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A two level mutation-selection model of cultural evolution and diversity

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ABSTRACT

Cultural evolution is a complex process that can happen at several levels. At the level of individuals in a population, each human bears a set of cultural traits that he or she can transmit to its offspring (vertical transmission) or to other members of his or her society (horizontal transmission). The relative frequency of a cultural trait in a population or society can thus increase or decrease with the relative reproductive success of its bearers (individual's level) or the relative success of transmission (called the idea's level). This article presents a mathematical model on the interplay between these two levels. The first aim of this article is to explore when cultural evolution is driven by the idea's level, when it is driven by the individual's level and when it is driven by both. These three possibilities are explored in relation to (a) the amount of interchange of cultural traits between individuals, (b) the selective pressure acting on individuals, (c) the rate of production of new cultural traits, (d) the individual's capacity to remember cultural traits and to the population size. The aim is to explore the conditions in which cultural evolution does not lead to a better adaptation of individuals to the environment. This is to contrast the spread of fitness-enhancing ideas, which make individual bearers better adapted to the environment, to the spread of "selfish" ideas, which spread well simply because they are easy to remember but do not help their individual bearers (and may even hurt them). At the same time this article explores in which conditions the adaptation of individuals is maximal. The second aim is to explore how these factors affect cultural diversity, or the amount of different cultural traits in a population. This study suggests that a larger interchange of cultural traits between populations could lead to cultural evolution not improving the adaptation of individuals to their environment and to a decrease of cultural diversity.

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1. Introduction

Cultural evolution is a complex process that can happen at three levels. At the level of individuals in a population, each human bears a set of cultural traits that he or she can transmit to its offspring (vertical transmission) or to other members of his or her society (horizontal transmission). The relative frequency of a cultural trait in a population or society (arbitrarily defined here as a set of individuals that interact more with each other than with other individuals) can thus increase or decrease with the relative reproductive success of its bearers.

At a lower level (here called, for simplicity, the idea's level) cultural traits can increase in frequency simply by being able to be communicated more often or more reliably between individuals in a population, thus not necessarily having any positive effect on the reproductive success of its bearers. A classical example would be the spreading of the preference for small size families among

late 20th century Italians (Cavalli-Sforza and Feldman, 1981) despite the presumably lower reproductive success entailed by this cultural trait.

At a higher level the spreading or decline of whole societies or social groups can affect the relative frequency of cultural traits without necessarily affecting the reproductive success of individuals. Thus, a social group can become extinct by the gradual adoption of its members by another culture. This can be due to multiple reasons: to military or political defeat or to the perception that life is better in another social group (Cronk, 1989). The adopted individuals are known to readily acquire (Soltis et al., 1995) many of the cultural traits in their host social group without necessarily compromising their reproductive success in a dramatic way.

These three levels fulfill the requirements to be considered levels of selection (Lewontin, 1970) because they exhibit variation that can be differently selected (selection at the social level has been suggested by Soltis et al., 1995 and many others (reviewed in Carneiro, 2003)).

This article studies a mathematical model on the interplay between the first two of these levels and their effect on cultural diversity. The first aim of the article is to explore when cultural

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evolution is driven by the idea's level, when it is driven by the individual's level and when it is driven by both. This is to explore the conditions in which cultural evolution does not lead to a better adaptation of individuals to the environment.

The present model is built on a similar set of simplifications and assumptions as the classical mutation-selection balance model of population genetics. Here, however, selection occurs at two levels, idea's and individual's, and the aim is in fact to understand their relative kinetics. These classical models focus on the kinetics of replacement between alleles in a population while in our case, as in other models in cultural evolution (Shennan, 2001; Eerkens and Lipo, 2005; Nowak, 2006), the focus is on the kinetics of replacement between cultural traits in a population without considering gene-culture co-evolution. These two previous studies, however, consider only neutral models without selection while here two levels of selection are considered. Nowak's work does use a mutation-selection balance model but only at one level, in an infinite population and intended to address some specific questions about the evolution of grammar. Other multilevel selection models are applied to questions like: mitochondrial evolution (Roze et al., 2005), the role of selection in early multicellularity (Roze and Michod, 2001), genetic group-selection (Wade, 1982), and social group formation (Janssens and Goldstone, 2006; Traulsen and Nowak, 2006). Let us emphasize here, that a cultural trait is defined in this article as any trait of human or animal activity acquired in social life and transmitted by communication. Thus, a cultural trait can be anything from a taste for the last fashionable shoes to the knowledge to make nuclear bombs.

Cultural traits can be composed of other traits and do not necessarily have a particulate nature. As it has been repeatedly argued, this does not preclude their study through mathematical models (Mesoudi et al., 2006; Henrich et al., 2008) as an extensive literature suggests (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Henrich and Boyd, 2001; Shennan, 2001; McElreath, 2003; Eerkens and Lipo, 2005; Henrich and Boyd, 2008). This model is equally applicable to concepts that are similar to the concept of cultural trait: *memes* (Dawkins, 1976) and *ideas* (Salazar-Ciudad, 2008a).

In addition, the model considers cultural trait interdependencies. The chances of an individual acquiring a new cultural trait depend on which cultural traits are already present in that individual. However, the model does not consider the interrelationship of cultural traits in the origin and content of new cultural traits. Thus, as in classical population genetic studies, there is production of new cultural traits (the analog to mutation) but there is no consideration on how, or in which way, the new variants are different from each other or on which cultural traits are most likely to arise. These things have a strong effect in the direction of evolutionary change (Alberch, 1982; Salazar-Ciudad, 2006). In cultural evolution that should, at least, depend on individual's psychology and experiences and likely on the cultural traits existing in a population (from which new cultural traits often arise). In the case of biological evolution, which phenotypic variation arises in each generation depends on how genetic and environmental variations affect the mechanisms of development. Although the study of these mechanisms is starting to be considered in evolutionary biology (Alberch, 1982; Raff, 1996; Salazar-Ciudad, 2008b), our current lack of understanding of the mechanisms by which cultural traits arise and are transmitted precludes general models about how the nature of specific cultural traits changes in evolution or how the "content" of some cultural traits affects the evolution of others. Population genetic models arose at a time when the understanding about development or even about the genetics of transmission was very limited. In spite of that, and of the many limitations they are known to

have (Alberch, 1982; Salazar-Ciudad, 2006), these models provided some valuable insights in evolutionary biology.

This article provides general tentative answers to several questions in cultural evolution employing a mostly "bean bag" model that should be further refined in the future. These questions are

1. How does the amount of communication between individuals in a population affect evolution at the idea's and individual's levels?
2. How does the intensity of selection at the level of individuals affect evolution at the idea's and individual's levels?
3. How does the rate at which new cultural traits arise (the innovation rate in this article) affect evolution at the idea's and individual's levels?
4. Innovation can arise at a fixed rate per individual and generation or as a consequence of individuals being exposed to new ideas (through communication). How does this affect evolution at the idea's and individual's levels?
5. As explained, the acquisition of a cultural trait by an individual will often depend in complex ways on the cultural traits already present in that individual. How does a complex relationship between cultural traits, compared to a simple one, affect the acquisition of new cultural traits and evolution at the individual's level?

The second aim of this article is to study, through the model, how the interplay between the individual and idea's level affects the evolution of cultural diversity. This work makes a distinction between cultural diversity, the number of different cultural traits present in a population, and cultural disparity, how different are the cultural traits present in a population. The same distinction already exists in biology for the species present in a phylogeny or geographic area (Raff, 1996). In the case of cultural evolution the limits of this distinction are arbitrarily based on how different two cultural traits need to be, so that they can be considered as distinct cultural traits (and of course on the complex issue of measuring these differences). As explained, this model only approaches cultural diversity.

Several studies indicate that both the amount of accumulated knowledge (Lehman, 1947; Basalla, 1989; Durham, 1991) and population has increased exponentially over historical times. The classical studies in socio-cultural evolution (White, 1959; Sahlins, 1970) conceive evolution as a progressive sequence of stages characterized, among other things, by progressively larger amounts of accumulated knowledge and cultural traits that steadily improve the adaptation of individuals and societies to the physical and social environment. Later studies (Steward, 1955; Carneiro, 2003) do not assume that this progressive evolution proceeds through a unique path but also suggest that there is some overall trend in accumulated knowledge and its adaptive value. More recently behavioral ecology has explained some cultural features of forager societies on the basis of arguments that also propose that cultural traits more adaptive for individuals tend to replace, in the long run, less adaptive ones (reviewed in Kelly, 2007). This increase in accumulated knowledge has occurred concomitantly with population growth over historical times. This suggests the possibility that there may be some connection between population size and cultural diversity. The questions addressed in this model concerning cultural diversity are as follows.

6. How does cultural diversity increase with population size? As stated, accumulated knowledge has increased exponentially

over historical times (Lehman, 1947). Since population has also increased exponentially it is not clear whether accumulated knowledge increased linearly or exponentially with respect to population size. Previous work (Enquist et al., 2008) suggests that cultural diversity can only increase exponentially through gene-culture co-evolution. This previous work uses a simple analytical model with an infinite population and individuals that can have any number of cultural traits. This article introduces an agent-based model with finite populations and individuals that have a finite number of cultural traits.

7. How does cultural diversity and its dependence on population size depend on communication rates and on the intensity of selection at different levels?
8. A large rate of appearance of new cultural traits can be expected to promote cultural diversity. At which rate does innovation, in the two forms considered, increase cultural diversity and how does it affect its dependence on population size?
9. How does a complex relationship between cultural traits, compared to a simple one, affect the acquisition of cultural traits and cultural diversity?
10. An individual can communicate with a fixed number of individuals or with a number of individuals that increases with increase in the population size. How does this change the dependence between cultural diversity and population size?

2. The models

This article introduces several models. First I will describe the simplest one. The other models are modifications of this one to accommodate different assumptions.

2.1. The basic model

This is a two level model: there is a population of individuals and within each of them is a population of cultural traits. The population of individuals has a size of P and the population of cultural traits within each individual has a size of N . In each generation there are selection at the individual's level and transmission (communication) of cultural traits between individuals (see Fig. 1). A number of individuals are eliminated from the population and an equal number of new individuals is introduced. The new individuals are simple copies of randomly chosen individuals within the population. For each individual the chances of being eliminated depend on the cultural traits it bears. In the model an individual is fully described by the list of cultural traits it bears (see Fig. 1). In each generation there is also communication of cultural traits between traits between individuals. A "communicated" cultural trait is incorporated by the individual that receives it depending on the *idea's level fitness* of the cultural trait communicated and the *idea's level fitnesses* of the cultural traits already existing in that individual. Thus, cultural traits are

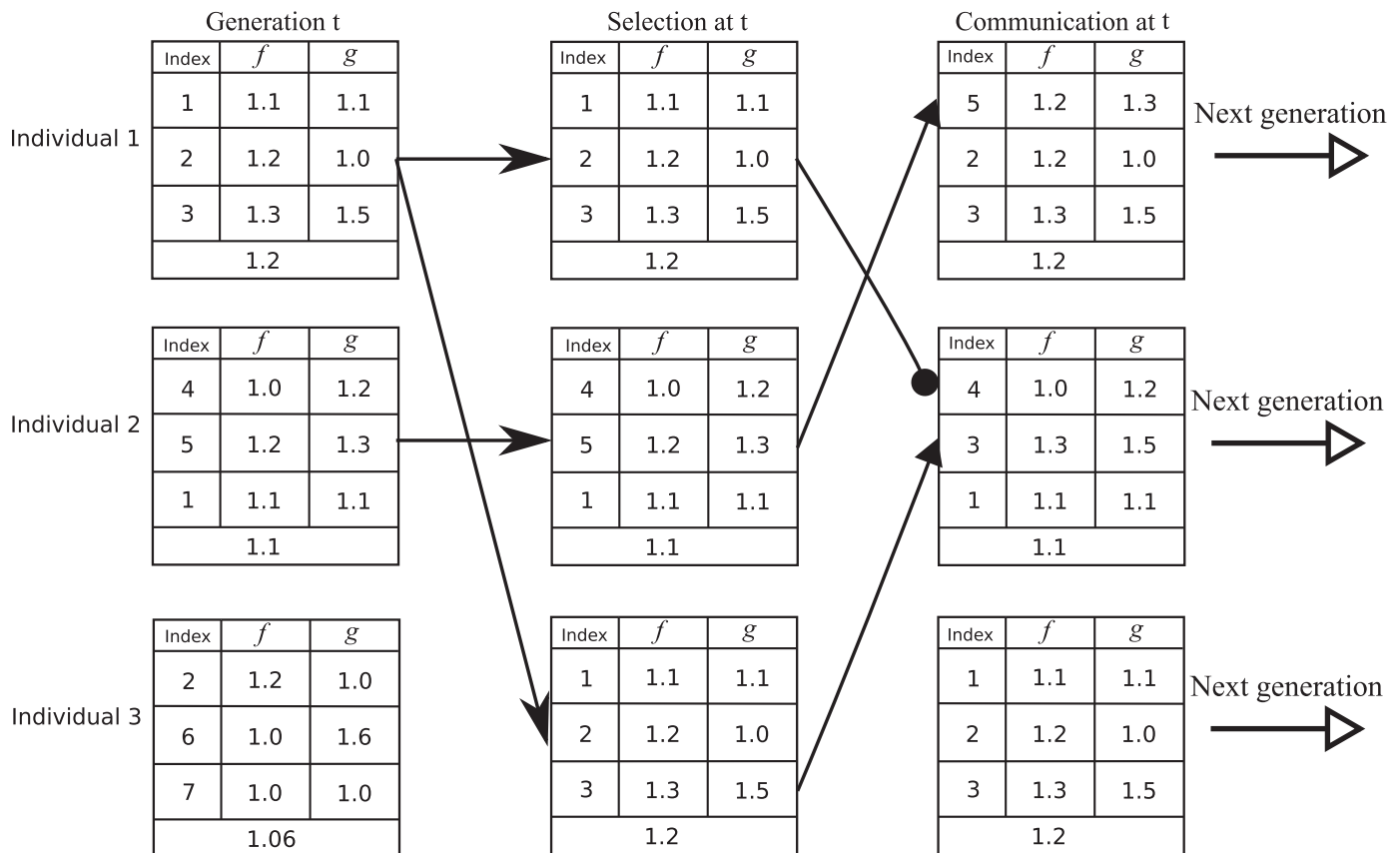


Fig. 1. The diagram depicts the basic model and an example of its dynamics. In this diagram each individual is represented by three columns describing the cultural traits it bears. The first column is simply a label for each cultural trait. The second column is the contribution of each cultural trait to the biological fitness of its bearer. The fourth row shows the average of these values per each individual. The third column shows the idea's level fitness of each cultural trait. In each generation there is selection among individuals and communication of cultural traits between individuals. The arrows between the first column of individuals and the second indicate which individuals are selected for and which ones are not. It can be seen that individual 3 dies and individual 1 remains in the population and also produces offspring. The net effect is that individual 3 is replaced by a copy of individual 1. This has to do with individual 1 having a higher average of cultural traits fitness contributions (as explained in the text). The arrows between the second and third column of individuals depict communication events. Lines with a round end indicate failed communication events in which an individual receives a cultural trait from another individual but it does not retain it. As it can be seen successful communication events lead to the replacement of an existing cultural trait by the communicated cultural trait. This process of selection and communication (plus mutation) is iterated in each generation.

differentiated on the bases of two numbers: one contributes to the capacity of its bearer to compete with other individuals and the other measures how well does a cultural trait compete with other cultural traits in its transmission between individuals. These two numbers, for a given cultural trait j , are, respectively, called in the model f_j and g_j . The model, thus, considers the spreading of cultural traits vertically, through the differential survivorship of its bearers, and horizontally through communication. Since each cultural trait is defined as two numbers the population can be fully described, in each generation, as the list, or array, of cultural traits each individual bears and these two numbers per each cultural trait. New cultural traits arise by a process analogous to mutation. The model keeps track of an array that includes the fitnesses of all the cultural traits that exist or existed in the population.

An important difference between those two levels is that there can be two, or more, identical individuals in a population but an individual cannot have two identical cultural traits. N represents the number of cultural traits an individual can remember. For simplicity all individuals have the same N . Writing and other means of recording cultural traits can increase N . Those, however, are subject to environmental decay and consequent information loss. Thus, N not only represents what can be remembered directly but also the cultural traits an individual can readily access from the records he/she can remember to access.

At each time step PS of these individuals die (S stands for selection). For each individual the chances of dying are inversely proportional to its biological fitness. This is determined by adding the fitness contributions of each of the N cultural traits an individual bears. This is:

$$F(i) = \frac{\sum_{k=1}^N f_{i(k)}}{\sum_{l=1}^P \sum_{k=1}^N f_{l(k)}} \quad (1)$$

where $F(i)$ is the relative biological fitness of individual i . $i(k)$ is the index, in the array that keeps track of cultural traits fitnesses, of the k th (of N) cultural traits in individual i . Thus $f_{i(k)}$ is the individual's level contribution of that cultural trait (see Fig. 1). Notice that the same cultural trait can occupy different positions in different individuals. The fitness contribution of a cultural trait to an individual fitness is called the individual's level fitness of a cultural trait. This fitness is invariable: it is the same in all individuals. Cultural traits, however, can be transformed into others and in that process change their fitness contribution, as explained later. Each individual i has a probability of being chosen for death, $P_d(i)$:

$$P_d(i) = \frac{\sum_{k=1}^N \frac{1}{f_{i(k)}}}{\sum_{l=1}^P \sum_{k=1}^N \frac{1}{f_{l(k)}}} \quad (2)$$

The ones that are chosen are replaced by new individuals. The cultural traits of the new individual are obtained by randomly choosing two living individuals (panmixia is assumed) in the population and taking a total of N cultural traits from them (each chosen randomly without repetition). The stochastic nature of this algorithm also allows incorporating drift directly. This model does not consider genetic-cultural co-evolution; there are already many existing models (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). For simplicity the fitness contribution of a cultural trait is considered to be independent of that of other traits.

The model also includes communication between individuals. A randomly chosen individual is exposed to a random cultural trait chosen from a random individual (that is called a communication event). N cultural traits are chosen per individual and generation from the cultural traits an individual had (from the

previous time step) plus the ones he/she has been exposed to, by communication, in a generation. The selection algorithm is similar to the one used at the individual's level. The chances of a cultural trait, j , in an individual, being selected for the next generation, in the same individual, are proportional to $G(j)$ an intrinsic idea's level fitness. This chance is

$$G(j) = \frac{g_j}{\sum_{k=1}^N g_k} \quad (3)$$

where the sum is over all the cultural traits in an individual. In each generation there are PC communication events in the population (where the parameter C is generically called communication or amount of communication). Therefore each individual communicates, on average, with the same number of partners irrespectively of population size.

There are two versions of the model according to how innovation is implemented. In the basic model, every cultural trait in each individual and generation has a chance M of becoming a new cultural trait. Thus communication and innovation are independent: innovation reflects new information acquired by an individual through its personal experience with the environment (including the social one). The new cultural traits have the f_j and g_j of their parent cultural trait plus a random number (with uniform distribution) ranging from $-A$ to A (a different random number is chosen for f_j and g_j). The minimum fitness value allowed is 0. A is thus another model parameter.

Each cultural trait is thus characterized by two independent fitnesses, one is related to the fitness contribution it provides to its bearer (for example the cultural trait can be the ability to use and construct bows and that may allow better hunting) and the other one can be related to the likelihood by which an idea is acquired by the individuals exposed to it through communication. This may depend on how easy it is to remember an idea (for example simpler cultural traits like proverbs may be easier to remember than poetry) or how appealing is that idea to the individuals exposed to it.

In all models, S and C are the parameters that effectively determine the intensity of selection at the individual's (S) and idea's level (C). Communication is a selective pressure because every time an individual is exposed to a new cultural trait this can replace an existing one with a probability proportional to their idea's level fitnesses. P and N are, effectively, the population size at each level.

The rules described determine the cultural change over time in a population. In the initial condition each individual has the same N cultural traits. These cultural traits have a fitness of 1 at the individual and idea's level. At any given moment the population can be described by the two kinds of fitnesses of each cultural trait and the distributions of each cultural trait among populations individuals.

Notice that this model does not consider the appearance of cultural traits that increase N (for example, writing). This initial condition is useful to study populations in which individuals are living in environments with a number of cultural traits that is much larger than the number of cultural traits an individual can possibly have. This is possibly a good approximation for most current human populations and for many historical ones. A different initial condition in which each individual has less than N different individual traits is presented in the discussion.

2.2. Model with communication partners increasing with P

In this model the number of communication events is not PC , as in the basic model, but $P^2C/3$. Thus, the number of communication partners per individual is not constant but increases with

P . The $1/3$ factor ensures that on average each individual only communicates with one third of the population. The motivation behind this model is question 6 of the introduction, of whether a non-linear increase in world's population should inevitably lead to an exponential increase in accumulated knowledge. For that question it may be important to consider whether communication partners increase with population size or not. Anything else is exactly as in the basic model.

2.3. Communication-enhanced innovation

In this model innovation is not independent of communication. Instead, innovation can only arise as a by-product of communication. Every time there is a communication event there is a chance M that the receiver produces a new cultural trait (that still has to pass through a round of selection). Thus, innovation results from an individual being exposed to new cultural traits (from other individuals) that trigger new experiences with the environment. From those, new cultural traits can arise. This form of innovation can also be interpreted as misunderstandings in communication that, rarely, lead to new cultural traits (in the basic model this simply leads to the non-communication of a cultural trait). Anything else is exactly as in the basic model.

2.4. Cultural trait interdependence model

Another version of the model assumes that there are strong interdependencies between cultural traits. Thus, the likelihood by which a cultural trait gets communicated to an individual depends on how that cultural trait interacts with the cultural traits existing in that individual. It is well known that having some cultural traits (for example a monotheistic religion) undermines or enhances the chances of acquiring others (for example a new monotheistic religion versus a new polytheistic religion). These interactions are likely to be very important in determining the number and spreading of cultural traits in a population. However, this “ecology of ideas” is not understood to the level to be accurately modeled. This dependence is implemented by randomly choosing which of the existing and communicated cultural traits in an individual are passed to the next generation. However, every time the same specific combination of cultural traits is present, the same cultural traits are chosen. In other words, for each combination of cultural traits there is a unique map that determines which N of them are passed to the next generation. This way the model effectively considers relationships of all complexities. This approach, thus, considers a random sample of all possible interdependences between cultural traits in determining their fitness at the idea's levels. Of course, this is still an idealization because, likely, in real cultural evolution only a subset of those is found. Notice that this approach is different from the infinite population Nowak's model on the evolution of grammar (Nowak, 2006) in which a transition matrix specifies the probability that a learner of a grammar learns a different one. The fitness or chances of acquisition of that grammar do not depend on N other grammars present on an individual. As previously stated, Nowak's model is not a two-level model that includes selection on the bearers of cultural traits as in here.

2.5. Simulations

All the models are implemented in a program written in fortran 90 (available in <http://bioinf3.uab.cat/grupgbe/images/stories/isaac/mevacu.f90>). The model was run 100 times (each time with a different random seed) for each combination of parameters. The parameter combinations were as follows: for S

0.01, 0.1, 0.2, 0.3; for C 0.01, 0.1, 1.0, 2.0; for M 0.0001, 0.001, 0.01, 0.1; for N 3, 5, 10, 100; for A 0.1, 1.0; for P 10, 100, 250, 500, 750, 1000. This gives a total of 307,200 different simulated cultural evolution experiments for the basic version of the model. For the model with interdependence between cultural traits N was 3 or 5. Then there is one set of simulations for each version of the model. Thus there is one version with interdependence between cultural traits, another with the number of partners increasing with population size and another with communication-enhanced innovation. Each run was continued until an equilibrium was reached in the number of cultural traits (absolute fitness does not normally reach an equilibrium as will be explained later).

3. Results

The first section of the results focuses in the results of the simulations of the basic model. Later sections describe the results of the multiple modifications of the basic model and how their results compare to the results of the basic model. The discussion describes how and to which extent the results address the questions proposed in the introduction. The discussion should be easier to follow for those interested in the implications of this model for social evolution and not so directly interested in how the model works.

3.1. Basic model

3.1.1. Fitness

The mean fitnesses of the cultural traits of a population at the individual and idea's levels (from now referred to as $\langle f \rangle$ and $\langle g \rangle$) can either remain fluctuating about the initial value of 1, increase steadily or increase with large fluctuations. Notice that $\langle f \rangle$ is the sum of the individual's level contribution of each cultural trait divided by the total number of different cultural traits existing in the population (thus each cultural trait is counted only once). For some parameter combinations both fitnesses increase over time (see Fig. 2a for an example simulation) while for others only $\langle f \rangle$ (see Fig. 2c) or $\langle g \rangle$ (see Fig. 2b) increase while the other remain fluctuating around 1. In some cases both fitnesses remain fluctuating close to the initial value (see Fig. 2d).

In general the ratio between $\langle f \rangle$ and $\langle g \rangle$ increases with S and decreases with C (see Figs. 3 and 4). If S is high, cultural traits that are received through communication tend to be, in fit individuals, less adaptive than the cultural traits inherited from the parents. In this way communicated traits that do not have a relatively large individual level fitness tend to be eliminated in each generation (through elimination of its bearers). In this case there is no evolution at the idea's level (no net increase of $\langle g \rangle$).

On the other hand, the more communication there is, the more chances there are that a cultural trait unfit at the individual level, but fit at the idea's level, replaces a cultural trait that is fit only at the individual's level. In fact, individuals can be regarded as meta-populations interchanging individuals (cultural traits) through communication. Thus, for larger C values there is more room for cultural traits that base their success in being more able to be communicated successfully irrespective of their adaptive effect on their bearers. As it can be seen in Fig. 5 for large values of C there are simply no increases in mean fitness at the individual's level. This simply implies that, in those conditions, cultural evolution is not adaptive for individuals.

In general N decreases the $\langle f \rangle / \langle g \rangle$ ratio (see Figs. 3 and 4). This is because the more cultural traits there are determining the fitness ($F(i)$) of an individual (that is N), the smaller is its variance (as a consequence of the central limit theorem) and thus the slower is evolution at the individual's level. This effect is

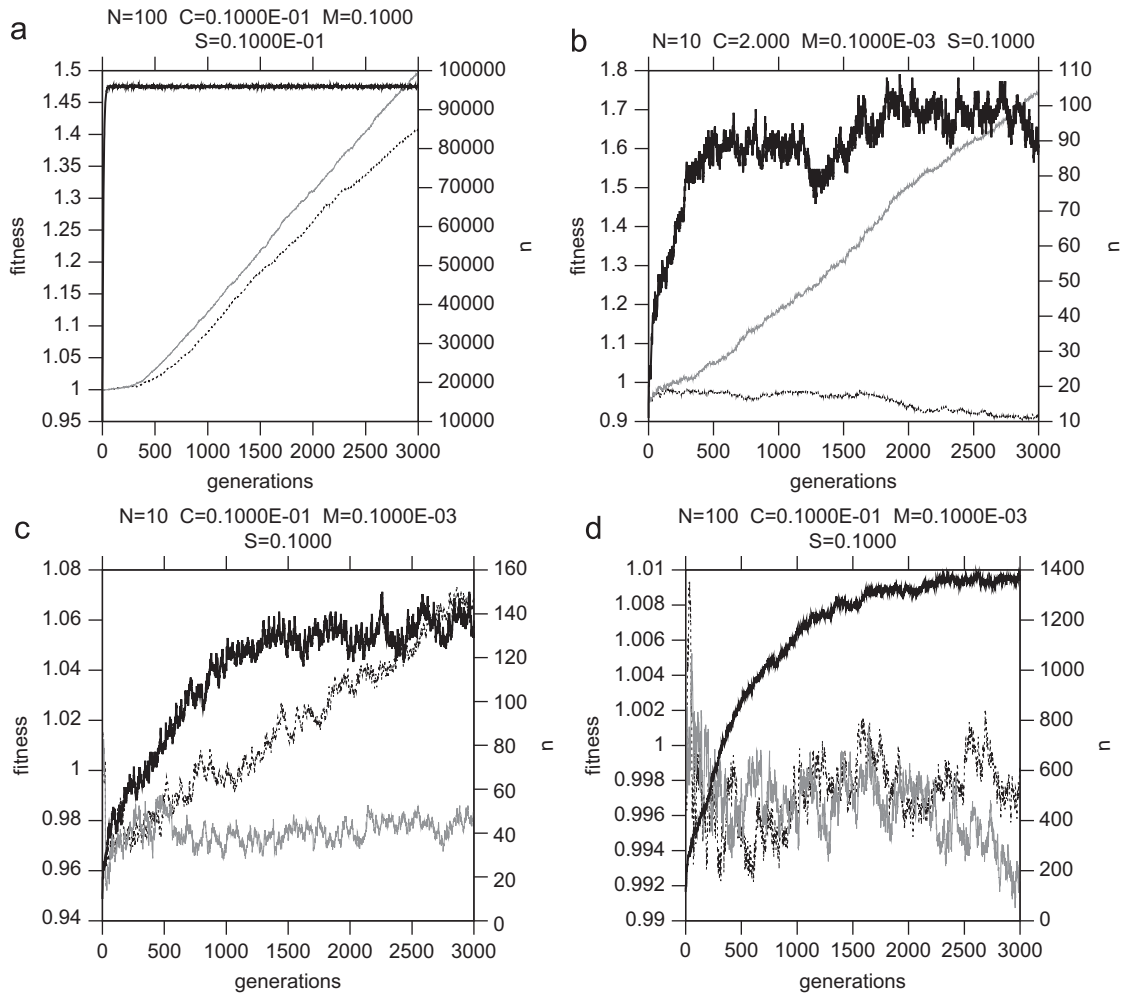


Fig. 2. Four examples of the dynamics over generations of the cultural diversity (darker line), mean idea's level fitness ($\langle g \rangle$, lightest line) and mean cultural trait fitness contributions to individual fitness ($\langle f \rangle$, intermediate gray line). These four simulations are chosen because they give examples of (a) a simulation in which both fitnesses increase over time, (b) a simulation in which $\langle g \rangle$ increases over time while $\langle f \rangle$ keeps fluctuating around the initial fitness (thus there is no adaptation at the individual's level), (c) a simulation in which $\langle f \rangle$ increases over time while $\langle g \rangle$ keeps fluctuating around the initial fitness (thus there is no adaptation at the idea's level), (d) a simulation in which both fitnesses keep oscillating around their initial value. The values of the parameters used for these simulations are indicated in the title of each plot except for A that is 0.1 in all the plots.

non-linear: small N values produce a larger decrease in the ratio (in fact, according to the central limit theorem the variance decreases as $1/N$) (see Fig. 4). When C is large and S very small, N has a small effect in decreasing the ratio because, effectively, there is no evolution at the individual's level.

P , M and A also affect the $\langle f \rangle / \langle g \rangle$ ratio. Their effect is simply multiplicative, when S and C are such that this ratio is larger than 1, any increase in P , M or A leads to an increase in this ratio. When this ratio is less than 1, increases in P , M or A further decrease this ratio. As in the mutation-selection balance model of populational genetics P and M increase the efficiency of selection. At which level they do it depends on S , C and N . A increases the variance in fitness of the cultural traits produced by innovation and thus trivially increases fitness (which of them depends on S , C and N).

As expected from these results maximal individual's level fitness is attained when N is the lowest, P is the largest, S is the largest and C is the lowest (and as stated A and M are the highest). However, when N is large or P is small the maximal individual's level fitness is attained for intermediate or large values of C (see Fig. 5). This is because when N is large and P is small communication becomes a relatively fast way to spread adaptive cultural traits (compared to only individual's level selection). In other words, for a cultural trait with relatively high individual level fitness and average idea's level fitness, N increases the

probabilities of spreading just by chance through communication. Small P , on the other hand, decreases the effectiveness of individual's level selection. This means that as the capacity of individuals to retain information increases intermediate levels of communication promote individual's adaptation (as far as S is large).

3.1.2. Cultural diversity

In all simulations the number of different cultural traits increases rapidly at the beginning and reaches an equilibrium with small fluctuations due to the stochastic nature of the model (see Fig. 2). Notice that the maximum cultural diversity is equal to NP . The amplitude of these fluctuations depends on N , the analog of population size at the idea's level, low values of N lead to larger fluctuations (see Fig. 2). The amount of cultural traits at the equilibrium (from now I will refer to that quantity as n_{eq}) depends on all the variables of the model except on A .

In general the model shows that cultural diversity is low for those parameter combinations that produce high fitness at either level. This is the same as in the mutation-selection balance model of populational genetics in which selection reduces standing genetic variation. However, in the present model there are two levels of selection with two different fitnesses. M and P always

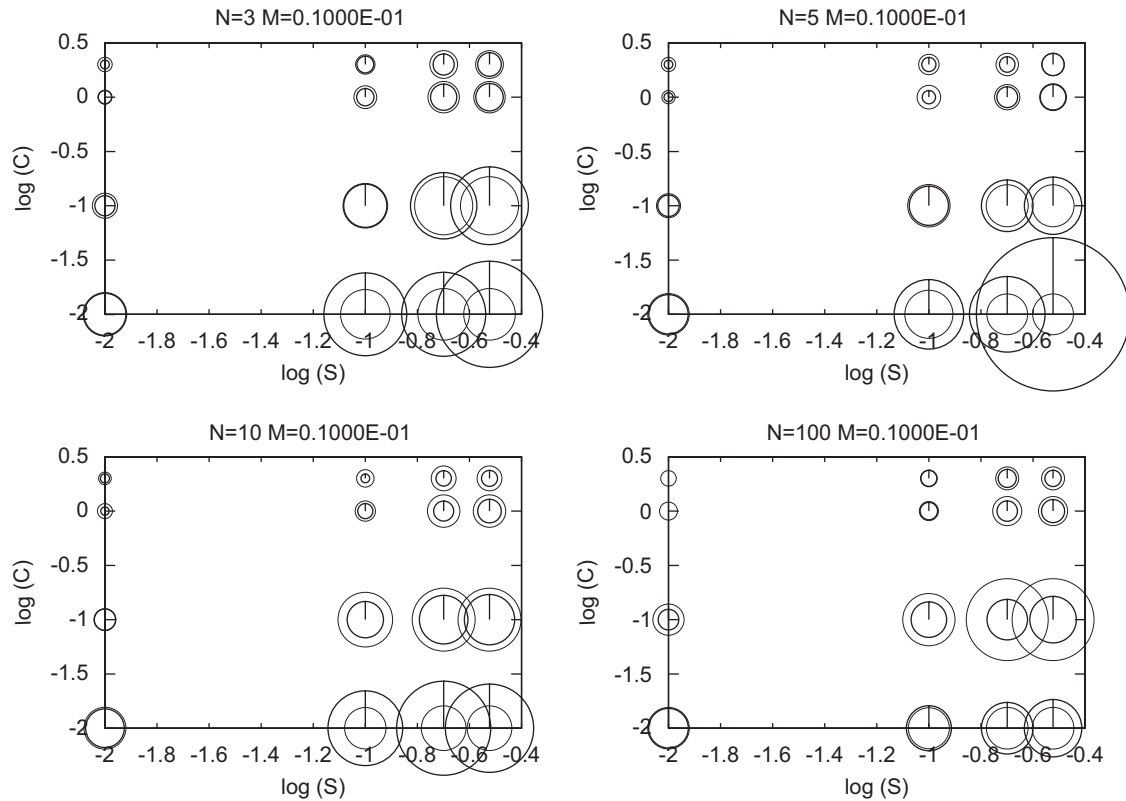


Fig. 3. Four plots of the $\langle f \rangle / \langle g \rangle$ ratio for $\log(S)$ (X axis), $\log(C)$ (Y axis) and P (full dots for $P=10$, empty dots for $P=1000$). The size of each dot is proportional to $\langle f \rangle / \langle g \rangle$. The four plots differ in the N value used, increasing from top left to bottom right. For reference $\langle f \rangle / \langle g \rangle$ is 1 in the last plot at $\log(S) = -2$ and $\log(C) = -2$ when $P=1000$. Thus, all circumferences larger than that one have a $\langle f \rangle / \langle g \rangle$ ratio larger than 1 while the rest have it proportionally smaller (meaning that evolution is faster at the idea's than individual's level). The plots show that $\langle f \rangle / \langle g \rangle$ increases with S and P and decreases with C and N . Notice also that for the largest N values and low P values the largest $\langle f \rangle / \langle g \rangle$ values are attained when C is low (but not minimal).

increase cultural diversity linearly. Both S and C , the analog of selection at the idea's level, decrease cultural diversity (see Fig. 6). The effect of S is smaller when N is large (for the same reasons that high N decreases individual's level fitness). S decreases n_{eq} in a non-linear way: large S values decrease n_{eq} proportionally less than small values of S . C decreases n_{eq} in a similar way. S and C decrease n_{eq} more strongly when P is small. The steepness of this decrease becomes smaller as M increases. Since selection at each level can only eliminate, in each generation, a proportion (instead of a fixed number) of cultural traits it is expectable that the decrease of n_{eq} is slower when n_{eq} is already small thus explaining these non-linearities. Since M increases n_{eq} it has an indirect effect on the steepness of the decrease produced by S and C .

n_{eq} grows linearly with N except when either S or C are large. In the latter case the rate of growth of n_{eq} with N decreases as N is increased. This is just a consequence of the non-linearity with which S and C decrease n_{eq} . A has a rather mild effect on n_{eq} . Only when M is very low A has a small, decreasing, effect on n_{eq} . This effect is also stronger when in addition to a low M value, P and N are also small and C or/and S are large. This is because A does not affect how many cultural traits have a different fitness (either g or f), it only affects how large this difference is. Thus, it has no effect on the elimination of cultural traits because irrespective of A there is going to be the same number of less fit cultural traits that are going to be eliminated in each generation. If M is very low then a single variant has time to replace a large proportion of other ideas before new mutations arise. In that case the larger is the fitness difference between this cultural trait and the rest, the larger is the proportion of different cultural traits that is going to be eliminated (thus explaining why A has an effect only when M is small). This is more likely in small populations with small N and large communication and selection.

4. Communication-enhanced innovation

4.1. Fitnesses

As seen in Fig. 7a the $\langle f \rangle / \langle g \rangle$ ratio tends to be larger in the basic model than in this model. The larger difference corresponds to small values of C . This is not the case when S is small and C is large. In the basic model this leads to a high $\langle f \rangle / \langle g \rangle$ ratio. This is not the case in this model because with low communication there is not much innovation either. Except for that this ratio seems to exhibit the same relationships with S and C as in the basic model. $\langle f \rangle$ also tends to be larger for the basic model (Fig. 7b), except when C is the largest. Thus, while in the basic model $\langle f \rangle$ decreases with C in this model it increases with C . This difference is larger when N is small (because then a larger proportion of the cultural traits of an individual can change by innovation). For large M values this trend is still present but then $\langle f \rangle$ is always larger for the basic model. Notice that even if $\langle f \rangle$ increases with C in this model $\langle f \rangle / \langle g \rangle$ does not. Thus, even if communication enhances innovation its overall effect is to enhance evolution at the idea's level more than at the individual's level.

4.2. Cultural diversity

As seen in Fig. 7c the basic model produces more cultural diversity than this model, except when C is large and P small. As in the basic model n_{eq} decreases with S and C (especial for small P). In this model, however, the largest C values lead to higher n_{eq} than the intermediate C values since in this model communication enhances innovation. Except for the case of very small P and M

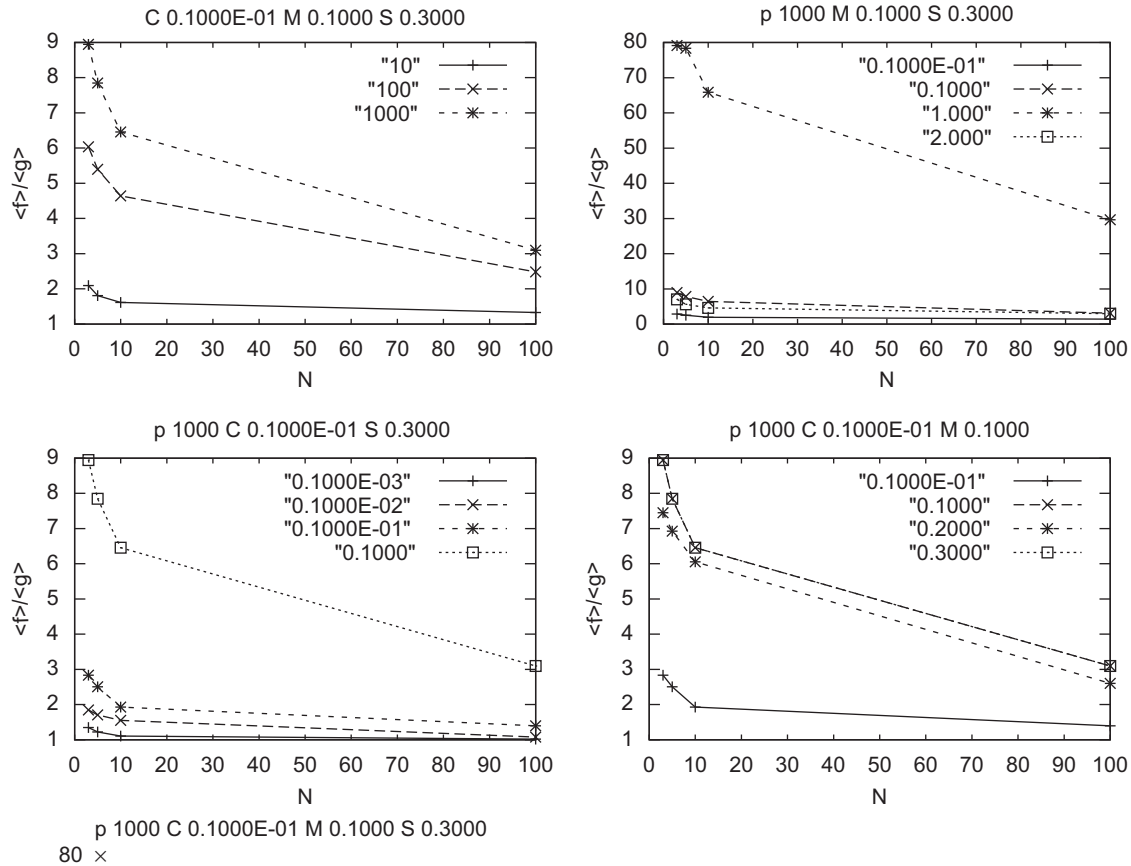


Fig. 4. Four example plots of the relationship between N and $\langle f \rangle / \langle g \rangle$. In each plot the parameters that are kept constant are indicated in the top. In the first plot the different lines indicate different values of P . The plot shows how this ratio increases with P and decreases with N . In the second the different lines indicate different values of C . The plot shows how $\langle f \rangle / \langle g \rangle$ is highest for intermediate values of C and decreases with N . In the third plot the different lines indicate different values of M . The plot shows how $\langle f \rangle / \langle g \rangle$ increases with M and decreases with N . In the fourth plot the different lines indicate different values of S . The plot shows how $\langle f \rangle / \langle g \rangle$ increases with S , although that increase saturates for the highest S values, and decreases with N .

large, the basic model still produces more cultural diversity (even if C is large). Notice that in the more extreme case when C is maximal ($C=0.2$) and N minimal ($N=3$) each individual gets $2/3$ of their cultural traits through communication.

5. Cultural trait interdependence model

5.1. Fitnesses

In the cultural interdependence model g and $\langle f \rangle / \langle g \rangle$ cannot be defined. As seen in Fig. 8a and b the cultural trait interdependence model leads to slightly lower values of $\langle f \rangle$ than the basic model. Thus, a complex relationship between cultural traits is a stronger impediment for adaptation at the individual level than the presence of an idea's selection level. However, for most parameter combinations there is a net increase in $\langle f \rangle$ over time in spite of the complex relationships between cultural traits. In contrast with the basic model, C does not decrease $\langle f \rangle$.

5.2. Cultural diversity

As shown in Fig. 8c the basic model leads to smaller values of n_{eq} than the cultural trait interdependence model. In addition n_{eq} does not depend on C as in the basic model. Thus, a complex relationship between cultural traits is less efficient in eliminating cultural diversity than idea's level selection.

6. Model with communication partners increasing with P

6.1. Fitness

This model behaves as the basic model with more communication (on average each individual communicates with $PC/3$, instead of C , individuals per generation). Thus, the ratio $\langle f \rangle / \langle g \rangle$ increases more slowly with P than in the basic model. In addition, this increase tends to de-accelerate with P . This is simply reflects the relatively larger number of communication events related to P in this model.

6.2. Cultural diversity

In this article only the changes of n_{eq} with respect to P are presented (see Fig. 9). Cultural diversity increases with P but at a smaller rate than in the basic model and this rate also tends to decrease with P . To visualize that I have calculated the rate of increase (the slope) of n_{eq} (its values have been normalized to 1 by dividing by the value of n_{eq} when $P=1000$) for each interval of P values (10, 100, 250, 500, 750, 1000) and then plotted the ratio of the sum of the first two slopes (between 10 and 100 and between 100 and 250) and the sum of the last two slopes (between 500 and 750 and between 750 and 1000). This quotient is close to one when there is a linear relationship between P and n_{eq} , smaller than one when the rate of growth of n_{eq} increases with P and larger than one when this rate decreases with P . As seen in Fig. 8 there are many cases in which this quotient is larger than one for this model

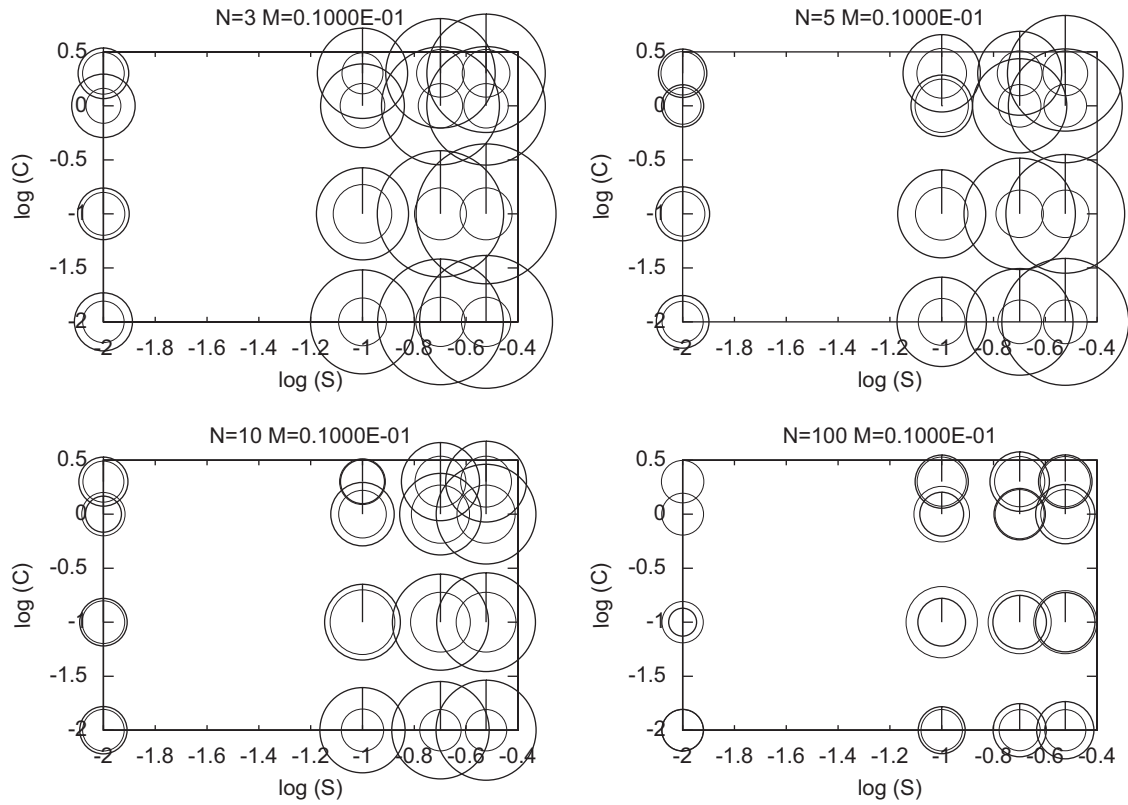


Fig. 5. Four plots of $\langle f \rangle$ for $\log(S)$ (X axis), $\log(C)$ (Y axis) and P (full dots for $P=10$, empty dots for $P=1000$). The size of each dot is proportional to $\langle f \rangle$. The four plots differ in the N value used, increasing from top left to bottom right. For reference $\langle f \rangle$ is 1 in the last plot at $\log(S)=-2$ and $\log(C)=-2$ when $P=1000$. Thus, all circumferences larger than that one have a $\langle f \rangle$ larger than 1 while the rest have it proportionally smaller (thus there is no adaptation at the individual level). The plots show that $\langle f \rangle$ increases with S and P and decreases with C and N . Notice also that for large N values and low P values the largest $\langle f \rangle$ values are attained when C is low (but not minimal).

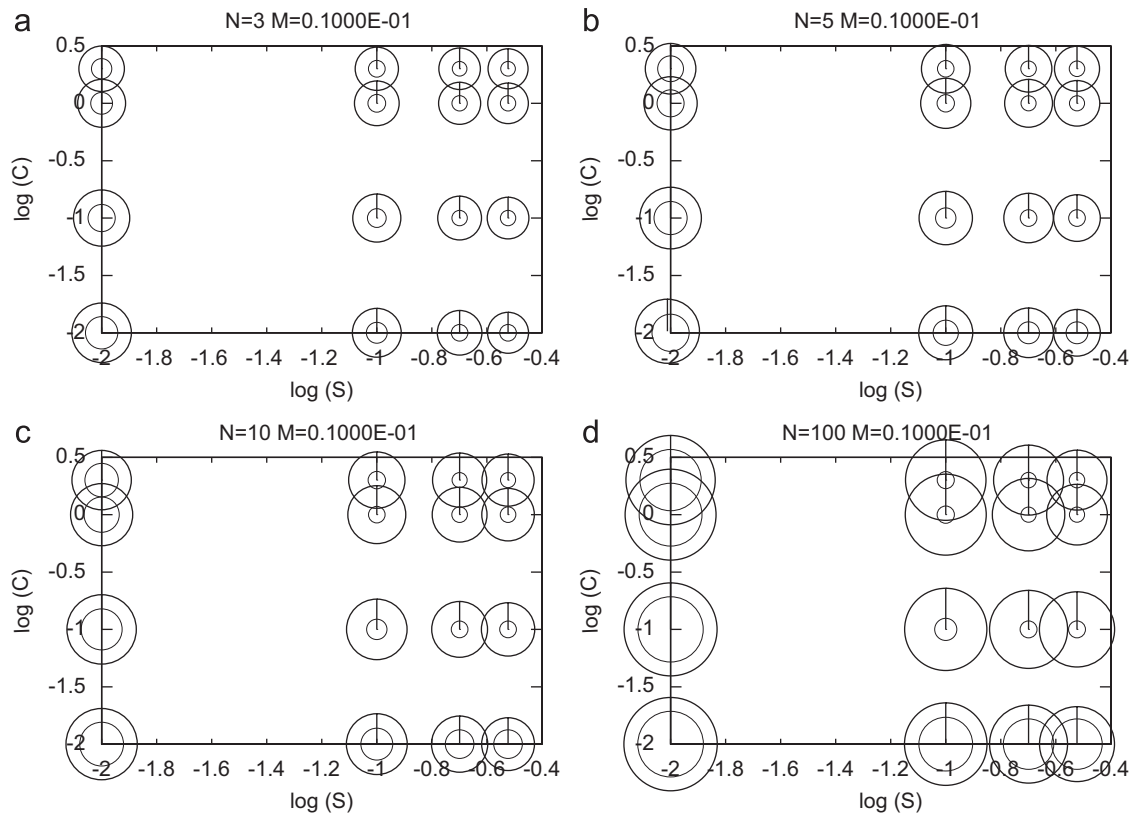


Fig. 6. Four plots of $\log(n_{eq})$ for $\log(S)$ (X axis), $\log(C)$ (Y axis) and P (full dots for $P=10$, empty dots for $P=1000$). The size of each dot is proportional to $\log(n_{eq})$. The four plots differ in the N value used, increasing from top left to bottom right. For reference n_{eq} is 53021 in the last plot at $\log(S)=-2$ and $\log(C)=-2$ when $P=1000$.

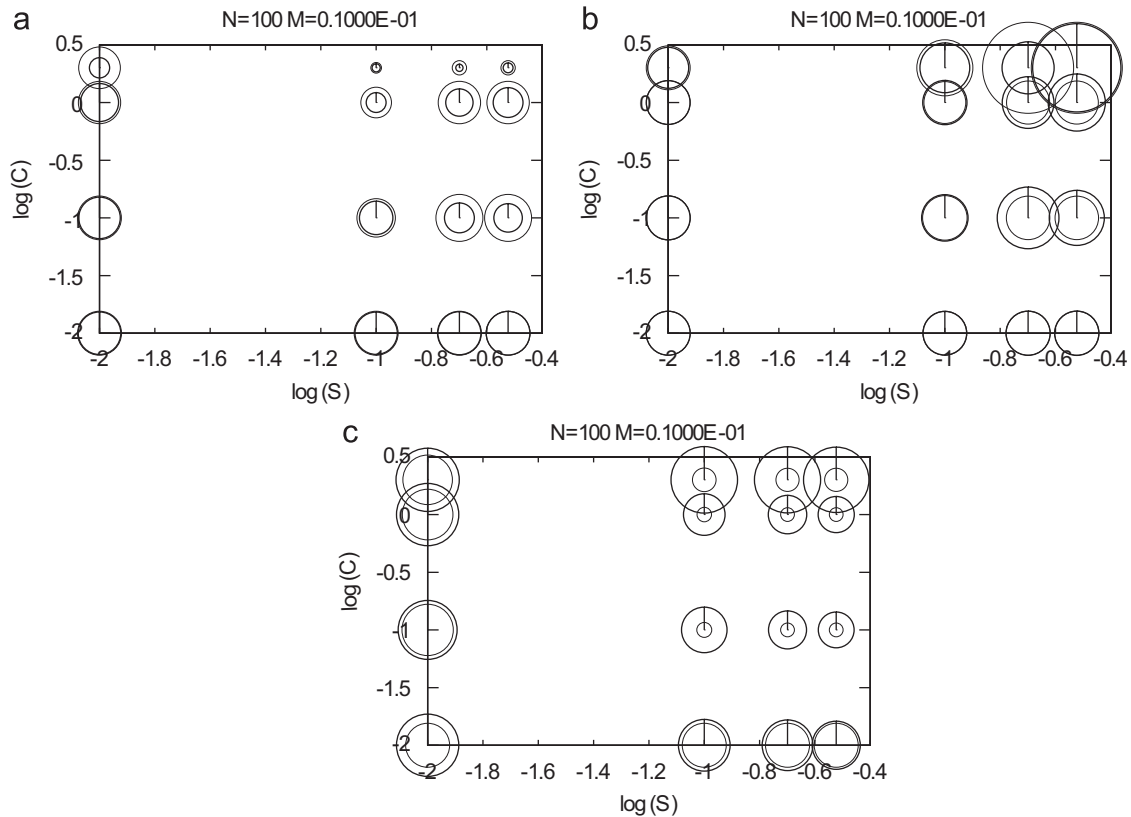


Fig. 7. Communication-enhanced innovation model. Three plots: (a) $\langle f \rangle / \langle g \rangle$, (b) $\langle f \rangle$ and (c) $\log(n_{eq})$ for the Communication-enhanced innovation model. In all plots the axis are $\log(S)$ (X axis), $\log(C)$ (Y axis) and P (full dots for $P=10$, empty dots for $P=1000$). The size of each dot is proportional to $\langle f \rangle / \langle g \rangle$ in (a), to $\langle f \rangle$ in (b) and $\log(n_{eq})$ in (c). The same value of N , M and A ($A=0.1$) are used in each plot. The reference sizes of each dot are as in previous figures.

(in comparison with the basic model). For the basic model this quotient is close to 1 except when S and C are large. This model exhibits a larger quotient, especially for small C values. Fig. 10 shows some examples of how n_{eq} increases with P (while keeping the rest of the parameters constant at an arbitrary set of values).

The difference between these two models is a consequence of the larger number of communication partners existing at high P values for the model with communication partners increasing with P . Thus, even if P increases n_{eq} , C decreases it and leads to the convexity of n_{eq} growth with P .

7. Discussion

7.1. Cultural diversity and isolation

The results indicate that in most models the amount of communication enhances evolution at the idea's level. This can lead to the extreme case (as seen in Fig. 3) where no adaptation occurs at the individual's level. Even in the communication-enhanced innovation model the overall pattern is that the increase C promotes adaptation at the idea's level and, mostly, precludes adaptation at the individual's level. S has exactly the opposite effect: promoting adaptation at the individual's level and not at the idea's level. P and N count as the population size at each of these levels and S and C as the selection pressures at each level. In some sense, the basic model can be regarded as a meta-population model with P meta-populations of size N and a selection pressure (S) acting on the meta-population as a whole (the individual) and a flux (C) of individuals between meta-populations. This C is effectively also a within meta-population selective pressure because the number of

individuals in a meta-population is fixed. However, this model is not a totally symmetric two level nested mutation-selection asexual model and, as it will be discussed later, this has relevant consequences for cultural evolution. First, the fitness of individuals is a sum of the fitness contributions of their cultural traits while the idea's level fitnesses of cultural traits is not the sum (or any other function) of any underlying entities. In addition, each individual can only have a single copy of any one idea. Our understanding of brain functioning is not good enough to ascertain that this is actually the case. If the model would not be implemented like that it could easily happen that a single idea takes over all the "head" space (of N ideas) of one or multiple individuals. The existence of single-idea persons does not seem very tenable.

It is generally accepted that in human history there has been an increase in population, population density and in the transportation of persons, objects and ideas. As mentioned in Section 1 there is also a substantial evidence of an increase in accumulated knowledge and diversity. It is clear that at least in technology the amount and diversity of devices has increased over time (Basalla, 1989). This could indicate that either the increase in the amount of population or the increase in the flux of ideas, or both, helped in the apparent increase in cultural diversity observed. However, this model indicates that the two latter options are very unlikely. The amount of interchange of ideas, that in the model is approximated by C the amount of communication, has a strong effect in reducing cultural diversity. This is the case even if innovation arises as a consequence of communication (unless P is as small as 10 individuals).

The model indicates that populations have a higher overall cultural diversity if they are isolated from each other.

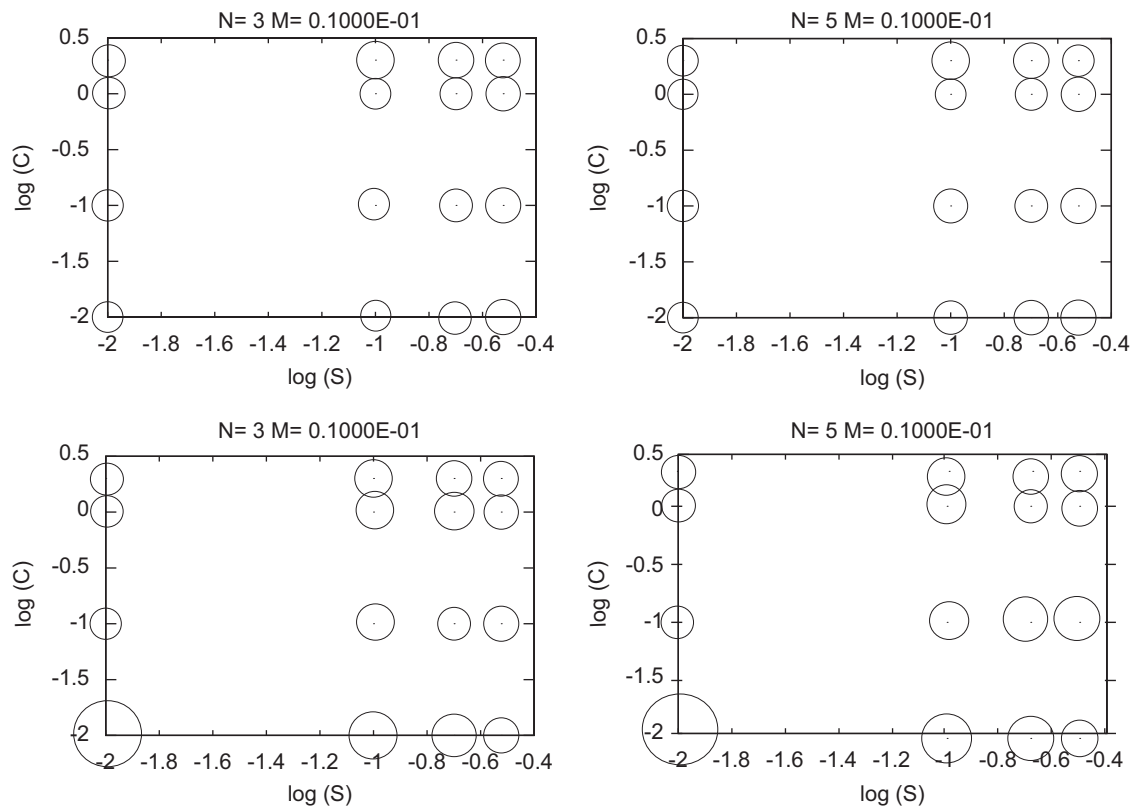


Fig. 9. Model with communication partners increasing with P . The upper two plots are for the basic model and the lower two for the mode with communication partners increasing with P . The plots show the value of the quotient between the sum of the rates of growth of n_{eq} for low P (between $P=10$ and $P=100$ and $P=100$ and $P=250$) and the sum of the rates of growth of n_{eq} for high P (between $P=500$ and $P=750$ and between $P=750$ and $P=1000$). For reference the quotient is 1 in the upper left plot at $\log(S)=-2$ and $\log(C)=-2$.

7.2. Communication evolutionary catastrophe

If communication leads to a decrease in cultural diversity because it exposes less fit ideas to more fit ideas then communication should increase fitness. Section 3 shows that this is indeed the case for idea's level fitness but, except for a few exceptions, not for individual's level fitness. In fact, excessive communication (i.e. excessive meaning as low as each individual communicating one idea to another individual per generation, see Fig. 3) can lead to no adaptation at the individual's level. This implies that as the amount of communication increases cultural evolution tends to happen at a level that does not improve the adaptation of individuals to their environment. This possibility will be called in this article a communication evolutionary catastrophe. If, as suggested, the amount of communication partners increases with P and the trend in increasing P remains, then the world population would be facing towards this communication evolutionary catastrophe. There are several factors not considered in the model that can mitigate or enhance this catastrophe.

7.3. Number of communication partners and time per communication event

A critical factor is what makes a cultural trait to have a high fitness at the individual and idea's level. This is clearly a complex issue not currently well understood and there are several possible

factors that may contribute to it. One of them, possibly a quite general one, is simplicity. Ideas that are easy to understand are more likely to be transmittable. If, as population grows the number of communication partners increases and the time spent per communication event decreases (as suggested), then simple cultural traits would spread much faster than complex cultural traits. In a complex social and physical environment it is possible that the cultural traits that are adaptive at the individual level are not simple. Even if that would not be the case, an increase in the number of communication partners and a decrease in the time per communication event are likely to facilitate the above explained communication catastrophe.

7.4. The evolution of N

The results show that this communication catastrophe is more likely to take place when N is large because then the contribution of each cultural trait to an individual biological fitness is smaller. This is especially the case when biological fitness is determined by the sum of the fitness contribution of several (N) cultural traits, as in the present model. $F(i)$ could be determined by a function different than [1] but, in general, as the number of cultural traits determining the biological fitness in an individual increases one can expect that the average importance of each cultural traits decreases. Over history there has probably been an increase of the effective N of individuals because technologies such as writing allow individuals to effectively remember more cultural traits. If technology is expected to further increase this effective N over time, as it has done in the past (for example with the invention of writing), then the chances of reaching this communication catastrophe increase.

Note that according to the present model, variation in N between individuals would lead to an increase on the average N in

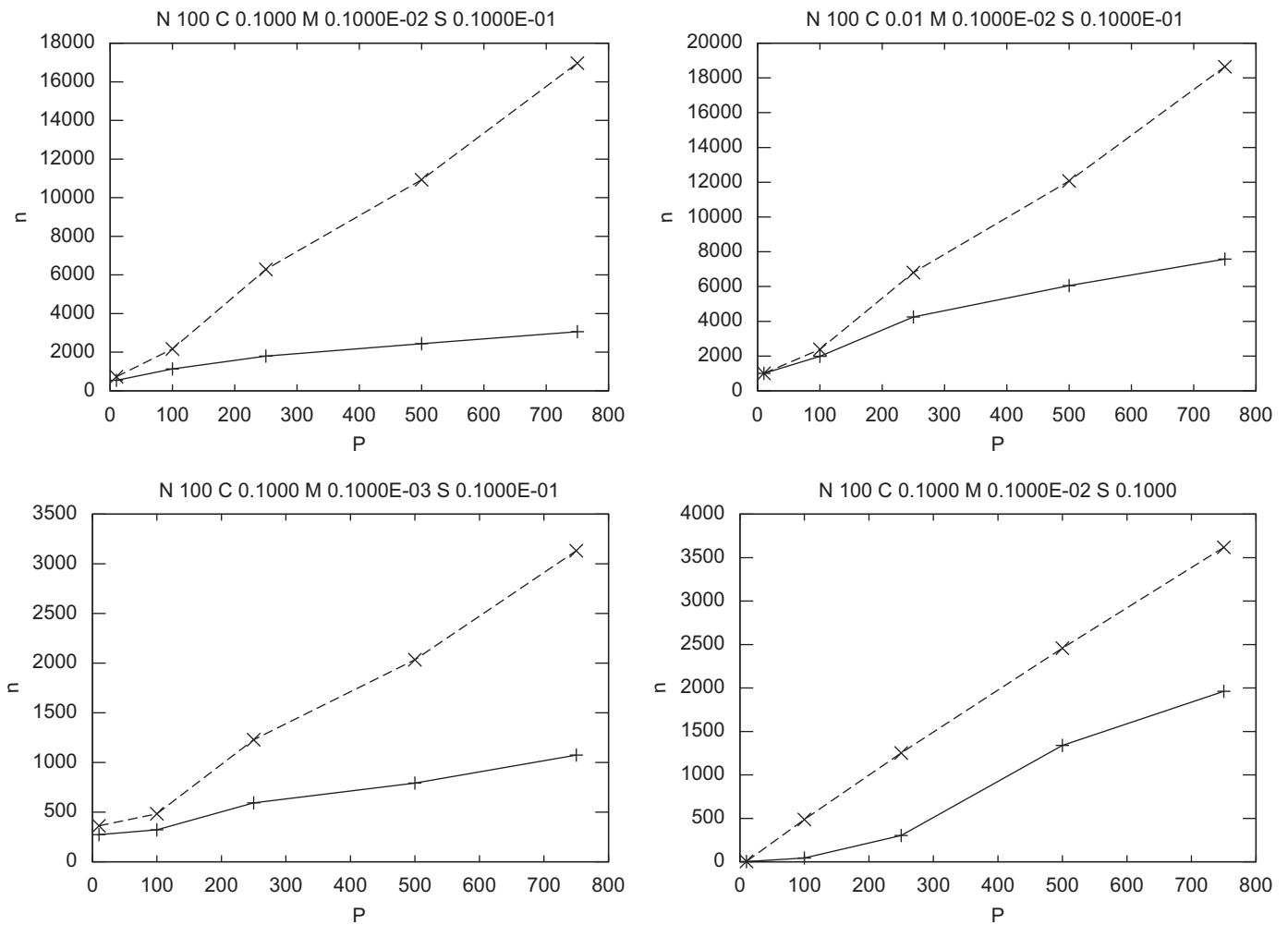


Fig. 10. This figure shows four example plots of the different cultural diversity allowed by the basic model (dashed line) and the model with communication partners increasing with P (solid line). The parameter values used are indicated in the top of each plot. As it can be seen the basic model exhibits higher cultural diversity. Moreover, in model with communication partners increasing with P the rate of increase of cultural diversity with P decreases for large values of P .

the population (simply because a larger N allows for a larger $F(i)$), implying that even without technology the catastrophe could be reached (except for neurobiological constraints in the value of N).

7.5. The effect of cognition

The model assumes that individuals have no cognitive capacity to discriminate the cultural traits according to their individual level fitness contribution. It is an open question to which extent or in which proportion individuals can choose to acquire one trait or another according to the individual's level fitness contribution of those. There are many documented cases of cultural traits that have not been adopted in spite of their high individual level fitness (Basalla, 1989). The reasons for that seem to be complex and manifold (i.e. the difficulty to estimate the utility of a cultural trait by either the individuals or the researchers studying them). It is clear, however, that improving the capacity of individuals to assess the fitness contribution of specific traits would delay, or even prevent, reaching the communication catastrophe.

7.6. Initial conditions and early cultural evolution

The initial conditions given to the model represent the situation in which individuals live in an environment where the

number of available cultural traits is much larger than the number of different cultural traits that an individual could possibly have. This is possibly a good approximation for most current human populations and for many historical ones. Cultural evolution in small isolated current populations or in early human evolution might have started with much fewer cultural traits. In the model, this would imply that individuals will have less than N different cultural traits in the simulation's initial condition. However, the dynamics arising from this kind of initial conditions are, likely, reducible to the ones arising from the initial conditions discussed in this article. From these initial conditions the model would lead to an early increase in cultural diversity and in the number of cultural traits per individual. This trend will last until that number equals N . This is because, in the model, communication does not lead to replacement between cultural traits in an individual's memory if such an individual has less than N cultural traits. As mentioned, N represents the number of cultural traits an individual can have. Cultural traits compete for that "space" and reach that space through communication. In other words, only when an individual has N cultural traits there is chance for competition (and only then one can define an idea's level fitness). In any other situation an individual exposed to a new cultural trait will simply acquire it. Moreover, in this situation an individual fitness will, on average, increase with the number of cultural traits he/she has (as can be seen from Eq. (1)).

7.7. Interdependences between cultural traits

The basic model assumes that the idea's level fitness of a cultural trait does not depend on the other cultural traits present in an individual. The cultural trait interdependence model assumes, on the contrary, that cultural traits do not have an intrinsic idea's level fitness but that their chances of being acquired depend on the cultural traits already present in each individual. In that latter model the results show that communication catastrophes are rare. Instead there tends to be cultural evolution at both levels. Since in this model the modes of interaction between cultural traits are chosen at random, these results are only valid for the bulk of interaction modes and it does not preclude that some specific ways of interaction between cultural traits lead to communication catastrophes.

It is not currently possible to estimate which of those two models reflects reality more accurately. Most likely some cultural traits have an idea's level fitness but this one is dependent, to some extent, on other cultural traits present in the individual to which this cultural trait is communicated. This may preclude a complete communication catastrophe.

The model presented in here assumes that any cultural trait can replace any other one in an individual. In reality it is more likely that there is a large number of idea types in the brain within which ideas can replace each other but between which replacements are more unlikely. Thus, for example a catchy song can replace another existing catchy song in the preferences of an individual but this catchy song is more unlikely to be replaced by a preference for blond women or for countries whose name starts with "S" (unless the catchy song is from a Swedish blond). Ultimately, at any given moment an individual is only thinking or paying attention to a small proportion of the ideas he or she bears and eventually the ideas that never get into an individual's attention are forgotten. This can impose some degree of all-against-all competition. A more realistic model would consider a set of different areas of the memory (with different N values) with possible but unlikely transmission between them. From this perspective the present model can be interpreted as considering only the evolution of a given category of cultural traits. As far as these categories are largely independent the model could apply to each different category. However, this suggests that the communication catastrophe may happen only on some of these categories (for example in those categories with a less important contribution to the individual's level fitness).

7.8. Tests

The above predictions could be tested by checking in different societies whether $\langle f \rangle$ and cultural diversity have decreased when, over time, population and/or communication has increased. There are, of course, a number of technical problems. First it is very difficult to estimate the f of a cultural trait. This should be easier in small societies with simple technologies and simple environments (ideally in the most isolated forager groups). Second, there is no absolute way to measure cultural diversity, although there are several possible proxies (Lehman, 1947; Eerkens and Lipo, 2005). Then there is the above-mentioned fact that in specific societies cultural trait fitnesses and diversity may be subject to many specific factors not considered in this model. The model should therefore be useful as it provides a null-hypothesis about how fitnesses and diversity should behave when none of these specific factors are in action (then departures from the model would indicate that there is something more going on) or when many different societies are considered (under the expectation that these more specific factors may on average cancel each other).

7.9. Accumulated knowledge

The above results suggest that the exponential increase in accumulated knowledge, for which cultural diversity would be a proxy, recorded by Lehman (1947) is not a consequence of cultural diversity increasing exponentially with P . This is not due, either, to a linear increase in N over time since N increases cultural diversity linearly. In fact, this model suggests that it is not possible to exponentially increase accumulated knowledge unless P and/or N increase exponentially.

It is also important to consider that there are many exceptions to these general trends. Some of these exceptions can last for a long time. A classical and often cited example (Russo, 2004) is the decline in accumulated knowledge in the societies in the Mediterranean region accompanying the decline of the Roman empire and the high middle ages. This was accompanied by either a population decline or redistribution from dense cities to less dense rural areas. The collapse of the Aztec societies has also been suggested to lead to a decrease in accumulated knowledge and population density (Demarest, 2004). Studies by Henrich (2004) suggest that the Tasmanian aboriginal lost, over the 10,000 years they were separated from the main land Australian aboriginals, a large number of cultural traits. Some of them were likely adaptive. Many forager societies kept fluctuating for centuries around low population densities and relatively low accumulated knowledge (Kelly, 2007). Also cultural traits of presumably high adaptive value for individuals have been lost several times independently in small populations (pottery, bows and arrows, canoes in several Polynesian islands) or more rarely in larger populations (fire weapons in 17th century Japan (Perrin, 1979)). In the case of the Tasmanian and Polynesian islands it has been suggested (Rivers, 1926; Henrich, 2004) that their small population sizes increased the chances that the bearers of specific cultural traits died before passing their knowledge. Many, although not all, of these examples still suggest that there may be some connection between population size and cultural diversity.

Another possibility is that N is always much larger than n_{eq} , then an exponential growth of accumulated knowledge is possible if previous knowledge in each generation is used to produce new knowledge in the next generation. For example in the form

$$\frac{\partial n(t)}{\partial t} = inP - dn/P \quad (4)$$

where P is the population size, n is the number of cultural traits, d is the decaying rate of cultural traits and i is the innovation rate by which individuals produce new cultural traits on the bases of existing ones. This equation can be solved as

$$n(t) = C \exp^{(P^2i-d)t} \quad (5)$$

Thus, as long as P^2i is larger than d , accumulated knowledge will grow exponentially without requiring genetic co-evolution as suggested previously (Enquist et al., 2008) (even without population growth). In that scenario, however, an exponential growth of n will inevitably lead to a situation where N is no longer much larger than n . From that perspective the observed exponential growth of accumulated knowledge may actually be the initial phase of a sigmoid growth (when $n > N$).

Another possibility is that the reasons of this exponential growth have to be searched, precisely, in what is left out of the model. That is the "content", nature or meaning of the different cultural traits. Thus, for example, it can be that new discoveries or knowledge open the door to ask or address more and more questions (thus leading eventually to an exponential growth in accumulated knowledge). Unfortunately, this kind of issues cannot be addressed from this model.

However, it is also possible that at a larger scale, when considering large number of different societies (and even if cultural diversity depends on specific processes in specific times) there is a general connection between population size and cultural diversity. This article suggests that this relationship could partly be understood, generically, from population genetics-like models. The specific outcomes of those would be affected by the population and idea's level variables considered in the model presented in this article as well as by case-to-case specific historical, psychological and sociological factors that are too complex to be considered in this model. Even if the assumptions in this article turn out to be too simplistic to be valuable for any specific society it can still be taken as a null model to be contrasted with more complex situations (analogously to how it was with the Hardy–Weinberg, Weinberg (1908) original model).

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