Modeling Demic and Cultural Diffusion: An Introduction

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ABSTRACT

Identifying the processes by which human cultures spread across different populations is one of the most topical objectives shared among different fields of study. Seminal works have analyzed a variety of data and attempted to determine whether empirically observed patterns are the result of demic and/or cultural diffusion. This special issue collects articles exploring several themes (from modes of cultural transmission to drivers of dispersal mechanisms) and contexts (from the Neolithic in Europe to the spread of computer programming languages), which offer new insights that will augment the theoretical and empirical basis for the study of demic and cultural diffusion. In this introduction we outline the state of art in the modeling of these processes, briefly discuss the pros and cons of two of the most commonly used frameworks (equation-based models and agent-based models), and summarize the significance of each article in this special issue.

The remarkable adaptive capacity of our species is testified by the dispersal of early human communities and their colonization of a diverse range of environmental settings. This successful process is underpinned by the fact that human culture is cumulative and can rapidly spread among human populations located at large distances. The study of the diffusion of cultural traits is thus of great interest, forming the basis for understanding human cultural diversity and complexity.

Demic and Cultural Diffusion

A new cultural trait can spread by different combinations of the following three processes: *demic diffusion*, the spread of human communities carrying the new trait; *cultural diffusion*, the spread of the cultural trait through social learning (without a concurrent substantial population movement); and *local innovation*, the independent invention of the same new trait by communities at different locations. The three processes are also pivotal to one of the most intriguing questions shared by a variety of disciplines (including but not limited to anthropology, genetics, archaeology, and linguistics): whether observed cultural similarities between different geographic regions are the result of shared ancestry and demic diffusion, cultural diffusion, or convergent adaptation to similar selective pressures. These processes are deeply intertwined, are not mutually exclusive, and often exhibit (at least superficially) similar spatial structures of cultural

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diversity/similarity (Nunn et al. 2006; Crema et al. 2014).

Earlier studies by Ammerman and Cavalli-Sforza (1971) focused on a specific, seminal case study: the spread of farming in Europe. According to archaeological data, the oldest farming sites are located in the Near East and date to about 12,000 years BP. From there, agriculture and stockbreeding spread across Europe until about 5,000 years BP. Local convergent innovation is widely disregarded for this instance, as most of the wild varieties of the domesticated plants and animals are found only in the Near East (Smith 1995). Genetic studies further support this argument, as several lines of evidence suggest that almost all European domesticates have a Near Eastern origin (Troy et al. 2001; Morrell and Clegg 2007). However, the roles of demic and cultural diffusion in the expansion of these domesticates into Europe have been strongly debated during the last 50 years. Edmonson (1961) hypothesized that farming propagated by cultural diffusion. In contrast, Ammerman and Cavalli-Sforza (1971) advocated for an important role of demic diffusion in the spread of farming. They argued that demic diffusion will be most relevant in situations with marked differences in demographic pressure (Ammerman and Cavalli-Sforza 1973) and that early farming promoted population growth. Crucially, they predicted that such a process would lead to genetic clines but that (a) these will not form as a consequence of a total replacement of Mesolithic groups by Neolithic ones and that (b) mixing or interbreeding between individuals of the Neolithic and Mesolithic genetic types is required for the emergence of such a spatial pattern (Ammerman and Cavalli-Sforza 1971).

Albeit both genetic and cultural transmission can be framed within a Darwinian and population-oriented framework, they are characterized by different inheritance systems (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). Cultural transmission can follow three different forms: vertical, horizontal, and oblique (Cavalli-Sforza and Feldman 1981). *Vertical cultural transmission* closely resembles a genetic inheritance system, as cultural traits are transmitted from parent to offspring. In the case of spread of farming, vertical transmission results in cultural change in cases of interbreeding between agriculturalists and hunter-gatherers, as offspring will inevitable choose the trait of one of the two parents (in this case agriculturalists; see Cavalli-Sforza 1986, esp. 409–411; Bentley et al. 2009). *Horizontal transmission* includes any social learning within the same generation, whereas *oblique transmission* is nonparental but intergenerational. Compared to vertical transmission, horizontal and oblique transmissions can often provide faster means of diffusion. Both pathways can be many-to-one (i.e., multiple teachers, one learner) and one-to-many (i.e., single teacher, multiple learners), rather than injective (one-to-one or two-to-one) as in vertical cultural transmission. Thus, in the case of the spread of farming, agriculturalists can teach specific skill sets to hunter-gatherers of both the same (horizontal transmission) and subsequent generations (oblique transmission).

Under any of the three forms (or combinations of them), the Neolithic genetic type will eventually mix with the Mesolithic one. If the proportion of people with the Mesolithic genetic type involved was sufficiently high (relative to those with the Neolithic genetic type), interbreeding will have led to a genetic gradient or cline, with highest frequencies of the Neolithic genes at the origin of the farming expansion in the Near East. This cline will gradually disappear over time as a result of admixture, but it may be still observed if not too much time has elapsed (so that populations have not substantially mixed since the cline was formed). The prediction of genetic clines centered in the Near East by Ammerman and Cavalli-Sforza (1971) was impressively confirmed by Menozzi et al. (1978), who analyzed genetic data from modern Europeans. Although other processes (e.g., the spread of modern humans) may have also played a role in the formation of some of those observed clines, the Neolithic spread is considered as an important cause (Barbujani 2013; Rasteiro and Chikhi 2013).

Ammerman and Cavalli-Sforza (1973) calculated the farming spread rate using Fisher's wave-of-advance mathematical model, which assumes a purely demic process. This has sometimes led to the wrong impression that the authors advocated for purely demic diffusion. On the contrary, they pointed out that demic and cultural diffusion are not mutually exclusive and that their relative importance was probably not the same across Europe (Ammerman and Cavalli-Sforza 1984). Recently, cultural transmission theory has been incorporated to extend demic wave-of-advance models in order to include cultural as well as demic diffusion (Fort 2012). This new demic-cultural theory has been used to estimate the relative importance of demic and cultural diffusion in different regions of Europe (Fort 2015; see the cover figure of this special issue).

Paralleling these studies that seek to assess the relative contribution of demic and cultural diffusion, an independent research agenda targeting the cultural and demic components separately has flourished during the last three decades. Cultural evolutionary studies, with early works inspired from population genetics (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), have matured into a cross-disciplinary field with a rich tradition in both theoretical and empirical studies (for a review, see Mesoudi 2011). The population-level consequences of a variety of transmission modes—ranging from simple random cultural drifts to more intricate context-biased (i.e., frequency- and model-based) and content-biased transmissions (e.g., functional, aesthetic)—have been first predicted mathematically and then examined against a variety of data, from the diffusion of crop types (Henrich 2001), to baby names (Bentley et al. 2004) and pottery decoration (e.g., Kandler and Shennan 2013). Other studies have contributed to a broader research agenda from slightly different standpoints, for instance, looking at the effect of convergent adaptation in relation to cultural inheritance (e.g., Beheim and Bell 2011) or using linguistic data and graph theory to discern vertical and horizontal transmission (Towner et al. 2012).

Studies dealing with the demic diffusion component also gradually grew with, for example, (a) reaction-diffusion equations with a time delay linked to the generation time (Fort and Méndez 1999); (b) a distribution of delay times (Vlad and Ross 2002); (c) advection due to nonisotropic dispersal (Davison et al. 2006); (d) cohabitation equations that further improve the description of the effect of the time interval during which offspring live with their parents (Fort et al. 2007); and (e) reaction-dispersal equations with a set of dispersal distances and probabilities (Isern et al. 2008), which are more precise that their second-order approximations (these approximations are usually called reaction-diffusion equations; for an excellent review on their applications to human dispersals, see Steele 2009). For some detailed comparisons between reaction-dispersal and reaction-diffusion equations, see Fort (2015: Section S5).

Purely demic diffusion models have been used to simulate the "out of Africa" dispersal of modern humans (Mithen and Reed 2002; Hughes et al. 2007) and the cline of genetic diversity that is expected by this process (Ramachandran et al. 2005). Demic diffusion theory has also been applied to understand the geographical rates of spread of postglacial recolonizations (Fort et al. 2004) and the initial Paleoindian occupation of America (Hamilton and Buchanan 2007). Purely demic analyses also include the role of waterways in the spread of human populations (Davison et al. 2006; Silva and Steele 2014), the evolution of Neolithic cultural diversity (Pérez-Losada and Fort 2011), the spread of Bantu populations (Russell et al. 2014), the geographical origins of rice cultivation in Asia (Silva et al. 2015), and the effect of topography and climate on the spread of farming (Bernabeu et al. 2015), among others.

Language competition is an important phenomenon involving both demic and cultural diffusion. The purely cultural model proposed by Abrams and Strogatz (2003) was extended through the inclusion of a demic component by Patriarca and coworkers (Patriarca and Leppänen 2004; Patriarca and Heinsalu 2009). Kandler and coworkers (Kandler 2009; Kandler et al. 2010) considered bilingual speakers as a third population and applied a demic-cultural model to the dynamics of Britain's Celtic languages. For a review on such models, see Solé et al. (2010). More recently, Isern and Fort (2014) pointed out some limitations of the original model by Abrams and Strogatz (2003) and its extensions, and introduced an alternative language-competition model with demic diffusion. This model was applied to predict the replacement speed of the Welsh language, yielding a speed consistent with the observed one.

Demic-cultural models have also been applied to simulate genetic clines (Rendine et al. 1986; Aoki et al. 1996; Currat and Excoffier 2005) and the formation of cultural boundaries (Ackland et al. 2007), as well as to model the survival of hunter-gatherers in regions where environmental conditions do not favor farming (Patterson et al. 2010).

The mathematical foundations of cultural and demic studies have eased the integration of recent simulation techniques since the early 1990s. In particular, the development of agent-based simulation has exponentially increased possibilities offered by model-based research in the social sciences. On one hand, this led to the development of rich, "whole-society" models, which enabled the formalization and integration of multiple behavioral assumptions drawn from different theoretical backgrounds (for a review, see Lake 2013). While these studies have undoubtedly increased the level of realism, offering multiproxy comparison with the empirical data, in some cases the cost of increased complexity outweighed the benefit derived by the addition of extra parameters. On the other hand, these technical developments have also encouraged the study of detailed aspects of the agent model and how small differences at this scale can lead to drastically different patterns at the population level. Several authors have tackled both ends of the spectrum, from abstract theoretical models (e.g., Premo and Scholnick 2011; Crema et al. 2014; Wren et al. 2014) to more empirically grounded models aimed to study specific historical and geographic contexts of demic and cultural diffusion (e.g., Mithen and Reed 2002; Bernabeu et al. 2015).

Reaction-dispersal models are often used when dealing with demic and/or cultural front propagation. In contrast, agent-based models are applied to many other anthropological, biological, and archaeological challenges involving demic and cultural diffusion and other processes. In this context, it is useful to compare when reaction-dispersal models are preferable to agent-based models and vice versa. This aspect has been often overlooked, but it is very relevant to this special issue (see also the contribution by Romanowska). The next section deals with this aspect; readers not interested in this technical problem can move directly to the last section, which summarizes the articles collected in this special issue.

Reaction-Dispersal versus Agent-Based Models

In *agent-based models*, a set of rules describes the behavior of agents (i.e., dispersal, reproduction, etc.). If such rules are sufficiently simple, we can replace them with mathematical equations (such that the evolution of the system predicted by those equations is the same as those predicted by the rules of the agent-based model). For example, consider the rule "the net reproduction (births minus deaths) of agents is proportional to their population density p." This rule can be replaced by the equation $dp/dt = kp$, where t is the time and k is a constant.

If individuals move in space, the equations are usually called *reaction-dispersal equations* (these include reaction-diffusion equations; see previous section). Reaction-dispersal models cannot be used if the rules driving the behavior of agents are so complicated that it is not possible to determine a formula for computing the front speed. As an example, consider the Sugarscape model by Epstein and Axtell (1996) that was later modified to simulate the population dynamics of the Anasazi (Axtell et al. 2002). In this agent-based model, different points on a surface have different amounts of sugar. Each agent has a value for its metabolism and a value for its vision. The motion rules are as follows: "Each agent looks around as far as its vision permits, finds the spot with the most sugar, goes there, and eats the sugar. Every time an agent moves, it burns some sugar (according to its metabolic rate). Agents die if they burn up all their sugar." It does not seem possible to describe this model as an equation and determine the front speed under such complex rules. This example clearly shows the limitations of reaction-dispersal models, compared with agent-based models.

Nevertheless, reaction-dispersal models are preferable to agent-based models when the evolution equations are simple enough that it is possible to determine a formula for computing the front speed. This provides several advantages. First, it allows for a substantial reduction in the computation time. For example, consider a recent model of Neolithic spread on a homogeneous surface. Let (x, y) stand for the spatial coordinates and t for time. The rules are as follows: "Every generation, the following events take place: (a) every individual has a number of offspring equal to R_0, provided that the initial local population density $p(x, y, t)$ is below its saturation value $p_{\max}$ (but if the local population density $p(x, y, t)$ is equal or above $p_{\max}$, not all individuals have offspring and the offspring population density is equal to $p_{\max}$); (b) all parents die; and (c) each offspring stays at the same location with probability p_e (the so-called persistence) or jumps a distance r in a horizontal or vertical direction (with probability $(1-p_e)/4$)." These rules are simple enough to be written with mathematical equations (Fort et al. 2007):

$$p(x, y, t+T) = R[\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} p(x+\Delta_x, y+\Delta_y, t) \phi(\Delta_x, \Delta_y)\, d\Delta_x\, d\Delta_y] \tag{1}$$

where T is the generation time; we further introduce the reproduction function

$$R[p(x,y,t+T)] = \begin{cases} R_0 p(x,y,t) \text{ if } p(x,y,t) < p_{\max} \\ 0 \text{ if } p(x,y,t) > p_{\max} \end{cases}, \tag{2}$$

and $\phi(\Delta_x, \Delta_y)$, the dispersal probability to jump from location $(x+\Delta_x, y+\Delta_y)$ to location (x, y), is in this very simple case

$$\phi(\Delta_x, \Delta_y) = p_e\delta(\Delta) + (1-p_e)\delta(\Delta - r) \tag{3}$$

where $\Delta = \sqrt{(\Delta_x^2 + \Delta_y^2)}$ is the jump length and $\delta(\Delta - r)$ is a function that vanishes everywhere except at $\Delta = r$ (so that only jumps of length r are allowed in this simple model). For systems evolving according to these equations, the speed of front solutions has been shown to be (Fort et al. 2007)

$$c = \min_{\lambda>0} \frac{\ln\{R_0[p_e + (1-p_e)I_0(\lambda r)]\}}{T\lambda}, \tag{4}$$

where $I_0(\lambda r)$ is the modified Bessel function of the first kind and order zero. We can use this equation and numerical values of the parameters (R_0, p_e, r, and T) into a mathematical computer program (e.g., Mathematica or Matlab), plot the function in the right-hand site of Equation 4, and find its minimum (i.e., the front speed c) very quickly. But if we decide instead to write down and run an agent-based computer program, we will surely need more time to find the front speed c. This is the main advantage of reaction-dispersal models compared with agent-based models. As a consequence, a second advantage is that we are also able to directly and rapidly estimate the dependence of the front spee c to one or more parameters (R_0, p_e, r, and T)), a process that will, again, require substantial computational time with agent-based simulations.

In some cases, the advantage of reaction-dispersal models becomes further relevant when we can identify instances where we do not even need to assume parameter values or ranges to know the dependency of the front speed on the variables. For example, Fisher's model (for details, see Steele 2009) leads to the wave-of-advance speed $c = \sqrt{(aD)}$, which immediately shows how the speed c depends on the net reproduction rate a and diffusion coefficient D. Thus, the formula $c = \sqrt{(aD)}$ also shows that the front speed does not depend on the carrying capacity. Obviously, such a general conclusion cannot be reached using agent-based models, simply because it is impossible to run a simulation an infinite number of times.

However, as explained above, reaction-dispersal models are useful only for sufficiently simple agent rules. Moreover, they have the following two additional limitations:

1. *Nonhomogeneous surfaces:* If the spread takes place in nonhomogeneous surfaces, usually we cannot find a formula for the front speed. For example, Equation 4 is valid only for homogeneous surfaces. However, for nonhomogeneous surfaces we can perform numerical simulations using the same reaction-dispersal equations (not necessarily agent-based models). For example, the reaction-dispersal Equations 1–3 above have been applied by Fort et al. (2012) to take into account the effect of seas and mountains in the spread of farming in Europe. The difference between such simulations and agent-based models is that simulations of reaction-dispersal equations find the population density, whereas agent-based models follow the dispersal and movement of individual agents. If both approaches are valid, they will yield the same results for the variable that can be compared with empirical data (e.g., the wave-of-advance speed). Incidentally, in the case of homogeneous surfaces, reaction-dispersal simulations are useful to check the validity of the formula for the front speed [this was done, e.g., by Fort et al. (2007) for Equation 4].
2. Even for homogeneous surfaces, reaction-dispersal models are of little use if we are interested not exclusively in the front speed but also in analytical results for other variables. For example, it is seldom possible to find an

equation for a front profile, a genetic cline, and so forth. However, we can again use the same evolution equations (e.g., Equations 1–3, thus not necessarily agent-based models) to perform computer simulations and find results that cannot be obtained analytically (e.g., a numerical front profile).

The Special Issue Contributions

This volume offers a series of contributions that provide insightful considerations of some details and assumptions that are often uncritically used in models of demic and cultural diffusion, ranging from drivers of dispersal processes (Wren and Costopoulos) to different modes of transmission (Crema and Lake, Wilder and Kandler). Some of the works are purely theory-building exercises, while others focus on specific historical contexts, from hominid dispersals (Wren and Costopoulos, Romanowska) to Neolithic landscape productivity (Shukurov et al.) and the evolution of computer programming languages (Valverde and Solé).

The article by Romanowska offers a comprehensive introduction to the theory and practice of the computational modeling of demic diffusion. She carefully describes equation-based modeling, cellular automata, and agent-based modeling. Her article provides an extensive overview that can guide nonexperts and students, with highlights on key aspects of the modeling cycle. Although tailored to hominid dispersal models, the review is relevant to a broader readership with interest in computational modelling.

Wren and Costopoulos also consider hominid dispersal. They offer a detailed exercise of agent-based theory building in a system with demic diffusion. Their simulation study demonstrates that the degree of environmental knowledge (resulting from individual or social learning) and the specific pattern of resource distribution can strongly affect dispersal dynamics. Their results suggest that a high degree of knowledge can lead to a particular form of "tragedy of the commons" (Hardin 1968) where agents converge to the same spatial destination, leading to instances of local overcrowding. Their model is based on the assumption that agents find high-resource patches attractive even if such a crowding decreases the reproduction rate. As the authors suggest, empirical data could be used in future models to introduce more detailed mechanisms (e.g., the inhibition of the attraction of high-resource patches above some population-density threshold), possibly leading to a weaker reduction of dispersal due to environmental knowledge.

Crema and Lake also show how an increase in knowledge is not necessarily always beneficial. Their article questions how the size of the sample pool of social "teachers" and the uncertainty in the payoff attributed to a specific cultural trait can profoundly drive cultural evolution. In particular, their agent-based model demonstrates that certain types of social learning strategy (e.g., copy the individual with the highest payoff), when associated with a large pool of social teachers and high payoff uncertainty, can slow the rate by which beneficial traits (i.e., traits with higher payoff) spread within a population.

The article by Wilder and Kandler also tackles the topic of social learning, focusing on whether different forms of cultural transmission can generate discernable patterns in the frequency of cultural variants, given the limitations imposed by the temporal resolution in the observed data. Their results provide useful guidance on the conditions where this inferential exercise is possible, as well as a cautionary tale on how increasingly incomplete samples will decrease our capacity to distinguish one mode from another.

Shukurov and colleagues offer a detailed paleoeconomic reconstruction of premodern agriculture for a case study, the Neolithic-Eneolithic Cucuteni–Trypillia cultural unity (CTU; 5,400–2,700 BC) in Ukraine, Romania, and Moldova. Other case studies in the future can apply their methodology, and probably some of their parameter values (they obtain some of them from modern experimental farms in other regions). Their results suggest that farming settlements of a few thousand people are sustainable only if technological innovations, such as the ard for land tilling, are available. The lack of such technological innovation could explain the dominance of small and medium-sized settlements during the early CTU. The authors also explain the observed lifetimes of early CTU villages. The work by Shukurov et al. contains an impressive amount of data, of interest in models of the spread and consequent development of farming systems. Furthermore, similar studies for hunter-gather societies could be useful for comparing the advantages of farming and hunting-gathering in diverse ecological settings, which might lead to new insights on the relationship between the environment and the relative importance of demic and cultural diffusion.

Finally, the article by Valverde and Solé applies many of the concepts of cultural diffusion tackled by the other authors and examines the evolution of computer programming languages. Their work is not limited to historical trends. Indeed, they also develop a cellular-automaton model of software developers (with innovation, adoption or diffusion, and forgetting rules) that reproduces the empirical power law observed in the frequency-rank distribution in programming language popularity. Their model also predicts a substantial decline in language diversity.

An overall conclusion from the works gathered in this special issue is that there are still plenty of important problems to be solved by means of demic, cultural, and demic-cultural models, which deserve further theoretical development and application to new case studies.

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