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# Genealogies and ages of cultural traits: An application of the theory of duality to the research on cultural evolution

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## HIGHLIGHTS

- An ancestral process is described to simulate the genealogy of a cultural trait.
- This ancestral process is dual to a forward-time process of cultural evolution.
- Metrics potentially useful for inferring ages of traits are defined.
- Limiting processes are derived for approximate computation of the metrics.
- Critical behaviors of the metrics are explained in terms of phase transition theory.

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## ABSTRACT

A finite-population, discrete-generation model of cultural evolution is described, in which multiple discrete traits are transmitted independently. In this model, each newborn may inherit a trait from multiple cultural parents. Transmission fails with a positive probability unlike in population genetics. An ancestral process simulating the cultural genealogy of a sample of individuals is derived for this model. This ancestral process, denoted by  $\mathcal{M}_-$ , is shown to be dual to a process  $\mathcal{M}_+$  describing the change in the frequency of a trait. The age–frequency spectrum is defined as a two-dimensional array whose  $(i, k)$  element is the expected number of distinct cultural traits introduced  $k$  generations ago and now carried by  $i$  individuals in a sample of a particular size  $n$ . Numerical calculations reveal that the age–frequency spectrum and related metrics undergo a critical transition from a phase with a moderate number of young, rare traits to a phase with numerous very old, common traits when the expected number of cultural parents per individual exceeds one. It is shown that  $\mathcal{M}_+$  and  $\mathcal{M}_-$  converge to branching or deterministic processes, depending on the way population size tends to infinity, and these limiting processes bear some duality relationships. The critical behavior of the original processes  $\mathcal{M}_+$  and  $\mathcal{M}_-$  is explained in terms of a phase transition of the branching processes. Using the results of the limiting processes in combination, we derive analytical formulae that well approximate the age–frequency spectrum and also other metrics.

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## 1. Introduction

An ultimate goal of research on cultural evolution is to understand observed trait distributions in terms of past cultural dynamics. There is a growing body of the literature showing the usefulness of phylogenetic approaches for inferring past events from cultural data sets (Gray and Jordan, 2000; O'Brien et al., 2001; Holden and Mace, 2003; Fortunato et al., 2006). Most of these

studies, however, concern histories on the scale of populations, while very few are about cultural genealogies on the scale of individuals. On the other hand, a number of mathematical models were developed to study how cultural changes accumulate over time in a population (Strimling et al., 2009; Lehmann et al., 2011; Aoki et al., 2011; Fogarty et al., 2015), but virtually none of them are aimed at inference of past events. This status of research on cultural evolution contrasts starkly with that of population genetics, in which coalescent theory has flourished (Wakeley, 2009). Thus, the theory of cultural evolution is far behind population genetics in terms of genealogical studies.

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However, [Aguilar and Ghirlanda \(2015\)](#) have recently made a landmark contribution by studying a continuous-time ancestral process which simulates the cultural genealogy of a trait. Their goal was to compute the expected time to the most recent unique ancestor (MRUA) of a sample, a concept analogous to the time to the most recent common ancestor (MRCA) in population genetics ([Aguilar and Ghirlanda, 2015](#)). This attempt is obviously desirable, potentially opening up a new area of research. However, they did not show formal duality between their backward-time process and a corresponding forward-time process. The notion of duality has been developed to establish a formal connection between two related Markov processes and applied to a variety of fields, in particular the theory of interacting particles ([Liggett, 2005](#)). Duality has also been used in population genetics to formalize ancestral processes of a sample of genes. Specifically, diffusion models of allele frequency change are dual to retrospective branching-coalescing processes ([Shiga and Uchiyama, 1986](#); [Krone and Neuhauser, 1997](#); [Neuhauser and Krone, 1997](#); [Möhle, 1999](#); [Athreya and Swart, 2005](#); [Mano, 2009](#)); a basic example is the duality between Kimura's diffusion model ([Kimura, 1955](#)) and Kingman's coalescent ([Kingman, 1982](#)). Duality reveals often non-intuitive connections between processes and allows results from one process to be used for another. It can be useful in research on cultural evolution as well if formal theories are developed for models of cultural transmission, which often differ from population genetic ones in essential properties.

In the present study, we derive forward- and backward-time processes of cultural evolution and establish a formal duality relationship between them. Our major goal is to demonstrate the usefulness of duality in the research on cultural evolution through its application to problems concerning genealogies and ages of cultural traits. How old can cultural traits found in a sample of individuals be and how do their ages depend on the rate of cultural transmission and intensity of social connection? The present study aims to provide a first step to tackle these intriguing and yet unexplored questions.

The remainder of the paper is structured as follows. In Section 2, we describe a discrete-generation model of cultural evolution in which multiple traits are independently transmitted from generation to generation by means of social learning. We derive an ancestral process which simulates the cultural genealogy of a trait carried by a sample of individuals and apply the theory of duality to establish its formal connection to a forward-time process. In Section 3, we compute some metrics which are potentially useful for inferring the ages of cultural traits in a sample of individuals. The central concept is the metric we call the age–frequency spectrum, which gives the numbers of distinct cultural traits in specific age–frequency classes found in a sample of individuals. Numerical calculations reveal that the age–frequency spectrum and related metrics undergo a critical transition from a phase with a moderate number of young, rare traits to a phase with numerous very old, common traits when the expected number of cultural parents per individual exceeds one.

In Section 4, we derive limiting processes in which population size tends to infinity; these processes allow us to interpret the critical behavior found in Section 3 in terms of phase transition theory. In Section 5, we show that some duality relationships hold between the limiting processes derived in Section 4. In Section 6, we use the limiting processes and their duality relationships obtained in Sections 4 and 5, respectively, to derive useful approximation formulae for the metrics under consideration. Finally, in Section 7, we summarize our results and discuss their implications. [Table 1](#) summarizes the major symbols used in this article.

Although we focus on a specific model of cultural transmission, our method is potentially applicable to other models as well. Thus, we hope that the present study provides a useful first step toward more general theory of cultural genealogies.

## 2. Model

### 2.1. Basic setup

Imagine a population composed of a fixed number  $N$  of individuals. Each individual may possess an arbitrarily large (but finite) number of traits, which are transmitted culturally from one generation to the next through social learning. Generations are discrete. In generation renewal, each newborn (i.e. an individual in the next generation) is assigned  $K$  potential role models drawn at random from the parental generation. Each trait possessed by each potential role model is transmitted to the focal newborn with probability  $\beta$ . Note that a newborn may redundantly inherit the same trait from multiple role models, but even in this case the newborn acquires only a single copy of the focal trait. Different traits are transmitted independently of each other, so that the probability of a trait's being successfully transmitted is not affected by whether other traits are successfully transmitted or not. Note that this mode of transmission is slightly different from the “best-of- $K$ ” transmission described by [Fogarty et al. \(2015\)](#), in which, if at least one among the  $K$  role models has the trait, the newborn acquires it (no matter how many other role models have it) with probability  $\beta$ . When  $K = 1$ , the transmission mode reduces to that called random transmission by previous authors, for which many results are known (e.g. [Strimling et al., 2009](#); [Lehmann et al., 2011](#); [Fogarty et al., 2015](#)).

Each newborn also invents on average  $\mu$  novel traits through individual learning. Reinvention of the same trait never happens; therefore, once a trait goes extinct, it is lost from the population forever. In this respect our model is similar to the infinite-site model of mutation in population genetics ([Kimura, 1969](#)). We assume that the traits do not have any effect on the biological fitness of a bearer.

### 2.2. Forward process $\mathcal{M}_+$

Given the above model, we derive a Markov process  $\mathcal{M}_+$  describing the change in the frequency of a trait in the population. We call this the “forward process” as opposed to the “backward process”, a retrospective process derived in the next subsection. The state variable is the number of the individuals having the focal trait. Let  $\pi_{i,j}$  be the probability that the state changes from  $i$  to  $j$ . It is given by

$$\pi_{i,j} = \binom{N}{j} (1 - f(i))^j (f(i))^{N-j}, \quad (1)$$

where

$$f(i) = \sum_{m=0}^K \frac{\binom{i}{m} \binom{N-i}{K-m} (1 - \beta)^m}{\binom{N}{K}} = \sum_{m=0}^K \frac{\binom{i}{K-m} \binom{N-i}{m} (1 - \beta)^{K-m}}{\binom{N}{K}} \quad (2)$$

gives the probability that a newborn fails to acquire the focal trait. The summand in the first summation in Eq. (2) gives the probability that  $m$  among  $K$  role models have the focal trait and the newborn fails to learn the trait from all of them.

The probability generating function  $g_i^+(\theta)$  for the number of the copies of the focal trait in the next generation, given that it is  $i$  in the current generation, is given by

$$g_i^+(\theta) = \sum_{j=0}^N \pi_{i,j} \theta^j = (1 - (1 - f(i))(1 - \theta))^N. \quad (3)$$

We call  $g_i^+(\theta)$  the one-step probability generating function.

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