A Darwinian Theory of Cultural Evolution Can Promote an Evolutionary Synthesis for the Social Sciences

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Abstract

The evolutionary synthesis of the 1930s and 1940s integrated the study of biological microevolution and biological macroevolution into the theoretically consistent and hugely productive field of evolutionary biology. A similar synthesis has yet to occur for the study of culture, and the social sciences remain fragmented and theoretically incompatible. Here, it is suggested that a Darwinian theory of cultural evolution can promote such a synthesis. Earlier non-Darwinian theories of cultural evolution, such as progress theories, lacked key elements of a Darwinian theory of cultural evolution (e.g., population thinking) that are necessary to promote a synthesis, while other contemporary theories of cultural evolution, such as memetics, make too stringent neo-Darwinian assumptions (e.g., high-fidelity replication) that are inconsistent with evidence regarding cultural transmission. Several examples are given which indicate the beginnings of an evolutionary synthesis for culture, where patterns of cultural macroevolution have been explained in terms of underlying cultural microevolutionary forces. Finally, it is argued that experimental simulations of cultural evolution can play an important role in this emerging synthesis.

Keywords

cultural evolution, cultural transmission, Darwinian evolution, evolutionary synthesis, gene-culture coevolution, population thinking

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1. The Evolutionary Synthesis in the Biological Sciences

Although the publication of *The Origin of Species* in 1859 (1968) is rightly seen as a pivotal moment in the history of evolutionary biology (Ghiselin 1969; Mayr 1982), it took several decades before the full impact of Darwin's ideas were felt by the biological sciences as a whole. This did not occur until the "modern synthesis" or "evolutionary synthesis" of the 1930s and 1940s (Mayr and Provine 1980; Mayr 1982; Kutschera and Niklas 2004), commonly seen as the result of six key works: Dobzhansky (1937), Huxley (1942), Mayr (1942), Simpson (1944), Rensch (1947), and Stebbins (1950). The major achievement of these researchers was to link biological microevolution (principles of change occurring within populations of single species) to biological macroevolution (large-scale patterns of change above the species level) and in so doing unifying biology into a coherent evolutionary science. The key development was the acceptance by most contemporary working biologists that the large-scale macroevolutionary temporal and spatial patterns of change and geographical distribution observed by paleontologists and naturalists, such as speciation and adaptive radiation, are extrapolations of the microevolutionary forces that cause changes in gene frequencies within populations, such as mutation, recombination, natural selection, and drift, as studied by experimentalists and mathematical modelers. In the words of one of the architects of the synthesis:

> The proponents of the synthetic theory maintain that all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transspecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species . . . it is misleading to make a distinction between the causes of micro- and macroevolution. (Mayr 1963: 586–587)

To give an example, consider the pattern of "punctuated equilibria" observed in the fossil record, in which species appear to undergo long periods of stasis interspersed with relatively shorter periods of morphological change. Although some have claimed otherwise (e.g., Gould and Eldredge 1977), Charlesworth et al. (1982) review extensive experimental and theoretical work demonstrating that different microevolutionary modes of selection can account for such patterns. Stabilizing selection, in which extreme phenotypes are selected against and eliminated from the population, can account for periods of stasis, while directional selection due to environmental change can drive populations to new body forms, resembling movement from one peak to another in an "adaptive landscape" (Wright 1932; Arnold et al. 2001).

This is not to imply, however, that the evolutionary synthesis has remained unchanged since 1950. The following decades have seen several major additions and revisions (Carroll 2000; Kutschera and Niklas 2004), including the details of molecular genetics (Watson et al. 1987), gene selectionism (Hamilton 1964), neutral theory (Kimura 1983), and multi-level selection (Okasha 2006). Other aspects of biology, such as development, have yet to be fully integrated into the synthesis, although the growing field of EvoDevo (Carroll 2005) suggests that an integration is likely. Nevertheless, these new theoretical and empirical advances were often made possible by the earlier integration of micro- and macroevolution into a single unified scientific discipline, and the evolutionary synthesis can be seen as a key determinant of the remarkable progress of the biological sciences in the past 50 years.

2. The Study of Culture is in a Pre-Synthetic State

In parallel to these events occurring in the biological sciences, the social sciences have also seen attempts to apply evolutionary principles to the study of human culture, although with very different results. Culture can be defined most usefully for present purposes as "information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission" (Richerson and Boyd 2005: 5). Viewing culture as an inheritance system in this way allows parallels to be drawn between cultural inheritance and biological/genetic inheritance, parallels which have led many scholars to propose theories of cultural evolution. Darwin ([1871] 2003) himself drew such parallels, as did several of his contemporaries (e.g., Muller 1870; Pitt-Rivers 1875; James 1880). Various theories of cultural evolution then proliferated, most prominently in cultural anthropology (Steward 1955; White 1959; Sahlins and Service 1960), but also in the form of evolutionary epistemology (Campbell 1974; Popper 1979; Plotkin 1982) and quantitative population-based models of cultural evolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland et al. 1995; Feldman and Laland 1996), continuing through to the present decade (Aunger 2000a, 2002; O'Brien and Lyman 2002; Plotkin 2002; Shennan 2002; Mesoudi et al. 2004; Pagel and Mace 2004; Richerson and Boyd 2005; Mesoudi et al. 2006b).

Yet none of this work has stimulated an evolutionary synthesis for the study of culture in the way that the evolutionary synthesis of the 1930s and 1940s fused evolutionary biology into a single coherent discipline. The current situation in the social sciences is not dissimilar to the state of pre-synthesis evolutionary biology, which, as Mayr (1982) notes, was divided along a sharp micro- versus macroevolutionary divide:

> Through the first third of the twentieth century the gap between the experimental geneticists and the naturalists seemed so deep and wide that it looked as if nothing would be able to bridge it . . . The members of the two camps continued to talk different languages, to ask different questions, to adhere to different conceptions. . . . (Mayr 1982: 566)

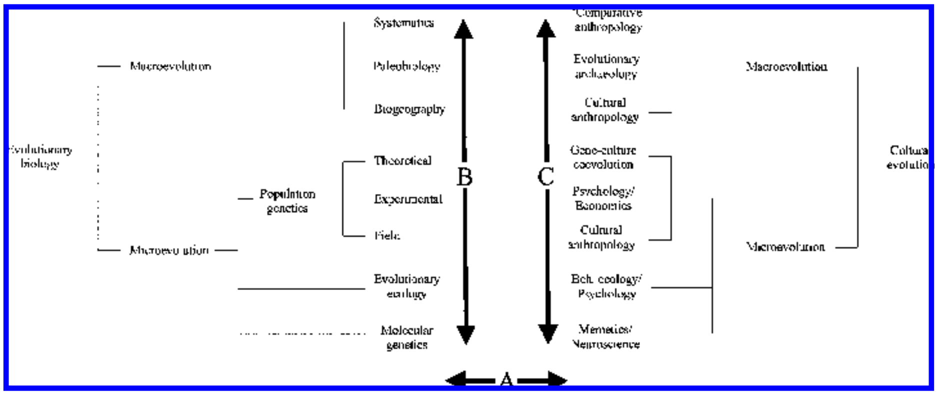

Figure 1.
The structure of modern-day evolutionary biology (left-hand side), as given by Futuyma (1998), and the corresponding structure of a science of cultural evolution (right hand side), as proposed by Mesoudi et al. (2006b). Mesoudi et al. (2006b) argued that methods, findings and theories can be exchanged between corresponding branches of the biological and cultural sciences (A), to the mutual benefit of both. Here it is argued that, just as evolutionary theory synthesised the biological sciences (B), it can do the same for a science of culture (C).

In fact, the social sciences are currently in a much worse state than pre-synthetic biology. Rather than two camps, there are several isolated camps, representing the different disciplines of cultural anthropology, archaeology, psychology, economics, sociology, and history, each with their own terminologies, theories, and methods. Still, a rough "micro versus macro" divide can also be discerned in the study of culture (Mesoudi et al. 2006b) and, doing so, reveals the same deep division as noted by Mayr for pre-synthetic biology. Some social science disciplines, such as archaeology and history, focus on large-scale changes in human culture over extended periods of time; these can be considered the study of cultural macroevolution. Seldom, however, are these macroevolutionary changes considered to be reducible to behavior and decision making at the level of the individual or small group. Other disciplines, such as psychology or (micro-)economics, deal with decision making in single individuals or small groups; these can be considered the study of cultural microevolution. Seldom, however, are these microevolutionary decisions extrapolated to the population level. Where culture *is* considered in these disciplines, such as in cross-cultural psychology, it is often treated as a static background variable that influences individual cognition (e.g., Chua et al. 2005), rather than also being the *result* of individual cognition. Cultural anthropology, the discipline that professes to be most engaged in the study of culture, remains the most isolated of these disciplines. Modern ethnographers seldom attempt to extrapolate their findings from single detailed case studies to more general theories of cultural change. Instead, each society is seen as unique and ungeneralizable, while culture is often viewed in a holistic manner that denies the possibility of reduction to lower-level causes (Ingold 2000, 2007).

It does not need to be this way. In the following sections I argue that the theory of cultural evolution can serve to unify the social sciences, by allowing an evolutionary synthesis to link the study of cultural microevolution to the study of cultural macroevolution. This proposal builds upon and extends a previous proposal (Mesoudi et al. 2006b) that concepts and methods from evolutionary biology can be used to study culture (Figure 1), given the similarities between biological and cultural change. Here I suggest that, as well as the exchange of concepts, methods, findings, and theories *between* corresponding branches of the biological and the social sciences (e.g., between paleobiology and archaeology), an evolutionary approach to culture can also stimulate the exchange of concepts, methods, findings, and theories across different disciplines *within* the social sciences (e.g., between psychology and archaeology). First, however, it is instructive to ask why none of the previous theories of cultural evolution have resulted in an evolutionary synthesis for the study of culture.

3. The Multiple Theories of Cultural Evolution

The term "cultural evolution" has been used in many different and often conflicting ways. Campbell (1965) reviews many of these different theories of cultural evolution (Table 1), dividing them into two groups. In the first group are "theories descriptive of the fact and course of socio-cultural evolution" (Campbell 1965: 21). These include so-called *transformation theories* (e.g., Greenberg 1959), which hold that all cultural forms share a common source; *unilinear progress theories* (e.g., Tylor 1871; Morgan 1877; Spencer 1896), in which all cultural change represents progress in a specific direction and societies progress along fixed, predetermined stages; and *multilinear progress theories* (e.g., Steward 1955; White 1959; Sahlins and Service 1960), in which societies progress through stages, but the exact course of this progress may differ in response to different environments.

The second category contains "theories descriptive of the process of [cultural] evolution" (Campbell 1965: 22). These are notable for providing details regarding how and why culture changes, and do not insist on progress or fixed

Table 1. Theories of cultural evolution, based on Campbell (1965: 20–22). Recent theories of cultural evolution (5 and 6) have been added to Campbell's original four.

Classification	Theory	Description
"Theories descriptive of the fact and course of socio-cultural evolution" (Campbell 1965: 21)	1. Transformation theories (Greenberg 1959)	The transformation of all cultural forms from a single common source (countering separate creation theories)
	2. Unilinear progress theories (Spencer 1896; Tylor 1871; Morgan 1877)	All cultural change in specific societies represents progress; all societies go through the same progressive stages; less advanced contemporary societies resemble earlier stages of more advanced contemporary societies
	3. Multilinear progress theories (Steward 1955; White 1959; Sahlins and Service 1960)	Progress or increasing adaptive adequacy in response to the environment; different environments may generate different courses of cultural evolution
"Theories descriptive of the process of [cultural] evolution" (Campbell 1965: 22)	4. Blind-variation-selective-retention (Campbell 1965)	Blind and haphazard variations differentially propagated due to exigencies of different environments
	5. Memetics (Dawkins 1976; Blackmore 1999)	Differential selection and inheritance of discrete cultural replicators—memes—which exhibit longevity, fecundity, and fidelity
	6. Gene-culture coevolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985)	Quantitative population-based models of cultural evolution and gene-culture coevolution

stages. Campbell (1965) placed his own *blind-variation-and-selective-retention* (BVSR) theory into this category, in which blind or random variations are subject to consistent selection criteria, and the positively selected variants are preserved. Table 1 additionally lists the two main approaches to cultural evolution to have emerged since Campbell wrote his summary (after Laland and Brown 2002): *memetics* (Dawkins 1976; Blackmore 1999), where cultural change occurs via the differential selection and inheritance of discrete cultural replicators, or memes; and *gene-culture coevolution* (e.g., Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), in which cultural change is modeled using quantitative population-based mathematical models, with culture often co-evolving with genetic evolution (although models of purely cultural change are also common). Note that this list is not intended to be exhaustive, nor is each category mutually exclusive (memetics, for example, can be studied using the mathematical modeling techniques of gene-culture coevolution: Kendal and Laland 2000).

Interestingly, a similar diversity of theories of biological evolution existed before the evolutionary synthesis in biology. Table 2 outlines five of these theories, as specified by Mayr (1980: 4–5). Mayr divided these theories along two dimensions. The first dimension is whether advocates of the theory saw species in *essentialist* (or typological) terms, where species constitute fixed and uniform types and evolutionary change occurs when one type abruptly turns into another type, or whether they adopted *population thinking*, focusing on the uniqueness of individuals and the consequent variation within each species, with evolution seen as gradual change in this variation within populations. The second dimension is whether the theory admitted the inheritance of acquired characteristics, where changes in the phenotype are transmitted directly to the genotype[1] or whether the theory maintained the separation of germ line and soma (Weismann's barrier). Early pre-Darwinian evolutionary theories such as *Geoffroyism* (e.g., Semon 1921) and *orthogenesis* (e.g., Lamarck 1809) were

Table 2. Theories of biological evolution, from Mayr (1980: 4–5).

Theory	Description	Essentialist or populationist?	Inheritance of acquired characteristics?
1. Geoffroyism (Semon 1912)	Evolutionary change caused by the direct influence of the environment	Essentialist	Exclusively
2. Orthogenesis (Lamarck 1809)	Evolutionary change caused by a built-in drive toward progress and perfection	Essentialist	Exclusively
3. Saltationism (Goldschmidt 1940)	Evolutionary change caused by large and sudden mutations	Essentialist	None
4. Darwinism (Darwin 1859)	Slow, gradual evolutionary change through natural selection	Populationist	Some
5. Neo-Darwinism (Weismann 1883)	Darwinian but with no inheritance of acquired characteristics	Populationist	None

essentialist and held that change occurred exclusively through the inheritance of acquired characteristics. Evolution according to these theories was seen as a progressive drive toward perfection. *Saltationism* (e.g., Goldschmidt 1940) retained the essentialism of those earlier theories, seeing change as occurring when macromutations abruptly appear and transform a species into a new type, but did not admit the inheritance of acquired characteristics, influenced by the discoveries of early geneticists. *Darwinism* (Darwin [1859] 1968) saw the introduction of population thinking, but still admitted the inheritance of acquired characteristics. Finally, *Neo-Darwinism* (Weismann 1883) featured both population thinking and the separation of germ line and soma.

It is instructive to compare the various theories of cultural evolution listed in Table 1 with the theories of biological evolution given in Table 2. The early theories of cultural evolution that Campbell (1965) labels unilinear or multilinear progress theories appear to most resemble orthogenetic theories of biological evolution, in that they share a progressive view of evolution as guided by a built-in drive toward perfection along fixed and predetermined stages. As Campbell (1965) notes, this view of evolution better resembles development, i.e., the progressive unfolding of an embryo over successive fixed stages, than selection-based evolution.[2] Indeed, we might attribute progressive theories of both biological and cultural evolution to the influence of Herbert Spencer, from whom many cultural anthropologists of that period acquired their theory of evolution (Freeman 1974).

Mayr (1980) argued that orthogenetic theories of biological evolution were fundamentally incompatible with an evolutionary synthesis because of their essentialist and progressive underpinnings. According to orthogenetic theories of biological evolution, evolutionary change is the abrupt transformation of one class of entity into another class, caused by some vaguely specified built-in drive along discrete predetermined stages and toward a specific endpoint. There was no room and no need in these theories for explanations of change in terms of microevolutionary mechanisms. It was only when population thinking became established within biology that the evolutionary synthesis could occur. Focusing on the variation between individuals within populations allowed macroevolutionary change to be seen as caused by microevolutionary forces, such as natural selection, drift, and recombination, which gradually change within-population variation over successive generations.

The same applies to progress theories of cultural evolution. Viewing cultural change as the abrupt transformation of a society from one stage to another, with this change caused by a built-in drive along discrete predetermined stages, left no room and no need for explanations of cultural change in terms of microevolutionary cultural mechanisms. It should also be noted that, besides their unsuitability for promoting a synthesis, orthogenetic/progressive theories of both biological and cultural evolution are empirically unsupported; neither species nor societies move along progressive stages toward fixed endpoints (Freeman 1974; Rindos 1985).[3] This is not to say that specific cultural trends may not demonstrate a "progressive" increase in some specific characteristic (e.g., the rapid increase in computer processing power in recent years), merely that this progress is neither fixed nor inevitable and does not take the form of discrete stages.

Saltationist theories of biological evolution have no direct parallel with any of Campbell's (1965) types of cultural evolution given in Table 1, although they might be said to resemble "great leaps by great minds" theories of cultural evolution which are sometimes held by historians (e.g., Constant 1980). Here, cultural change is seen as resulting from large, discontinuous change ("great leaps") caused by a small number of highly influential individuals ("great minds"), somewhat similarly to Goldschmidt's (1940) macromutations. Like the progress theories of cultural evolution, great leap theories leave no room for microevolutionary processes acting on within-population variation. They are, moreover, inconsistent with evidence that cultural change is typically gradual and cumulative (Basalla 1988; Petroski 1994; Ziman 2000).

What of later theories of cultural evolution? Both Campbell's (1965, 1974) BVSR theory of cultural evolution, in its insistence on "haphazard, random and blind" variation, and memetics (Blackmore 1999), which is predicated on the existence of replicators (memes) that possess longevity, fecundity, and fidelity, appear to most resemble the neo-Darwinian theory of biological evolution. Although these do not suffer from the essentialist or progressive flaws of the earlier theories of cultural evolution, certain assumptions of BVSR theory and memetics appear to be inconsistent with data from psychology regarding the details of cultural microevolution. As highlighted by Sperber (2000) and Atran (2001), "replication" seems to provide a poor model for cultural transmission, which more resembles biased reconstruction rather than high-fidelity replication (Bartlett 1932). An insistence on blindness also appears to be unnecessary (Mesoudi, in press), given the existence of various cognitive mechanisms that act to guide cultural change.

4. Darwinian Cultural Evolution

I suggest that the most useful model for a theory of cultural evolution, and the one most likely to facilitate an evolutionary synthesis for the study of culture, is the fourth in Mayr's list in Table 2: "Darwinian" evolution. This theory was introduced by Darwin in *The Origin of Species*, is based on population thinking, yet lacks many of the details of genetic inheritance later established by the neo-Darwinians, such as the strict separation of genotype and phenotype, or the existence of high-fidelity replicators, that may not apply to cultural evolution.

This Darwinian theory of cultural evolution resembles that modeled by practitioners of gene-culture coevolution (Table 1), such as Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985). This work takes an explicitly population-based approach, borrowing the mathematical tools of population genetics to track changes in the frequencies of cultural traits within populations over successive generations. The microevolutionary forces that cause cultural variation to change may be the same as those that cause genetic variation to change, such as natural selection or drift (Cavalli-Sforza and Feldman 1981). Crucially, however, these models also incorporate microevolutionary cultural forces and assumptions that are different from those found in neo-Darwinian biological models, including horizontal, many-to-one, or one-to-many cultural transmission (Cavalli-Sforza and Feldman 1981), conformist or prestige-biased cultural transmission (Boyd and Richerson 1985), and blending inheritance and non-discrete cultural traits (Boyd and Richerson 1985; Henrich et al., in press). The following sections briefly outline the key components of this Darwinian theory of cultural evolution.

4.1. Evolution as "Variation, Selection, and Inheritance"

As stated most clearly by Lewontin (1970), Darwin's theory of evolution by natural selection can be conceptualized in abstract terms as embodying three principles: (1) variation exists between individuals within a population; (2) there is differential fitness, such that different variants are more or less likely to be passed on to subsequent generations; and (3) a correlation exists between parent and offspring in that variation, such that selected variants are preserved. Lewontin (1970) notes the generality of these principles, arguing that they can be applied to different levels of biological selection (e.g., replacing "individual" with "group" to give group selection, or with "gene" to give genic selection), and also hints at their application to cultural evolution: "No particular mechanism of inheritance is specified . . . the population would evolve whether the correlation between parent and offspring arose from Mendelian, cytoplasmic, or cultural inheritance" (Lewontin 1970: 1).[4] Applying these abstract principles more explicitly to culture, we can specify a Darwinian theory of cultural evolution: (1) cultural traits may vary within a population of individuals; (2) these cultural variants differ in their likelihood of persisting and being passed on to other individuals; and (3) there is some form of cultural transmission that causes a correlation between cultural parent (the model from whom a cultural trait is acquired) and cultural offspring (the individual acquiring the cultural trait). Mesoudi et al. (2004) present evidence for the existence of variation, selection, and inheritance in culture, drawing an explicit parallel with the argument presented by Darwin in *The Origin*.

Okasha (2006: 13–18) has recently argued that this abstract variation-selection-inheritance conceptualization of evolution is preferable to an alternative conceptualization proposed by Dawkins (1976) and Hull (1980), which requires the existence of replicators and interactors. Replicators are entities that exhibit copying fidelity (are faithfully transmitted accurately), fecundity (generate many copies), and longevity (persist long enough to affect their own replication), while interactors are entities that interact with the environment as expressions of those replicators. Okasha (2006) argues that this alternative replicator theory of evolution is inferior to the Darwin/Lewontin variation-selection-inheritance conceptualization because replicator theory imposes additional, unnecessary requirements for evolution—that replicators exhibit fidelity, fecundity, and longevity, and the existence of distinct and cohesive interactors—that should more properly be seen as characteristics that *result from* the evolutionary process: "if we wish to understand how copying fidelity and cohesiveness [of interactors] evolved in the first place, we cannot build these notions into the very concepts used to describe natural selection" (Okasha 2006: 16). Moreover, Henrich et al. (in press) use formal models to demonstrate that replicators are not necessary for cultural evolution; all that is required is some form of inherited variation. In essence, the existence of replicators and interactors are requirements of *neo-Darwinian* evolution, not *Darwinian* evolution (as defined in Table 2), and are not required by a Darwinian theory of cultural evolution. This does not preclude the possibility that some aspects of culture may be appropriately analyzed in terms of replicators/memes, if this can be empirically justified. Hence memetics can be viewed as a potentially useful sub-branch of the Darwinian theory of cultural evolution advocated here (Mesoudi et al. 2006b: 375).

4.2. Population Thinking

As noted above, a key prerequisite of the biological synthesis was population thinking: individuals within a species vary, and selection and other forces act to gradually change this variation over time. This contrasts with the essentialist orthogenetic theories of biological evolution and the corresponding progressive theories of cultural evolution. Richerson and Boyd (2005: 5–8) stress the importance of population thinking in analyzing cultural change, as demonstrated by their and others' population-based mathematical models of cultural evolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985, 2005). The evolutionary archaeologists O'Brien and Lyman (2000: 352–375) similarly argue, and present a detailed case study to demonstrate, that population thinking provides a better understanding of archaeological change than essentialist thinking, which has been the dominant mode of archaeological theorizing for much of the 20th century.

4.3. No Progressive Stages

Unlike unilinear and multilinear progress theories of cultural evolution, a Darwinian theory of cultural evolution does not prescribe the progression of societies along predetermined stages. Rather than appealing to vague, built-in drives, or stages that appear to come from nowhere, Darwinian cultural evolution explains cultural change in terms of specific and measurable microevolutionary mechanisms (see below).

4.4. The Possibility of the Inheritance of Acquired Characteristics

Table 2 highlights the fact that Darwin accepted to some degree the inheritance of acquired characteristics. It was not until Weismann (1883) and the rise of neo-Darwinism that a strict separation between genotype and phenotype was established. As noted in Section 4.1, a Darwinian theory of cultural evolution does not require a replicator-interactor separation: all that is required is that there is a trait correlation between cultural parent and cultural offspring. In this case, therefore, the issue of the inheritance of acquired characteristics becomes an invalid one, based on a false assumption (Hull 2000). On the other hand, Section 4.1 also left open the *possibility* of replicator-interactor dynamics in cultural change, where this is empirically justified. Even here, however, there is no reason why the inheritance of acquired characteristics (from interactor to replicator) cannot occur. Examples might include inferring the recipe of a cake from the cake itself (Blackmore 1999) or imitating overt behavior (assuming cakes and behavior are classed as interactors, and recipes and mental programs are classed as replicators). Indeed, mathematical models of cultural evolution have been developed that assume the inheritance of acquired characteristics (Boyd and Richerson 1985).

4.5. Unique Cultural Transmission Mechanisms

Darwin knew little about the precise mechanisms of biological inheritance, stating that "the laws governing inheritance are quite unknown" (Darwin 1859 [1968]: 76). As time went by, new findings from genetics provided details of these mechanisms, such as the aforementioned separation of genotype and phenotype, the details of recombination and diploid inheritance, and so on.

For cultural evolution, many of the details of cultural transmission (as well as the sources of cultural innovation and the forms of cultural selection) will differ from the biological case, although analogies with biological evolution may still be useful. Cultural transmission may be conformist, where the cultural trait exhibited by the majority of the population is disproportionately more likely to be adopted (Boyd and Richerson 1985; Henrich and Boyd 1998). Other biases involve preferentially copying individuals with certain indicator traits, such as success, prestige, age, or health (Henrich and Gil White 2001; Henrich and McElreath 2003). Content biases specify what kind of information is transmitted best (Henrich and McElreath 2003), such as a "social bias" that favors information concerning third party social interactions over equivalent non-social information (Mesoudi et al. 2006a), or emotional biases that favor social norms that prohibit disgust-eliciting actions (Nichols 2002). Cultural transmission may also be affected by the particular mechanism of social learning that is operating (e.g., motor imitation, emulation, stimulus enhancement, spoken language, or written language; Whiten et al. 2004) and the form of the information being transmitted (e.g., beliefs, values, attitudes, schemas, motor plans).

4.6. Drift and Historical Contingency

Stochastic processes such as drift (Kimura 1983) and founder effects (Mayr 1942) are known to play an important role in biological evolution. The same factors are likely to influence cultural evolution also, and this is consistent with a Darwinian theory of cultural evolution. Drift, in the form of undirected copy errors in cultural transmission, has been shown to account for certain archaeological phenomena (Cavalli-Sforza and Feldman 1981; Neiman 1995; Shennan and Wilkinson 2001) as well as aspects of more contemporary cultural data, such as the popularity of dog breeds or baby names (Bentley et al. 2004).

4.7. Multi-Level Selection

As illustrated by the above quote from Lewontin (1970), one benefit of an abstract variation-selection-inheritance conceptualization of biological evolution is that these processes can be applied to any level (or multiple levels simultaneously) of the biological hierarchy: genes, individuals, groups, or species (Sober and Wilson 1998; Okasha 2006). The same multi-level selection can also apply to a Darwinian theory of cultural evolution, where the hierarchical levels may be memes, individuals, and groups of various types (e.g., firms, villages, or nations). Cultural group selection has been studied using formal models (Boyd and Richerson 1985) and empirical analyses (Soltis et al. 1995).

5. Towards an Evolutionary Synthesis for Culture

The theory of Darwinian cultural evolution outlined above provides the necessary conditions for an evolutionary synthesis in the social sciences. This theory (1) views cultural change in terms of variation, selection, and inheritance/transmission, (2) adopts population thinking, (3) is non-progressive, (4) allows for the inheritance of acquired characteristics, (5) acknowledges the operation of unique cultural transmission mechanisms, and also incorporates (6) drift and (7) multi-level selection. This Darwinian theory of cultural evolution most closely resembles the quantitative population-based models of Cavalli-Sforza and Feldman (1981), Boyd and Richerson

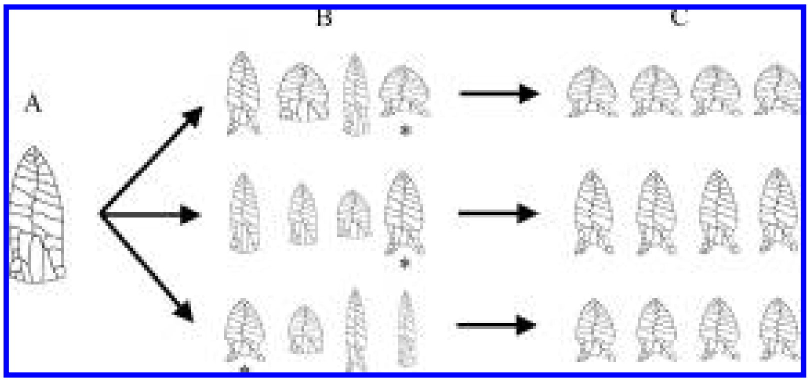

Figure 2.
The evolutionary scenario proposed by Bettinger and Eerkens (1999) to explain variation in projectile point designs from the prehistoric Great Basin. An ancestral point design (A) spreads to different groups (B) where it diverges due to idiosyncratic individual learning. In C, indirectly biased cultural transmission causes the single point design used by the most successful hunter (marked with a * in B) to spread within each group. According to Bettinger and Eerkens, prehistoric California resembled B, where point attributes correlated poorly with one another, while prehistoric Nevada resembled C, where point attribute inter-correlations were high. This scenario (A→B→C) was simulated experimentally by Mesoudi and O'Brien (in press).

(1985) and other proponents of gene-culture coevolution (Table 1).

The other theories of cultural evolution lack one or more of these features, and this has prevented them from facilitating an evolutionary synthesis for culture. Transformation and progress theories (1–3 in Table 1) lack population thinking, which is necessary to link individual-level decisions and transmission biases to population-level patterns. Previous calls for an evolutionary synthesis for cultural evolution (e.g., Schwartz and Mead 1961) have likely failed for this reason. Theories of cultural evolution that are based on neo-Darwinism, such as Campbell's BVSR theory or memetics, make individual-level assumptions (e.g., that variation is blind, or that replicators and replication must be present) that appear to be inconsistent with data from psychology. Proposals for a science of memetics (e.g., Hull 2000) have likely failed for this reason.

The beginnings of this synthesis can be found in the formal models of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) and others, who provide several examples of how microevolutionary decision-making forces and transmission biases, such as those listed in Section 4.5, can account for specific macroevolutionary population-level patterns observed in the anthropological, archaeological, or sociological record. A good example of this can be found in a recent study by Bettinger and Eerkens (1999), who used cultural transmission rules modeled by Boyd and Richerson (1985) to explain patterns of variation in projectile points found in the Great Basin region of the southwestern United States and dated to around A.D. 300–600. Bettinger and Eerkens (1999) observed that two sites differed in the degree to which the points' attributes, such as height, width, and thickness, correlate with each another. The attributes of points found in eastern California were found to be poorly correlated with each other, giving a diverse set of point designs. In contrast, the attributes of points found in central Nevada were found to be highly correlated with one another, making these points more uniform in their designs. Bettinger and Eerkens (1999) interpreted these differences in terms of the manner in which prehistoric people of the two regions acquired and transmitted projectile-point technology (Figure 2). In this proposed scenario, the diverse Californian points originally spread via what Boyd and Richerson (1985) called "guided variation," where cultural traits are copied from a model and are then subject to separate individual trial-and-error experimentation. This latter trial-and-error phase caused point attributes to vary independently, and hence increase correlations between attributes. The uniform Nevadan points, in contrast, originally spread via what Boyd and Richerson (1985) called "indirect bias," where the cultural trait exhibited by a particularly successful individual is preferentially copied. If everyone is copying wholesale the design of a single successful model, soon everyone within a group will have the same point design, generating high correlations between point attributes. Hence, Bettinger and Eerkens (1999) argued that microevolutionary differences at the individual level (guided variation versus indirect bias) generated macroevolutionary differences at the population level (uncorrelated attributes versus correlated attributes).

In a similar manner, Cavalli-Sforza and Feldman (1981: 307–325) used a model of cultural drift to explain patterns of prehistoric projectile point variation documented by Binford (1963), finding that certain point attributes (length and width) exhibit large between-group variation which is indicative of drift, while other point attributes (thickness) exhibit lower between-group variation that is more consistent with stabilizing selection. The application of neutral drift models to archaeological data has been extended by Neiman (1995), who found evidence for drift operating in Woodland period ceramics from Illinois, and Shennan and Wilkinson (2001), who found evidence of anti-conformist cultural transmission (or selection for novel cultural traits) in early Neolithic central European pottery.

Other studies have identified signatures of microevolutionary processes in ethnographic and sociological data. Boyd and Richerson (1985) found in their models that prestige bias (preferentially copying models who have high social status) can generate runaway selection for extreme and exaggerated cultural traits, just as sexual selection can cause runaway selection of biological traits. They proposed that this runaway process might explain exaggerated traits that have been observed in the ethnographic record, such as giant yams on the Micronesian island of Ponapae or elaborate tattoos in Polynesia. More recently, Henrich (2001) has shown how conformist cultural transmission can generate the distinctive S-shaped cumulative distribution curves found by sociologists to be characteristic of the spread of innovations through societies (i.e., a slow initial uptake of the innovation, then a rapid spread through most of the population, then a slowdown as the population becomes saturated: Rogers 1995). Similarly, Bentley et al. (2004) have shown that the power law frequency distribution (a small number of very popular traits and a large number of uncommon traits) exhibited by various cultural datasets, such as first names, dog breeds, or pop songs, can be generated by random copying at the individual level. Models in which microevolutionary forces have been used to explain macroevolutionary phenomena can also be found in the evolutionary economics literature (Nelson and Winter 1982) and occasionally in history (Turchin 2003).

In all of these examples, microevolutionary forces—e.g., random copying, prestige/indirect bias, conformist cultural transmission and guided variation—have been found in formal models to generate distinct population-level macroevolutionary patterns—e.g., power law distributions, runaway selection, S-shaped cumulative distribution curves and different patterns of between- and within-group variation—which have then been observed in the archaeological, anthropological, or sociological record. While none of these studies are conclusive, and many of the findings are open to alternative interpretations, they at least point to the beginnings of an evolutionary synthesis for culture, where distinct macroevolutionary patterns are seen to result from specific microevolutionary forces.

6. The Need for Experiments

A major driver of the evolutionary synthesis in biology was the experimental study of microevolution in the laboratory, where experiments with model species such as *E. coli* or *Drosophila* resulted in important insights into the effects of different forms of selection or the mechanisms of genetic inheritance (Mayr 1982). The findings of these experiments were used to inform the assumptions of theoretical population genetic models, which, via the evolutionary synthesis, informed the study of biological macroevolution.

The same should be true of the study of cultural evolution. The work cited in the previous section demonstrates how formal mathematical models of microevolutionary processes have been used to simulate a range of macroevolutionary patterns (e.g., power-law distributions or exaggerated traits), with these patterns then identified in actual observational or historical cultural datasets. These models, however, contain many explicit and implicit assumptions about individual decision-making and learning. At worst, these assumptions reflect the uninformed intuitions of the modeller. At best, modellers have drawn on existing empirical data from experimental social psychology to inform their models, such as where Boyd and Richerson (1985) used empirical work demonstrating the strength of conformity (e.g., Asch 1951) when modeling conformist cultural transmission. However, as they themselves acknowledged (Boyd and Richerson 1985: 296), much of this evidence is inadequate and/or not collected with their specific hypotheses in mind. In general, cultural evolutionary models and theories would be greatly improved if their assumptions were verified using experimental methods. Encouragingly, this is beginning to happen, and recent experimental studies have begun to explicitly test the predictions of formal cultural evolution models (Kameda and Nakanishi 2002, 2003; Baum et al. 2004; McElreath et al. 2005). A similar situation exists for content biases in cultural transmission, which can be studied by passing written information along chains of participants and measuring the changes in the material or comparing the degradation rates of different types of material. Although once common (Bartlett 1932), this "transmission chain method" fell out of favor in mainstream social psychology, but has recently seen a revival of interest (Bangerter 2000; Kashima 2000a, 2000b; Mesoudi and Whiten 2004; Mesoudi et al. 2006a; Mesoudi 2007b).

As well as using experiments to inform the assumptions of models which are then used to simulate macroevolutionary patterns, experiments can also be used to directly simulate macroevolutionary change, serving the same function as the mathematical models themselves[5] (akin to recent experiments that simulate long-term biological macroevolution in microorganisms: Elena and Lenski 2003). The pioneering studies of Insko et al. (1980, 1983) attempted just this. Insko et al. (1983) sought to test two competing anthropological hypotheses for the origin of large-scale cooperative societies. One hypothesis, proposed by Service (1975), held that large-scale societies originated when different villages produced different goods and one village was economically central, such that all trade had to pass through it. An alternative hypothesis proposed by Carneiro (1970) held that large-scale societies only emerged when one village had military superiority, and could confiscate the goods of other villages. Insko et al. (1983) simulated these scenarios in groups of participants who were taught to produce and trade paper models, finding that cooperative Service groups significantly outperformed coercive Carneiro groups. This result suggests that cooperative groups would have been more likely to persist due to cultural group selection (Soltis et al. 1995) than coercive groups, hence supporting Service's hypothesis.

More recently, Mesoudi and O'Brien (2008) conducted an experimental simulation of the aforementioned archaeological scenario proposed by Bettinger and Eerkens (1999) to account for prehistoric Great Basin projectile point variation (Figure 2), in order to verify that these forms of learning really do generate the proposed patterns of variation when real people face a similar task. In our study (Mesoudi and O'Brien 2008), groups of participants played a simple computer game in which they designed "virtual projectile points" and tested them in "virtual hunting environments." Different phases of the game simulated the different microevolutionary learning rules specified by Bettinger and Eerkens (1999): either indirectly-biased cultural transmission, where participants could copy the point design of another member of their group (given information about each person's success); or independent individual learning, where participants had no access to social information and had to rely on individual trial-and-error learning to improve their design. As predicted, periods of indirectly-biased cultural transmission were associated with significantly stronger inter-attribute correlations than were periods of individual learning, supporting Bettinger and Eerkens' (1999) hypothesis regarding differences between their prehistoric Nevadan and Californian data sets. We also found that participants who could engage in indirectly biased cultural transmission significantly outperformed individual-learning controls, and that this advantage was greater when individual learning was costly. This latter finding provides a potential reason why the two prehistoric sites differed in the type of learning employed: perhaps the prehistoric Nevadan environment was harsher in some respect, making individual trial-and-error experimentation more costly, resulting in a greater reliance on cultural transmission. This illustrates how experiments, via the manipulation of variables, can elucidate past cultural evolution in a way that archaeological data alone cannot.

We also found that the advantage of cultural transmission was in part caused by our assumption of a multimodal adaptive landscape underlying the evolution of projectile point design, with cultural transmission allowing participants to jump from their locally adaptive fitness peaks to higher fitness peaks found by more successful group members. So, just as Arnold et al. (2001) linked punctuated equilibria (biological macroevolution) to adaptation in a multimodal adaptive landscape (biological microevolution) (see Section 1), we similarly linked the patterns of projectile point variation observed by Bettinger and Eerkens (cultural macroevolution) to cultural transmission in a multimodal adaptive landscape (cultural microevolution).

Generally, experiments offer several advantages over macroevolutionary methods found in archaeology and anthropology, such as the ability to re-run history, to replicate results in multiple groups, to manipulate variables, to randomly assign participants to control and experimental groups, and to collect complete, uninterrupted, and unbiased data (Mesoudi 2007b). Used together, these methods can all contribute to a synthetic science of cultural evolution: psychology experiments can reveal details of microevolutionary mechanisms, formal theoretical models can reveal what these microevolutionary mechanisms would look like at a population level and over extended periods of time, and macroevolutionary (e.g archaeological, historical, or ethnographic) methods can be used to identify these signatures in actual cultural datasets. Finally, it should be noted that the study of cultural microevolution is not the sole preserve of psychology: recent experiments conducted by economists have generated important findings regarding cultural transmission (e.g., Schotter and Sopher 2003), while suitably rigorous ethnographic studies can provide important details of microevolutionary forces operating under natural conditions, such as the studies of cultural transmission in traditional societies conducted by Hewlett and Cavalli-Sforza (1986) and Aunger (2000b).

7. Conclusions

A Darwinian theory of cultural evolution provides the necessary conditions for an evolutionary synthesis for the study of culture, wherein the microevolutionary forces studied by psychologists, economists, and ethnographers can be used to explain the specific macroevolutionary patterns observed by archaeologists, historians, and sociologists. A Darwinian theory of cultural evolution facilitates such a synthesis because, unlike earlier theories of cultural evolution, it is non-progressive and based on population thinking, allowing change to be seen in terms of microevolutionary forces acting on within-group variation. At the same time, a Darwinian theory of cultural evolution, unlike other contemporary theories such as memetics, does not make neo-Darwinian assumptions regarding cultural microevolution, such as the existence of replicators or blind mutation, that are inconsistent with how cultural transmission appears in many cases to operate.

To foster such a synthesis, psychologists, (micro-) economists and ethnographers must think beyond individuals and small groups and consider how their findings would affect large-scale cultural change. They must also treat culture as a dynamic process that results from individual behavior, rather than a static background factor that only affects individual behavior. Experiments need to explicitly test the assumptions and predictions of formal cultural evolution models (e.g., McElreath et al. 2005), and experimental simulations are needed of specific cultural phenomena that have been documented by anthropologists and archaeologists (e.g., Insko et al. 1983; Mesoudi and O'Brien 2008). For their part, archaeologists, historians, and sociologists need to think in terms of individual level decision-making forces and cultural transmission biases when collecting and analyzing their data (e.g., Neiman 1995; e.g., Bettinger and Eerkens 1999). Finally, cultural anthropologists need to abandon the anti-scientific, post-modernist, constructivist, and dualist approaches that pervade their discipline and instead adopt a scientific, quantitative, reductionist, and evolutionary approach to culture, and recognise that attempts to engage with their discipline are not hostile invasions (as portrayed, for example, by Ingold 2007) but rather invitations to contribute to a more inclusive and more productive science of culture.

As noted in Section 1, the evolutionary synthesis in biology is ongoing, recently incorporating (or beginning to incorporate) phenomena such as EvoDevo (Carroll 2005), epigenetic inheritance (Jablonka and Lamb 1995), multilevel selection (Okasha 2006) and niche construction (Odling Smee et al. 2003). Interestingly, these new additions make neo-Darwinism more similar to Darwin's original theory of biological evolution, and hence also more similar to the Darwinian theory of evolution that has been advocated here for culture (Jablonka and Lamb 2005; Mesoudi 2007a). For example, the presence of epigenetic inheritance means that Weismann's barrier is not quite as strict as neo-Darwinians believed. These additions to the biological synthesis may provide important insights for cultural evolution once a cultural synthesis is established. For example, a "cultural EvoDevo" would specify the cognitive processes that describe how information stored in the brain is expressed as behavior or material artifacts, and how these cognitive processes affect large-scale cultural macroevolution (Mesoudi et al. 2006b). There are already interesting parallels between biological EvoDevo and cultural EvoDevo, for example the parallel findings that both the genetic processes that control development (Halder et al. 1995) and the cognitive processes that structure the expression of verbal information during cultural transmission (Mesoudi and Whiten 2004) both appear to be hierarchically organized.

According to the analysis presented here, all of the ingredients for an evolutionary synthesis for culture were in place by the mid-1980s: Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) had developed appropriate theoretical models, ethnographers were beginning to test these theories in the field (Hewlett and Cavalli-Sforza 1986) and social psychologists were simulating cultural evolution in the lab (Insko et al. 1983). Yet these works had little impact in their respective fields of cultural anthropology and social psychology. Why did this work not spark a synthesis for the study of culture? Perhaps the aforementioned anti-evolution and anti-science stances of cultural anthropology, or the individualistic focus of most mainstream psychology and economics, posed too a great barrier. But perhaps the delay is not surprising. We should not exaggerate the speed with which the biological synthesis occurred: 80 years elapsed between publication of *The Origin* and the evolutionary synthesis in biology, and Mayr (1980: 39) notes that even when every individual element of that synthesis was present, it still took several decades for the synthesis to occur. Perhaps the recent proliferation of studies applying evolutionary principles to culture (Mesoudi et al. 2006b) indicates that it will not be much longer.

Notes

1. The inheritance of acquired characteristics is often equated with Lamarckism. However, as noted by Mayr (1980: 4), "the frequently used dichotomy, Darwinism versus Lamarckism, is not very satisfactory because both labels usually lumped rather different theories." As shown in Table 1, the inheritance of acquired characteristics, often associated with Lamarckian evolution, actually describes three of the theories listed by Mayr, including that held by Darwin. This generates confusion when theories of cultural evolution are labeled Darwinian or Lamarckian (e.g. Hodgson 2001). I suggest Mayr's statement is as true for cultural evolution as for biological evolution, and so I avoid this distinction and the term "Lamarckian". I use "Darwinian" (as distinct from "neo-Darwinian") in the historically accurate sense defined by Mayr and given in Table 1.

2. More recent accounts of development are far less fixed and progressive, and more interactionist, than these early views of development. Nevertheless, the historical point remains that these early cultural evolution theories were modeled after the contemporary (progressive) idea of development.

3. Progress theories of cultural evolution are also notable for their past use to justify racist ideologies, given that the form of society placed at the top of the "cultural ladder" invariably resembled the proponent's own (white, middle-class, Anglo-American) society (Campbell 1965: 25).

4. Lewontin has since argued against the application of evolutionary theory to culture (Fracchia and Lewontin 1999).

5. Note that I am not making the strong claim that theories can be definitively verified or rejected with experimental methods (or mathematical models) alone, rather that experimental simulations and mathematical models can tell us what is theoretically possible and what is empirically plausible, and hence what to look for in actual cultural datasets in order to successfully test a theory.

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