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Modelling 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 amongst different fields of study. Seminal works have analysed 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 papers 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 modelling of these processes, briefly discuss the pros and cons of two of the most commonly used frameworks (i.e. equation-based models and agent-based models), and summarise the significance of each paper published in this special issue.

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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, cultural diffusion, and local innovation. Demic diffusion is the spread of human communities carrying the new trait; cultural diffusion is the spread of the cultural trait through social learning (without a concurrent substantial population movement); and local innovation is the independent invention of the same new trait by communities located at different places. 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), namely to infer whether observed cultural similarities between different geographic regions are the result of: 1) shared ancestry and demic diffusion; 2) cultural diffusion; or 3) convergent adaptation to similar selective pressures. These processes are deeply intertwined, not mutually exclusive, and often exhibit (at least superficially) similar spatial structures of cultural 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 dated at about 12,000 yr Before Present (BP). From there, agriculture and stockbreeding spread across Europe until about 5,000 yr 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) hypothesised 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: (i) these will not form as a consequence of a total replacement of Mesolithic groups by Neolithic ones; and that (ii) mixing or interbreeding between individuals of the Neolithic and Mesolithic *genetic* types are 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-thinking framework, they are characterised 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). The first one, vertical cultural transmission, resembles closely a genetic inheritance system, as cultural traits are transmitted from parent to offspring. In the case of spread of farming, vertical transmission results into cultural change in case of interbreeding between agriculturalists and hunter-gatherers, as offsprings will inevitable choose the trait of one of the two parents (in this case agriculturalists, see Cavalli-Sforza 1986; Bentley *et al.* 2009).. The second pathway, referred to as horizontal transmission, includes any social learning within the same generation while the third —generally referred to as oblique transmission— is non-parental but inter-generational. 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 being injective (one-to-one or two-to-one) as in vertical cultural transmission. Thus, in the case of the spread of farming, agriculturalists can both teach specific skill-sets to hunter-gatherers of the same (horizontal transmission) or 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

centred in the Near East by Ammerman and Cavalli-Sforza (1971) was impressively confirmed by Menozzi, Piazza and Cavalli-Sforza (1978), who analyzed genetic data from modern Europeans. Although other processes (such as 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 (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 were 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 in addition to 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; cover figure of this special issue).

In parallel to 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 (see Mesoudi 2011 for a review). The population-level consequences of a variety of transmission modes — ranging from simple random cultural drifts to more intricate context (i.e. frequency and model-based) and content biased transmissions (e.g. functional, aesthetic, etc.) — 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 2014). Other studies have contributed to a broader research agenda from slightly different standpoints, looking for instance 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: (i) reaction-diffusion equations with a time delay linked to the generation time (Fort and Méndez

1999); (ii) a distribution of delay times (Vlad and Ross 2002); (iii) advection due to non-isotropic dispersal (Davison *et al.* 2006); (iv) 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 (v) reaction-dispersal equations with a set of dispersal distances and probabilities (Isern *et al.* 2008), which are more precise than their second-order approximations (these approximations are usually called reaction-diffusion equations, see Steele 2009 for an excellent review on their applications to human dispersals). 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 re-colonisations (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), the effect of topography and climate on the spread of farming (Bernabeu *et al.* 2015), and 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 *et al.* (2004, 2009). Kandler and co-workers (2009, 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), the formation of cultural boundaries (Ackland *et al.* 2008), as well as to model the survival of hunter-gatherers in regions where environmental conditions do not favour farming (Patterson *et al.* 2010).

The mathematical foundations of cultural and demic studies have eased the integration of recent simulation techniques since the early 90s. 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 formalisation and integration of multiple behavioural assumptions drawn from different theoretical backgrounds (Lake 2013 for a review). While these studies have undoubtedly increased the level of realism, offering multi-proxy comparison to 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 (e.g. Mithen and Reed 2002, Bernabeu *et al.* 2015) of demic and cultural diffusion.

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 and readers not interested in this technical problem can move directly to the last section, which summarises the papers collected in this special issue.

Reaction-dispersal versus agent-based models

In agent-based models, a set of rules describes the behaviour 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 $\frac{dp}{dt} = kp$, 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 equation models cannot be used if the rules driving the behaviour of agents are so complicated that it is not possible to determine a formula for computing the front speed. As an example, consider the *Sugarspace* 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, as compared to agent-based models.

Nevertheless, reaction-dispersal models are preferable to agent-based models when the evolution equations are simple enough so that it is possible to determine a formula for computing the front speed. This provides several advantages. Firstly, this allows for a substantial reduction in the computation time. For example, let us 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: “Every generation, the following events take place: (i) every individual has a number of offspring equal to R_0 , provided that the 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 of above p_{max} , not all individuals have offspring and the new population density is equal to p_{max}); (ii) all parents die; and (iii) each offsprings 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, as follows (Fort *et al.* 2007)

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

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

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

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

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

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)

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

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 side of Eq. (4), and find out 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 out the front speed c . This is the main advantage of evolution-equation models, as compared to 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 speed 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 more 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 (see Steele 2009 for details) 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. Non-homogeneous surfaces. If the spread takes place in non-homogeneous surfaces, usually we cannot find out a formula for the front speed. For example, Eq. (4) is valid only for homogeneous surfaces. However, it is worth noting that for these 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. Both approaches will be valid if they yield the same results for the variable that can be compared to 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 Eq. (4)).

2. Even for homogeneous surfaces, reaction-dispersal models are of little use if we are not exclusively interested in the front speed, but also to other variables. For example, it is seldom possible to find an equation for a front profile, a genetic cline, etc. However, we can again use the same evolution equations [e.g., Eqs. (1)-(3)] to perform computer simulations (as explained in the previous paragraph) and find results that cannot be obtained analytically.

The special issue contributions

This volume offers a series of contributions that provide insightful considerations over 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, whilst other 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 paper by Romanowska offers a comprehensive introduction to the theory and practice of the computational modelling of demic diffusion. She carefully describes equation-based modelling, cellular automata, and agent-based modelling. Her paper provides an extensive overview that can guide non-experts and students, with highlights on key aspects of the

modelling 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 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 decrease 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 threshold for the population density), 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 paper 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 down the rate by which beneficial traits (i.e. traits with higher payoff) spread within a population.

The paper 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 palaeo-economic reconstruction of pre-modern agriculture for a case study, the Neolithic-Eneolithic Cucuteni-Trypillia cultural unity (5,400-2,700 BC) in Ukraine, Romania and Moldova. Other case studies can in the future 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 paper 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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