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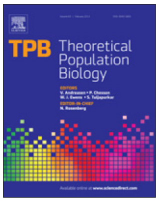

Invasion fitness for gene–culture co-evolution in family-structured populations and an application to cumulative culture under vertical transmission

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ABSTRACT

Human evolution depends on the co-evolution between genetically determined behaviors and socially transmitted information. Although vertical transmission of cultural information from parent to offspring is common in hominins, its effects on cumulative cultural evolution are not fully understood. Here, we investigate gene–culture co-evolution in a family-structured population by studying the invasion fitness of a mutant allele that influences a deterministic level of cultural information (e.g., amount of knowledge or skill) to which diploid carriers of the mutant are exposed in subsequent generations. We show that the selection gradient on such a mutant, and the concomitant level of cultural information it generates, can be evaluated analytically under the assumption that the cultural dynamic has a single attractor point, thereby making gene–culture co-evolution in family-structured populations with multi-generational effects mathematically tractable. We apply our result to study how genetically determined phenotypes of individual and social learning co-evolve with the level of adaptive information they generate under vertical transmission. We find that vertical transmission increases adaptive information due to kin selection effects, but when information is transmitted as efficiently between family members as between unrelated individuals, this increase is moderate in diploids. By contrast, we show that the way resource allocation into learning trades off with allocation into reproduction (the "learning-reproduction trade-off") significantly influences levels of adaptive information. We also show that vertical transmission prevents evolutionary branching and may therefore play a qualitative role in gene–culture co-evolutionary dynamics. More generally, our analysis of selection suggests that vertical transmission can significantly increase levels of adaptive information under the biologically plausible condition that information transmission between relatives is more efficient than between unrelated individuals.

0. Introduction

Cultural evolution, which is the change in non-genetically transmitted phenotypes (or information) carried by individuals in a population, is thought to have played a major role in human's ecological success (e.g., Laland et al., 2010; Boyd et al., 2011; van Schaik, 2016). Cultural evolution rests on mechanisms by which individuals learn and communicate, which themselves depend on behavior or cognitive rules that are at least partially genetically determined. Conversely, cultural evolution can significantly affect reproduction and survival, which in turn affects selection on genes determining behavior. Hominin evolution is therefore influenced by gene–culture co-evolution, whereby genetically determined behavior rules co-evolve along culturally transmitted information (Feldman and Cavalli-Sforza, 1976; Lumsden and Wilson, 1981; Aoki, 1986; Boyd and Richerson, 1985; Feldman and Laland, 1996; van Schaik, 2016).

It is useful to distinguish between two broad cognitive mechanisms that underlie cultural evolution. First, cultural evolution depends on individual learning (IL), which is a generic term for the cognitive processes that lead to the creation of *de novo* non-innate information by an individual, including trial-and-error learning, statistical inference, or insight (Boyd and Richerson, 1985; Rogers, 1988; Dugatkin, 2004; Aoki and Feldman, 2014; Wakano and Miura, 2014). Second, cultural evolution is underlain by social learning (SL), which refers to the cognitive processes that lead to the acquisition of non-innate information from others (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Rogers, 1988; Dugatkin, 2004; Aoki and Feldman, 2014; Wakano and Miura, 2014). If genes are almost always transmitted vertically from parent to offspring, cultural information can be acquired and transmitted in multiple ways via SL. It can be transmitted vertically from parent to offspring, but also horizontally from peer-to-peer,

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or obliquely between unrelated individuals belonging to different generations (Cavalli-Sforza and Feldman, 1981).

While IL results in the generation of novel information, SL enables the acquisition of skills or information that an individual would be unable to acquire alone by IL over the course of its lifetime. SL thus enables cumulative culture, which is a hallmark of cultural evolution in human populations (e.g., Boyd et al., 2011; van Schaik, 2016). A necessary but not sufficient condition for cumulative culture to occur in a population is that individuals use a composite learning strategy in which SL precedes IL (Boyd and Richerson, 1985; Enquist et al., 2007; Aoki et al., 2012).

Since both IL and SL strategies determine cultural evolution, much population work on gene–culture co-evolution has been devoted to understand the co-evolution between genetically determined IL and SL learning on one hand, and the amount of cultural information they generate in evolutionary stable population states on the other. This has led to a rich literature investigating the role of various factors, such as the type of cultural information, the regime of environmental change, or the structure of the population for the evolution of IL and SL and their impact on cumulative culture (e.g., Boyd and Richerson, 1985; Feldman et al., 1996; Wakano et al., 2004; Wakano and Aoki, 2006; Enquist et al., 2007; Rendell et al., 2010; Nakahashi, 2010; Aoki et al., 2012; Lehmann et al., 2013; Nakahashi, 2013; Aoki and Feldman, 2014; Wakano and Miura, 2014; Kobayashi et al., 2015; Ohtsuki et al., 2017).

The vast majority of such theoretical work has focused on horizontal and oblique transmission, assuming that information is transmitted independently from genotype via SL (i.e., between randomly sampled individuals in the population, from the same generation for horizontal transmission and different generations for oblique transmission). In this case, the fate of a mutant strategy, here a genetically determined phenotype affecting IL and SL, that arises as a single copy in a resident population can be studied under the assumption that the mutant is in a cultural environment determined only by the resident (i.e., "evolutionary invasion analysis"). In other words, SL among mutants is so rare that it can be neglected (no mutant–mutant interactions), which greatly simplifies mathematical analysis (see Metz, 2011 for general considerations on evolutionary invasion analysis and Aoki et al., 2012 for applications to cultural evolution).

When information is transmitted vertically via SL, however, non-random interactions occur between individuals as transmission occurs in a way that is correlated to genotype. As a result, transmission of cultural information among mutants can no longer be neglected and influences the fate of a mutant strategy. In other words, kin selection occurs (i.e., natural selection when individuals interact with others that are more likely to share a recent common ancestor than individuals sampled randomly from the population, Hamilton, 1964; Michod, 1982; Frank, 1998; Rousset, 2004; van Baalen, 2013; Lehmann et al., 2016). Intuitively, kin selection will favor learning strategies that promote the transmission of adaptive information since related individuals in downstream generations preferentially benefit from this information. This should influence cultural transmission from parent to offspring and hence the selection pressure on IL and SL, which will depend on multigenerational effects of genetically determined phenotypes.

Despite the potential importance of vertical transmission and its prominent role in cultural evolution theory (e.g., Cavalli-Sforza and Feldman, 1981; Feldman and Zhivotovsky, 1992; McElreath and Strimling, 2008), few studies have investigated the evolution of IL and SL and its effect on cumulative culture under vertical transmission. Models with vertical cultural transmission either do not allow for the transformation of cultural information by genetically determined phenotypes (and therefore do not allow to consider cumulative cultural evolution with multigenerational effects, e.g., Feldman and Zhivotovsky, 1992); or make specific assumptions on learning dynamics and the trade-off between resource allocation into learning and into reproduction (Kobayashi et al., 2015; Ohtsuki et al., 2017), from which it is difficult to get a broad view of the impact of vertical transmission on cultural evolution. The learning-reproduction trade-off, which reflects biologically realistic constraints between life-history components, can significantly compromise the accumulation of culture (Nakahashi, 2010; Lehmann et al., 2013; Wakano and Miura, 2014; Kobayashi et al., 2015; Ohtsuki et al., 2017). However, its general importance is not fully understood because most previous studies assume that the marginal cost of learning (i.e., the effect of learning on reproductive success holding everything else is constant), which influences the learning-reproduction trade-off, is constant (Lehmann et al., 2013; Wakano and Miura, 2014; Kobayashi et al., 2015; Ohtsuki et al., 2017, but see Nakahashi, 2010 for an exception).

The above considerations highlight that currently, there exists no framework to systematically carry out an evolutionary invasion analysis for gene–culture co-evolution under vertical transmission with multigenerational effects (i.e., gene–culture co-evolution family structured populations). Since a primary form of transmission of information in humans is vertical (Cavalli-Sforza and Feldman, 1981; Guglielmino et al., 1995; Hewlett et al., 2011; Konner, 2010), such a framework would be useful to understand cultural evolution. In particular, it would allow determining how the level of culture generated by evolving IL and SL departs under vertical transmission from oblique and horizontal transmission, and assess the importance of the learning-reproduction trade-off.

The aim of this paper is therefore two-fold: (1) develop a mathematical model to perform evolutionary invasion analysis for gene–culture co-evolution in a diploid family-structured population; and (2) study the effects of vertical transmission on the evolution of IL and SL and the concomitant level of adaptive information they generate. In the first part of this paper, we derive the invasion fitness of alleles in a diploid, family-structured population, when each individual carry cultural information, which can be a stock of knowledge, skill, or any other form of biotic or abiotic capital. The cultural information of an offspring depends deterministically on the cultural information in the parental generation, and therefore on transmission modes, but also on the alleles in the offspring and in the parental generation. In turn, cultural information in the population affect the reproductive success of individuals, resulting in eco-evolutionary feedbacks between genes and cultural information. Second, we apply our framework to the evolution of IL and SL strategies and the concomitant level of adaptive information they generate.

1. Gene–culture co-evolution in a family-structured population

1.1. Life-cycle

We consider a diploid monoecious population of large and constant size (large enough to neglect random genetic drift) that is structured into families, each founded by a mated individual. The discrete time life-cycle of this population is as follows. (1) Each individual produces offspring and then either survives or dies (independently of age so that there is no explicit age-structure). (2) Random mating among juveniles occurs and then each juvenile either survives or dies (possibly according to density-dependent competition) to make it to the next generation of adults.

Each individual carries a cultural information variable $\mathcal{E}$, which is possibly multidimensional and which can represent the total amount of knowledge or skill held by that individual at the stage of reproduction. The cultural information variable $\mathcal{E}$ is indirectly influenced by the genetic composition of the population and affects the survival of adults or juveniles, and/or individual fecundity.