

CULTURAL REPLICATION AND MICROBIAL EVOLUTION

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The aim of this paper is to argue that cultural evolution is in many ways much more similar to microbial than to macrobial biological evolution. As a result, we are better off using microbial evolution as the model of cultural evolution. And this shift from macrobial to microbial entails adjusting the theoretical models we can use for explaining cultural evolution.

Introduction

We have a very elegant and efficient theory for explaining certain biological changes from population to population: the theory of natural selection. The theory of natural selection has a remarkable explanatory power: it can explain something very complex, such as the structure of the human eye or the fit between the organism and the environment in terms of something very simple, the dumb causal processes of births and deaths. A tempting idea is that the same explanatory scheme could be used to explain some complex non-biological, more precisely, cultural phenomena (Richerson and Boyd 2005; Sterelny 2006a; Lumsden and Wilson 1981; Hull 1988, 2001; Fracchia and Lewontin 1999; Dawkins 1976, 1982a, 1983; Cavalli-Sforza and Feldman 1981; Auger 2000; Dennett 1995; Campbell 1956, 1960, 1974; Toulmin 1967, 1970, 1972; Kantorovich 1989; Bradie 1986; Popper 1963, 1972, 1974, 1978; Nanay 2011b – the list is obviously far from being complete). This is exactly what theories of cultural evolution attempt to do.

There are numerous important differences between biological and cultural evolution. The question is whether the explanatory scheme of the theory of natural selection could be applied in the cultural domain *in spite of* these dissimilarities.

In this paper, I want to focus on three salient differences between biological and cultural evolution:

- 1) Cultural evolution is very fast, much faster than biological evolution.
- 2) In the case of biological evolution, information transmission is vertical: we inherit our genes from two individuals only (our parents). This is not true for cultural evolution, where information is also transmitted laterally, from peers to peers.
- 3) The fidelity of information transmission in the case of biological evolution is much higher than in the cultural case.

There are many more widely discussed differences: it has been claimed that cultural evolution is Lamarckian, whereas biological evolution is Weismannian, etc. (Hull 1980, 1981). But I will focus on (1), (2), and (3) here.

The aim of this paper is to argue that when it comes to (1), (2), and (3), cultural evolution is much more similar to microbial than to macrobial biological evolution. As a result, we are better off using microbial evolution as the model of cultural evolution. And this shift from macrobial to microbial entails adjusting the theoretical models we can use for describing cultural evolution.

Macrobial versus microbial evolution as a model for cultural evolution

Here is an odd fact about the literature on cultural evolution. It invariably takes macrobial evolution to be the model of cultural evolution. When it compares the biological and the cultural domain, it really compares the domain of macrobial biology and culture.

But macrobes are not the only biological entities – in fact, they are not even the most widespread ones. Evolutionary biologists and philosophers of biology have been actively ignoring microbes, and this, arguably, has been a mistake. We may be able to understand important facts about biological evolution if we understand the microbial world (see, for example, O'Malley and Dupré's 2007 manifesto). And my proposal in this paper is that we may be able to understand something important about cultural evolution if we take microbial evolution, and not macrobial evolution, as its model.

- 1) Microbial evolution is in many respects very different from macrobial evolution. Here are three important (and conspicuously numbered) differences:
Microbial evolution is very fast, much faster than macrobial evolution (see e.g., Lawrence 2002).
- 2) In the case of macrobial evolution, information transmission is vertical: we inherit our genes from one or two individuals (the parent[s]). This is not true for microbial evolution, where information is also transmitted laterally – this is called *lateral gene transfer*, where the transfer of genetic material from one organism to another happens by conjugation, transduction, or transformation (Bushman 2002; Thomas and Nielsen 2005; see O'Malley and Dupré 2007: 167–168 especially for a philosophical analysis of this phenomenon).
- 3) The fidelity of information transmission in the case of macrobial evolution is much higher than in the microbial case (see e.g., Lawrence 2002; O'Malley and Dupré 2007).

In other words, the three differences I considered in the last section between biological and cultural evolution were in fact differences between macrobial and cultural evolution. And we find the exact same differences between macrobial and microbial evolution. The conclusion is that we would be much better off using microbial evolution for modeling cultural evolution.

The aim of this paper is to cash out what this shift of emphasis from macrobial to microbial evolution in the analysis of cultural evolution would entail in terms of the theoretical framework we can use to model cultural evolution.

Two ways of thinking about natural selection

There are two distinct ways of conceiving of selection processes. According to one, selection is the heritable variation of fitness. According to the other, it consists of repeated cycles of replication and interaction. These two models of selection⁷⁵ give us very different ways of formulating evolutionary explanations, and they even yield different kinds of evolutionary explanations.

According to the first model (Lewontin 1970; Maynard Smith 1987), selection should be described as the heritable variation of fitness. A typical formulation is the following (see also Lewontin 1970: 1; Endler 1986: 4; Ridley 1996: 71–72; Godfrey-Smith 2007: 515).

A sufficient mechanism for evolution by natural selection is contained in three propositions:

- 1) There is variation in morphological, physiological, or behavioral traits among members of a species (the principle of variation).
- 2) The variation is in part heritable, so individuals resemble their relations more than they resemble unrelated individuals, and, in particular, offspring resemble their parents (the principle of heredity).
- 3) Different variants leave different numbers of offspring either in immediate or remote generations (the principle of differential fitness). (Lewontin 1980: 76).⁷⁶

According to the alternative concept, selection consists in repeated cycles of two separate processes. As Ernst Mayr says, “natural selection is actually a two-step process, the first one consisting of the production of genetically different individuals (variation), while the survival and reproductive success of these individuals is determined in the second step, the actual selection process” (Mayr 1991: 68; see also Mayr 1982: 519–520; Mayr 2001: 117; Mayr 1978). David Hull calls these two steps replication and interaction (Hull 1981; Hull 1988; Hull et al. 2001). Hull defines selection as “[t]he repeated cycles of replication and environmental interaction so structured that environmental interaction causes replication to be differential” (Hull et al. 2001: 53).

In turn, Hull (1988: 408) defines the unit of replication, the *replicator*, as “an entity that passes on its structure largely intact in successive replications” (see Hull 1980: 318 for a slightly different definition). The unit of interaction, the *interactor*; on the other hand, is de-

⁷⁵ I will refer to these two ways of conceiving of selection as two *models* of selection, acknowledging that my use of the concept of models is different from the way this term is used in biology.

⁷⁶ According to Lewontin (1980: 76), each of these three propositions is necessary for evolution by natural selection (besides being jointly sufficient).

defined as the “entity that interacts as a cohesive whole with its environment in such a way that this interaction causes replication to be differential” (Hull 1988: 408; see Hull 1980: 318).

This replication–interaction model of selection was introduced as an improvement on the heritable variation of fitness model, and it is supposed to clarify a number of details left implicit therein. More precisely, the replication–interaction model has been thought to help us to understand what is at stake in the units of selection debate: if selection is replication plus interaction, then we should not talk about the units of selection, but rather about the units of replication and the units of interaction, which may not be (and in fact most often are not) the same. The thought is that the replication–interaction distinction in itself will not solve this problem, but it is supposed to help us to formulate the problem in such a way that would make it possible to tackle it (see e.g., Lewontin 1970: 7; Brandon 1982, 1988, 2006; and especially Lloyd 2001).

In the last decade or so, more and more evolutionary biologists and philosophers of biology have been arguing against the replication–interaction model. Their main claim is that replication is not necessary for evolution by natural selection, or, as I will put briefly, for selection.⁷⁷ As a result, the *heritable variation of fitness* model has become more and more widely used.

In the cultural evolution literature, both of these models are used. The most famous, but not the only, example of the replication–interaction model in the domain of cultural evolution is meme theory. These two models are also often applied to the cultural domain without a clear attempt to distinguish the two – as in Richerson and Boyd (2005: Chapter 3), where the first half of the chapter uses the heritable variation of fitness model, whereas the second half uses a version of the replication–interaction model, without any explicit acknowledgement of the difference between the two.

My aim is to point out that regardless of whether the heritable variation of fitness model or the replication–interaction model is better suited for describing microbial evolution, the heritable variation of fitness model faces serious problems when applied to microbial evolution. And it faces the same problems when applied to cultural evolution. In other words, we are better off using the replication–interaction model for describing microbial and cultural evolution.

The heritable variation of fitness and microbial evolution

The heritable variation of fitness model may look straightforward, but in fact it is not. What this account of selection entails very much depends on the way in which we interpret the concept of fitness. And there is no agreement on a number of important features of this concept.

⁷⁷ There is an important terminological difference in the way the concept of selection is being used in the literature. Some ask whether replication is necessary for *evolution by natural selection* (Okasha 2007; Godfrey-Smith 2007), others ask whether replication is necessary for *selection* itself (Hull 1988; Neander 1995; Hull 2001; Nanay 2005). I assume that these are two different ways of asking the same question (the question of whether replication is necessary for *evolution by natural selection*) and I will use the latter formulation because it is simpler. If the reader prefers the former one, he/she should read ‘evolution by natural selection’ instead of ‘selection’ in what follows.

Is fitness a causal or a statistical concept (Matthen and Ariew 2002)? Is it a population-level or an individual-level concept (Millstein 2006)? What entity do we attribute fitness to, individuals or to trait types (Sober 1981; see also Nanay 2010b; Nanay 2011c)? If the former, is an individual's fitness the same throughout its life (Ramsey 2006)? If the latter, how should we individuate these trait types (Nanay 2010a)?

The two most influential questions about fitness and about selection are whether they should be taken to be population-level or individual-level phenomena, and whether they are causal or statistical concepts (Matthen and Ariew 2002; Walsh et al. 2002; Millstein 2006; Brandon 2006; Bouchard and Rosenberg 2004; Rosenberg and Bouchard 2005; Stephens 2004). It has been pointed out that the concept of fitness is used in two different ways: as an "ecological descriptor" and as a "mathematical predictor" (Sober 2001: 319; this distinction may be traced back to Kitcher 1984: 50). Building on Sober's distinction, Mohan Matthen and André Ariew (2002) made a distinction between "vernacular" and "predictive" fitness.⁷⁸

Vernacular fitness is a measure of the "overall competitive advantage traceable to heritable traits" (Matthen and Ariew 2002: 56). Predictive fitness, in contrast, is the "expected rate of increase (normalized relative to others) of a gene, a trait, or an organism's representation in future generations" (Matthen and Ariew 2002: 56). Vernacular fitness plays a role in the informal presentations of natural selection, whereas predictive fitness is used in mathematical formulations of population genetics. Vernacular fitness is a comparative measure, whereas predictive fitness is a quantitative one. Vernacular fitness is usually taken to be a cause of selection, whereas predictive fitness is taken to be a measure of selection, not its cause.

Matthen and Ariew (2002) argue that we should only use the concept of predictive fitness. Others defend the concept of vernacular fitness and insist that it is an individual-level concept (Bouchard and Rosenberg 2004; Rosenberg and Bouchard 2005). Yet another group of philosophers concede that it is a population-level concept, but maintain that it is a causal one (Stephens 2004; Millstein 2006). There are some further questions about fitness. Is it fixed throughout the organism's lifetime (Ramsey 2006)? In what way does it depend on the environment and how can we characterize the environment it depends on (Abrams 2007)?

Before we get entangled in the Byzantine debates surrounding the concept of fitness, we should take a step back and ask: why should we conceive of selection as the heritable variation of fitness at all? There are important cases of natural selection where it is not clear how the heritable variation of fitness account could even be formulated.⁷⁹

An important aspect of the heritable variation of fitness account is that it talks about parents and offspring. Both what Lewontin calls "the principle of variation" and what he calls "the principle of differential fitness" (Lewontin 1980: 76) are principles about the parent-offspring relation. But there are cases of natural selection where it is unclear what should be considered as the parent and what should be considered as the offspring. Here are two such

⁷⁸ Ariew and Lewontin (2004) refer to these two concepts of fitness as "Darwinian" and "reproductive" fitness.

⁷⁹ I leave aside some further potential problems with the heritable variation of the fitness account, for example, that it presupposes that the parent and offspring generations do not overlap (see Ariew and Lewontin 2004). I assume that the heritable variation of the fitness account could be modified in such a way that it could deal with this potential problem.

cases: selection among clonal organisms and in the microbial world. For the purposes of this paper, I will focus on microbial evolution (but see Nanay 2011a on clonal selection). It is important to note that these are not marginal cases of natural selection (on how widespread and important clonal reproduction is, see Godfrey-Smith 2009: 71–72, and Bouchard 2008; on the importance and relevance of the microbial world, see O’Malley and Dupré 2007’s manifesto).

As we have seen, a striking feature of most microbial population is lateral gene transfer, the transfer of genetic material from one organism to another by conjugation, transduction, or transformation (Bushman 2002; Thomas and Nielsen 2005; see O’Malley and Dupré 2007: 167–168 especially for a philosophical analysis of this phenomenon). Lateral gene transfer makes natural selection (and evolutionary change in general) in the microbial world more rapid and more frequent than it is among macrobes (see e.g., Lawrence 2002).

But how can we talk about the heritable variation of fitness in the case of lateral gene transfer? Lateral gene transfer is not from parent to offspring. It is from offspring to offspring. This, again, makes it difficult to even formulate the principle of variation and the principle of differential fitness of the heritable variation of fitness account (see O’Malley and Dupré 2007 for a summary of how lateral gene transfer in the microbial world challenges our existing evolutionary accounts).

Could we not defend the heritable variation of fitness account by arguing that lateral gene transfer should be considered a simple mutation from the point of view of the organism that is on the receiving end of the transfer? This move is indeed open to the proponents of the heritable variation of fitness account, but it is difficult to see how it will help. Lateral gene transfer can have varying degrees of fidelity. Thus, it can, in principle, give rise to *bona fide* evolution by natural selection that may even lead to adaptation. But lateral gene transfer is (by definition) not an intergenerational change. And this makes it impossible to talk about the change of fitness values, as fitness is defined with reference to (some features of) the parent generation and (some features of) the offspring generation. When lateral gene transfer gives rise to evolution by natural selection, this cannot be described with the help of the heritable variation of fitness account.

It seems then that, while the heritable variation of fitness account may or may not be the right model for macrobial evolution, it is unlikely to be the right way to describe microbial evolution. But, because of the structural similarities between microbial and cultural evolution, it is also unlikely to be the right way to describe cultural evolution. The argument I gave in the last couple of paragraphs can be easily rephrased with regards to horizontal information transfer in the case of the cultural domain. If we want to understand cultural evolution (and microbial evolution), we are well advised not to use the heritable variation of fitness account. We should turn to the replication–interaction model.

The replication–interaction model and microbial evolution

The replication–interaction account of selection is a genuine alternative to the heritable variation of fitness account, but it has different versions and the most widespread of these is widely assumed to be highly problematic. We can distinguish two versions of this account, the *replicator–interactor account* and the *property–replication account*. The former

has been repeatedly criticized. I argue that we should use the latter when modeling microbial and cultural evolution.

The replicator–interactor account

According to the first version of the replication–interaction account, replication is the copying of an entity, the *replicator*. Hull defines the replicator as “an entity that passes on its structure largely intact in successive replications” (Hull 1988: 408; see also Godfrey-Smith 2000; Brandon 1990; see Nanay 2002 on the concept of replicator). The unit of interaction, the *interactor*; on the other hand, is defined as the “entity that interacts as a cohesive whole with its environment in such a way that this interaction causes replication to be differential” (Hull 1988: 408). I will call this version of the property-replication account the *replicator–interactor account* as it identifies replication with the copying of an entity, the replicator.

In the last decade or so, many philosophers and biologists have argued against this replicator–interactor account of selection (Okasha 2007: 15–16; Godfrey-Smith 2007: 515; Godfrey-Smith 2009; Avital and Jablonka 2000: 359; Jablonka and Lamb 1995; Richerson and Boyd 2005: Chapter 3; Griesemer 2000: 74–76; Griesemer 2002: 105). Their main claim is that the copying of replicators is not necessary for selection; hence, selection cannot consist of repeated cycles of replication (conceived of as the copying of replicators) and interaction.

There are ways of transmitting information (for example, extragenetic inheritance) that do not count as replication but that are (given other conditions) sufficient for selection (Okasha 2007: 15; Avital and Jablonka 2000: 359; Jablonka and Lamb 1995: 3). Samir Okasha summarizes this line of objection: “evolutionary changes mediated by cultural and behavioural inheritance cannot be described as the differential transmission of replicators” (Okasha 2007: 15). To put this objection in more general terms, selection can happen if there is sufficient phenotypic parent–offspring resemblance. Replication is not needed (Okasha 2007: 15). One example is maternal effects, i.e., cases in which large mothers have large offspring as a result of laying eggs with larger food reserves (Uller 2008).

The property-replication account

It is important that these problems are problems for the replicator–interactor account and not for the replication–interaction account in general. Remember that the original alternative to the heritable variation of fitness account was the view that selection consists of repeated cycles of replication and interaction. It is an additional requirement that replication should be thought of as the copying of an entity, namely, the replicator.

We may be able to salvage the general gist of the replication–interaction account if we deny that replication is the copying of an entity. We could conceive of replication as the copying of property-instances (Nanay 2011a; see also Nanay 2002: 113). The hope is that this version is not vulnerable to the objections raised against the replicator–interactor account. I will use the term *property-replication account* for this version of the original replication–interaction account to contrast it with the replicator–interactor account.

It is important to clarify the difference between these two versions, i.e., what is meant by entities and properties here. The cup in front of me is an entity. It has lots of properties, some interesting, some others less so. Its color is one property, its shape is another one, etc. Thus, the copying of an entity and the copying of one of the properties of this entity are very different processes. Properties are always properties of entities, of course. But it is possible to copy a property of an entity without thereby copying the entity itself. The claim is that replication is the copying of properties: we can have a replication process without there being a replicator that is being copied.⁸⁰ The definition of replication would then be the following (Nanay 2011a: Section 4): property P of object (a) is a replica of property Q of object (b) if and only if: (1) P is similar to Q and (2) Q is causally involved in the production of P in a way responsible for the similarity of P to Q.

An important feature of this definition is that (a) and (b) are not necessarily objects of the same kind. Object (b) may be an apple, and object (a) a color photograph of this apple. The color of the photograph can be a replica of the color of the apple under my definition, but this does not mean that the objects themselves are replicas or copies or replicators in the old sense of the word.

This notion of replication is very weak: many non-biological copying processes, like photocopying, will also qualify as replication. Is this a problem? No. The same is true of the traditional concept of replication as the copying of replicators (Godfrey-Smith 2000; Nanay 2002). Importantly, any account that conceives of selection as the repeated cycles of replication and interaction needs to acknowledge that not every replication process will be particularly interesting from an evolutionary point of view. But this is what we should expect: the notion of replication is only the starting point for an account of selection. Further additional criteria need to be met in order for replication to lead to selection: replication needs to give rise to an interaction process that makes the next round of replication differential.

How can this property-replication account handle the objections to the replicator–interactor account? First, according to the property-replication account, both extragenetic inheritance and cultural transmission can count as replication. Nothing in the definition of replication suggests that the replicated property needs to be a property of the DNA. Thus, extragenetic properties can replicate as much as the properties of the DNA can. If property P of the offspring is similar to property Q of the parent, and the latter is causally responsible for this similarity, then we do have replication, regardless of whether these properties can be called genotypic or not.

Crucially, the transfer of cultural information also counts as replication if we understand replication in the way that property-replication suggests: cultural properties are being replicated. Remember that the definition of replication was the following: property P of object (a) is a replica of property Q of object (b) if and only if: (1) P is similar to Q and (2) Q is causally involved in the production of P in a way responsible for the similarity of P to Q. As P and Q can be any property in this definition, cultural information transfer would qualify as replication, as long as both (1) and (2) are satisfied.

⁸⁰ Biologists call the properties of organisms ‘traits.’ If someone prefers this concept to the concept of properties, he/she can rephrase my definition of replication as ‘the copying of traits.’ But as the replicated properties are not necessarily properties of an organism, I will talk about properties, rather than traits, in what follows in order to preserve generality.

More generally, if we accept the property-replication account, then phenotypic traits can replicate. Take the maternal effects example I mentioned in the last subsection. According to the property-replication account, there is a property that replicates in this case: the property of being large. The offspring's instantiation of this property is similar to her mother's (in as much as the degree of similarity between the size of the two individuals is higher than it is between the size of two randomly chosen individuals in the population), and her size is causally responsible for this similarity. Thus, we do have selection in this population, but we also have replication. We do not have replicators though.

Property-replication and lateral gene transfer

So far, everything looks promising: the property-replication account is not susceptible to the objections that were raised against the replicator–interactor account. But the real question is whether the property-replication account is a genuine alternative to the heritable variation of fitness account. More precisely, can it handle the cases of selection in the microbial world that were problematic for the heritable variation of fitness account?

If we accept the property-replication account, then microbial evolution will pose no problem as lateral gene transfer will count as a replication process. Lateral gene transfer is the copying of an entity (and its many property-instances) from one organism to the other. And this counts as replication under any account of replication: both the replication–interaction conception and the property-replication conception. Some replication processes will happen from parent to offspring, some others from offspring to offspring.

If either kind of replication processes gives rise to environmental interaction that makes the next round of replication (again, either parent to offspring, or offspring to offspring replication) differential, we have a selection process, conceived as the repeated cycles of replication and interaction. We can talk about selection in microbial populations without running into the problems that the concept of fitness poses in this context.

And the same goes for horizontal information transfer in the case of cultural evolution: it counts as replication in the sense that the property-replication view uses the term. Some replication processes will happen from parent to offspring, some others from offspring to offspring. If either kind of replication processes gives rise to environmental interaction that makes the next round of replication (again, either parent to offspring, or offspring to offspring replication) differential, we have a selection process, conceived as the repeated cycles of replication and interaction.

We then get the following picture: there are three ways of modeling natural selection, the heritable variation of fitness account, and two versions of the replication–interaction account, the replicator–interactor account and the property-replication account. We have seen that the heritable variation of fitness account is unlikely to be able to be the right way to think about cultural and microbial evolution because it cannot handle lateral gene transfer and horizontal information transfer. The replicator–interactor account has been facing various objections. The best bet for those who want to understand cultural and microbial evolution is then the property-replication account.

Property-replication and cultural evolution: Cultural replication without memes

As the most famous account of applying the replication–interaction model to cultural evolution is meme theory, one may worry that the shift from the heritable variation of fitness model to the replication–interaction model I am encouraging in the context of cultural evolution would amount to a return to meme theory.

Much of the recent discussion of cultural evolution has been revolving around the concept of meme. The distinction between replicator and interactor was originally famously introduced “as a generalization of the traditional genotype–phenotype distinction” (Brandon 1990: 125). This means that there can be, and supposedly there are, entities other than the gene that would count as replicators. The main candidates for such replicators have been memes.

Memes are defined as the “units of the cultural transmission” (Dawkins 1976/1989: 192; see also Dawkins 1982a, 1982b). According to meme theory, cultural phenomena can be explained, at least partially, with the help of the following evolutionary model: memes are pieces of information, and they compete for survival in a way quite similar to genes; the difference is that they compete for the capacity of our minds. A meme can be a tune, the idea of liberalism, or the habit of brushing one’s teeth. Those tunes will survive that can get into and stay in many minds. The ones that fail to do so will die out. Meme theory is clearly a way of applying the replicator–interactor model to the cultural domain.

Meme theory is still extremely popular (see Blackmore 1999; Dennett 2003, 2006; Aunger 2002; Distin 2005), but it has been severely criticized for various reasons, partly for worries about the ontological status of memes (Sperber 1996; Wimsatt 1999; Fracchia and Lewontin 1999; Richerson and Boyd 2005; Sterelny 2006a, 2006b). What are these cultural replicators supposed to be?

There have been various attempts to answer this question (Dennett 2006: 80–81, and 349–350; Dennett 2003; Aunger 2002: 311–322; Distin 2005). An influential strategy is to say that both genes and memes are really just pieces of information, and there is nothing ontologically worrying about the concept of information (this is Dennett’s and Distin’s response; but see Aunger’s more restrictive version). Note that this view violates the concept of replicator the original replication–interaction model was presupposing.⁸¹

It is important to note that meme theory applies the replicator–interactor model to cultural evolution. My proposal, in contrast, has been that we should apply the property-replication model instead. If we do so, we can bypass the ontological worries meme theory faces. This move would replace the notion of cultural replicators, that is, memes, with replicated cultural properties.

It has been argued that whether or not we buy into meme theory, there are processes in the cultural domain that can be described as replication (Richerson and Boyd 2005; Sterelny

⁸¹ They are not reproducers either: a meme and its copy do not have any material overlap.

2006a, 2006b).⁸² If we accept my definition of replication, then we can explain these processes without postulating ontologically suspicious entities, like memes.⁸³

It is important to note that if we acknowledge that there are processes that could count as cultural replication, we do not need to be thereby committed to allow for cultural selection (as replication is not sufficient for selection), let alone cumulative cultural selection that could explain why certain cultural features are the way they are. If we accept my definition of replication, this will not salvage meme theory, or even the very idea of memes. But it would make it possible to talk about cultural replication, without specifying what the replicated entities would be, or without positing the existence of memes.

Conclusion

The aim of this paper has been to argue that we should use microbial, rather than macrobial evolution as the model for understanding cultural evolution. And the emphasis on the similarities between microbial and cultural evolution as well as on the differences between microbial and cultural evolution should persuade us to abandon both the heritable variation of fitness model and the replicator–interactor model when it comes to understanding cultural evolution, and use the property-replication view instead.

References

- Abrams, M. (2007) Fitness and propensity's annulment? *Biology and Philosophy* 22, 115–130.
- Ariew, A. and Lewontin, R. (2004) The confusions of fitness. *British Journal for the Philosophy of Science* 55, 347–363.
- Aunger, R. (2002) *The Electric Meme: A New Theory of How We Think and Communicate*. New York: Free Press.
- Aunger, R. (ed.) (2000) *Darwinizing Culture: The Status of Memetics as a Science*. Oxford: Oxford University Press.

⁸² Of course, there are ways of giving an evolutionary account of cultural change without talking about cultural replication (see Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981). My point is that if we want to talk about *cultural replication*, we can do so without positing memes.

⁸³ Note that this application of the account I proposed here would have interesting consequences with regard to an important debate about cultural evolution that has emerged within the context of meme theory. A crucial question about cultural replication is whether it needs to be specific to one kind of physical substrate. In the context of meme theory, this question is about whether meme replication needs to be specific to one kind of physical substrate. Robert Aunger (2002: 154 and 157) argues that it is. Kate Distin (2005: Chapter 11; see also Dennett 2003, 2006), in contrast, argues that memes can replicate in different substrates. If we accept my definition of replication, then replication does not have to be specific to one kind of physical substrate: it is properties that get copied, regardless of the substrate. And the same is true of cultural replication. Hence, my account is siding with Distin and Dennett (and not with Aunger) in this question. It is also important to note that the question of substrate-specificity is an important one as long as we allow for cultural replication, regardless of whether we talk about memes.

- Avital, E. and Jablonka, E. (2000) *Animal Traditions: Behavioural Inheritance in Evolution*. Cambridge: Cambridge University Press.
- Blackmore, S. (1999) *The Meme Machine*. Oxford: Oxford University Press.
- Bouchard, F. (2008) Causal processes, fitness and the differential persistence of lineages. *Philosophy of Science* 75, 560–570.
- Bouchard, F. and Rosenberg, A. (2004) Fitness, probability and the principles of natural selection. *British Journal for the Philosophy of Science* 55, 693–712.
- Bradie, M. (1986) Assessing evolutionary epistemology. *Biology & Philosophy* 1, 401–459.
- Brandon, R.N. (1982) Levels of selection. *Proceedings of the Philosophical Science Association*. Vol. 1, 315–323.
- Brandon, R.N. (1988) Levels of selection: A hierarchy of interactors. In: H.C. Plotkin (ed.) *The Role of Behavior in Evolution*. Cambridge, MA: MIT Press, 51–71.
- Brandon, R.N. (1990) *Adaptation and Environment*. Princeton: Princeton University Press.
- Brandon, R.N. (2006) The principle of drift: Biology's first law. *Journal of Philosophy* 102, 319–335.
- Bushman, F. (2002) *Lateral DNA Transfer: Mechanisms and Consequences*. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.
- Campbell, D.T. (1956) Perception as substitute trial and error. *Psychological Review* 63, 331–342.
- Campbell, D.T. (1960) Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review* 67, 380–400.
- Campbell, D.T. (1974) Evolutionary epistemology. In: P.A. Schilpp (ed.) *The Philosophy of Karl Popper*. LaSalle: Open Court, 413–463.
- Cavalli-Sforza, L.L. and Feldman, M.W. (1981) *Cultural Transition and Evolution*. Princeton: Princeton University Press.
- Dawkins, R. (1976/1989) *The Selfish Gene*. 2nd edition. Oxford: Oxford University Press.
- Dawkins, R. (1982a) *The Extended Phenotype*. Oxford: W.H. Freeman.
- Dawkins, R. (1982b) Replicators and vehicles. Reprinted in: R.N. Brandon and R.M. Burian (eds.) (1984) *Genes, Organisms, Populations: Controversies over the Units of Selection*. Cambridge, MA: MIT Press.
- Dawkins, R. (1983) Universal Darwinism. In: D.S. Bendall (ed.) *Evolution from Molecules to Man*. Cambridge: Cambridge University Press, 403–425.
- Dennett, D.C. (1995) *Darwin's Dangerous Idea*. New York: Touchstone.
- Dennett, D.C. (2003) *Freedom Evolves*. New York: Viking.
- Dennett, D.C. (2006) *Breaking the Spell: Religion as a Natural Phenomenon*. New York: Viking.
- Distin, K. (2005) *The Selfish Meme*. Cambridge: Cambridge University Press.
- Endler, J. (1986) *Natural Selection in the Wild*. Princeton: Princeton University Press.
- Fracchia, J. and Lewontin, R. (1999) Does culture evolve? *History and Theory* 38, 52–78.
- Godfrey-Smith, P. (2000) The replicator in retrospect. *Biology and Philosophy* 15, 403–423.
- Godfrey-Smith, P. (2007) Conditions for evolution by natural selection. *Journal of Philosophy* 104, 489–516.
- Godfrey-Smith, P. (2009) *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.
- Griesemer, J. (2000) The units of evolutionary transition. *Selection* 1, 67–80.
- Griesemer, J. (2002) What is 'epi' about epigenetics? *Annals of the New York Academy of Sciences* 981, 97–110.
- Hull, D.L. (1980) Individuality and selection. *Annual Review of Ecology and Systematics* 11, 311–332.
- Hull, D.L. (1981) Units of evolution: A metaphysical essay. In: U.J. Jensen and R. Harré (eds.) *The Philosophy of Evolution*. Brighton: Harvester Press, 23–44.

- Hull, D.L. (1988) *Science as Process*. Chicago: Chicago University Press.
- Hull, D.L. (2001) *Science and Selection*. Cambridge: Cambridge University Press.
- Hull, D.L., Langman, R.E. and Glenn, S.S. (2001) A general account of selection: Biology, immunology and behavior. *Behavioral and Brain Sciences* 24, 511–528.
- Jablonka, E. and Lamb, M.J. (1995) *Epigenetic Inheritance and Evolution: The Lamarckian Dimension*. Oxford: Oxford University Press.
- Kantorovich, A. (1989) A genotype-phenotype model for the growth of theories and the selection cycle in science. In: K. Hahlwed and C.A. Hooker (eds.) *Issues in Evolutionary Epistemology*. Albany: State University of New York Press, 171–184.
- Kitcher, P. (1984) *Vaulting Ambitions: Sociobiology and the Quest for Human Nature*. Cambridge, MA: MIT Press.
- Lawrence, J.G. (2002) Gene transfer in bacteria: Speciation without species. *Theoretical Population Biology* 61, 449–460.
- Lewontin, R. (1970) The units of selection. *Annual Review of Ecology and Systematics* 1, 1–18.
- Lewontin, R. (1980) Adaptation. Reprinted in R. Levins and R. Lewontin (eds.) (1985) *The Dialectical Biologist*. Cambridge: Harvard University Press, 65–84.
- Lloyd, E. (2001) Units and levels of selection. In: R.S. Singh, C.B. Krimbas, D.B. Paul and J. Beatty (eds.) *Thinking about Evolution*. Cambridge: Cambridge University Press, 267–291.
- Lumsden, C.J. and Wilson, E.O. (1981) *Genes, Mind and Culture*. Cambridge, MA: Harvard University Press.
- Matthen, M. and Ariew, A. (2002) Two ways of thinking about fitness and natural selection. *Journal of Philosophy* 49, 53–83.
- Maynard Smith, J. (1987) How to model evolution. In: Dupré, J.A. (ed.) *The Latest on the Best*. Cambridge, MA: MIT Press, 119–131.
- Mayr, E. (1978) Evolution. *Scientific American* 239, 46–55.
- Mayr, E. (1982) *The Growth of Biological Thought*. Cambridge, MA: Harvard University Press.
- Mayr, E. (1991) *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought*. Cambridge, MA: Harvard University Press.
- Mayr, E. (2001) *What Evolution Is*. New York: Basic Books.
- Millstein, R. (2006) Natural selection as a population-level causal process. *British Journal for the Philosophy of Science* 57, 627–653.
- Nanay, B. (2002) The return of the replicator: What is philosophically significant in a general account of replication and selection? *Biology and Philosophy* 17, 109–121.
- Nanay, B. (2005) Can cumulative selection explain adaptation?, *Philosophy of Science* 72, 1099–1112.
- Nanay, B. (2010a) A modal theory of function. *Journal of Philosophy* 107 (8), 412–431.
- Nanay, B. (2010b) Population thinking as trope nominalism. *Synthese* 177, 91–109.
- Nanay, B. (2011a) Replication without replicators. *Synthese* 179, 455–477.
- Nanay, B. (2011b) Popper’s Darwinian analogy. *Perspectives on Science* 19, 337–354.
- Nanay, B. (2011c) Three ways of resisting essentialism about natural kinds. In: J.K. Campbell and M.H. Slater (eds.) *Carving Nature at its Joints: Topics in Contemporary Philosophy*. Vol. 8. Cambridge, MA: MIT Press, 175–197.
- Neander, K. (1995) Pruning the tree of life, *British Journal for the Philosophy of Science* 46, 59–80.
- Okasha, S. (2007) *Evolution and the Levels of Selection*. Oxford: Oxford University Press.
- O’Malley, M.A. and Dupré, J. (2007) Size doesn’t matter: Towards a more inclusive philosophy of biology. *Biology and Philosophy* 22, 155–191.

- Popper, K.R. (1963) *Conjectures and Refutations*. London: Routledge.
- Popper, K.R. (1972) *Objective Knowledge*. Oxford: Clarendon.
- Popper, K.R. (1974) Darwinism as a metaphysical research programme. In: P.A. Schilpp (ed.) *The Philosophy of Karl Popper*. La Salle, IL: Open Court, 133–143.
- Popper, K.R. (1978) Natural selection and the emergence of mind. *Dialectica* 32, 339–355.
- Ramsey, G. (2006) Block fitness. *Studies in the History and Philosophy of Biological and Biomedical Sciences* 37, 484–498.
- Richerson, P.J. and Boyd, R. (2005) *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
- Ridley, M. (1996) *Evolution*. 2nd edition. Oxford: Blackwell.
- Rosenberg, A. and Bouchard, F. (2005) Matthen and Ariew's obituary to fitness: Reports of its death have been greatly exaggerated. *Biology and Philosophy* 20, 343–353.
- Sober, E. (1981) Evolutionary theory and the ontological status of properties. *Philosophical Studies* 40, 147–176.
- Sober, E. (2001) The two faces of fitness. In: R.S. Singh, C.B. Krimbas, D.B. Paul, and J. Beatty (eds.) *Thinking About Evolution*. Cambridge: Cambridge University Press, 309–321.
- Sperber, D. (1996) *Explaining Culture: A Naturalistic Approach*. Oxford: Blackwell.
- Stephens, C. (2004) Selection, drift, and the “forces” of evolution. *Philosophy of Science* 71, 550–570.
- Sterelny, K. (2006a) The evolution and evolvability of culture. *Mind & Language* 21, 137–165.
- Sterelny, K. (2006b) Memes revisited. *British Journal for the Philosophy of Science* 57, 145–165.
- Thomas, C.M. and Nielsen, K.M. (2005) Mechanisms of, and barriers to, horizontal gene transfer between bacteria. *National Review of Microbiology* 3, 711–721.
- Toulmin, S. (1967) The evolutionary development of natural science. *American Scientist* 55, 456–471.
- Toulmin, S. (1970) From logical systems to conceptual populations. *Boston Studies in the Philosophy of Science* 8, 552–564.
- Toulmin, S. (1972) *Human Understanding*. Oxford: Clarendon.
- Uller, T. (2008) Developmental plasticity and the evolution of parental effects. *Trends in Ecology and Evolution* 23, 432–438.
- Walsh, D.M., Lewens, T. and Ariew, A. (2002) The trials of life: Natural selection and random drift. *Philosophy of Science* 69, 429–446.
- Wimsatt, W.C. (1999) Genes, memes, and cultural heredity. *Biology and Philosophy* 14, 279–310.