humans to grow and evolve for its own benefit. It is more like a parasite turned symbiont than an adaptation.

This makes a big difference not only to how we understand human evolution but to our predictions for the future. Memetic evolution constructed human brains and is now building better, higher fidelity meme machines, including computers, the Internet, and digital media. For the moment we humans are essential to the further evolution of the memosphere, but there are already many memes created that never have contact with a human being, and there will be more. Memetics alone makes sense of this and will help us understand what is happening.

Analogies are powerful and dangerous things

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Abstract: The analogy between biological and cultural evolution is not perfect. Yet, as Mesoudi et al. show, many of the vaunted differences between cultural and genetic evolution (for example, an absence of discrete particles of cultural inheritance, and the blurred distinction between cultural replicators and cultural phenotypes) are, on closer inspection, either illusory or peripheral to the validity of the analogy. But what about horizontal transmission? We strongly agree with the authors that the potential for horizontal transmission of cultural traits does not invalidate an evolutionary approach to culture. We suggest, however, that it does require a different evolutionary treatment.

Here, not to admonish the authors for oversight but to emphasize potential pitfalls in conceiving of the culture–biology analogy too narrowly, we list some common misconceptions about transmission modes.

1. First, any trait can be fed into a software program to produce, or map, a phylogeny. This does not mean that the phylogeny is the most accurate depiction of the trait's history, nor that vertical transmission best accounts for its distribution. This may seem obvious, but a number of studies cited in the target article are founded on such erroneous logic.

The absolute value of a goodness-of-fit measure, such as RI or CI or even the familiar R^2, is rarely informative. Rather, the same data must be analyzed with multiple models to make sense of measures of fit. Statistical measures developed to test for "treeness" are also of little help. They are based on strong assumptions about evolutionary process that cannot be casually applied to data produced by any evolutionary process. Indeed, all existing phylogenetic methods make strong assumptions about independence of lineages, rates of evolution, and other important aspects of descent, and biologists rarely employ any such method without first exploring its sensitivity to violations of these assumptions with simulated data. We fail to see how, without explicit models of cultural evolution and simulation studies, we can infer from published work that phylogeny provides the most accurate depiction of a trait's history.

2. Most cultures are of course made up of multiple traits, each of which may have a different phylogeny. Untangling the distinct phylogenies of separate traits is complicated (McElreath 1997), but assuming that all traits have the same tree simply avoids the issue. Using a narrow range of conserved vocabulary to construct language classifications yields a narrow view of language evolution – other aspects of language typically have different histories (Thomason & Kaufman 1988). Even among well-behaved biological species, different loci sometimes have different phylogenies (Enard & Pääbo 2004). Indeed, few geneticists would even attempt to construct a single phylogeny for the entire genome. The bulk of what we know about human history suggests strong mixing at many scales. Hence, assuming populations evolve independently, as typical maximum likelihood does, for example, is something few biologists are now willing to assume (Relethford 1998).

3. The authors support the use of a phylogenetic approach in comparative analyses to deal with Galton's problem, claiming (sect. 4, para. 2) that "evolutionary methods . . . (e.g., the phylogenetic analyses) work equally well for both biological and cultural evolution." Unfortunately, this is not true. A recent simulation study shows that as the prevalence of horizontal transmission of cultural traits between populations increases, so do Type I errors (rejection of a true null hypothesis) (Nunn et al. 2006). Importantly, a tiny amount of horizontal transmission is sufficient to cause serious problems. This parallels recent empirical work in biology which shows that trying to correct for phylogeny when working with rapidly evolving traits such as bird song can introduce serious error (Rheindt et al. 2004). More to the point, how can we claim that methods developed for analyzing genetical evolution work "equally well" for culture when we know, for example, how sensitive phylogenetic contrast analyses are to topological inaccuracies (Symonds 2002)?

4. The authors scrupulously differentiate macroevolutionary from microevolutionary questions, but others they cite have been less careful. Cavalli-Sforza and Feldman (1981) adopted the terms vertical and horizontal transmission from the field of epidemiology to denote, respectively, parent-offspring transmission and transmission between any two (usually unrelated) people. Soon these terms were adopted for use at the intergroup level, referring to traits that were spread from parent to daughter populations and between neighboring populations. Is an extrapolation from micro- to macroevolutionary processes legitimate? For example, from a study of Aka pygmies showing vertical transmission (parent-to-child) to account for a large majority of skills learned by children (80% of skills studied), is it appropriate to infer that Aka culture *as a whole* is highly conservative (Hewlett & Cavalli-Sforza 1986, p. 933)? The unstated assumption here is that the transmission patterns that occur within populations are the same as those that occur between populations. This, however, is untested because we have no measure of the extent of horizontal transmission between different populations, for example, between Aka and other pygmy populations, or between Aka and non-pygmy populations. Furthermore, even if all transmission is vertical, if there is any intermarriage between groups (or other kinds of immigration), vertical transmission within groups will not preserve variation between groups. A particularly clear example of the mismatch between transmission modes within and between populations, specifically inferring micro from macro patterns, comes from language. There is good reason to believe that portions of language are highly conserved within cultural lineages (Cavalli-Sforza et al. 1992), and yet we know that parents have limited influence on the language of their children after an early age; immigrant children do not speak their new national languages with their parents' accents.

To be clear, we are not arguing that cultural evolution, because of horizontal transmission, invalidates an evolutionary approach, only that it requires novel treatment within a general evolutionary framework. More specifically, we think that some tree-based approaches are highly flawed (Borgerhoff Mulder et al. 2006) and need more thought (Eerkens et al. 2006). Analogies are powerful things. But returning to first principles and considering how cultural evolution functions in its own right are, in the long run, more powerful yet.

More generally, we think that this is a fabulous article – a wide-ranging and truly creative review, bristling with insight

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and offering an inspirational glimpse into a very new kind of social science that may exist in the future. Our only concern is that readers may run with the ideas without thinking carefully about each step.

Evolutionary theory and the riddle of the universe

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Abstract: An effective restructuring of the social sciences around the evolutionary model requires that evolutionary theory has explanatory power with respect to the spread of cultural traits: The causal mechanisms involved should be structurally analogous to those of biological evolution. I argue that this is implausible because phenotypical consequences of cultural traits are not causally relevant to their chances of "survival."

That there exists a certain likeness between the evolution of species and the manner in which cultural traits are propagated, stands beyond doubt. Before we jump to conclusions and start remodeling the social sciences according to the evolutionary blueprint that biology provides, however, it is important to have a clear indication that the evolution of cultural traits is not merely similar to biological evolution, but structurally analogous to it. Therefore, the important question is not whether models based on evolutionary theory are roughly *descriptive* of the spread of cultural traits, but whether the evolutionary model has *explanatory power* with respect to the process by which that spread occurs. And for this to be the case, the model has to get the causal mechanisms of the process right.

In the story "The Riddle of the Universe and Its Solution," Czerniak (1981) describes a situation that would allow for a positive verdict on this score. It is useful to examine this situation, because it rather glaringly differs from the situation that we find ourselves in with respect to the propagation of ideas and other cultural traits. Czerniak imagines that, for humans, there exists an idea analogous to a Gödel sentence for computers. People who have this idea go into a catatonic state from which they are unable to recover. The propagation of such an idea (or rather, the process by which it goes extinct) would be truly analogous to biological evolution. The reason for this is that the causal system at work would be structurally analogous to selection of genes by biological evolution: A phenotypical consequence of having the Gödel idea (namely, going into catatonic state) is itself responsible for its lower chances of being propagated – just as the phenotypical properties associated with genes may cause their bearers to go extinct.

The fact that this story strikes us as science fiction suggests that, in reality, it does not work like this. At least on the face of it, the propagation of ideas and other cultural traits does not involve selection on their phenotypical properties (if that term is at all well defined). Ideas, artifacts, and other cultural traits are subject to changing levels of popularity, sometimes as a result of their becoming more or less useful over time, sometimes because of other factors. But surely the decline in popularity of, say, Dixieland music is not due to any phenotypical consequences of liking Dixieland music. In point of fact, liking Dixieland music does not prevent one from giving away Dixieland records for free, however much the decline in popularity of such records in the human population may resemble the evolutionary process by which genes become infrequent in a population of animals. In contrast, such a connection does exist between having a gene and being able to propagate it (namely, if the gene is bad for you, you die before you get the chance to propagate).

Mesoudi et al. attempt to anticipate the problem of identifying such causal mechanisms by stating that "just as Darwin formulated his theory of evolution with little understanding of genes or Mendelian inheritance, a theory of cultural evolution likewise does not necessarily have to rest on the existence of memes or particulate cultural transmission" (sect. 1, para. 12). But this confuses an ontological condition with an epistemological one. The relevant issue here is not whether Darwin *knew* about the mechanisms of inheritance via genetics; the relevant issue is that such mechanisms *exist* and are *causally relevant* to the biological phenomena that we want to explain. In other words, what convinces us of the usefulness of the evolutionary framework in biology has nothing to do with the epistemological position Darwin was in when working out the principles of evolutionary theory; it has to do with the fact that his theory, by and large, appears to be true.

The biological sciences are organized around evolutionary theory because evolution has causal relevance for each of the disciplines involved. For a similar organization of the social sciences to be an effective restructuring, rather than a case of plastic surgery, it is important to show that such causal relevance also exists for the various disciplines that make up the social sciences. Hence, the mechanisms by which cultural traits are propagated cannot be sidestepped as easily as Mesoudi et al. suggest, and they would, therefore, do well to offer some convincing arguments for the existence of such mechanisms. Otherwise our restructured social science, modeled after the biological plan, will be like a toy model of a Boeing 747. It will look just the same, but it won't fly.

It is not evolutionary models, but models in general that social science needs

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Abstract: Mathematical models are potentially as useful for culture as for evolution, but cultural models must have different designs from genetic models. Social sciences must borrow from biology the idea of modeling, rather than the structure of models, because copying the product is fundamentally different from copying the design. Transfer of most cultural information from brains to artificial media increases the differences between cultural and biological information.

Mesoudi et al. make a plea for the use of evolutionary models, developed for analyzing genetic evolution, in analyzing cultural influence and change. Indeed, they provide many illuminating examples of the usefulness of modeling in social sciences, but the connection to mathematical models of biological evolution is often indirect, sometimes only metaphorical. For example, in section 2.1.2 the authors cite Mace and Pagel (1994), who treat cultural traits as equivalent to biological characters, with independent instances of cultural change occurring when a cultural trait is invented, acquired from another culture, changed, or lost. This situation is very different from biological evolution, though, where "acquired" is not a possibility. Further, cultural traits are not like Mendelian units, independent of one another – they influence one another, they have different sizes and different nestings, and, as Mesoudi et al. note, they are frustratingly difficult to define.

Under these conditions, it is surprising that models developed to analyze biological evolution are also useful for looking at cultural development. But the value of the models may stem not so much from their link to evolutionary theory as from the way that they force investigators to define terms, use consistent categories, and in general discipline their data. Mathematical

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