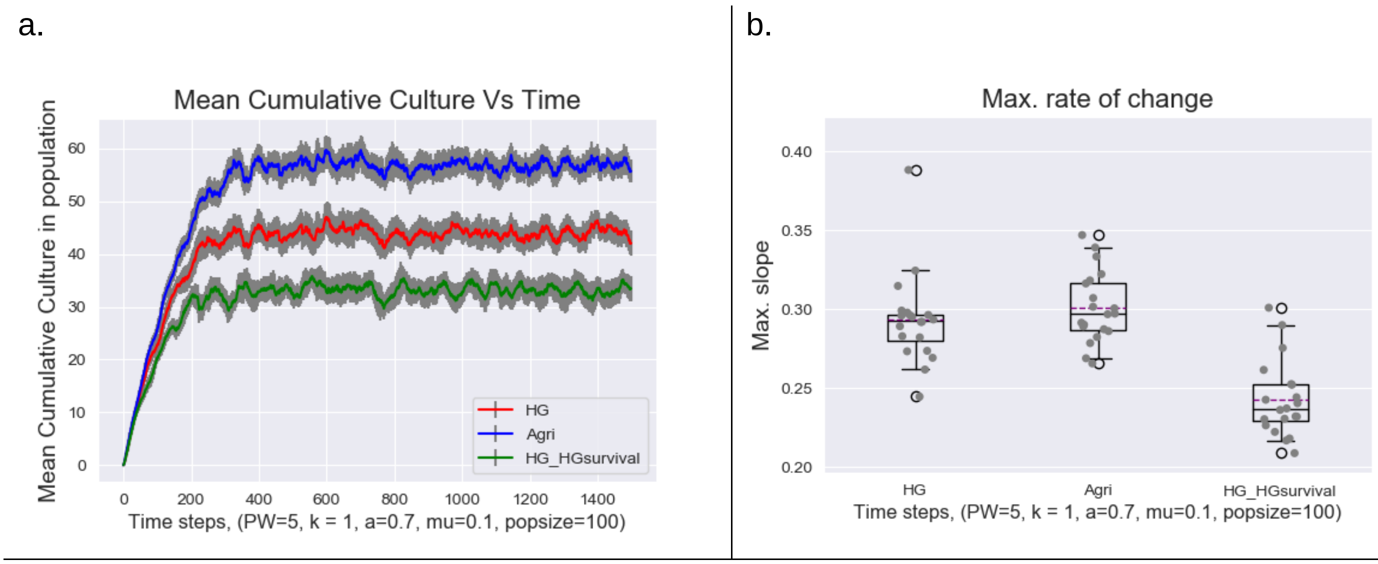



*Figure 17: a) Time series comparing the Hunter-Gatherer (red), Agriculturalist (blue), and Hunter-Gatherer with corrected survival (green). b) Box plot for maximum rate of change comparing HG and Agri. Solid black horizontal line in box plot denotes the median and purple dashed line denotes the mean. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

This result also implies that the cumulative cultural dynamics also depends on the overall survival of the individuals in the population. Higher biological survival appears to be aiding the population to maintain culture that is more complex. This might be the case because, as explained in section 3.1.1 and seen in figure 10, age positively correlates with cultural value possessed by an individual. Hence, higher survival would imply accumulation of culture over longer duration making it more complex. Using this observation, we can speculate that survival enhancing cultural practices would also boost the accumulation of other cultural traits showing some kind of ‘cultural epistasis’. New studies are emerging in this area (Pascual et al., 2019) and the scenario described above could be a possible area of future investigation.

### *3.3. Model 3: Comparing different mechanisms of learning defined in terms of hierarchy and cost of learning*

In this section the four mechanisms of learning, namely, hierarchical non-costly (H-NC), hierarchical costly (H-C), non-hierarchical costly (NH-C), and non-hierarchical non-costly (NH-NC) are compared against each other in the context of the four transmission modes (VT, HT, OT, and AIT). These mechanisms are defined and illustrated in section 2.3.

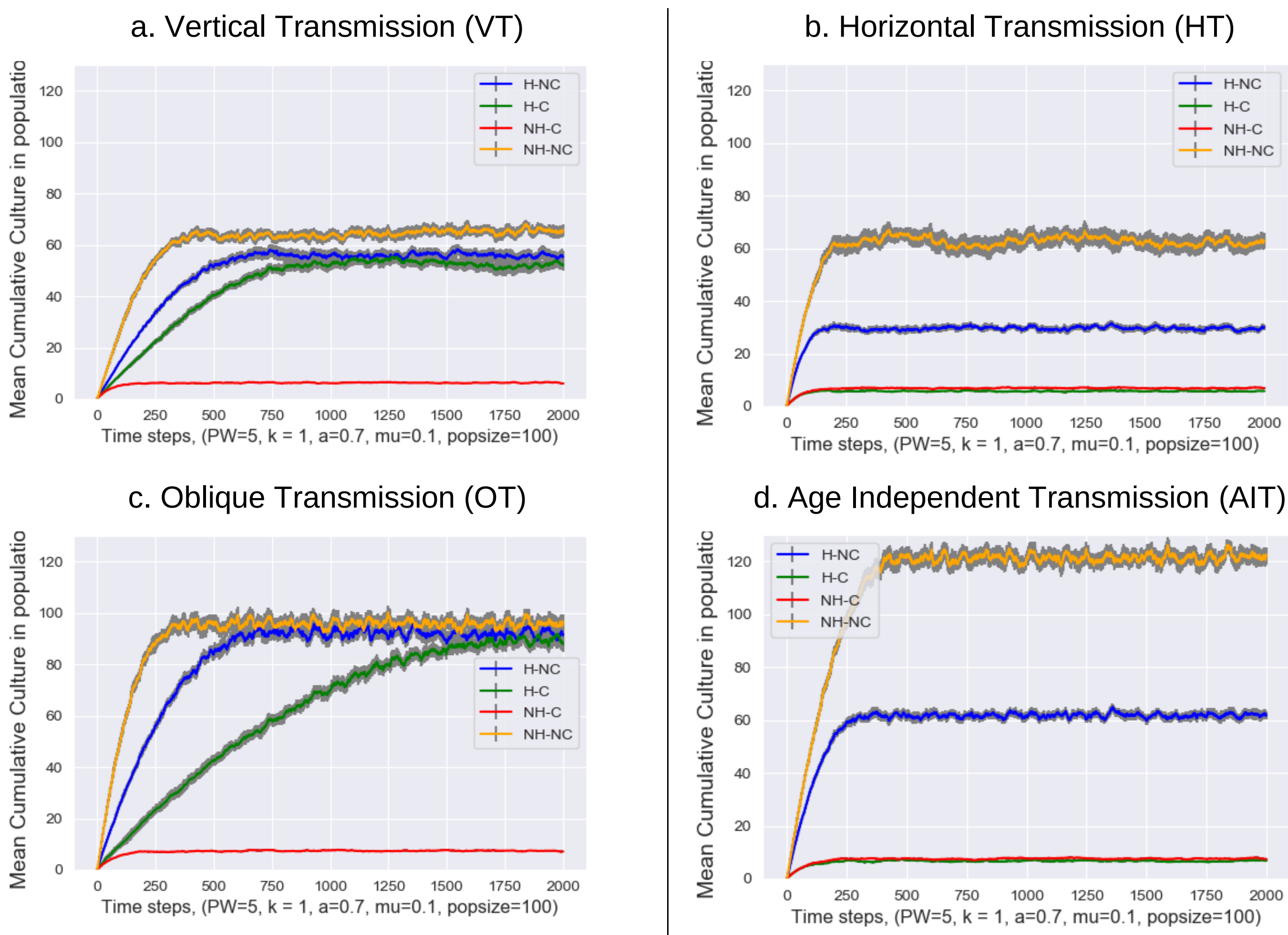



*Figure 18: Time series plots comparing the learning mechanisms. Blue - Hierarchical Non-Costly (H-NC). Green - Hierarchical Costly (H-C). Red - Non-Hierarchical Costly (NH-C).Orange - Non-Hierarchical Non-Costly (NH-NC). Plot a, b, c, and d correspond to VT, HT, OT, and AIT respectively. Error bars are 95% confidence intervals calculated over values from 20 replicates*

For VT and OT, hierarchical transmission (both costly (H-C) and non-costly (H-NC)) and non-hierarchical non-costly transmission (NH-NC) leads to approximately similar equilibrium cultural values (figure 18a and 18c). Even though H-C involves costly learning, the unidirectional flow (only elders act as demonstrators) and hierarchy (demonstrators are defined and cost is applicable only to the learner) rescues it and takes its equilibrium cultural value closer to non-costly mechanisms. NH-C mechanism remains very low, in terms of equilibrium cultural value, for all the transmission modes.

For HT and AIT, costly transmission, H-C and NH-C, leads to very small equilibrium cultural values. H-C is not rescued in HT and AIT (similar to VT and OT) because even though H-C is hierarchical; bidirectional flow of culture in HT and AIT, which allows learner demonstrator roles to be switched in subsequent transmission events, results in the cost being applicable to all the individuals. The non-costly transmission is effective in the case of HT and AIT; especially NH-NC mechanism reaches high equilibrium cultural values since, in NH-NC transmission, at every transmission event individual with lower cultural value always gain cultural levels.

The comparison of maximum rate of change for these transmission mechanisms can be done in figure 19. VT and OT show highest rate of change for NH-NC, followed by H-NC, H-C, and NH-C. HT and AIT also show highest rate of change for NH-NC, followed by H-NC, but H-C and NH-C have similar (and very low) rate of change.

Taken together, results from figure 18 suggest that learning from your elders is always favourable (in terms of equilibrium culture) in the case of hierarchical transmission mechanisms (be it costly or non costly) as well as in the case of non-hierarchical non-costly mechanism. Since following oblique or vertical transmission mode is beneficial (in terms of equilibrium cultural value) in most of the cases; we can speculate why, societal norm of respecting and learning advantageous cultural traits from your elders would have come into existence.

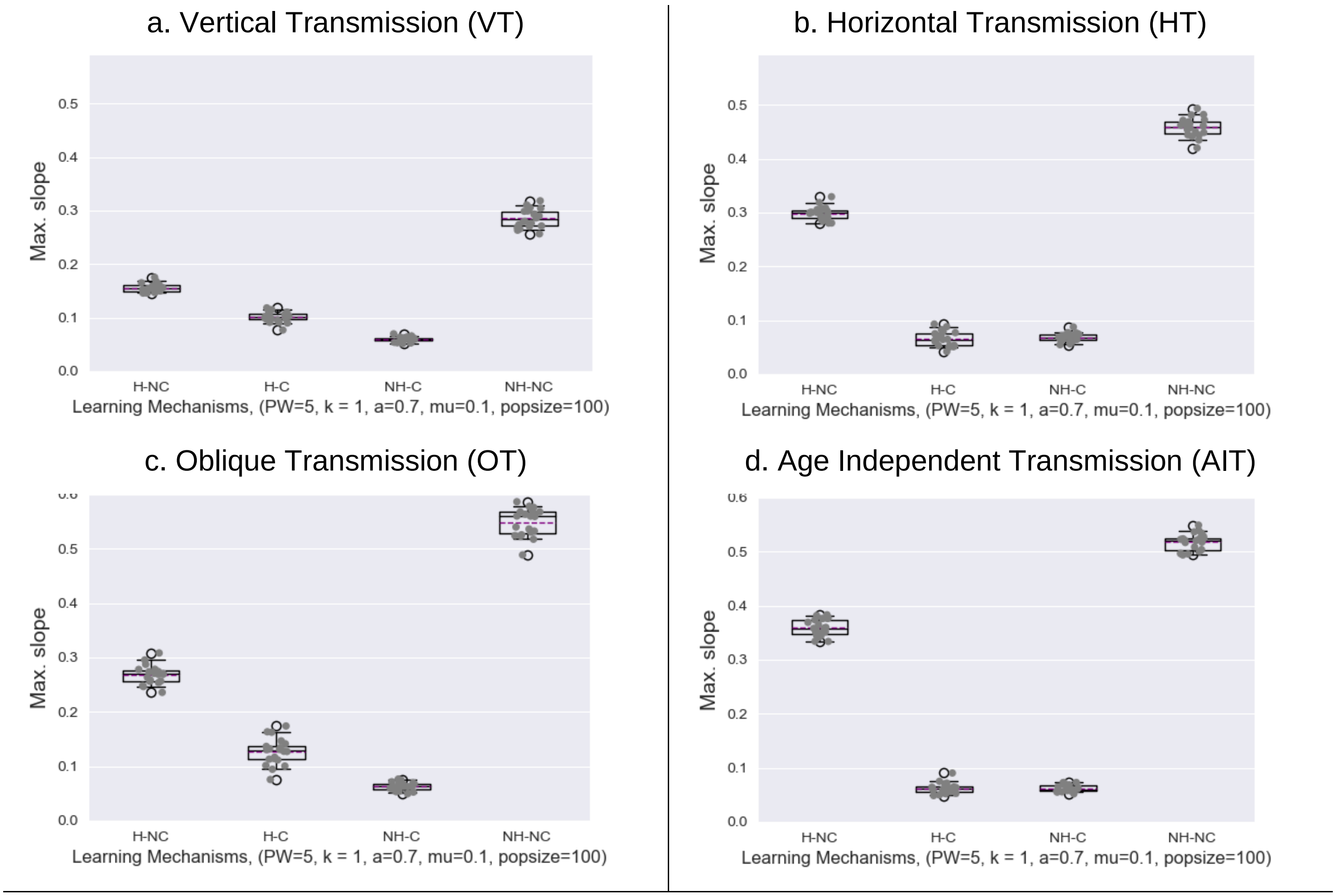



*Figure 19: Box plots comparing the maximum rate of change of learning mechanisms. Hierarchical Non-Costly (H-NC). Hierarchical Costly (H-C). Non-Hierarchical Costly (NH-C). Non-Hierarchical Non-Costly (NH-NC).Plot a, b, c, and d correspond to VT, HT, OT, and AIT respectively. Solid black horizontal line in box plot denotes the median and purple dashed line denotes the mean. Error bars are 95% confidence intervals calculated over values from 20 replicates.*

## 4. Conclusions and Future Directions:

Culture provides a second inheritance system (Whiten, 2005) and has the capacity to provide adaptive advantage to animals as well as humans (Whiten et al., 2017). On the other hand, cumulative culture, i.e. knowledge accumulated across generations, is considered unique to humans (Salali et al., 2016; Stout et al., 2019) and considered to be an important factor that provides adaptive advantage to humans (Castro and Toro, 2014; Hill et al., 2009; Richerson and Boyd, 2005).

Culture can spread via transmission modes such as vertical, horizontal, and oblique transmission (Cavalli-Sforza and Feldman, 1981). Previous studies have shown that oblique transmission (OT) is slower than horizontal transmission (HT) in terms of rate of spread of a cultural trait, and vertical transmission (VT) is the slowest (Kandler et al., 2017). However, these studies do not invoke cumulative culture. The main aim of the study was to compare the cumulative cultural dynamics under pure and mixed modes of transmission. This comparison was done based on two parameters namely the rate of accumulation of culture and the amount of culture accumulated at equilibrium. We also explored the effects of pure modes of transmission under different mechanisms of learning, defined on the basis of cost and hierarchy, on the dynamics of cumulative culture.

Our results suggest that the pure transmission modes do show differences in cumulative cultural dynamics. Agreeing with previous results, the rate of change is the slowest for VT, followed by OT, and the highest for HT and age independent transmission (AIT). However, the cumulative cultural value at equilibrium was the highest for OT, followed by AIT and VT, and was the lowest for HT. These differences resulted in the efficiency of each transmission mode being dependent on the time frame in which the cultural complexity is being compared. We attribute these differences to the characteristics of the pool of demonstrators, such as size of the pool and age of individuals in the pool, and the direction of the flow of innovations. The results in terms of equilibrium cultural value are robust as they are independent of the initial cultural value. Further, the cultural dynamics are mostly preserved throughout the parameter ranges, the differences between transmission modes being most prominent at higher values of learning ability ‘a’.

We also observe that the mixed modes of transmission, defined in the context of learning life history strategies, called ‘agriculturalist’ (Agri) and ‘hunter-gatherer’ (HG), also show differences in terms of equilibrium cumulative culture. Keeping all else equal, Agri strategy could sustain higher equilibrium culture than the HG strategy. When we correct for the survival curves of hunter-gatherers the difference is further enhanced, suggesting that longer life spans would increase the capacity of the population to sustain complex culture. At the end we compared pure transmission modes under four mechanisms of learning and established the importance of learning from elders in order to achieve higher levels of equilibrium cumulative culture.

Our individual-based model has captured cumulative cultural transmission in an age-structured population. Moving forward, the model could be expanded to study cultural epistasis as discussed in section 3.2.2. The age structure can be used to incorporate age dependent phenomena that can affect cumulative cultural transmission. For example, we have already incorporated transmission modes, learning life histories, and different survival curves. Age dependent rise and decline in different types of cognitive abilities (empirical data can be found in Tucker-Drob, 2009) can be used to modulate the learning and innovation abilities with age. Apart from humans, the presence of cumulative culture in other animals has been gaining traction in recent years (Sasaki and Biro, 2017; Schofield et al., 2018). Although our model has been parameterized using human survival and fecundity data, it can easily be parameterized for other animals. With suitable data from experiments on animals (or transmission chain experiments in humans), empirical verification of our results is possible. Apart from biological systems, our model can be modified to fit the dynamics of organizations or institutions where individuals usually enter in the lower tiers and move towards the top, and the information can transfer vertically (one to one, top down), obliquely (many to one, top down), or horizontally. Such model would potentially be able to predict the dynamics of knowledge transfer in organizations of different structures.

## 5. **Appendix:**

*1. Survival curve data transformation*

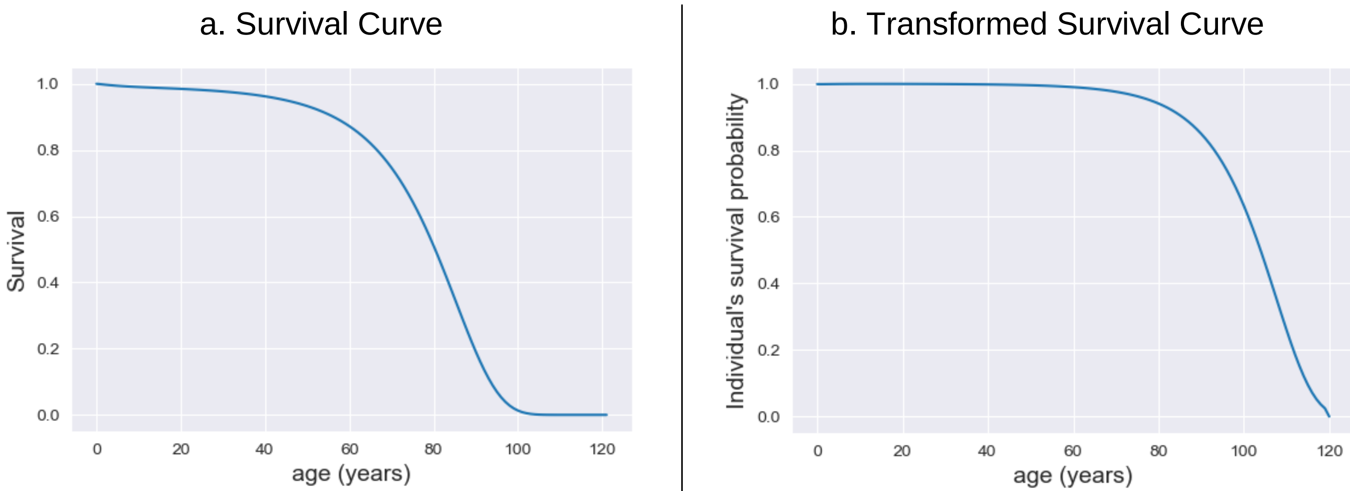



*Figure A1: a) Survival curve. b) Transformed Survival Curve.*

The survival curve in figure A1a, adopted from Weon (2003), tells us the proportion of individuals surviving to a particular age. Therefore, survival at the age of 40 is not the probability of surviving through the time period from age 39 to 40 but it is the proportion of the individuals survived till the age of 40 or in other words it is the probability of surviving from birth till the age of 40. In the simulations we had to use the probability that an individual will survive a time step (a year) given its age. In order to get this probability we transformed survival data in the following way:

Consider F(t) to be the survival and G(t) to be the transformed survival at the age of t. Then, we defined

$$G(t) = F(t), \qquad \text{for } t = 0 \ \&$$

$$G(t) = F(t)/F(t-1), \qquad \text{for } t > 1$$

Figure A1b plots this G(t).

The transformation is valid because F(t) is the probability of survival from birth till time t and G(t) gives the probability of survival from time t-1 to t, assuming survival events in each time steps are independent we can define F(t) = G(0)*G(1)*.....*G(t) Putting G(t) = F(t)/F(t-1) into this equation equates LHS and RHS.

*2. Adapting learning life history data from Fogarty et al. 2019 in the form of figure 3*

*Table A2.1: Learning life history data adapted from Fogarty et al. 2019*

| Discrete Age Classes | Class - Width (in years) | Hunter-Gatherer Data | | Agriculturalist Data | |
|---|---|---|---|---|---|
| | | Proportion of learning time given to VT | Proportion of learning time given to NVT | Proportion of learning time given to VT | Proportion of learning time given to NVT |
| 1 | 0 -12 | 1 | 0 | 1 | 0 |
| 2 | 13 - 24 | 0.85 | 0.15 | 0.5 | 0.5 |
| 3 | 25 - 36 | 0.6 | 0.4 | 0.1 | 0.9 |
| 4 | 37 - 48 | 0 | 1 | 0 | 1 |
| 5 | 49 - 60 | 0 | 1 | 0 | 1 |

Note: 1) VT stands for Vertical Transmission and NVT stands for Non-Vertical Transmission (oblique or horizontal).

Table A2.1 was adopted from the figure 1 of Fogarty et al. (2019). The data is in the form of discrete age classes. In order to assign proportions to each time step (age in years) we decided the width of each age class to be 12 years. Then we assigned the mid-point of each age class to the values given in the table and fit a polynomial curve (quadratic) for the data till the fourth age class (see table A2.2). From fifth age class onwards, proportion of learning time given to VT is assigned to zero. We fitted the curves for VT, and used those values to get the NVT curve by doing one minus VT data.

*Table A2.2: Conversion of data in table A2.1 into continuous curves*

| X, mid-point of age class | Y, Hunter-Gatherer Data | Y, Agriculturalist Data |
|---|---|---|
| 6 | 1 | 1 |
| 18 | 0.85 | 0.5 |
| 30 | 0.6 | 0.1 |
| 42 | 0 | 0 |
| Quadratic Equation → | $Y = -(0.000781*(X^2)) + (0.0104*X) + 0.966$ | $Y = (0.000694*(X^2)) - (0.0617*X) + 1.36$ |

*3. Procedure followed to calculate maximum rate of change and equilibrium cultural value*

For every simulation we store the cultural values of each individual at every time step. There are 20 simulation replicates for each simulation study. Equilibrium cultural value is calculated by averaging the last 500 data points (making sure that the mean cultural value has been saturated well before that point) of each replicate separately. The average of these 20, one for each replicate, values along with its 95% confidence interval gives us the equilibrium cultural value.

Maximum rate of change is calculated by the sliding window method. Since our data is dense, for each replicate, we take window of length 75 time steps in the time series data and fit a straight line through those points and get its slope. We slide this window shifting it by one point and do the same procedure again. The procedure is repeated till the 200$^{th}$ point. Out of all the slope value for each of the window, the maximum value is considered as the maximum rate of change for that replicate. We get 20 such values, one for each replicate, and the mean of this along with the 95% confidence interval gives us the maximum rate of change of the mean cumulative culture.

*4. Time series with only innovation as the driving force*

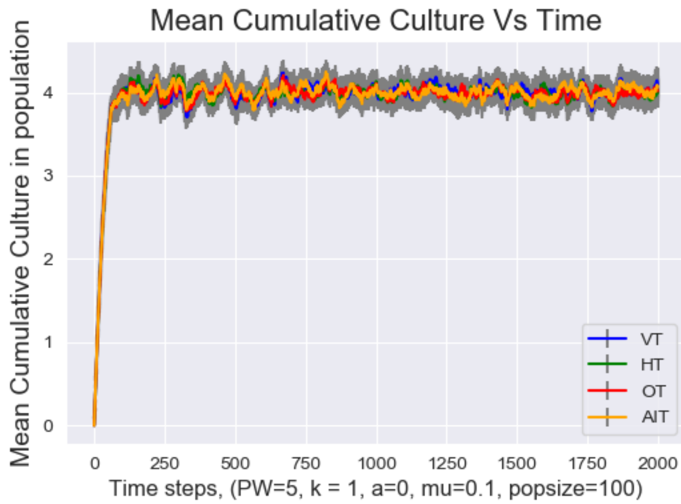



*Figure A4: Time series with learning ability 'a' to be zero i.e. only innovation can contribute to increase in culture levels. All transmission modes reach the same equilibrium cultural value of around 4.*

*5. Learning and innovation stops after certain age*

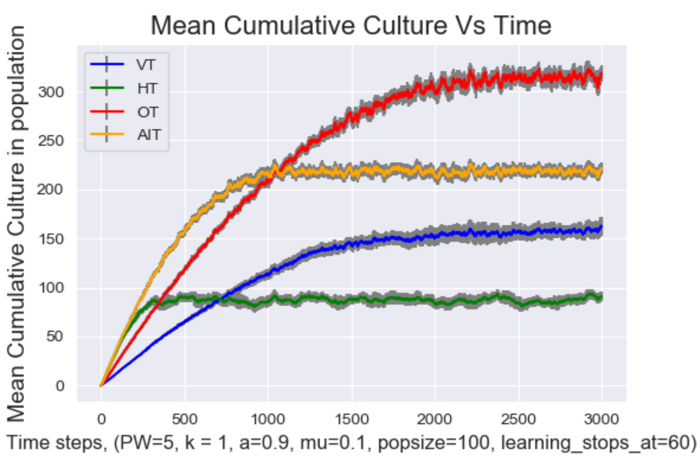



*Figure A5.1: Time series plot for the case where learning stops after age 60. There is no qualitative difference as compared to section 3.1.1. Fogarty et al. (2019) use an age structured model where learning stops after the reproductive age.*

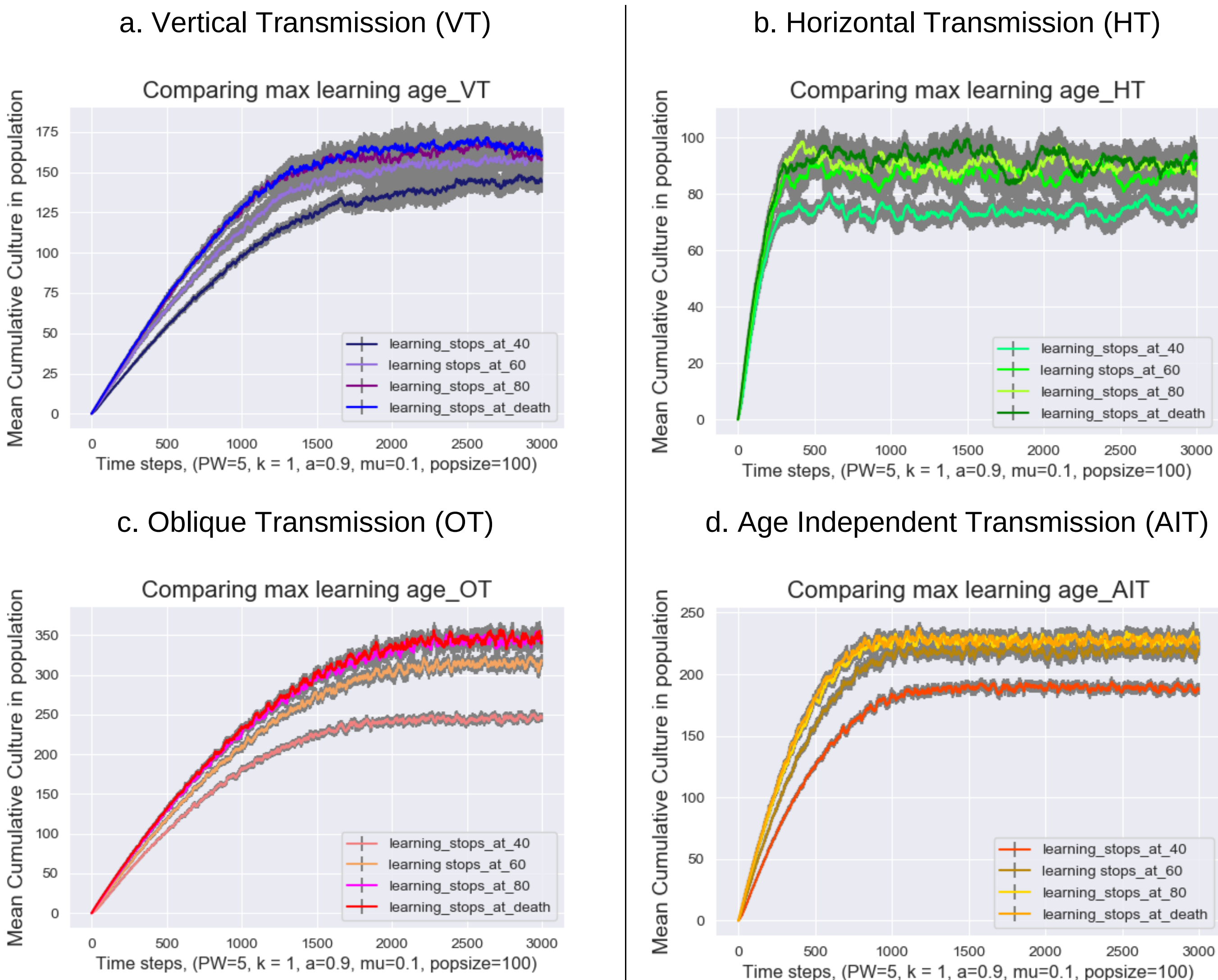
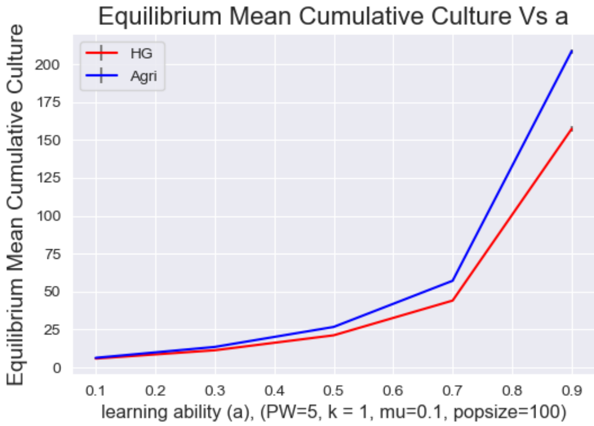


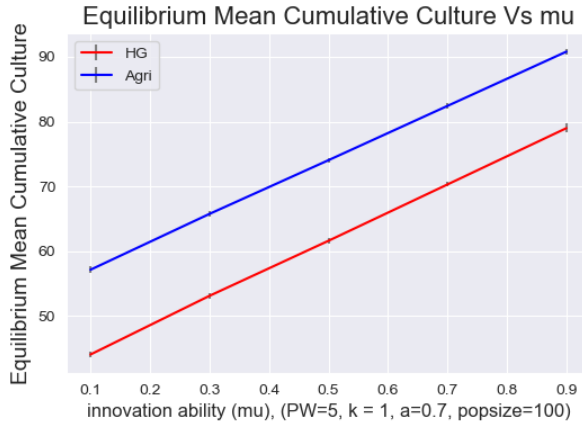

*Figure A5.2: Time series for comparing the effect of learning and innovation stopping at age 40, 60, 80, and at death. The equilibrium cultural values are not that different and an expected trend of slight reduction in equilibrium cultural value with drop in the age when learning stops. These trends do not affect the between cultural mode comparisons to large extent.*

*6. Equilibrium cultural value for ‘HG’ and ‘Agri’ compared across the parameters*

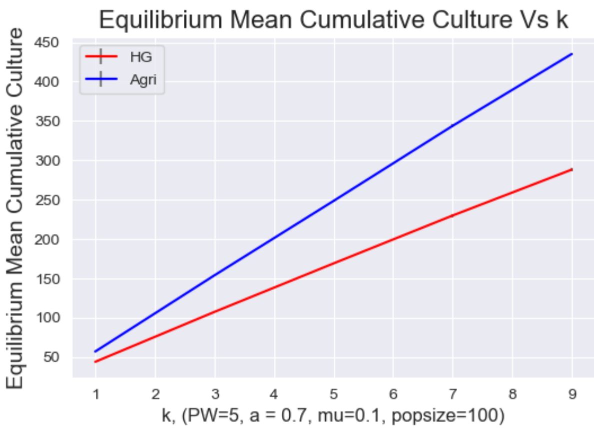
a. Learning ability ‘a’



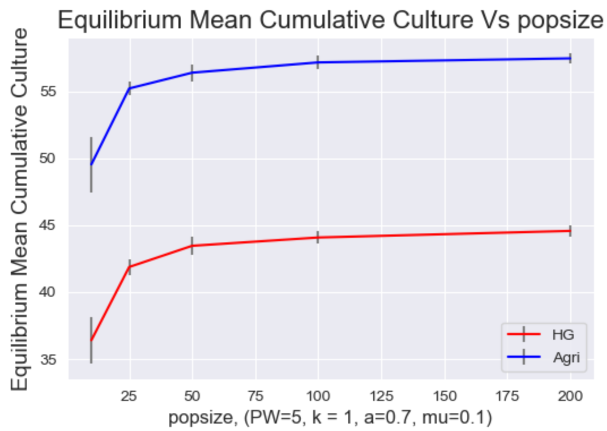

b. Innovation ability ‘mu’




c. Number of demonstrators ‘k’




d. Population size ‘popsize’




e. Peer Width ‘PW’

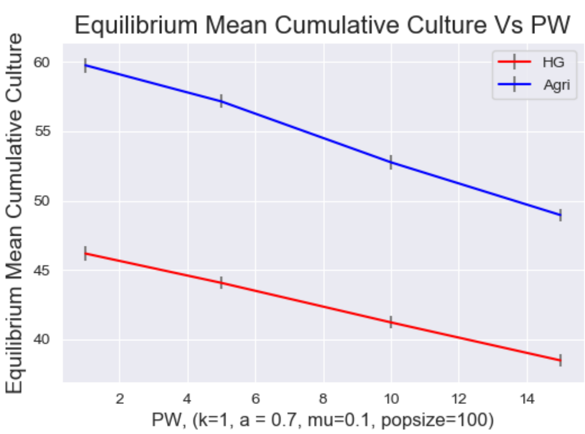



*Figure A6: Equilibrium cultural value against the parameter space. Blue denotes ‘Agri’ whereas red denotes the ‘HG’ life history of learning strategies. ‘Agri’ is above ‘HG’ for all the parameters. Reasoning behind the trends can be given by arguments similar to section 3.1.4.*

*7. Survival curve with juvenile mortality*

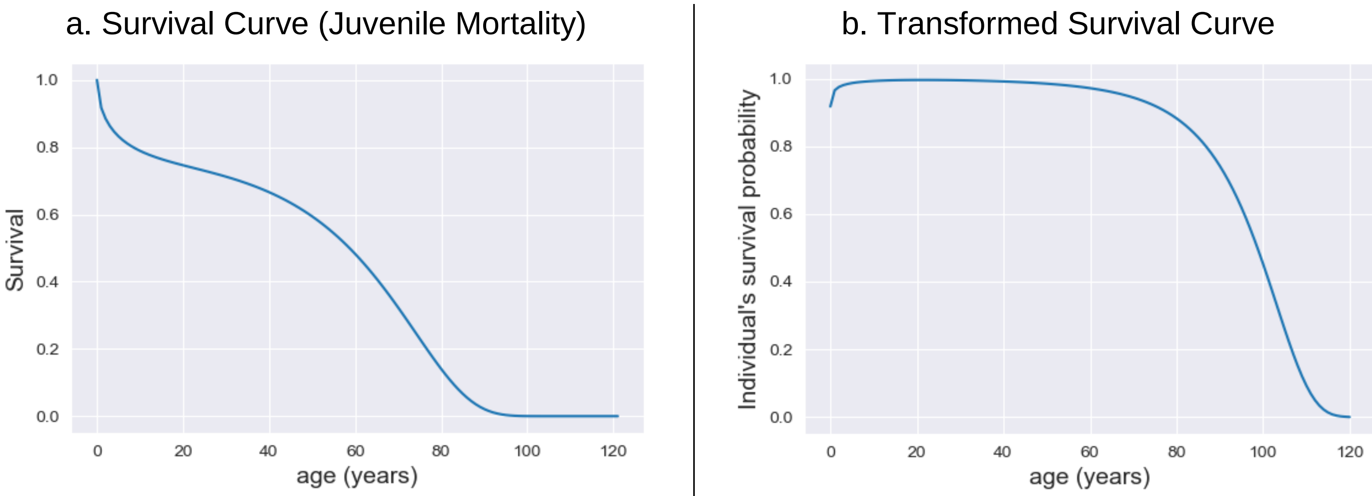



*Figure A1: a) Survival curve and b) Transformed Survival Curve for population with juvenile mortality. Adopted from Weon, (2003). The survival curve in plot a is qualitatively similar to hunter gatherer survival curve empirically calculated by Gurven and Kaplan, (2007). The transformation to the survival curve is done according the method described in appendix 1.*

## 6. References:


Aoki, K. (2010). Evolution of the social-learner-explorer strategy in an environmentally heterogeneous two-island model. Evolution (N. Y). *64*, 2575–2586.

Aoki, K., and Feldman, M.W. (2014). Evolution of learning strategies in temporally and spatially variable environments: A review of theory. Theor. Popul. Biol. *91*, 3–19.

Aunger, R. (2000). The Life History of Culture Learning in a Face-to-Face Society. Ethos *28*, 445–481.

Bailey, R.C., and Aunger, R. (1995). Sexuality, Infertility and Sexually Transmitted Diseases Among Farmers and Foragers in Central Africa.

Baldini, R. (2014). Estimating the evolution of human life history traits in age-structured populations. BioRxiv 002584.

Baldini, R. (2015). Revisiting the Effect of Population Size on Cumulative Cultural Evolution. J. Cogn. Cult. *15*, 320–336.

Borenstein, E., Feldman, M.W., and Aoki, K. (2008). Evolution of learning in fluctuating environments: When selection favors both social and exploratory individual learning. Evolution (N. Y). *62*, 586–602.

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

Boyd, R., and Richerson, P.J. (1988). An evolutionary model of social learning: The effects of spatial and temporal variation. Soc. Learn. Psychol. Biol. Perspect. 29–48.

Castro, L., and Toro, M.A. (2014). Cumulative cultural evolution: The role of teaching. J. Theor. Biol. *347*, 74–83.

Cavalli-Sforza, L.L., and Feldman, M.W. (1981). Cultural Transmission and Evolution: A Quantitative Approach (Princeton University Press).

Cavalli-Sforza, L.L., Feldman, M.W., Chen, K.H., and Dornbusch, S.M. (1982). Theory and observation in cultural transmission. Science *218*, 19–27.

Creanza, N., Kolodny, O., and Feldman, M.W. (2017). Cultural evolutionary theory: How culture evolves and why it matters. Proc. Natl. Acad. Sci. U. S. A. *114*, 7782–7789.

Dean, L.G., Vale, G.L., Laland, K.N., Flynn, E., and Kendal, R.L. (2014). Human cumulative culture: a comparative perspective. Biol. Rev. *89*, 284–301.

Derex, M., and Boyd, R. (2016). Partial connectivity increases cultural accumulation within groups. Proc. Natl. Acad. Sci. U. S. A. *113*, 2982–2987.

Enquist, M., and Ghirlanda, S. (2007). Evolution of social learning does not explain the origin of human cumulative culture. J. Theor. Biol. *246*, 129–135.

Enquist, M., Ghirlanda, S., Jarrick, A., and Wachtmeister, C.-A. (2008). Why does human culture increase exponentially? Theor. Popul. Biol. *74*, 46–55.

Enquist, M., Ghirlanda, S., and Eriksson, K. (2011). Modelling the evolution and diversity of cumulative culture. Philos. Trans. R. Soc. B Biol. Sci. *366*, 412–423.

Feldman, M.W., Aoki, K., and Kumm, J. (1996). Individual Versus Social Learning: Evolutionary Analysis in a Fluctuating Environment. Anthropol. Sci. *104*, 209–231.

Fogarty, L., and Creanza, N. (2017). The niche construction of cultural complexity: interactions between innovations, population size and the environment. Philos. Trans. R. Soc. B Biol. Sci. *372*, 20160428.

Fogarty, L., Creanza, N., and Feldman, M.W. (2013). The role of cultural transmission in human demographic change: An age-structured model. Theor. Popul. Biol. *88*, 68–77.

Fogarty, L., Creanza, N., and Feldman, M.W. (2019). The life history of learning: Demographic structure changes cultural outcomes. PLOS Comput. Biol. *15*, e1006821.

Gurven, M., and Kaplan, H. (2007). Longevity among Hunter-Gatherers: A Cross-Cultural Examination.

Henrich, J. (2004). Demography and Cultural Evolution: How Adaptive Cultural

Processes Can Produce Maladaptive Losses—The Tasmanian Case. Am. Antiq. *69*, 197–214.

Hewlett, B.S., Fouts, H.N., Boyette, A.H., and Hewlett, B.L. (2011). Social learning among Congo Basin hunter-gatherers. Philos. Trans. R. Soc. B Biol. Sci. *366*, 1168–1178.

Hill, K., Barton, M., and Magdalena Hurtado, A. (2009). The emergence of human uniqueness: Characters underlying behavioral modernity. Evol. Anthropol. *18*, 187–200.

Kandler, A., Wilder, B., and Fortunato, L. (2017). Inferring individual-level processes from population-level patterns in cultural evolution. R. Soc. Open Sci. *4*, 170949.

Kempe, M., Lycett, S.J., and Mesoudi, A. (2014). From cultural traditions to cumulative culture: parameterizing the differences between human and nonhuman culture. J. Theor. Biol. *359*, 29–36.

Kline, M.A., Boyd, R., and Henrich, J. (2013). Teaching and the Life History of Cultural Transmission in Fijian Villages. Hum. Nat. *24*, 351–374.

Kobayashi, Y., and Aoki, K. (2012). Innovativeness, population size and cumulative cultural evolution. Theor. Popul. Biol. *82*, 38–47.

Kobayashi, Y., Ohtsuki, H., and Wakano, J.Y. (2016). Population size vs. social connectedness — A gene-culture coevolutionary approach to cumulative cultural evolution. Theor. Popul. Biol. *111*, 87–95.

Lehmann, L., Feldman, M.W., and Kaeuffer, R. (2010). Cumulative cultural dynamics and the coevolution of cultural innovation and transmission: an ESS model for panmictic and structured populations. J. Evol. Biol. *23*, 2356–2369.

Lewis, H.M., and Laland, K.N. (2012). Transmission fidelity is the key to the build-up of cumulative culture. Philos. Trans. R. Soc. B Biol. Sci. *367*, 2171–2180.

Mesoudi, A. (2011a). Cultural evolution : how Darwinian theory can explain human culture and synthesize the social sciences (University of Chicago Press).

Mesoudi, A. (2011b). Variable Cultural Acquisition Costs Constrain Cumulative Cultural Evolution. PLoS One *6*, e18239.

Mesoudi, A. (2016). Cultural Evolution: A Review of Theory, Findings and Controversies. Evol. Biol. *43*, 481–497.

Mesoudi, A. (2017). Pursuing Darwin's curious parallel: Prospects for a science of cultural evolution. Proc. Natl. Acad. Sci. *114*, 7853–7860.

Mesoudi, A., and Thornton, A. (2018). What is cumulative cultural evolution? Proc. R. Soc. B Biol. Sci. *285*, 20180712.

Noord-Zaadstra, B.M. Van, Looman, C.W.N., Alsbach, H., Habbema, J.D.F., te Velde, E.R., and Karbaat, J. (1991). Delaying Childbearing: Effect Of Age On Fecundity And Outcome Of Pregnancy. JSTOR *302*, 1361–1365.

Ohtsuki, H., Wakano, J.Y., and Kobayashi, Y. (2017). Inclusive fitness analysis of cumulative cultural evolution in an island-structured population. Theor. Popul. Biol. *115*, 13–23.

Pascual, I., Aguirre, J., Manrubia, S., and Cuesta, J.A. (2019). Epistasis between cultural traits drives paradigm shifts in cultural evolution.

Pradhan, G.R., Tennie, C., and van Schaik, C.P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. J. Hum. Evol. *63*, 180–190.

Ram, Y., Liberman, U., and Feldman, M.W. (2018). Evolution of vertical and oblique transmission under fluctuating selection. Proc. Natl. Acad. Sci. U. S. A. *115*, E1174–E1183.

Ram, Y., Liberman, U., and Feldman, M.W. (2019). Vertical and oblique cultural transmission fluctuating in time and in space. Theor. Popul. Biol. *125*, 11–19.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M.W., Fogarty, L., Ghirlanda, S., Lillicrap, T., and Laland, K.N. (2010). Why copy others? insights from the social learning strategies tournament. Science (80-. ). *328*, 208–213.

Richerson, P.J., and Boyd, R. (2005). Not by genes alone : how culture transformed human evolution (University of Chicago Press).

Richerson, P.J., Boyd, R., and Henrich, J. (2010). Gene-culture coevolution in the age of genomics. Proc. Natl. Acad. Sci. U. S. A. *107*, 8985–8992.

Salali, G.D., Chaudhary, N., Thompson, J., Grace, O.M., van der Burgt, X.M., Dyble, M., Page, A.E., Smith, D., Lewis, J., Mace, R., et al. (2016). Knowledge-Sharing Networks in Hunter-Gatherers and the Evolution of Cumulative Culture. Curr. Biol. *26*, 2516–2521.

Sasaki, T., and Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. Nat. Commun. *8*.

Schofield, D.P., McGrew, W.C., Takahashi, A., and Hirata, S. (2018). Cumulative culture in nonhumans: overlooked findings from Japanese monkeys? Primates *59*, 113–122.

Stout, D., Rogers, M.J., Jaeggi, A. V., and Semaw, S. (2019). Archaeology and the Origins of Human Cumulative Culture: A Case Study from the Earliest Oldowan at Gona, Ethiopia. Curr. Anthropol. *60*, 309–340.

Tennie, C., Call, J., and Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. B Biol. Sci. *364*, 2405–2415.

Tomasello, M. (1999). The cultural origins of human cognition (Cambridge: Harvard University Press).

Tucker-Drob, E.M. (2009). Differentiation of Cognitive Abilities Across the Life Span. Dev. Psychol. *45*, 1097–1118.

Weon, B. (2003). General functions for human survival and mortality.

Whiten, A. (2005). The second inheritance system of chimpanzees and humans. Nature *437*, 52–55.

Whiten, A., Ayala, F.J., Feldman, M.W., and Laland, K.N. (2017). The extension of biology through culture. Proc. Natl. Acad. Sci. U. S. A. *114*, 7775–7781.