serious ontological divergences like those which have split the traditional social sciences.

In support of a unified theoretical framework that is conceptually flexible and inclusive, Mesoudi et al. propose a program of research that is methodologically pluralistic, incorporating techniques imported from evolutionary biology as well as ones that are better established in the social sciences. Unfortunately though, it appears that the authors take such a dismal view of social anthropology that they rather downplay the role that ethnography could play in this enterprise by subsuming it within ethnology – the synthesis of ethnographic case studies into cross-cultural databases (e.g., Murdock 1967) – and a more generic and less well-defined category of "anthropological field studies." The latter encompasses a wide range of research styles, some of which differ markedly from ethnographic fieldwork – particularly in the degree to which they employ a "top-down" rather than a "bottom-up" approach. Thus, questionnaire-based studies (e.g., Hewlett & Cavalli-Sforza 1986), psychological experiments (e.g., Barrett 2004), and economic games (Henrich et al. 2005) in small-scale societies are designed to investigate specific anthropological problems using highly structured data-collection strategies that are implemented over relatively short periods of time. The time frame of ethnographic research is much greater, requiring months and often years of fieldwork, the aims and outcomes of which are only loosely contained within the parameters set by a predetermined research question. Compared to other approaches, ethnographic methods are more informal and typically consist of unstructured or semi-structured interview techniques and "participant-observation," which involves immersing oneself in the lifeways of a community and learning the language and habits of its members firsthand (e.g., Bradburd 1998).

Rather than focusing on isolated subsets of cultural complexes, ethnographers attempt to situate behaviours within wider contexts of cultural meaning, event histories, and social relationships. For example, whereas an economic game experiment (e.g., Henrich et al. 2005) would investigate norms of reciprocity and punishment through performance in a money allocation task, an ethnographer might focus instead on different orders and currencies of exchange within a particular culture. Thus, an ethnographic analysis might compare and contrast the sorts of expectations that individuals have of monetary transactions with strangers, with the social and moral obligations implied by the giving and receiving of gifts among kin, friends, and allies (Bloch & Parry 1989). Moreover, ethnographic accounts of the "natural" settings in which cultural behaviours are expressed and evaluated are certainly compatible with more structured experimental studies (e.g., Astuti et al. 2004; Henrich et al. 2004). Using the framework developed by Mesoudi et al., these approaches could be combined to investigate cultural micro-evolution within populations in exactly the same way as field-based studies of animal behaviour in the wild complement studies carried out in captivity and in laboratory conditions.

Ethnographic studies can also make a useful contribution to our understanding of cultural macro-evolution. Although studies indicate that cladistic methods can be as useful for reconstructing cultural histories as they are for recovering and classifying the relationships among species (e.g., Collard et al. 2005; 2006), the underlying mechanisms responsible for generating and maintaining cultural lineages remain poorly understood. Using evidence from the ethnographic record, Durham (1990; 1992a) has proposed that the apparent prevalence of warfare, language barriers, endogamy, and ethnocentricism in human societies may act in a similar way to reproductive isolating mechanisms that restrict gene flow among biological populations and which are believed to be important in speciation. Collard and I found evidence of these mechanisms in the phylogenesis of Turkmen textile designs, which, we argued, might be explained by ethnographic reports relating to the extent of intertribal warfare and endogamous marriage practices (Tehrani & Collard 2002). However, it should be noted that the presence and influence of these mechanisms cannot be assumed to be universal (e.g., Jordan & Shennan [2003] found branching processes to be much less dominant in Californian basketry traditions) and nor can they be assumed to be constant: Blending among Turkmen textile traditions increased in importance following the pacification of the Turkmen tribes in the late nineteenth century and the introduction of commercial craft production (although branching continued to dominate). Thus, as well as varying from case to case, the processes responsible for generating patterns of cultural diversity can change significantly within a few generations. Ethnographic studies can advance our understanding in this area by shedding more light on the specific social, economic, and political conditions that cause groups to become isolated from one another or encourage them to interact. Moreover, long-term participant-observation studies of cultural learning can help to establish which traditions are likely to be strongly affected by social change and rates of inter-group contact, and which ones are more stable and long-lasting (e.g., Pétrequin & Pétrequin 1999).

Unfortunately, in recent decades there have been relatively few ethnographic studies that have directly addressed the issues that I have raised here. This can largely be accounted for by the rise of so-called hermeneutic approaches (e.g., Clifford & Marcus 1986; Geertz 1973) which focus on the problems of interpreting meaning and experience in different cultures, and which are inspired more by movements in literary criticism and philosophy than by the social or biological sciences. However, while the idea of a science of culture has fallen out of fashion in mainstream social anthropology, I have attempted to show that there is considerable potential for developing an ethnographic research agenda within the framework proposed by Mesoudi et al. The starting point for this agenda is recognising that by carrying out long-term fieldwork in a single community and observing the interactions and behaviours of its members in the absence of experimental controls, ethnographers can provide important insights into the evolution of culture that would complement – or possibly challenge – those obtained by the approaches discussed in the article.

Generative entrenchment and an evolutionary developmental biology for culture

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Abstract: Mesoudi et al.'s new synthesis for cultural evolution closely parallels the evolutionary synthesis of Neo-Darwinism. It too draws inspiration from population genetics, recruits other fields, and, unfortunately, also ignores development. Enculturation involves many serially acquired skills and dependencies that allow us to build a rich cumulative culture. The newer synthesis, evolutionary developmental biology, provides a key tool, *generative entrenchment*, to analyze them.

In 1982, Mayr and Provine celebrated the evolutionary synthesis, the articulation of disciplines into a population genetic – driven theory of evolution (Mayr & Provine 1980). Sewall Wright's absence was widely felt (Mayr did not invite him). His place and that of mathematical theory had to await Provine's (1986) masterful biography. Present but *not* felt was Viktor Hamburger, representing embryology, the disenfranchised mother of evolution (Richards 1992). But not disenfranchised for long: Discoverers of HOX genes, phylogeneticists, embryologists, and renaissant paleontologists recruited partners to a fusion as evolutionary developmental biology became the *newer* synthesis, one increasingly overreaching the original. Raff (1996), Arthur

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(1997), Davidson (2001), Schlosser and Wagner (2004), Carroll (2005), and others drive an expansive adaptive radiation of the new theory that even reaches culture, with Oyama et al. (2001), Jablonka and Lamb (2005), and Odling-Smee et al. (2003). This list could have been quadrupled (Maienschein & Laublicher 2006).

Mesoudi et al. survey and inform a synthesis increasingly stimulating research throughout the human sciences. They embrace the mathematics that Mayr avoided but reproduce the other mistake: development is far too central to be ignored in an account of cultural change, even more so than for biological evolution. Crucial to the architecture of the theory, development also gives handles on classes of phenomena not addressed effectively by any part of their new synthesis (Wimsatt & Griesemer 2006).

Biological life cycles begin with zygotic genomes, complete at birth, participating on cue in rich downstream interactions with their embodying and embedding contexts. Surviving organisms differentially become parents to make new zygotes. In this framework, one can abstract and separate out heredity, development, and selection (Wimsatt 1999), simplifying components not being directly studied or modeled, often treating problems as "nearly decomposable" without major distortions of evolutionary dynamics. In this problematic limit (Griesemer 2005), development is commonly lumped with selection as a black-box scalar multiplier for gene frequencies, and then ignored.

By contrast, transmission of cultural information is *not* complete at birth: it has barely begun. As the authors note, cultural transmission is commonly horizontal, generating different dynamics from those possible for biology. As they fail to note, individual enculturation is most often sequentially dependent: We *must* learn arithmetic (and many other things) well before calculus. Agents accumulate, coadapt, and construct contents and practices throughout the life cycle. Earlier assimilations potentiate, filter, and amplify, selecting and often transforming (Sperber 1996) later acquisitions. New contents may transform agents' connections in the social network mediating reception and transmission. Such sequential dependencies are not modeled in any extant theory. Furthermore, in development, selection and heredity are almost impossibly confounded and path-dependent, and details of individual history matter (Wimsatt 1999). Evolutionists and creationists taking the same curriculum in population genetics and developmental biology would draw, systematically, quite different lessons from it.

Why are some elements of a different culture readily diffusible, others rejected, and others transformed nearly unrecognizably? Epidemiological models of infectibility and resistance can utilize networks to model contacts but ignore cultural contents. Conformity bias and broad categories of "content-based bias" do not have the structure to deal with sequence-dependent skill acquisition or model the specificity and relatedness of ideas or technologies. One needs structures capable of dealing with the content.

One way looks promising. Developmental dependency of elements in the life cycle characterizes both biological and cultural evolution: You generate what comes later from what you have earlier. Inferential structures (including scientific theories and legal codes) have dependencies too. Biological, cognitive, and cultural architectures are all constrained by and tuned to creatively elaborating these dependencies. We can use them to build theory.

To Lewontin's (1970) three requirements for evolution (heritable variance in fitness) add two more: (4) developmental trajectories show sequential dependencies (*generativity*), and (5) systemic elements differ in downstream consequences and magnitude of effect (*differential generative entrenchment*). These provide a minimal but absolutely general account of development. All nontrivial evolutionary systems satisfy all five assumptions (Wimsatt 2001). And much more follows. Differential generative entrenchment yields a robust evolutionary dynamics and many new consequences (B. Arthur 1994; Schank & Wimsatt 1988; 2000; Wimsatt & Schank 1988; 2004). The key is neo-Darwinian: Larger mutations give more places for something to go wrong and so are exponentially less likely to be adaptive. So they are also less likely to be incorporated in evolution, generating a differential conservatism. An evolutionary dynamics arises simply from differential dependency, a general feature of organizational structure.

Here are some of the new consequences:

1. Features earlier in development that are more generatively entrenched should tend to be more evolutionarily conservative.
   1a. This yields von Baer's "laws," roughly, that earlier developmental stages tend to look more alike than later stages (Gould 1977).
   1b. Generative entrenchment in early development also predicts life *cycles*: Successive generations must start in places like their parents, however much they diverge later, until reproduction "closes" the cycle (Wimsatt 2001).
2. New population-genetics models of entrenchment (Schank & Wimsatt 1988) give purchase on "complexity catastrophes" and the evolution of modularity (Wimsatt & Schank 1988; 2004) that are also suggestive for culture.
3. An entrenchment account of phenomena spoken of as "innate" captures the maximal consistent subset of criteria for innateness and predicts new ones (Wimsatt 1986; 2003).
4. For culture, as things get more deeply entrenched, we resist changing them, suggesting how things become conventional, standardized, and acquire a normative loading.
5. Standardization is crucial to technological progress when further developments require common components, a more general feature of the truly *cumulative* culture sought by Richerson and Boyd (2005).
6. In literary theory, Turner (1991) employs entrenchment to explain differences between literal and figurative meaning.
7. Differences between biology and culture in how we can generate and deal with deeply entrenched changes are crucial to the rapidity and sometimes revolutionary character of cultural change (Wimsatt & Griesemer 2006).

Evolutionarily recent changes in deep structures provide apparent exceptions worth closer study (Raff 1996). Some changes (e.g., *bicoid*; Schmitt-Ott & Wimmer 2004) first appear as fine-tuning for a control structure, then co-opting and amplifying the role of that control structure to become deeply entrenched (like our information technologies). Other organizational features matter in determining entrenchment. Selection in evolutionary genetics is modulated by linkage, drift, and population structure and makes a richer theory for that. Similarly, a mature theory of generative entrenchment should articulate with other systematic organizational factors, such as redundancy, sequestration, modularity, and canalization. All decrease entrenchment in diverse ways with further implications. There are other fruitful complications for biology and many more for culture (Wimsatt & Griesemer 2006).

Differential dependencies – what remains invariant, and what changes with what – can produce organizational information from comparative data. In 1987 Rasmussen proposed a tentative architecture for *Drosophila* development inferred from 22 developmental mutations (Rasmussen 1987) – still often correct despite massive amounts of new data. Still key in evolutionary developmental biology, analyses of relative stasis and dependency help to unravel developmental programs and predict phylogenetic relationships (Arthur 1997; Davidson 2001). They can be used to good advantage in studying cultural change: Dependency relations are often more readily discovered and analyzed than is selection, and complement other methods in the powerful new paradigm.

Population structure is crucial for biological evolution (Wade & Goodnight 1998), but the breeding population for one trait does for all. Enculturated individuals getting traits piecemeal have as

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many breeding populations as reference groups and the salience of these groups shifts over time. Acquisition of sequential skills organizes many of these transitions (Wimsatt 2001). Divergent specialties and values midwife heterogeneous societies and subcultures as we bootstrap institutions, technologies, and material cultures to maintain and elaborate them (Basalla 1988). Molar structures – settlements, schools, governments, legal codes, religions, firms, and markets that scaffold our enculturation – organize, regulate, and contribute to its content. Entrenchments organize contingencies of practice into more stable structures, only to be modulated by the next round of contingencies. This produces for history and culture a fractal organization of relevant detail on many size and time scales (Gaddis 2002). Entrenchments thereby help to generate a qualitative understanding of the organization and richness of even "thick" culture through the development of individuals and the more stable superindividual structures (Wimsatt & Griesemer 2006).

Authors' Response

A science of culture: Clarifications and extensions

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Abstract: We are encouraged that the majority of commentators endorse our evolutionary framework for studying culture, and several suggest extensions. Here we clarify our position, dwelling on misunderstandings and requests for exposition. We reiterate that using evolutionary biology as a model for unifying the social sciences within a single synthetic framework can stimulate a more progressive and rigorous science of culture.

R1. Introduction

We are pleased and encouraged by the generally positive tenor of the commentaries. The majority of commentators (**Barkow**; **Borgerhoff Mulder**, **McElreath**, **& Schroeder** [**Borgerhoff Mulder et al.**], **Cronk**; **Dennett & McKay**; **Kincaid**; **Lyman**; **Mende & Wermke**; **O'Brien**; **Pagel**; **Reader**; **Tehrani**; **Wimsatt**) accept the core features of our evolutionary framework, and many of them go on to recommend additions or extensions to our approach. These additions are discussed in more detail in section R2.

Several other commentators (**Aunger**; **Blackmore**; **Fuentes**; **Kelly**, **Machery**, **Mallon**, **Mason**, **& Stich** [**Kelly et al.**]; **Knudsen & Hodgson**; **Sopher**) agree with the need for an evolutionary approach to culture, but take issue with our particular framework or appear to reserve judgement until certain key issues are dealt with. Finally, **Borsboom**, **Bridgeman**, and **Read** appear to reject the premise that any (Darwinian) evolutionary approach can be applied to culture. The objections of all of these commentators are dealt with in section R3.

R2. Suggested extensions

We are very encouraged that the commentators have already proposed new branches to the synthetic evolutionary framework for studying culture that we illustrated in Figure 1, either by drawing new parallels with subfields of evolutionary biology that we omitted, or by drawing our attention to existing subfields of the social sciences that might appropriately fit into a unified science of cultural evolution. We do not see this as a failing of our original proposal and are broadly receptive to their suggestions. On the contrary, a significant test for our synthetic framework is whether it can usefully accommodate such additions, which we believe it can and does. After all, the modern synthesis that unified evolutionary biology (Huxley 1942) was far from complete when it was first outlined in the 1930s and 1940s, and evolutionary biology continues to incorporate new subdisciplines to this day (Carroll 2000; Kutschera & Niklas 2004).

R2.1. Omitted social science literatures

Kincaid, **Knudsen & Hodgson**, and **Sopher** point to areas of the social sciences that have already adopted evolutionary methods with some success, but which we failed to acknowledge in the target article. Kincaid and Knudsen & Hodgson cite "organisational ecology" in sociology (Hannan & Freeman 1989), whereas Knudsen & Hodgson and Sopher reference "evolutionary economics" (Nelson & Winter 1982). We welcome this opportunity to draw attention to such work and encourage its integration with our broader evolutionary framework. Given these fields' emphasis on large-scale and long-term interactions between entire organisations, this might require a new branch of the macroevolution section of Figure 1, perhaps drawing a parallel between population or community ecology (biology) and organisational ecology (culture).

Kincaid also mentions evolutionary game theory (Danielson 2004; Gintis 2000), which, although currently used extensively within economics, in fact represents a methodological tool that can be used to model cultural evolution more generally. This would complement the methods derived from population genetics discussed in section 3.1.2, and although game-theoretic methods are already used extensively within gene-culture coevolutionary theory (e.g., Boyd & Richerson 1985), there are clear opportunities to broaden their application to cultural phenomena.

Agent-based modelling (Axelrod 1997; Epstein & Axtell 1996; Kohler & Gumerman 2000) represents yet another means to model cultural evolution, and we are happy to highlight the potential utility of this within our framework. Indeed, this is a methodology that we ourselves have used to explore the coevolution of paternity beliefs and genetic variation underlying human mating behaviour (Mesoudi 2005). All of these mathematical tools have strengths and weaknesses, and each can be applied, in a "horses

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