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“Agent-based models in social learning in nonhuman animals and opinion dynamics: a case study of evolutionary social science.”

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Abstract of article

Alex Mesoudi has argued that cultural evolution can provide a theoretical synthesis as well as a practical method for social science. Meanwhile, agent-based models, originally developed for social science applications, have seen increasing use in studies in cultural evolution. In this article, I test the validity of Mesoudi's claims in the specific case of opinion dynamics and social learning in nonhuman animals, both of which employ this type of models. This case study demonstrates possibilities for collaboration between the two fields, which are more mutual than is implied in arguments for understanding social phenomena in terms of cultural evolution concepts.

Agent-based models in social learning in nonhuman animals and opinion dynamics: a case study of evolutionary social science

Introduction

I own a 1979 Dutch translation of Auguste Comte's *Discours sur l'ésprit positive* (1844). In his introduction to the text, J.M.M. De Valk writes the following:

"Some sciences had made the positivist method their own by Comte's time, others hadn't yet. To explain this fact, Comte created a hierarchy of sciences. Ascending from mathematics via astronomy, physics, chemistry and biology, the object of study becomes more and more complicated, and the results less and less generally applicable. The last science in this sequence, and the summit of the sciences, is sociology. For the practice of each science, knowledge of the preceding is necessary, however it cannot be hereto reduced. Every science contains the principles of the foregoing, yet has, on top of that, its own specific object. This is why Comte resists the reduction of sociology to biology, something that in his time (and again in ours, in the so-called sociobiology) was in vogue. The representation of societal relations in mathematical formulas, too, is insufficient. It may not be incorrect, because mathematics enjoys universal validity; though what is gained hereby is but a shadowy picture of the social reality, because it is missing the essential" (Comte 1979, 16-17).

Writing in 1979, De Valk reminded readers that Comte's 19th century ideas were still relevant to a contemporary audience. Though the temptation is great to quantify social relations, and to translate the abstract notions of sociology into the more scientifically secured language of natural selection or physical determinism, both these tendencies will result in losing sight of what sociology describes. Considering that sociobiology, like social Darwinism, has since come to be understood as a mostly political ideology forcing a scientifically unsound view of human evolution on a backwards view of human society, De Valk's words of warning seem in retrospect to have been wise.

Today, according to some, there is a new contender for the title of a joint social and biological science: cultural evolution. Cultural evolution studies culture as the person-to-person transmission of cultural traits, such as skills and ideas. Over the course of the last four decades, cultural evolution has grown from applying population genetics models to culture, to a movement spanning among other disciplines psychology, anthropology, demography, linguistics, and zoology. The development is so great that we may be tempted to reconsider again the relationship between biological and social sciences.

Specifically, Alex Mesoudi's arguments, as set out in *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences*, will in this paper fulfill the role of defending such a reconsideration (Mesoudi 2011). Mesoudi argues that the theory of cultural evolution provides a unified way of understanding the methodologically and theoretically diverse social sciences, and in addition, that the formal models developed by cultural evolution may provide a scientific method for social science research.

The aim of this paper is to study these large-scale claims about the relationship between sciences at the level of actual scientific practice. To do so, I examine two fields, one in sociology and one in cultural evolution, that show a promising degree of similarity.

The sociological field is opinion dynamics. Opinion dynamics refers to formal models that simulate processes of consensus and polarization, by having populations of agents update opinion values based on interactions with other agents.

The cultural evolution field is the study of social learning in nonhuman animals. Social learning is the ability of individuals to learn from other individuals. Since cultural evolution is founded on studying the social transmission of information, this is a central concept in cultural evolution. The study of social learning in nonhuman animals, providing a rich body of comparative empirical evidence, has become a major part of the cultural evolution project.

I compare these specific fields because both of them have employed agent-based models to simulate their populations. Agent-based modeling is an approach to computer simulations created to generate complex outcomes by specifying simple rules of interactions between simple agents. This approach has proved useful for the fields examined here, both of which are concerned with the way social interactions between individuals drive population-level distributions and diffusions of behaviors and ideas.

The observations that agent-based models are shared across cultural evolution and opinion dynamics, and that models from cultural evolution may be written as agent-based, are not mine, but owed to cultural evolution minded researchers working on modelling social phenomena with cultural evolution techniques (Turner and Smaldino 2018; Mesoudi, Acerbi and Smolla 2020). Rather, my contribution is to develop the similarity between the fields in detail, and my interest is in what the comparison may teach us about the interaction between cultural evolution and social science.

So we have two comparable fields, one from a sociological and one from a biological discipline. The aim is to determine whether this sociological field may be better understood in terms of the biological one. Hence, my research question:

In the specific case of agent-based models in opinion dynamics and in social learning in nonhuman animals, does cultural evolution provide a method for studying social science?

Several things will have to be discussed before addressing this question. In the first section, I set up the theoretical context necessary to have this discussion. I explain the intention and basic concepts of cultural evolution, agent-based models, and opinion dynamics. I argue that agent-based models can be used to conceptualize both cultural evolution and opinion dynamics. Furthermore, I motivate the choice, amidst cultural evolution applications, for social learning in nonhuman animals.

In the second section, I examine models in both traditions in detail in order to establish what they can and cannot do. I do so by, for each of the two fields, discussing the concepts used in agent-based models, their fit with empirical evidence, and the major problems that face the models and their representation of reality.

In the third section, I draw conclusions from the foregoing. First, I summarize ways in which agent-based models can combine concepts from both fields. I argue for three specific ways in which such combinations may help address the problems discussed in the second section, and therefore contribute to a shared approach to culture. Second, I assess to what extent Mesoudi's claims apply to this case, and argue that the way forward for an evolutionary social science is not understanding opinion dynamics in terms of cultural evolution, but using the formal platform of agent-based models to incorporate sociological as well as biological concepts.

1. Context: cultural evolution, opinion dynamics, and their common formal framework

1.1. Cultural evolution and its claim on social science

1.1.1. What is cultural evolution?

The works generally agreed to be the foundation for cultural evolution modelling, those of Cavalli-Sforza and Feldman in 1981 and of Boyd and Richerson in 1985, still described their projects in terms and in the context of sociobiology (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). Today, cultural evolution is (rightly) seen as a rather different project, and it's worth it, both for understanding this project and its relation to social science today, to briefly consider the differences, before going into the ideas of cultural evolution and their flirtations with social science.

In his 1991 *Coevolution: Genes, Culture, and Human Diversity*, Durham proposes a distinction based on two questions, the first of which is: "Is culture a second inheritance system? "[1] (Durham 1991, 155). Those theories that answered this question in the negative are generally the sociobiological theories of the 1970s, which, as Durham explains, tackled culture by appealing to the same processes that drive biological evolution. These theories keep behavior on a very short genetic leash, explaining contemporary cultural phenomena with direct reference to their contribution to sexual selection and measures of fitness applicable to any wild animal. This is how one would get explanations of religious institutions as enhancement of personal persistence and influence, or of the self-sacrificing behavior of soldiers as the result of selective retention of altruistic genes in order to enhance the reproductive success of the group (Wilson 1978, 3; ,112). Such a theory is best described as sociology reduced to biology:

[1] And the second is "What are the best units to use in the study of cultural transmission?"; an important question I'll return to below, but one for the moment beside the point.

behavior, culture, is understood as practically a surface level effect, almost or entirely reducible to the forces of genetic evolution.

Those theories that answer “yes” to Durham’s question may be called theories of cultural evolution. In addition to the Darwinian process of evolution by variation, selection and retention of genes, these theories hypothesize an additional process of evolution in the variation, selection, and retention of culture. As evolutionary scientists started to take seriously the enormous variation in human behavior observed in the social sciences, the cultural influences on the development and behavior of individuals, and the influences human behavior may have on human biological evolution, theories with a more autonomous role for culture were developed. It is in this context that we encounter Cavalli-Sforza and Feldman and Boyd and Richerson.

Cavalli-Sforza and Feldman demonstrated that cultural processes can be described using classical models from population genetics. Before considering the analogy, consider how these models work. In the basic genetic case, we start with two variables A and B, which represent the groups in the population that carry, respectively, genetic trait a and b; say, hairy and not hairy. Between this generation and the next, natural selection (the environment is very cold, so the hairy a-individuals survive better) and sexual selection (non-hairy b-individuals are sexually popular and therefore reproduce more) happen, so that some traits are carried on more than others. The frequency of some trait *a* in the second generation (A_{t+1}), then, depends on its frequency in the first (A_t), multiplied by a variable r_a representing the reproductive rate, determined by selective fitness, of that trait. Hence:

$$A(t+1) = r_a(A(t))$$

According to Cavalli-Sforza and Feldman, in the cultural case, a “cultural trait” follows roughly the same rules- or at least can be formally described using the same rules. Instead of some genetically transmitted trait like hairiness, we now consider culturally transmitted traits: behaviors, skills and ideas picked up *during* life via interactions with others, or from learning from the environment.[2] Again, for two cultural traits *a* and *b* in a population, say, in this case, hairstyles, we have frequencies A and B in the population. Reproduction is replaced by social interactions that lead to adopting one of the hairstyles. The question, and this becomes a central question for cultural evolution, arises: what determines selection in this case; what determines *r*?

That is to say: if culture evolves like species do, what kind of forces operate in the cultural case, that make one cultural trait's propagation more likely than another's? Cavalli-Sforza and Feldman themselves, sticking close to the biological generations of population genetics models, distinguish three major mechanisms of cultural transmission: vertical, horizontal and oblique. Vertical is intergenerational transmission, from parent to offspring; horizontal (as in horizontal gene transfer and horizontal disease transmission) is intragenerational transmission; and oblique is again intergenerational, but from non-parent individuals. Between these kinds of transmission, a difference they had in mind was that vertical transmission is more conservative and acts on a slower timescale, while horizontal transmission can act faster, but is worse at preserving traits (Guglielmino et al. 1995).

Notice how the selective mechanisms distinguished by Cavalli-Sforza and Feldman are exclusively specifications on who information is copied from. In Boyd and Richerson's theory, these specification are called model-based biases (Boyd and Richerson 2006). "Bias" is to be understood here as more or less synonymous with the cultural selective forces we're looking for: any effect that has an influence on how likely one cultural trait is to be copied, and therefore how likely the trait is to be propagated. Model-based biases specify from which "models" (think "model-citizens") in the population an

[2] This is a common definition of cultural trait, but its precise interpretation is a subject that will have to be discussed once we get to problems with these models.

individual will pick up cultural traits. If an individual is an influential model, or copy target, the traits they carry will be more likely to propagate. A prominent example of model-based bias is prestige-bias, where individuals preferentially copy individuals with some kind of higher social status, to whose behavior they pay more attention. This is an effect regularly found among the rigid social structures of primates, and, for example, I will discuss below one recent study that concluded such a bias in to be used in a population of vervet monkeys (Canteloup, Hoppitt, and van de Waal 2020).

Model-based biases are distinguished from content-based biases, which specify preferential copying of traits directly, due to the properties or "content" of the trait. Some information is more important to individuals than other information; in a survival setting, I'd rather learn to hunt properly than to adopt a new hairstyle. Presumably, different traits therefore have a different impact on our attention and memory, and therefore on our behavior. An interesting application of this concept has been suggested by (Boyer 1994): those folk tales are more popular and better preserved that contain memorable elements like some (but not too many) supernatural events.

Finally, there's frequency-dependent biases, also known in the literature as conformity biases. The most frequent trait in a population, simply due to its being the most frequent trait in a population, will be copied more often. Conformity bias is the *additional* tendency to copy the majority. In a survival or otherwise pressured situation, copying the majority is often a good guess that doesn't cost much thinking or time, and the tendency to do so is often observed (Acerbi et al. 2016).

These model-and content-based selective forces of cultural traits form the basis of the original models of cultural evolution. Alongside the models and concepts, however, these foundational works also developed a much larger vision for the intended application of these models.

1.1.2. Applications of cultural evolution to social science subjects

While developing the analogy with population genetics, Cavalli-Sforza and Feldman as well as Richerson and Boyd had a definition of cultural trait in mind that could mean anything from specific actions and skills, to whole systems of belief and opinions. In other words, cultural evolution wasn't developed on its own and later applied to social subjects, but the intention has always been to study human culture, using evolutionary tools.

Cavalli-Sforza and Feldman conducted their own early application of their ideas in a survey of college students and their parents which illustrates their intent. Asking students, their friends, and their parents opinions about several subjects, they mapped which of these opinions were shared between parents and children, and which between friends, and inferred respectively vertical and horizontal transmission. They concluded that religious and political beliefs were mostly vertical in this sense, while the horizontal influence of friends was higher on more ephemeral matters like sports and music (Cavalli-Sforza et al. 1982). Cavalli-Sforza and Feldman, then, when they thought about cultural transmission in a modern setting, pictured belief systems and preferences as a reasonable application.

Richerson and Boyd cited this study in *Culture and the Evolutionary Process* among a list of similar studies of parent and child opinions and behavior as social science evidence for vertical (and horizontal) transmission in modern humans (Boyd and Richerson 1985, 50–55). They observe: "Sociological traits like skills, norms, and political and religious attitudes seem to us much less likely to be genetically acquired than basic psychological characteristics. Assuming that the reader agrees with this assessment, the observed parent-offspring correlations provide evidence of vertical cultural transmission" (Boyd and Richerson 1985, 52). Here, Boyd and Richerson agree with the idea that cultural traits can be, among other things, political and religious attitudes, and even treat them as synonymous with “sociological traits.”

This early vision is still today an ambitious one, and serves as an end-goal for cultural evolution: applying concepts from the human evolution of culture and culture’s own evolutionary process to the whole set of interrelated ideas, beliefs, know-how and everything else that makes up global human cultural variation (Boyd and Richerson 2006). With such a science, to name just a few things, we could exactly track the spread of ideas, their influence on decisions, behavior and biological evolution, and map the whole of culture as a collection of behaviors and ideas being iterated by, build upon, and communicated between individuals. We could drop a hypothetical human into a culture like a test particle into an electromagnetic field, and predict precisely what information could flow into and out of them.

Where one the one hand we have this brilliant vision, though, on the other we have the performance of both past and current models. Both Boyd and Richerson, and Cavalli-Sforza and Feldman recognized the gap between models and reality, both emphasizing repeatedly that their models are toy models, but better to start with simple models than to have no quantitative theory at all (Boyd and Richerson 1985, 24; Cavalli-Sforza and Feldman 1981, 34). In this paper, I consider two traditions that provide a picture of how hard this goal is to attain in practice. One is a major observation-oriented application of cultural evolution concepts: social learning in nonhuman animals. The other, opinion dynamics, has developed independently from cultural evolution, but has set itself a goal very much like these original applications of cultural evolution: to study, quantitatively, the social influence on and spread of abstract mental state entities like beliefs and opinions, in contemporary human populations. We’ll see that social learning has been able to develop models that study single traits and single bias effects more or less in isolation, while running into the fact that the reality of individuals is that multiple factors go into observed behavior, and the reality of culture is that traits don't exist in isolation. Opinion dynamics, meanwhile, has struggled to apply models to empirical results in any but the most controlled situations, and can only study traits quantifiable into numerical values. The details of these problems are the subject of the second section of this paper below. For the moment, the point is that the shortcomings of both traditions point out that there is still a big difference between what models can actually do, and the original goal of cultural evolution.

Accordingly, I propose that there are two distinct arguments at stake when we consider the relationship between social science and cultural evolution. The first is the very reasonable argument that society is somehow the product of evolution: *in principle,* human culture, while studied as the proper "object of sociology" in Comte's terms, has some evolutionary function and history, as socially transmitted information which allows adaptation to social and physical environment. The second is the much harder claim that cultural evolution models already provide a method ready for studying social science subjects.

Both claims are defended by Mesoudi in his 2011 book. Explicitly about the relationship between social science and cultural evolution, his argument is threefold: 1) some social sciences do not study culture using quantitative methods, while cultural evolution does; 2) the social sciences that do employ quantitative methods, primarily economics and psychology, hardly incorporate change over time or social influences on rational individual processes, while cultural evolution does; 3) the social sciences have such different methods and paradigms that they contain fundamental contradictions, and cultural evolution can provide a common theoretical framework (Mesoudi 2011, 22–23, 205–6).

According to Mesoudi, then, claim 1 is true, because cultural evolution would explain human culture, by providing an in principle, unifying understanding of what it is that social sciences study. Claim 2 is also true, because cultural evolution can provide testable, quantifiable hypotheses instead of verbal descriptions and arguments, a methodological improvement for much of social science. A complete assessment of these claims will have to wait until I've said more about what models can currently do in section 2. To anticipate my argument, however, I think one problem is that Mesoudi underestimates and does not engage with traditions within even the 'softer' social sciences that do employ formal methods. More or less coincidentally, one of these traditions, to which I now turn, shares with cultural evolution the formal approach of agent-based models.

1.2. Agent-based models and opinion dynamics

Agent-based models are, within the broader and older field of computational sociology and social simulation, a specific approach to using computers to simulate social phenomena. Earlier, more traditional approaches use computers to perform large-scale statistical or exact analysis of social datasets (Squazzoni 2010). In terms agent-based researchers are fond of, these calculations provide conclusions on macro-level patterns and variables in populations, while, in contrast, agent-based models simulate micro-level, individual variables in order to *generate* conclusions about macro-level patterns. How they do so requires some explanation.

The concept of agent-based modelling is based on cellular automata, an idea first developed by John Von Neumann in 1948, and closely analogous to how biological cells interact (Von Neumann 1976). Cells can grow complex tissues not by somehow planning or coding out the precise structure beforehand, but by following simple rules of interaction that could be summarized by statements like "if another cell is encountered, stop dividing in this direction and go the other way." We only need one or some of these simple rules to generate the intricate branches of lungs or trees. In a cellular automata model, cells have a position on a grid. At every timestep, every cell follows a global (the same for every cell) update rule that specifies what every cell's action is, based on the position of their direct neighbors on that grid. This action can consist in spawning new cells, or moving to another location. In this way, simple micro-level (cell-to-cell) interactions can generate complex patterns on a population level.

Agent-based models are cellular automata models where cells are agents. Agents can be a lot of things, but the present application is about models where agents are individuals. The interaction, then, which in the standard cellular automata model is spatial (the relative position of neighbors on a grid), becomes social. The idea of applying cellular automata to the simulation of social interactions between individuals was pioneered by Hegselmann and Flache (Hegselmann and Flache 1998). In the models considered in that paper, the action at each timestep of the agents is not to grow or move, but to update a certain state value associated with them. Having the application of social influence on opinion formation in mind, Hegselmann and Flache call these states opinion values. Explaining the idea of agent-based models, then, naturally leads us to explaining what is known as opinion dynamics, because the latter is an early and major application of the former (Mastroeni, Vellucci, and Naldi 2019).

Opinion dynamics models are agent-based models where agents are individuals, and their update rule updates an opinion value based on neighboring opinion values. The idea is to capture social influence, by way of social interactions like conversations, on opinion formation in individuals. The method is to express these opinions as some value, a 1 or 0 for opinions like yes/no or for/against, or a more abstract continuous value between 1 and 0 for other cases. The values of neighbors influence, at each timestep, in some defined way, the values of agents. I'll call this "defined way" the update rule of a model. The basic case of opinion dynamics is neatly summarized by Deffuant and colleagues in the following way (Deffuant et al. 2000). The updated opinion value $x_i(t+1)$, that is, that of agent *i* at the new timestep *t+1*, is arrived at by taking the current value $x_i(t)$, and adding the difference between that current value and the interacting neighbor's current value $x_j(t)$. The full update rule, then, is:[3]

$$x_i(t+1)= x(t) + (x_j(t) – x_i(t))$$

Difference between values is just one proposal for how agents adapt their values to social influence. I'll discuss different update rules, and the extent to which they are based on observed behavior in groups, in the second section below. For now, let's return to reasons why this type of modeling is considered to be valuable for social science research.

Agent-based models were developed as a way to directly simulate the micro-level individual processes that lead to the macro-level statistical patterns that social science observes. In a sense, nothing is different in that description from any empirical study where individual processes are observed and represented in data, and statistical analysis concludes patterns and correlations. But proponents of agent-based models argue that their use comes in where these individual processes aren't observed. An agent-based model cannot only *represent* collected data, but also *generate* new data. If an agent-based model can match some real observed macro-pattern, the update rule (which is its micro-level process of agent interaction) that model uses to generate that pattern provides a possible explanation for that pattern. Joshua Epstein has called this capacity of agent-based models *generative explanation* (Epstein 1999). Epstein envisioned a research program for agent-based models where micro-rules compete to generate patterns, and the decision between different rules that generate the same pattern is made

[3] To be precise, the basic case of Deffuant and colleagues includes a convergence parameter and a bounded confidence check, both of which are concepts I'll discuss in section 2.

on the basis of empirical testing.

In the next subsection, I argue that agent-based models provide a formal basis common to opinion dynamics and cultural evolution models.

1.3. Writing cultural evolution models as agent-based models

Agent-based models provide an approach to answering what I described as a central question of cultural evolution, namely which individual forces act as selective in one generation such that one trait becomes more frequent than another in the next. Replace "cultural trait" *a* carried by individual *i,* with opinion value $x_i(t)$, and "macro-level pattern" with the distribution of cultural trait values in a population A and B, and suddenly the possible update rules of opinion dynamics are among the transmission modes of Cavalli-Sforza and Feldman and the biases of Richerson and Boyd as possible micro-mechanisms behind that mysterious reproductive rate *r* of trait frequencies. The macro-patterns of culture, envisioned as cultural traits transmitted by social learning, are generated by the micro, individual interactions between agents 'carrying culture.'

The population genetic models that Cavalli-Sforza and Feldman used in their original application to culture stay at what agent-based modelers would call a macro-level (they are, after all, population genetic models, and evolution-oriented researchers call this the population level). Between generations, the individual reproductions (and therefore selective replication) that lead to population-wide distributions of traits A and B are assumed, but what is represented explicitly, mathematically, is the only the total fraction of the population that carries that trait; not every individual interaction (reproduction) via which these traits spread (Cavalli-Sforza and Feldman 1981, 31-35).

Cultural transmission lends itself well to agent-based models because agent-based models are designed to generate these population level outcomes by explicitly programming the individual interactions that give rise to them. In principle, this concept was always possible in models of cultural transmission, but the population genetic and epidemiological models used for these early analogies to culture were first developed in the 1920s and 1930s, and designed for describing elegantly, and on paper, processes on the scale of an entire population (Cavalli-Sforza and Feldman 1981, 1-40; Kermack and McKendrick 1927; Fisher 1937). For these approaches it may have in simple cases been possible, but certainly not intuitive or practical to calculate population outcomes by designing calculations for every single interaction and solving them by hand. Such an approach became intuitive only with the aid of computers and computing approaches that made this order of calculation doable, and is in this context that agent-based models first saw serious development (Squazzoni 2010; Flache et al. 2017). Still in 1985, Boyd and Richerson wrote that they used models way simpler than the complex realities they were intended to describe because more computationally complex approaches weren't tractable then "even with the fastest computers" (Boyd and Richerson 1985, 26). Agent-based models, based as they are on a computational framework designed specifically to simulate complex phenomena, have grown increasingly well-suited to simulating processes including cultural transmission on a more fine-grained scale. Cultural evolution researchers have increasingly recognized the possibilities of this agent-based basis for their models, recently explicitly so (Mesoudi, Acerbi, Smolla 2020).

So agent-based models are a formal framework both in opinion dynamics and in cultural evolution models. To establish specific links between the two areas, however, we cannot simply consider cultural evolution as a whole and compare it to opinion dynamics. Several fields have employed the concepts of cultural evolution in practice. Among them, the best candidate for this comparison is social learning in nonhuman animals.

1.4. Why social learning in nonhuman animals?

Discussing their application to human subjects, Boyd and Richerson remarked on animal culture in 1985 that "cultural transmission of phenotype is apparently rare in nature, and where it does exist it is generally restricted to a narrow range of traits." (Boyd and Richerson 1985, 82). This picture has since been proven wrong. Culture, in the sense developed by Boyd, Richerson, Cavalli-Sforza and Feldman of the use of social learning and copying, has since been established in species including primates, cetaceans, bees, fish, birds and rats (Galef and Laland 2005; Rosenthal et al. 2015; Kopps et al. 2014; Aplin et al. 2015; Ingraham, Perry, and Søvik 2017). Culture complex enough to vary locally has been mapped out in chimpanzees and humpback whales (Garland et al. 2011; Whiten et al. 2001). Animal culture, studied in terms of social learning, has become one of the pillars of cultural evolution research, mostly due to this impressive body of empirical evidence.

This empirical evidence, based primarily on the observation of actual behavior, is one argument for using social learning in nonhuman animals. For the present comparison. Another is that researchers employ agent-based modeling methods to quantify and simulate the spread of cultural traits transmitted via social learning. Thirdly, this field uses these models to study social influence on a timescale of individual transmissions, instead of whole generations.

To motivate these distinctions, let's look at two examples from two major fields in which the quantitative approach to culture was embraced as a research program: anthropology and zoology. Anthropologists Eerkens and Lipo, in 2005, used computer models later written as agent-based models (Gravel-Miguel 2013) to simulate possible cultural transmission mechanisms behind the variation of the base width and thickness of projectile points in

California from about 500 to 1300 AD, a well-documented and quantifiable pattern in the archeological record. The cultural trait that is transmitted in this case is the ability to produce these projectile points, and according to cultural evolution theory, variations would show up due to copying errors and innovations, and be counteracted by culture-preserving biases like Richerson and Boyd's concept of conformist transmission. Among other things, they conclude that simulating conformist transmission generates a variation over time that is consistent for at least part of the timeline with the observed data (Eerkens and Lipo 2005).

Eerkens and Lipo's approach is a perfect example of what Epstein means by using models for providing generative explanations. In lieu of being able to observe the actual behavior of the population that produced these projectile points, they employ a computer simulation that tries to fit plausible assumptions to observed patterns. Moreover, even if they were writing about presently living populations, they are interested in a timescale that would, again, render observation impossible. Their timesteps (their t to $t+1$) are 25 years long, meant to simulate an entire (biological) generation, and the archeological variation pattern they see is across many generations. In my second example, researchers also conclude presence of conformist transmission, the same process in theory. In sharp contrast, however, they do so in an observable amount of time in an observable population: one of wild birds.

In their field study, Aplin and colleagues introduced a "puzzle box" into a population of great tits. The two possible ways to open it and find food inside are picked up by members of the population, and considered as two cultural traits spreading over a population through learning. They concluded that individuals preferentially copied the trait most common in the population: an instance of conformist transmission. Whereas in Eerkens & Lipo's model, agents were strictly computational entities and the interactions between them theoretical, here the researchers used meticulous observation to closely track interactions between the birds and their puzzle box (Aplin et al. 2015). The model used is still a hypothetical or ‘generated’ explanation that is fit with the evidence, but this fit is very closely coordinated with actual observations. More importantly, this means that the timescale of these models is an observable amount of time; not one of human generations, but of 20 days.

Both studies use simulations of the individual interactions, of x_i’s, a’s, and biases, instead of the macro-logic of A, B, r and intergenerational transmission. This is a major step up in precision, facilitated by the use of computer models in a way envisioned by agent-based model developers. Still, in one case of applying the theory of cultural evolution, theoretical models provide a possible explanation; in the other, models provide a way of quantifying detailed observation, and testing claims in practice. On the one hand, such enormous differences in possible interpretations of these theoretical models should make us skeptical about sweeping claims about cultural transmission as a method ready for social science, even before we start talking about the application of animal and evolutionary models to modern human culture.

On the other hand, studies such as that of Aplin and colleagues show a promising precision and empirical basis for cultural evolution models. More pertinently to the present argument, these real-time studies of the diffusion of traits over a population via social interactions are the better candidates for a comparison with opinion dynamics, which simulates social influence on an observable scale. Also, as we will see, these models in turn could use the evidence-based wisdom of the nonhuman animal models.

Before we agree with Mesoudi’s argument that these precise cultural evolution models can provide an exact method for social science, however, beware that there are major problems even with these more exact and empirical models. The next section of this paper is dedicated to surveying these models, and what they currently can and cannot do. Only after that can we do the same for opinion dynamics models and the application to human culture, and start looking for paths to collaboration.

2. What can the models currently do?

In the preceding section, I've explained and talked about the theory and concepts of cultural evolution and opinion dynamics mostly in principle, to introduce the concepts involved, understand where these models come from, and what agent-based models are doing in these two fields. To get to an assessment of the possibilities of using cultural evolution models for social science such as envisioned by Mesoudi, we need to consider things in more detail. In the following pages, I consider the major theoretical terms, empirical support, and problems encountered in the two fields I selected above as comparable: social learning (in nonhuman animals), and opinion dynamics (in contemporary humans). I do so from the perspective of modeling these populations using agent-based models.

The major trend, therefore, that runs through this section, is a classical dichotomy in science: the relationship between the quantitative and exact relationships possible in the models, and the complex reality of the populations they are meant to simulate. The models here are agent-based models that consider social influence on diffusions of cultural traits and opinion values; the populations are nonhuman and human animals exchanging information on a timescale of individual interactions.

The stakes are outlined by the two claims about cultural evolution and social science I distinguished above. Should the models, upon closer examination, turn out to remain a theoretical exercise, then we are limited to arguing for a synthesis *in principle* between these social and biological sciences. Should they, however, succeed in securing quantified statements about their populations, then we may consider more seriously harder claims about a scientific study of culture.

Consequently, in this section, I first consider the concepts used in both traditions, from an agent-based perspective. Secondly, I assess what models within social learning in nonhuman animals can currently do, arguing that some problems are solved by new modeling approaches, and some remain more persistent and fundamental. Thirdly, I turn to opinion dynamics models, and do the same.

2.1. Agent-based modeling of social learning in nonhuman animals

2.1.1. Concepts

The simplest case for any agent-based model is a well-mixed population of agents that interact via a simple, universal update rule. "Well-mixed" means that there is no spatial structure to the model: any agent can interact with any other agent, and so the specification of which interaction partner to choose for a timestep can be entirely random.

Translating this to cultural evolution, our agents need to represent a population of individuals (nonhuman or human animals), and our update rule needs to capture how one's personal inventory of cultural traits is updated (every timestep) by social learning interactions with others. Distinguishing the simplest case from Boyd and Richerson's concept of biased transmission, a good place to start is unbiased transmission. Since bias means the preferential selection of traits (content-based) or of agents (model-based) above others, in an unbiased model agents copy all traits according to the same rules, and do so from any other agent. Note that therefore a non-model-biased model is a well-mixed model: there are no spatial restrictions for interaction. In a real population, this would reflect the assumption that all individuals interact freely and randomly, like particles in a gas. Of course, individuals hardly behave this way, and this is a first step in which the aforementioned difference between modelling possibilities and real populations becomes clear.

To get to more realistic models, we start introducing biases. Vertical and horizontal transmission, and model- and content-based biases still form the major categories of theoretical terms distinguished in these models. I'll discuss them in the order just given.

Vertical transmission would be one example of a model-based bias: biological offspring selectively copies from their parents. This could mean several things in practice, including observing parents more than others, and paying more attention to their behavior. Both would show up in a model as a preferential selection of agents specified as parents, but we can be more precise: more observation events would mean more timesteps are spent copying from a parent, while paying closer attention would mean that one interaction is more likely to lead to copying of a trait from that parent.

In the second case, the expression "more likely" underscores that in general, not every interaction leads to the spread of a trait from agent to agent. Over the entire population, some traits may be more likely to be copied at all than others, but in real human as well as nonhuman animals, learning only happens over the course of multiple repeated interactions. Again, several possibilities of interpreting relevant mechanisms present themselves. We may introduce a universal value for how much influence social interactions have on the cultural inventory of individuals. This has been posited as a "learning rate" of agents (Acerbi and Parisi 2006). The learning rate is multiplied by the update rule, so that scaling the value of this variable from 0 to 1 means scaling from no influence at all, to the full value, and upwards of 1, more than the full value. The updated value may then be said to be *weighted* by the value of that learning rate.

Alternatively, a learning rate may differ per individual, or over time, which means we take another step up in complexity, from universal and static update rules to local and dynamic ones. As real individuals generally don't move randomly about, so their behavior and relevant characteristics change over time under all manner of influence. To capture such an effect as increased attention to a parent by a child, we need to add, furthermore, a learning rate specific to a certain *pairing* of individuals, a pairing which is asymmetrical. That is to say, parents and offspring don't learn from each other equally, and therefore the interaction between these agents is *directed*.

The terms weighted and directed are used in network modelling, and reflect the fact that both in social learning and in opinion dynamics agent-based models are often network models. In an agent-based network, agents are nodes, between which run links. Links can be weighted and directed. Since we were already interested in interactions between agents, this isn't a major difference from the models we were already considering, but it's worth noting that model-based and content-based biases lend themselves not just to the agent-based concepts of spatial structure and update rules, but also to network structure and update rules. By connecting agents, networks can easily translate the selective preference for a subset of individuals of model-based biases, to links between individuals or differently weighted links between individuals. In practice, social network links may be formed by different phenomena including frequent observation, interaction, or kin relation, more on the differences between which below.

Horizontal transmission is modelled very similarly, the only difference being that the preferentially selected group is members of the same biological generation instead of biological parents. It's worth mentioning here, however, that cultural models don't necessarily need to distinguish between biological generations. This is done primarily in models that take biological generations for timesteps, either because modelers have such lifetime cultural complexes as belief systems in mind, as in the early cultural evolution applications I considered above, or because they are considering a process of change that takes place over a very large timescale compared to human lives, as in Eerkens and Lipo's archeological record data. I distinguished this from the real-time models used in social learning above because though the concepts employed are the same, timescale matters a great deal for what a model is describing.

Other prominent model-based biases are prestige and success bias. Prestige, some kind of social status that is correlated with preferential copying from or attention to prestigious individuals, can again be modelled by either network structure such that there are a lot of links running from this individual to others, or by directed and/or weighted links that make copying from them more likely (Canteloup, Hoppitt, and van de Waal 2020). Success-bias is different, because we need to introduce some measure of success, and some way for individuals to observe this success. The measure of success is, at least for tasks with obvious objectives such as foraging and tool reproduction, interpretable as some kind of payoff in the sense of game theory models. This is done in literature on social learning strategies, about which I go into more detail below. Though full knowledge of payoffs can be simply assumed in theoretical models (Acerbi and Parisi 2006), individuals must have some way of knowing that some individual is successful, or of connecting observable markers with success (Kendal et al. 2018).

As to content-based biases, several effects can be included in the update rule to capture effects that make one trait more popular than others. The most straightforward way to do so is to interpret a weighting variable such as the learning rate considered above as an effect due to the content of a cultural trait, and not to the psychological characteristics of individuals. Note that in this case, the learning rate would be the same thing as the reproductive rate *r,* summarizing all forces that lead to increased or decreased frequency of the trait in a population- the only difference being, again, that these frequencies change per timesteps of cultural reproduction, by social interactions and observations, and not by biological reproduction. If this, then, is another macro-level variable, content-based effects have been distinguished to serve as micro-level mechanisms of selection, to lead to such an outcome.

Lastly, let's consider frequency biases. In a model with a limited number of traits A,B,… it makes sense to have agents copy the most common trait; in models concerned with more continuous quantities, such as we'll encounter in opinion dynamics but also, for example, in Eerkens and Lipo's measurable variations, conformity is captured by agents copying the average value of a population. This, as well as any other bias, may be combined with network structure/model-based biases: agents may copy the most common trait or average variation only from a specific group, such as kin (Acerbi et al. 2016).

Other content-based effects may include differences in impact on memory and differences in saliency of information (as I mentioned above, hunting skills are often a more relevant thing to remember than hairstyling), effects that may be generally categorized as information-based. In addition, content-based biases may also be influenced by payoff-based considerations.

2.1.2. Some problems solved by modelling approaches

In the above exposition of theoretical terms, we've already come across several assumptions. Some problems with these assumptions are addressed or even solved by existing modeling approaches, and these I'll consider in this paragraph.

Since the original models rest upon an analogy with population genetics, a fundamental assumption of cultural evolution models is that cultural traits have their own process of replication: that they are copied between individuals via imitation. Imitation has since been recognized as only one (though the most common) type amidst a wider repertoire of social learning and teaching behavior. The assumption that this behavior constitutes a form of replication or copying has been called into question (Sperber and Claidière 2008; Godfrey-Smith 2012). Let's say that a behavior is observed to be performed by one individual, then a second individual observes that behavior, and then that second individual performs the same behavior. How can we be sure that this is an instance of 'replication,' and not just the decision of the second individual, perhaps due to similar environmental stimuli, to arrive at a similar behavior?[4]

To an extent, this question points to what I will define below as a deeper problem of both social learning and opinion dynamics models, namely that observation of behavior has limits in making conclusions about cognitive 'internal' processes. That being said, I argue that two specific approaches allow for a sharper distinction between social and other influences on the adoption of a behavior. First, the concept of social learning strategies was introduced into the study of social learning to incorporate the fact that learning and copying from others isn't always adaptive, and that therefore certain conditions must be met before animals switch from asocial to social learning (and vice versa) (Laland 2004). By assigning payoffs to different behaviors and outcomes, social learning strategies allow us to capture the circumstances under which social learning happens in more detail. Second, network-based diffusion analysis allows us to distinguish mathematically between the social and asocial influences on the adoption of a specific

[4] Apart from the general approaches considered here, one ingenuous practical solution to this problem is employed by Rosenthal and colleagues in their study of the spread of a predator avoidance behavior through a school of golden shiners, a species of freshwater fish (Rosenthal et al. 2015). To isolate social from asocial causes, they exploit the fact that fish will sometimes spontaneously or mistakenly initiate the reflexive flight behavior. In these cases, a 'cascade' of flight behavior still spreads through the population by observation of others, in absence of environmental stimuli.

behavior, effectively solving the problem of disentangling the two as influences on observed cultural traits (Franz and Nunn 2009).

In his paper introducing the social learning strategies concept, Laland proposes that, based on available empirical studies, animals roughly follow a three-step decision tree. First, if current behaviors are satisfactory, nothing changes. Second, if they aren't, animals switch to asocial learning; and third, only if that isn't productive either do they switch to social learning (Laland 2004, 11). In contrast and in addition to biases, in which we distinguish between different types of social learning, this leads to concepts of the circumstances under which social learning is opted for amidst the broader context of information sources available to individuals. These are called "when-strategies", and Laland distinguishes three of them: copy others when current/established behavior is unproductive, when asocial learning is costly, or when uncertain (Laland 2004, 5). When-strategies are distinguished from who-strategies, which, except for the fact that they are considered as possibly strategies between which individuals switch to yield higher payoffs, reduce to model-based biases. Most who-strategies are known model-based biases: copy successful individuals, copy kin, copy friends, and copy older individuals have been discussed as network structure options above. In general, social learning strategies may be considered as a different perspective on and adding some new cultural transmission biases, or more precisely, as adding payoff-based considerations to cultural transmission.

In network-based diffusion analysis, social learning is modelled not with attention to chances of adopting a behavior socially or forces operating on that chance, but to the predicted time it will take for an individual to learn a behavior (inferred from that individual expressing said behavior), and forces operating on this learning time. The learning curve (over time) for asocial learning is established first, and is a separate term from the one expressing social influence. Specifically, the term for social influence on an individual, a sum over all network neighbors (so everyone connected to an individual) is weighted by a value *S*. If *S* is zero, social influence has no effect at all and the expression reduces to the asocial learning curve; if it isn't, social contact has influenced the learning process and the curve deviates (Franz and Nunn 2009; Hasenjager, Leadbeater, and Hoppitt 2021). In studies using network-based diffusion analysis, networks are meant to express the social structure of a group, and are usually generated by observing interactions between individuals (Aplin et al. 2015; Canteloup, Hoppitt, and van de Waal 2020). In their most straightforward interpretation, links between individuals indicate that they have interacted at all, and links are weighted increasingly with the number of interactions. What is summed over, then, in the social influence term weighted by S, is the value of these weighted links, expressing the relative strength of influence of these individuals.

So how exactly do these two approaches address the problem that repeated occurrence in different individuals doesn't have to constitute copying? Social learning strategies adds to a clearer distinction by adding when-strategies, or, payoff-based conditions to be met before social learning is used. Network-based diffusion analysis offers a way of clearly distinguishing between a null-condition of asocial learning and added influence by social observations and interactions. Though, as I mentioned, a part of the problem remains and will be discussed in the dedicated subsection, these are major contributions to distinguishing more precisely between asocial and social influences on behavior, and generally the best methods available for studying social learning in nonhuman animals.

2.1.3. Observation

In a 2005 survey, Galef and Laland listed the available evidence for social learning, predominantly from mothers to offspring, in a variety of species. They reported that food choice, foraging behavior, predator avoidance and mating choices were found to be socially influenced in species of rats, fish, blackbirds, and monkeys, while techniques and even tool use locally differed and were socially transmitted in populations of chimpanzees, crows, and finches (Galef and Laland 2005). The findings are considered in the context of establishing that social learning exists at all, and in that of developing the concept of social learning strategies. In addition, however, they function as evidence for Cavalli-Sforza and Feldman's vertical transmission taking place in a variety of nonhuman animals. More recently, Kendal and colleagues surveyed the evidence for social learning strategies available since then, updating the picture of animal culture to include among others bees, cetaceans, and a varied landscape of biases and strategies used (Kendal et al. 2018).

My aim in this section is not to provide a complete survey the field; the papers already mentioned do an excellent job at this. Rather, the topic at hand is the way social learning researchers use observation as a way to move between the theory explained above, and the populations under study. To discuss this in detail, let's look at one recent study.

Canteloup, Hoppitt and van de Waal have employed network-based diffusion analysis in a study of wild vervet monkeys (Canteloup, Hoppitt, and van de Waal 2020). As in Aplin's and colleagues' study, described above, they introduced a puzzle-box into a population, which can be solved in two different ways. As the authors of network-based diffusion analysis instruct, different network models reflecting different biases and strategies are here used as possible hypotheses, and the aim is to establish what kind of diffusion network fits best with observation. Observation here is detailed: every interaction with the puzzle box is closely monitored, with attention also payed to how much naïve individuals observe those who have learned the task and now serve as demonstrators. This allows for a network model to be closely based on observation: links are to be fitted with observed observation between individuals, and there is a clear picture of who learned which behavior at what time. Additional information included the social rank of the individuals. Testing the fit of different models and different values for relative strength of social transmission *S*, the researchers conclude that the results are best captured by a network in which social observation does indeed predict a faster learning/adoption rate, and moreover, they find that observations of higher-ranked individuals carry more weight in this influence of social transmission. Therefore, a model-based bias effect is concluded that may be understood as a type of prestige or 'dominance' bias, or as a copy-higher-ranked-individuals learning strategy.

The authors do specify, however, that the number of social observations an individual makes, and consequently the effect observation has towards a social influence on the learning rate, may be composed of any combination of several strategies, in this case perhaps also including performance-based/ success bias or selective attention effects (Canteloup, Hoppitt, and van de Waal 2020, 2)The fact that these individual mechanisms are hard to distinguish brings me to two of the three major problems currently observed in social learning modelling.

2.1.4. Problems

Three major problems facing social learning are agreed upon in the literature. Because these three problems tie into both agent-based modeling and cultural evolution more generally, and especially because they will carry over into the applications of similar models to human populations in opinion dynamics, they are worth discussing here.

The first problem is this: several different individual-level social learning mechanisms can lead to the same or very similar population-level outcomes. In the survey mentioned above, Kendal and colleagues write that one of the new insights from recent findings is the fact that "population-level patterns are not necessarily indicative of particular SLSs [social learning strategies]" (Kendal et al. 2018, 6). More analytically, Acerbi and colleagues demonstrated that the population-level S-shaped diffusion curve[5] often taken as sufficient evidence for concluding conformity bias, can be generated by 7 out of 10 different plausible social learning mechanisms taken from the literature (Acerbi et al. 2016). The problem may also be observed in Canteloup and colleagues' study: the method for establishing individual strategies and biases is fitting different hypothetical networks reflecting these biases to the observed data, but several of them may fit it equally well.

If the aim of these models is to establish "micro-evolutionary processes" that drive the spread of cultural traits over populations (to establish the selective forces that lead to the survival or extinction of cultural traits) (Mesoudi 2011, 55), it's a problem that distinct mechanisms are associated with indistinguishable outcomes. Also without our eye on cultural evolution modeling in general, however, it's a problem for a field establishing different strategies of learning that some of these strategies can't be told apart.

I argue that an important part of this first problem is inherent to the use of agent-based models. As explained in section 1, agent-based modeling was developed as an alternative to top-down analytical calculations (like those of Cavalli-Sforza and Feldman), and inspired by and designed to simulate emergent, complex patterns using simple rules. They give rise to "generative" explanations, where individuals are directly simulated but the pattern generated by their interaction quickly becomes complex and opaque. For this reason, Hegselmann and Krause, in their foundational paper on opinion dynamics, are careful to distinguish linear from nonlinear models, and explain

[5] Mapping the diffusion of a single behavior over a population visually is often done by creating graphs with the number of adopters of this behavior (or, in terms explained above in the context of Cavalli-Sforza and Feldman, the fraction A/N, trait-carrier group A over the whole population) on the y-axis, and time on the x-axis. An s-shaped curve is formed by a process of diffusion which starts slow, becomes fast when spreading over the larger population, and ends slow again.

that they use (agent-based) computer models *because* and *in so far as* analytical results are hard to obtain when complexity starts to increase (Hegselmann and Krause 2002, 2). Introducing these computer models into the study of cultural evolution, as was done in the study of social learning, has allowed more direct attention to the individual interactions that drive population distributions, but at the cost of losing sight of the precise relationship between these micro-level mechanisms and macro-level outcomes.

In a sense, this was the idea of agent-based models. As I mentioned, Epstein set out a research program in which different micro-rules generating the same pattern may be distinguished from each other on the basis of empirical scrutiny. If we consider social learning as an example of this research program, we are faced with a further problem with it: as Canteloup and colleagues observe, just observing behavior does not decide between different reasons individuals have to copy, and the reality is more likely that multiple strategies overlap. The problem that the evidence points to multiple strategies being used at once, while current models usually test for one mechanism, is also pointed out by Kendal and colleagues as one of the new developments challenging current models (Kendal et al. 2018, 6).

Regarding the first problem, I said that "an important part" is due to using agent-based simulation. Relatedly, I wrote that network-based diffusion and social learning strategies tackle a part of the problem of distinguishing social influences from individual considerations. The rest of the problem is due to this second, underlying ambiguity of observation. Though studies can observe the absence or presence of a behavior, co-foraging events, and animals observing specific behaviors and demonstrators, it takes harder psychological assumptions and a different kind of observation to neatly distinguish the reasons and mechanisms behind this observed behavior. "When-" strategies are easier to establish empirically, partially because the decision to start using social learning is itself an individual process, and an animal can be observed to switch to social imitation and observation under certain circumstances. “Who-“ or model-based strategies or biases may be observed simply as frequent association or observation between individuals. However, within model-based biases, distinguishing between some of the mechanisms that may lead to the same effect, such as the success-based bias, selective attention, and rank-based biases mentioned as possible explanations by Canteloup and colleagues, requires more fine-grained knowledge and assumptions than this observation of behavior allows. This problem is especially relevant for content-based biases, which are entirely cognitive hypotheses.

In so far as these assumptions that cannot be distinguished by currently employed observation are present, social learning researchers have to rely on the fit of different hypothetical network-models that reflect different biases. In other words, to that extent they have to rely on generative explanations.

The third and last problem is similar to the second, and will become more relevant when we start to consider human applications. While current models test for diffusions of single or a small number of traits, the reality in complex social species, and especially in the complexity of human culture, is that multiple traits exist in populations simultaneously. Furthermore, these traits bear relationships: they compete for similar uses, and may depend on or change in use with the combination of other traits, creating a functional structure that researchers have only just begun to explore with an eye on formal modelling (Buskell, Enquist, and Jansson 2019; Mesoudi, Smolla, Acerbi 2020). Mesoudi and Thornton have defined the existence of multiple traits and multiple ‘lineages’ as criteria for cumulative cultural evolution[6], pointing out that the actual complexity of culture will pose a future challenge

[6] Cumulative cultural evolution is the idea that new cultural traits can become stable enough in populations to accumulate.

for modelling culture that has not at present been met by models that, as we have seen, test for single individual-level mechanisms as well as for a small number of usually independently considered behaviors (Mesoudi and Thornton 2018).

Ironically, finding solutions for this second and third problem within agent-based simulation models will worsen the first. Were such relationships to be found, including multiple interacting strategies in update rules is completely possible, but it will increase the complexity of the simulation and therefore the opacity of the relationship between these micro-rules and their generated population-level patterns.

To summarize, social learning has established a vocabulary of terms, empirical evidence, and network models to capture the copying of behaviors in populations of nonhuman animals. While the fact that there is social influence (and under which circumstances there is), the extent of that social influence, and the path by which these traits can "travel" through a population are admirably well-established, the more fine-grained behavioral rules that individuals use, while distinguished theoretically, are in practice harder to pin down because they are not simply observable from behavior.

All of these problems will carry over into opinion dynamics, which has developed similar agent-based network models to simulate social influence in human populations.

2.2. Agent-based models of opinion dynamics

In the opinion dynamics case, as in the cultural evolution case, the simplest case of an agent-based model is a well-mixed population with a simple and universal update rule.

This, at least, is what is intuitive from a cultural evolution perspective, because from this blank slate of random interaction, introducing model-based biases means introducing restrictions on spatial or network structure.

Remember that the forces intended to be modelled by cultural evolution are selective forces, and that these forces are modelled as any influence on the chance of individuals to adopt a trait. This is one way of conceptualizing selection and adaptation that is often used in cultural evolution: any trait having a higher chance of being adopted by others is understood as more adaptive (Mesoudi 2011, 56).

In the opinion dynamics case, modelling has remained closer to the logic of cellular automata modelling, and as a consequence, the simplest case is often considered to be a spatially explicit one: models where agents copy their direct neighbors. By spatially explicit, I mean that instead of entirely mathematical models, these models employ the direct simulation of some spatial structure, in this case a grid or lattice (but generalizable to networks). In fact, in their original concept for cellular automata-based models social phenomena Hegselmann and Flache consider local instead of global interactions, and spatial explicitness, as requirements for these types of models (Hegselmann and Flache 1998, 1). Cultural evolution models came from the population-wide logic of genetic selection, and later incorporated the individual-level interactions of agent-based models. Opinion dynamics, a major and early application of agent-based models, stayed closer to the conceit of these models as a method of generating complex outcomes by simple local interactions between cells.

A second reason for differences between these two uses of agent-based models is the phenomena they intend to simulate. First of all, the concept of a cultural trait differs from that of an opinion value. In the models considered above, the object of study is the social influence on observed behavior, like tool use, bird or whale song, and foraging techniques. In opinion dynamics, the concept is, ironically, much closer to what Cavalli-Sforza, Feldman, Boyd, and Richerson seemed to have in mind: modelling social influence, in human populations, on more abstract ideas and opinions.

In addition, the dynamics of interest differ. In social learning, the theoretical background is in the cultural variation, selection and replication of cultural traits. In opinion dynamics, the idea is to study differences and similarities between opinion values, and therefore to capture polarization and consensus in populations. Because of this focus, the update rules used in opinion dynamics are invariably some function of the difference in opinion values between interacting agents.

2.2.1. Concepts

The simplest case is Deffuant's expression as I gave it above: agents update their opinion value by the difference with their current interaction partner, weighted by some value to make this updating realistic. This basic rule amounts to the assumption that people grow more similar over time (concerning a certain topic, quantified as a value between 1 and 0) via social interactions. The difference $(x_j(t) - x_i(t))$ is negative when x_i is higher than x_j, and hence x_i will be updated in the direction of the lower value x_j; and if x_i is lower than x_j, the difference will be positive and x_i updates towards the higher value x_j. Without adding any further variables, then, this model will always lead to a population consensus (agents have very similar opinion values), any weight-value just determining how fast consensus is reached. A variable such as the learning rate considered above may in opinion dynamics simply be considered a consensus speed variable (Flache et al. 2017). The full update rule would in that case be $x(t)+ \sigma((x_j(t) - x_i(t)),$ where σ is the learning or scaling variable.

The idea that these models always lead to consensus does assume there is free, spatially unrestricted interaction among agents. As in the cultural, and indeed in the genetic case, spatial and interaction restrictions will lead to local cultures of similar traits, in this case opinion values. And as in the cultural evolution case, social networks have been introduced into opinion dynamics modelling to capture these restrictions (Cercel and Trausan-matu 2014). In the consensus model, as long as there is contact at all between these groups, agents will still grow similar over time, albeit slower. If the network creates entirely isolated groups, however, local groups will reach consensus around a local mean value, determined, as happens in the simpler model on a population scale, by the distribution of the initial values held by agents in the interacting group. In a recent survey of models, Mastroeni and colleagues distinguish pairwise interaction, any-to-any (unrestricted interaction) and closest neighbors (either in networks or in a regular lattice) but in principle we may add any model-based bias and any network structure (Mastroeni, Vellucci, and Naldi 2019).

The extent to which the assumption that individuals grow more similar in their opinions by interacting is true, is debatable. The fact that people don't always reach consensus, however, seems intuitive enough; and two popular mechanisms of opinion dynamics posit ways in which agents fail to agree, and form different groups.

The first way in which this is done is to introduce a threshold of difference for agents to have influence on each other at all. Opinion dynamics models often include what is called bounded confidence to capture such an effect a maximum value of difference between opinions above which agents don't change their values based on the interaction (Hegselmann and Krause 2002). Setting such a condition on interaction means that even without spatially being isolated, communities can form that converge locally around a certain value, while not or barely interacting with other communities.

Secondly, models of more extreme polarization include a negative influence: if agent's opinion values are sufficiently different, their values are updated not towards each other, as in consensus, or not at all, as in bounded confidence, but further apart. Negative influence intensifies the grouping caused by bounded confidence, and tends to polarize the population into two or a low number of extremes, or poles.

As I discussed, in models used in cultural evolution, the object of study is cultural traits. In the social learning models considered above, the focus is on a single, observable behavior which spreads through a population through social contact. It makes sense, in these models, to consider two or a low number of discrete states in which an animal can be; the individual either does or does not carry the trait, that is, does or does not exhibit the studied behavior. Most opinion dynamics models, focused more on the difference and variation in a population than on diffusions of single opinions, instead employ the large (in fact, theoretically infinite) variety of continuous values between 1 and 0. Differences are gradual, and social influence doesn't lead to either adopting or not adopting, but to updating based on the other agent's value (Flache et al. 2017).

In addition to the use of continuous values, some opinion dynamics models have multiple values per agent. Every agent is associated not with a single value but with a vector or matrix of values, either all of which interact with all others from an interacting agent, or values are grouped into specific topics which interact with each other and not with others. (Quattrociocchi, Caldarelli, and Scala 2014; Flache et al. 2017; Alaali et al. 2008).

2.2.2. Observation and Problems

When agents are taken to represent real people, the major assumptions of opinion dynamics models are that social interactions can cause either (1) less or (2) more difference in positions on some topic. The first of these assumptions amounts to the consensus model, which predates the term opinion dynamics and refers to a collection of social psychology studies ranging from 1935 to 1982 (Flache et al. 2017, 6). Though this modelling tradition therefore in principle has some empirical basis, it can hardly be considered to be based on state of the art knowledge. Moreover, while there is a rich body of literature on new theoretical demonstrations and modeling possibilities, there is also an almost complete lack of testing of these hypotheses on actual populations.

In other words, the major problem with opinion dynamics models is that they aren't much based on observation. More so than in social learning models, models have remained theoretical, and papers, written for a large part by computer scientists and physicists, demonstrate modeling possibilities rather than applications (Squazzoni 2010). Much like Galef and Laland's early survey of the evidence and development of the concept of social learning strategies, Hegselmann and Krause's 2002 paper collected a wide array of results spanning several decades, and synthesized out of it concepts now considered standard in opinion dynamics modeling. Unlike that other survey however, which was one of empirical results, this was a survey of modelling ideas.

Another example: the term for relative social influence *S* in network-based diffusions analysis is equivalent to the convergence parameter determining consensus speed in consensus models. In both Hegselmann and Krause and Hasenjager 's model, this variable is multiplied by (and therefore scales) a sum over the influence of (network) neighbors x_j on individual x_i. While in network-based diffusion analysis, however, the entire point is to fit *S* to observed social interactions, opinion dynamics models are more interested in finding values of this parameter for tipping points, optimization, and other analytically interesting demonstrations. The models remain the same, yet the intention of their use differs completely.

Summarizing the status of empirical observation in opinion dynamics, the authors of a more recent paper remark: "Empirical ground for these models is however largely missing, which confines them to the level of mere metaphors of the real phenomena they aim at explaining" (Chacoma and

Zanette 2015, 1).

This being the general state of the field when it comes to observation, there are some exceptions, and discussing one in more detail makes clear what the challenges are to such an application.

Writing in 2016, Vande Kerckhove and colleagues called their study “the first time the predictive power of a quantitative model of opinion dynamics is tested against a real dataset.” (Kerckhove et al. 2016, 1). Their simulation includes a confidence threshold, here called influenceability, varying between 1 and 0. Agents update their opinion values by multiplying this influenceability by the difference between their current value and the mean value of the group, and adding this to the current value. Disregarding network structure for a moment (that is, assuming that all agents know the mean opinion of the entire population at each timestep), this is the standard model described by Hegselmann and Krause. Vande Kerckhove and colleagues make interactions controlled and quantified by looking at online interactions and defining the opinion values as numerical guesses in a gauging and a counting game. Like in Canteloup and colleagues’ study, the aim is to find the model best fitting with the data, hypothesis-networks with different variables are tried out, and one central question is how and when individuals use socially acquired information. Unlike that study, the researchers are interested in a human population, interacting online in the controlled environment of a set of rounds, and the main theoretical terms to be tested in observation are influenceability and opinion values. Where Canteloup and colleagues found that social interaction was a reliable predictor for increased learning rate of a new foraging behavior, Vande Kerckhove and colleagues find that those who use social information are more accurate in both guessing and gauging.

One very interesting difference is that this experiment in opinion dynamics includes a section describing a method for determining different degrees of predictability that their models can achieve, given different levels of available knowledge. Even in their most optimal case, they conclude that one third of the unreliability of prediction is due to the ”intrinsic unpredictability of the decision revision process” (Kerckhove et al. 2016, 7). In other words, even in very controlled, quantified circumstances, we encounter the fact that observing behavior doesn’t allow us to distinguish between the reasons and factors that led to that behavior. We encountered this problem already in the pragmatic, observation-oriented field of social learning, but if we want to take seriously the theory of opinion dynamics and its claim to simulate real social processes by postulating such psychological concepts as opinions, the problem posed by this limitation increases enormously. The complexity of multiple factors influencing decisions and behaviors only increases in the human populations that opinion dynamics applies its models to, and so do the many interrelated traits that form the structure of culture.

Considering all this complexity, it’s not very surprising that opinion dynamics has struggled to make their field more empirical. It’s tempting to suggest that opinion dynamics has been neglecting empirical application out of a sort of disciplinary alienation. An underlying problem, however, is the obvious truth that finding a set of simple yet realistic (or even very complex yet realistic) rules for simulating human behavior is just very hard. Theoretical demonstrations of possible mechanisms are many, but quickly become computational speculation when not checked with real populations; while in the few observational studies that do exist, researchers have to take care to use wide margins of error and caveats, even in limited controlled environments looking at one or two variables. Getting anywhere near a “wild” population of humans makes the current models practically, in Chacoma & Zanette’s words, metaphorical.

3.

In section 1, I noted that when population models of culture were first introduced, population geneticists Cavalli-Sforza and Feldman as well as anthropologists Richerson and Boyd recognized a gap between their intended eventual application and the extent of their formal models. Their intended application, in both cases, was to understand, in human populations, the diffusion of whole systems of beliefs, behavior and opinions as they are transmitted and shared across and between generations. Over the course of the last section, we have seen several reasons why this goal is hard to reach by existing models. What is conceptualized in those early interpretations of cultural traits turns out to consist of multiple interrelated traits. Furthermore, even the processes that do turn out to be easier to establish exactly, such as single traits and single biases or mechanisms, may not represent reality accurately, and this becomes worse the closer we get to human culture.

Along the same lines, I distinguished two different claims, both of which were defended by Mesoudi in 2011:

1) this picture of culture is *in principle* an explanation (or unified definition) of culture as it is studied under different names in social sciences.

2) formal models currently used in cultural evolution can already provide a (more) scientific way of studying social phenomena as culture.

The point of this last section is to asses to what extent these claims are true for the specific case of agent-based models in social learning and opinion dynamics. First, I emphasize the positive conclusions to be drawn:

there are promising ways in which the two fields could collaborate towards shared models of evolution- as well as sociology-inspired phenomena. Second, I consider what we learn about the bigger picture of these traditions as a specific case of interaction between social and biological science

3.1. Possibilities for collaboration

To put it succinctly, the similarities are overwhelming, and the two fields should interact more. From the perspective of agent-based modelling, both use network models to capture social influence on behavior, one tradition searching for techniques to quantify more abstract and hypothetical measures of it and one focused on observable behaviors. Both find out that simulating and observing social influence in general is something these models excel at. This is an exciting conclusion: both in nonhuman and human animals, these models allow researchers to quantifiably simulate social paths of information flow that influence and constrain individual behavior and cognition, results which hold even without further investigating this individual cognition.

On the other hand, both traditions also reflect the fact that distinguishing specific mechanisms remains theoretical to the extent to which we need to postulate harder psychological assumptions. These are the kind of assumptions that would be necessary for the original vision for human cultural evolution models including content biases and complex traits, as well as the vision for agent-based models of opinion dynamics of simulating social difference.

At least in the particular traditions I have examined here, these visions have not yet been met with adequately detailed models. Single-trait and single-mechanism/single-bias models should be thoroughly upgraded before approximating the complexity of human as well as nonhuman culture and cognition.

At the same time, the fields have developed largely independent from each other, and different intentions of modelling have led to different variables and modeling ideas. This is another exciting conclusion: because these traditions share a formal framework, any of these terms may be combined. Hence, we may include more evolution-oriented effects in the social applications of opinion dynamics, and we may consider more social effects such as polarization and social group formation in evolutionary models. Below is a table summarizing effects I have talked about in this paper, considered from the perspective of agent-based networks.

Update rule variables	Network structure	Traits associated with agents
Bounded confidence	Well-mixed	Binary trait values
Positive and negative influence	Lattice or grid neighbors	Multiple trait vectors or matrices
Frequency-dependent: copy-most-common if discrete, averaging if continuous	Vertical transmission; parent-bias; also kin biases, prestige and dominance biases, age-based, and any other model-based bias that may be observed simply by selective attention to specific individuals[7].	Continuous trait values (defined on any set of numbers)
Learning rate (individual or global), relative social influence, consensus speed , and other scaling parameters	Success-based bias, and knowledge-based bias; require agent knowledge of success markers and / or payoff	Discrete trait values (defined on any set of numbers)
Information- or affect-based bias	Directed and weighted links for fine-tuning specific relations	
Payoff-based bias		

Fig.1: Cultural evolution and opinion dynamics concepts in agent-based network models. This is not an exhaustive list, and I refer the reader again to excellent existing surveys in both fields (Kendal et al. 2018; Flache et al. 2017; Mastroeni, Vellucci, and Naldi 2019). Omitted here are when-biases, which specify the circumstances under which social learning is used, and may warrant further combinations. Rows in this table mean nothing.

[7] These effects are empirically different, but in networks just variations of structure.

Specifically, I'd like to highlight here three ways in which combining these agent-based models may help solve the problems facing these traditions such as I have outlined them above.

First, while in the context of cultural evolution, the structure of more than single, isolated traits is just being examined, opinion dynamics has always used models of multiple interrelated traits. When we consider opinion dynamics as an application of agent-based models to human culture, as well as that the more-than-single-trait structure of culture becomes more pronounced the further we move to human complexity, this difference is unsurprising. In any case, multiple-trait models will almost certainly help a great deal in modelling more complex culture.

Second, and not unrelatedly, due to a focus on gradual difference instead of diffusion opinion dynamics has always used continuous values for the 'cultural inventory' associated with an agent. Such a focus on degrees of variation may prove valuable in cultural evolution models that examine variation in the context of the Darwinian trinity of variation, selection and heredity. In addition, it allows for a more fluid definition of cultural traits than one based on single observed behaviors or 'discrete culture units,' allowing instead more noisy statistical distributions of more and less similar traits. Though one disadvantage is that continuous values are more abstract and relate less directly to observable behavior, this also means that we widen the scope of what we can model as a cultural trait to include the kind of numerical guesses explored by Vande Kerckhove and colleagues, and, though with greater caveats of ambiguity, other quantitatively expressable kinds of evidence like voting behavior and survey data (Redner 2019). Notice, however, that without further work on detailed modeling of cognitive and cultural complexity, the latter application would just be the same as the survey-based application Cavalli-Sforza and Feldman. The strength is in combining different modelling ideas.

Third, opinion dynamics may learn a lot from the closely observation-based field of social learning in nonhuman animals. Though we have explored good reasons why observation of behavior can say less about human populations, this objection may to a large extent also be raised for other socially and cognitively complex animals, which have been insightfully studied nonetheless by social learning researchers. At least within opinion dynamics, researchers have room to employ a lot more exact methods of observation such as those used in studying nonhuman animals. Only to the extent to which this behavioral observation fails do we need to employ the more cognitive kinds of explanations from a first-person, reasoning perspective.

This would certainly not be the first time cultural evolution concepts would be applied empirically to human populations. We've seen one kind of application in Eerkens and Lipo's use of the archeological records. Another is studies of chains of transmissions in human groups such as those developed by Kirby, and field studies of social transmission such as those by Hewlett (Scott-Phillips and Kirby 2010; Hewlett and Roulette 2016). It would be useful to view opinion dynamics as another one of these applications, and integrate its ideas for modelling into more empirical evidence.

Though I have outlined serious problems with what these models can do, all of these new approaches may lead us a little bit closer to that ridiculously ambitious vision of cultural evolution as a science able to quantitatively model the flow of culture through populations.

3.2.

In section 1, I distinguished sociobiological from cultural evolution explanations by the fact that the former reduce culture to biology. Frankly, there is still a reductive streak in arguments such as those made by Mesoudi that social science lacks a unifying theoretical framework, and that cultural evolution models can study social phenomena in a better way. Sure, quantitative and observation-based modeling, in general, is better science than verbal description. But it's highly doubtful whether, considering the performance of the models I've examined here, cultural evolution methods and models trump existing social science methods and models. In fact, in this specific case, the formal framework used in a cultural evolution field was borrowed from computational sociology, and originally intended for sociological application; not the other way around.

Moreover, the interaction between the two traditions here studied are interesting not in so far as social phenomena can be modelled in terms of cultural evolution, but precisely in so far as opinion dynamics has developed its own variables and mechanisms to study the not evolutionary but social problems of consensus, decision and polarization. Even if, in a final theory, sociological questions and terms like this would be understood as evolved and evolving culture, it is these terms and interests that would make a cultural science sociological, and useful for the study of the social. Arguing instead that we should study these phenomena entirely in term of concepts from cultural evolution, would just be sociobiology with extra steps.

To reiterate, this specific collaboration between a social and a biological science would be productive precisely in so far as both fields can incorporate terms from the other; in so far as there is not a hierarchical flow of concepts up or down, but a horizontal and mutual relationship of exchange and combination. In this specific case, this exchange is feasible and promising because the fields already share the formal framework of agent-based models, and combination would therefore just consist of adding variables and techniques from the other field. Driscoll has made a similar anti-reduction argument about cultural evolution and the social sciences, conceptualizing cultural evolution as a "bridge-field" instead of a embedding it as a higher or lower state in a hierarchical tree (Driscoll 2018). In fact, promising directions of cultural evolution collaborating with social science seem to follow this kind of horizontal structure. Colleran has worked on integrating cultural evolution concepts with data and insights from demography to study the many factors that go into the fertility decline in many rich societies (Colleran and Snopkowski 2018; Colleran 2016). Henrich has developed collaborations with, among others, historians to study the effect of the Church on global psychological variation (Schulz et al. 2019). On a smaller and more model-oriented scale, collaboration between the sociologically oriented field of opinion dynamics and the rich body of empirical results from social learning would follow a similar structure.

To return to Comte's terms, then, there still seems to be wisdom in the idea that social and biological sciences have their own sets of irreducible terms. At the same time, the fields I have examined here make a case for considering the relationship between these sciences less hierarchical, and more mutual. Moreover, embracing the arduous task of developing more mathematical methods, instead of preventing us from capturing the 'essence of the social,' has in this case provided the platform making a more horizontal collaboration between these sciences possible.

Conclusion

In this paper, I have aimed to establish a thorough comparison and agenda for collaboration between two fields, where before there was only the suggestion that cultural evolution and opinion dynamics should engage more. In the process of doing so, I have demonstrated and argued for several things. Through a discussion of the history of cultural evolution and opinion dynamics, I have pointed out how the original cultural evolution models may be transformed into agent-based ones. I have argued for a related difference in timescale in the application of these models to cultural evolution, in favor of the more fine-grained and observation-based use in social learning in nonhuman animals. I have argued that network-based diffusion analysis and social learning strategies can help in solving the problem of distinguishing between asocial and social information. I have argued that one major problem with social learning models is inherent to agent-based modelling, but also that the more fundamental problem with social learning, as with opinion dynamics, is differentiating between different reasons and causes for individual behavior. I have listed several ways in which, through this common formal framework, opinion dynamics and social learning concepts may be combined, and shown several theoretical terms to be equivalent. I have argued for three ways (multiple trait vectors, continuous values, and observation-based modeling) in which approaches from the one field can help solve problems from the other, and that the prospects for a shared approach using concepts from both fields in the same type of models are promising.

The main question, however, which I asked in the introduction to this paper, was whether, in the specific case of agent-based models in opinion dynamics and in social learning in nonhuman animals, cultural evolution provides a method for studying social science. The answer is yes, in the sense that models, concepts and empirical results used in cultural evolution may be used to study the human populations of interest to social science. However, I have considered here a case where the formal framework used does not come from the "lower" biological science into the "higher" sociological science, but provides a platform for horizontal collaboration. Moreover, the social phenomena that may be studied by cultural evolution or shared models are not interesting in so far as they can be understood theoretically in terms of cultural evolution. In fact, the opposite is true: in so far as these traditions have developed different approaches and terms, they provide fruitful avenues for future research which may study both social and evolutionary phenomena. I therefore consider the present case study to be a counterexample to both claims defended by Mesoudi: cultural evolution, in this case, can neither be said to have provided a better or more scientific method for social science, nor would it be productive to understand the social object of study in terms known from cultural evolution.

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